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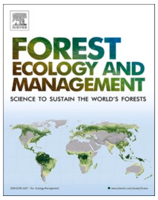

From mixtures to monocultures: Bird assemblage responses along a production forest conifer-broadleaf gradient

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A B S T R A C T

Increasing the prevalence of broadleaf trees in conifer-dominated production forests is a recommended means of improving habitat availability for broadleaf and mixed-forest species. The implications for biodiversity are often measured by contrasting broadleaf-conifer mixtures with conifer-dominated stands. However, few studies include broadleaf-dominated stands in these assessments. Here we contrasted the bird assemblages of even-aged production forests along a mixture gradient from Norway spruce (*Picea abies*) dominated, to birch (*Betula* spp.) dominated stands in southern Sweden. We conducted point count surveys of bird individuals exhibiting breeding behaviour within 30 stands varying from <0.5% to over 98.5% broadleaf by basal area. A total of 355 birds were detected, comprising 36 bird species, seven of which are classified as near threatened by the Swedish Red-list. Our results indicate i) a distinct shift in bird community composition linked to the percentage of broadleaf trees at stand and landscape scales, ii) significantly higher bird species richness, evenness, and abundance in stands with a higher proportion of birch, iii) higher bird abundance in birch-dominated stands than in mixtures, and iv) shifts in bird species guilds as related to stand basal area, the amount of shrubs in the understory, and quantities of dead wood. All of these results have implications for the ways in which production forest management could be altered to enhance avian diversity, and we discuss these with respect to the use of broadleaf versus mixed-species stands.

1. Introduction

Conserving forest ecosystems is critical to tackling global biodiversity loss (Ceballos et al., 2017; IPBES, 2019). However, only 13% of the world's forests are formally protected for biodiversity conservation, and most of the remaining forest area is used for wood production and other commodities (FAO, 2016). As a result, both protected forests and forests actively managed for the production of biomass and other goods and services are important for forest biodiversity (Lindenmayer and Franklin, 2002). Despite widespread reliance on managed production forests for meeting conservation goals (Brockerhoff et al., 2017), these environments often diverge from natural forest conditions and the habitat requirements of many native species. This can be due to differences in the anthropogenic disturbance regimes employed, tree species composition provided, and forest structures retained (Felton et al., 2016a).

Current trends indicate that reliance on intensively managed production forests will continue to increase this century (Warman, 2014; Payn et al., 2015), which will further increase the distinction between natural forest conditions and those found in many production forests. Countering these trends, there is growing international awareness of the potential biodiversity and ecosystem service benefits from diversifying silviculture (Felton et al., 2020a). Diversified forestry includes the use of a wider variety of less intensive practices (Puettmann et al., 2015), better aligned with natural disturbance regimes and tree species composition (Angelstam, 1998; Augustynczik et al., 2019). Less intensive silvicultural practices can provide greater structural complexity, small-scale variability (Kuuluvainen et al., 2012) and tree species diversity (Pretzsch et al., 2017) than the even-aged monocultures commonly used by intensive forestry, with expected benefits to habitat availability, and thus forest biodiversity (Lindenmayer and Franklin, 2002; Gustafsson et al., 2020).

Mixed species stands are one such production forest alternative, in which stands are designed around the targeted production of two or

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more tree species. To be classified as a mixture, thresholds are often set for the proportion of the stand's volume or basal area (e.g. 65%, 70%, 80%) that any one tree species can provide. Whereas monocultures may excel at providing large quantities of wood per unit area, mixed species stands can support higher levels of biodiversity (Felton et al., 2010; Ampoorter et al., 2020), broaden the range of ecosystem services provided (Gamfeldt et al., 2013; Felton et al., 2016b), help to counter the uncertainties and risks associated with climatic change (Jactel et al., 2017), while providing managers with alternative directions for stand development (Millar et al., 2007). The biodiversity benefits of mixtures are generally linked to the increased range of environmental conditions and resources provided, and thus the increased availability of distinct niches to exploit (Cavard et al., 2011; Ampoorter et al., 2020). The extent of this niche space depends on whether the tree species are phylogenetically and functionally distinct (e.g. combining broadleaf and conifer tree species), and thereby provide the habitats and resources used by flora and fauna evolved to exploit each individual tree species (Jonsell et al., 1998; Felton et al., 2010; Ampoorter et al., 2020). Mixture specialists, which are those species evolved to exploit the variety of complementary resources provided in mixed-species stands, are also likely to benefit (Cavard et al., 2011).

Birds are a key element of forest biodiversity, because they fulfill diverse and important ecological functions, including seed dispersal, pest control, and ecosystem engineering (Sekercioglu, 2006). Birds are also highly useful study organisms because their populations can vary in response to fine scale habitat requirements (Hewson et al., 2011; Rosenvald et al., 2011; Lindbladh et al., 2017; Pedley et al., 2019), and because their visually and acoustically conspicuous behavior (Bibby et al., 2000; Whelan et al., 2008) enable the efficient evaluation of habitat differences in forest systems (Gardner et al., 2008). Whereas few forest bird species in Europe are strongly associated with single tree species, many exhibit a preference for broadleaf or conifer forests (Bibby et al., 1989). As a result, many forest birds can be usefully categorized as broadleaf, conifer, or mixture specialists (Roberge and Angelstam, 2006). In mixed stands of broadleaves and conifers, bird diversity is often enhanced because of the occurrence of both broadleaf- and conifer-associated bird species (Donald et al., 1998; Hausner et al., 2002). In such mixtures, plant diversity and structural complexity are thought to mutually enhance niche space provided by the tree species composition and structure of the forest. Diverse structural attributes alter bird mobility and the range of nesting and shelter sites available, and thus the efficiency by which birds obtain key resources (e.g. food, mates) or escape predators; whereas floristic composition generally influences the quality, type and breadth of resources available (Cavard et al., 2011; Seavy and Alexander, 2011; Lemaitre et al., 2012). The inclusion of broadleaf trees in a conifer stand can also allow sufficient light to reach the understory for a more structurally complex and floristically diverse understory to develop (Saetre, 1999; Brandtberg et al., 2000; Hedwall et al., 2019), and thereby facilitate the increased prevalence of ground or shrub-associated bird species (Hobson and Bayne, 2000; Hausner et al., 2002). The resultant bird diversity and community composition will, in turn, depend on a range of context dependent contributing factors, including the proportions of the different tree species grown (Lindbladh et al., 2011), site productivity (Hausner et al., 2002), forest age (Roberge et al., 2018), the prevalence of dead wood structures (Donald et al., 1998; Hausner et al., 2002), as well as regional species pools and the amount of suitable habitat in surrounding landscapes (Jokimäki and Huhta, 1996; Lindbladh et al., 2019).

Numerous studies have examined avian diversity and composition in monocultures and mixed species stands (Donald et al., 1998; Archaux and Bakkaus, 2007; Sweeney et al., 2010; Cavard et al., 2011). However, there are often some limitations in such studies due to a lack of inclusion of pure broadleaf stands, the prevalence of confounding influences of age and forest composition variables, or due to the comparison of unmanaged mixed species stands with intensively managed plantation monocultures (Young et al., 2005; Cavard et al., 2011). Here we attempt to overcome some of these limitations by contrasting the bird assemblages of production stands that varied along a conifer-broadleaf mixture gradient from Norway spruce (*Picea abies*) monocultures to birch (*Betula* spp.) dominated broadleaf stands. For our purposes, mixtures are those stands in which no single tree species exceeds 70% of basal area. We focus on differences in species richness, evenness and abundance, as well as changes in the abundance of representatives of ecological guilds based on migratory status, broadleaf association, and breeding site requirements. Our study was conducted in Sweden, a country with extensive production forests, where recent government support was provided for the increased use of broadleaf and mixed species stands (Felton et al., 2020a).

2. Methods

2.1. Background to study region

In Sweden, forests cover 70% of land area, and extend from the temperate to the subarctic/alpine zone. Most of Sweden's productive forest area (i.e. producing ≥ 1 m^3 of wood ha^{-1} yr^{-1}) is managed using the rotational clearcutting of even-age stands for the production of timber, pulp wood and bioenergy. Production stands primarily rely on the native conifer tree species Norway spruce (*Picea abies*) or Scots pine (*Pinus sylvestris*), whereas Betula spp. (*Betula pendula* or *B. pubescens*, hereafter birch) is the most commonly harvested broadleaf tree species. In the early 1990 s the Swedish Forestry Act provided equal status to environmental and production objectives (Gov. bill 1992/93:226, 58; Lämås and Fries, 1995; Bush, 2010). Since this time Sweden has increased the spatial extent of protected forest areas and voluntary set-asides, and integrated conservation considerations (e.g. green tree retention) within production forests (SFA, 2014; Gustafsson et al., 2020). Nevertheless, recent evaluations indicate that Sweden will not meet its 2020 environmental goals for sustainable forests (SEPA, 2018; Angelstam et al., 2020), and the Swedish Forest Agency (SFA) has suggested that broadleaf and mixed broadleaf-conifer production forests should be encouraged (Bergquist et al., 2016). The increased use of broadleaf and broadleaf-conifer mixtures would not only diversify forestry practice (SFA, 2017, 2020), and aid climate change adaptation (Felton et al., 2016a), but is also expected to improve the biodiversity provided by production forest stands.

2.2. Study area

Our study was performed in southern Sweden, a temperate and hemiboreal climatic region with 60% forest cover, where almost 80% of productive forest land is controlled by private owners. Due in part to production forestry (Lindbladh et al., 2014), the region's forests are dominated by spruce (46% of standing volume), as well as Scots pine (26%; *Pinus sylvestris*) and birch spp. (11%; *Betula pendula* or *B. pubescens*, hereafter birch) (SLU, 2018), with<5% of forest areas formally protected (SFA, 2014). Production forestry in this region is largely defined by the rotational clearcutting of even-aged stands, planting of conifers, the active removal of competing vegetation and production stem density control (i.e. thinning), with final harvest after 50–80 years. Whereas spruce and pine are generally planted, birch establishes primarily by natural regeneration and frequently occurs in mixtures with the two conifers (Holmström et al., 2017). Spruce and pine are prioritized as production stems, with birch often removed during thinning, depending on owner/manager objectives and the success of conifer establishment (Holmström et al., 2021). As forest certification schemes require the retention of a minimum percentage of broadleaf tree species (10% in southern Sweden; FSC, 2010), a varying proportion of birch is retained throughout the entire rotation. In addition, a small proportion of forest owners actively cultivate birch as the primary production tree species.

2.3. Stand selection

Using a data base of production forest stands in the region, which provided information on tree species composition, forest age and site fertility, we randomly selected 30 stands that varied from<0.5% to over 98.5% broadleaf by basal area. Norway spruce comprised 97% of conifer trees, whereas birch accounted for the majority of broadleaf trees (86%). Other broadleaves included European alder (*Alnus glutinosa*, 4%), European aspen (*Populus tremula*, 4%), pedunculate oak (*Quercus robur*, 3%), goat willow (*Salix caprea*, 1%), and additional broadleaf species (2%). Stands were limited in age to between 20 and 60 years of age. This was to exclude younger age categories with large amounts of naturally regenerating additional tree species. We used a minimum stand size of 3 ha (average 3.7 ha) to reduce the influence of bird assemblages associated with stand border zones.

2.4. Bird surveys

Bird surveys were conducted using point counts, for which abundance estimates act as indices correlated with the true abundance of the bird species present (Bibby et al., 2000). Caveats are warranted when interpreting such indices, because variability in bird detectability influences results (Buckland and Handel, 2006). Whereas modeling approaches can address detectability issues in point count data, these approaches introduce additional uncertainties (see Barry and Walsh, 2001; Johnson, 2008; Banks-Leite et al., 2014). For our purposes we assumed that a detected increase or decrease in the abundance of a species across the spectrum of stands surveyed is indicative of a relative increase or decrease in abundance, though the absolute abundance of that species may only be correlated with these results (Bibby et al., 2000). We used an *a priori* "study design" approach to minimizing detectability concerns in the field (Johnson, 2008; Banks-Leite et al., 2014), by only including birds detected within 30 m of the observer; a distance within which the vast majority of birds that occur, are likely to be detected. Four survey points were located towards the centre of each stand (approximating the four corners of a square), which reduced the influence of ecotone bird assemblages found in some stand edges. This constraint also helped to ensure that survey points were not placed over larger areas in larger stands, which can inflate avian diversity results due to the increased range of environments surveyed. It also provided opportunities to reassess detections made at previously surveyed points. Bird survey points were placed to be as close to 80 m apart as possible, but no closer, while also being > 40 m from stand edges. Survey points were located beforehand using aerial photographs to avoid onsite selection bias. The 30 m radius limit that was applied to the point-count survey distance, also acted to limit the birds assessed to those located within the stand, and reduced the likelihood of double counting birds at two survey points. A laser rangefinder was used to calibrate distances. Stands were surveyed four times in 2018; twice in early spring (early April) and twice in late spring (late May), with each of the four survey points surveyed on each of the four visits to a stand. The survey periods coincided with annual peaks in the singing activity of breeding resident and migrant passerines respectively, with most tropical migrants arriving during the second survey period. Daily surveys began at dawn during the daily peak in bird vocalization; approximately 6:00 am in early spring, and 4:30 am in late spring, and finished at 9:00 am and 7:30 am respectively.

All point count surveys were conducted by researchers experienced with both bird identification and point count surveys (AF, ML). The stand types were randomly distributed among the observers and then adjusted to ensure that no one observer's surveys were skewed towards a particular stand category, and each point on each occasion was surveyed for five minutes (Bibby et al., 2000), after a 1 min pause to reduce influences from the surveyors' approach (Bonthoux and Balent, 2012). Two stands were surveyed daily by each surveyor. The order in which stand types were visited was varied systematically to avoid bias in the time of the morning or survey period they were surveyed. Surveys were conducted in suitable weather (i.e. minimal wind, no rain) to reduce environmental influences on bird detectability and activity. Most identifications were made acoustically (>99%). If there was uncertainty regarding the number of individual birds calling, we used the most conservative abundance estimate. Only individuals performing territorial behaviour (song in almost all cases, nest attendance in others) were included in analyses, to increase our confidence that the bird individual's occurrence was tied to the vegetation conditions provided within the stand. For each stand, we used the highest abundance value attained for a bird species across the four stand surveys conducted (after first summing abundance results for a species across the four survey points in each stand survey), as the within-stand estimated abundance for that bird species. We did so because 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 detectability of residents and migrants.

2.5. Bird ecological characteristics

We used descriptions of dietary preference, and nest sites from the Birds of the Western Palearctic (https://birdsoftheworld.org/bow/home) to classify bird ecological characteristics and specific habitat requirements. Bird species were classified as migrants (only present in the study area during the breeding season), partial migrants (some populations of the species are migratory), or residents (present in the study region throughout the year) depending on whether populations undergo partial or near total migration from the study non-breeding season (Lindell, 2002; BWPi, 2007; Ohlsson, 2008). We also classified species using the Swedish Red List of threatened taxa (https://artfakta.se/artbestamning/).

2.6. Stand vegetation

In each stand six randomly assigned (using ArcGIS) and four centrally located (overlapping with bird survey points) 10 m radius sample plots were established. Plots were located at least 40 m from the stand border to reduce edge effects. Within these plots basal area and tree species composition were determined by measuring the diameter of each tree (>4 cm) at 1.3 m height (diameter breast height, dbh) and identifying the tree species. A tree was included if its centroid was within 10 m of the plot center. The availability of dead wood was quantified by measuring the dbh and height of all standing dead trees and snags > 10 cm dbh. The volume of all lying coarse woody debris (CWD) was quantified by measuring the length and diameter of dead wood items with diameters of $\geq$ 10 cm. The presence of taller understory vegetation (shrubs) was assessed by counting the number of stems of all woody vegetation > 0.3 m in height but < 4 cm dbh (e.g. tree saplings, small trees and shrubs, ericaceous shrubs).

2.7. Landscape level vegetation

Landscape analysis of forested vegetation surrounding the stand was sourced from k-NN Sweden 2010 http://skogskarta.slu.se, which provided an estimate of standing tree volume (m^3 ha^{-1}) on land areas classified as forest (Reese et al., 2003). The data is developed from satellite imagery and inventory data compiled by the National Forest Inventory of Sweden, using a kNN-method (k-Nearest Neighbors algorithm). Each pixel in the kNN-Sweden dataset is 25 by 25 m, with a relative root mean square error of 10% for standing volume when assessed on 100 ha size estimations (Reese et al., 2003). For a one km circle (314 ha) surrounding the center of each stand (i.e. the center of the four survey points) we calculated the percentage of forest land, deciduous forest, old forest, and old deciduous forest, from this kNN-Sweden data (Table 1). We defined old forest as over 80 years of age,

Table 1
Descriptive statistics of the vegetation variables included in the analyses. The first eight variables summarize data collected within each of the 30 stands' 10 survey points. The final four variables summarize kNN-Sweden data extracted for the one km circle surrounding the centre of each stand. The variables included were the percentage of old deciduous forest (Old Dec 1 km (%)), old forest (Old 1 km (%)), forest (Forest 1 km (%)) and deciduous forest (Dec 1 km (%)). COV broadleaves refers to the coefficient of variation in the amount of broadleaf trees in the stands.

	Mean	SD	Min	Max
Spruce BA (m^2 ha^{-1})	16.2	11.7	0.2	37.9
Birch BA (m^2 ha^{-1})	6.3	5.1	0.0	19.0
Total BA (m^2 ha^{-1})	24.1	8.5	11.4	42.4
Birch (%)	32.5	27.1	0.0	85.9
Broadleaves (%)	37.0	31.9	0.3	98.7
Cov broadleaves	0.8	0.6	0.0	2.4
CWD (m^3 ha^{-1})	3.2	2.6	0.0	9.8
Shrubs (n ha^{-1})	4170	5210	20	23,320
Old Dec 1 km (%)	0.2	0.6	0.0	3.3
Old 1 km (%)	9.9	6.0	0.6	21.4
Forest 1 km (%)	73.9	17.0	19.0	93.5
Dec 1 km (%)	13.7	7.6	5.8	32.9

and broadleaf forest as forest with>50% of standing volume provided by broadleaf species.

2.8. Data analysis

All statistical analyses were done in R 3.6.1 (R_Core_Team, 2019). To analyze the effects of vegetation variables (Table 1) on bird assemblages, an unconstrained ordination using non-metric multidimensional scaling (NMS) was performed on the bird abundance data by applying the metaMDS function in the Vegan package (Oksanen et al., 2019). The correlation between site locations in ordination space and the vegetation variables (Table 1) was analyzed using the envfit function in Vegan and projected on the final graphical NMS solution. The output illustrates the strength (length of arrows) and the direction of the strongest correlations. The distance metric employed was Bray-Curtis dissimilarity, and the number of permutations in the ordination was 999. The effect of the vegetation variables on all univariate response variables (species richness, abundance, etc.) was modeled using Generalized Linear Models (GLM) with a Poisson error distribution and log-link. To account for collinearity among the vegetation variables and to avoid over-parameterization we ran a Principal Component Analysis (PCA) on these variables and used the first three components as predictors in the GLMs.

We also used a GLM as described above to test for non-linear effects of the proportion of birch on the total abundance. The full GLM included the proportion of birch and the second and third degree polynomials of this variable, as well as the scores of PC2 and PC3 (described above), to control for other vegetation variables. We then performed a backward model selection removing variables for which exclusion decreased the AIC. 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.

3. Results

A total of 355 birds exhibited territorial behaviour within the sampled points during bird surveys, comprising 36 bird species from 18

Table 2
Birds encountered during stand surveys organized by scientific name. Swedish red list status is of June 2020 (artfakta.se). Migratory status (M = migrant, PM = partial migrant, R = resident), forest preference (Broadleaf associated, Conifer associated, Broad/Con = generalist), and general nest site usage (AG = above ground, GN = ground nesting, CN = cavity nesting) was sourced from Birds of the Western Palearctic, and supplemented using regional data on migratory status.

Family	English	Shortened scientific	Scientific	Redlist status	Migratory status	Forest preference	Nest site
Aegithalidae	Long-Tailed Tit	Aeg_caud	*Aegithalos caudatus*		R	Broadleaf	AG
Motacillidae	Tree Pipit	Ant_triv	*Anthus trivialis*		M	Broad/Con	GN
Fringillidae	European Greenfinch	Car_chlo	*Carduelis chloris*		PM	Broad/Con	AG
Fringillidae	Eurasian Siskin	Car_spin	*Carduelis spinus*		PM	Broad/Con	AG
Certhiidae	Eurasian Treecreeper	Cer_fami	*Certhia familiaris*		R	Broad/Con	AG
Columbidae	Common Wood Pigeon	Col_palu	*Columba palumbus*		PM	Broad/Con	AG
Picidae	Great Spotted Woodpecker	Den_majo	*Dendrocopos major*		R	Broad/Con	CN
Picidae	Black Woodpecker	Dry_mart	*Dryocopus martius*	NT	R	Broad/Con	CN
Emberizidae	Yellowhammer	Emb_citr	*Emberiza citrinella*	NT	PM	Broad/Con	GN
Muscicapidae	European Robin	Eri_rube	*Erithacus rubecula*		M	Broad/Con	GN
Muscicapidae	European Pied Flycatcher	Fic_hypo	*Ficedula hypoleuca*	NT	M	Broad/Con	CN
Fringillidae	Common Chaffinch	Fri_coel	*Fringilla coelebs*		PM	Broad/Con	Ag
Fringillidae	Brambling	Fri_mont	*Fringilla montifringilla*		M	Broad/Con	AG
Corvidae	Eurasian Jay	Gar_glan	*Garrulus glandarius*		R	Broad/Con	AG
Acrocephalidae	Icterine Warbler	Hip_icte	*Hippolais icterina*		M	Broadleaf	AG
Paridae	European Crested Tit	Lop_cris	*Lophophanes cristatus*		R	Conifer	CN
Fringillidae	Red Crossbill	Lox_curv	*Loxia curvirostra*		PM	Conifer	AG
Paridae	Eurasian Blue Tit	Par_caer	*Parus caeruleus*		PM	Broadleaf	CN
Paridae	Great Tit	Par_majo	*Parus major*		R	Broad/Con	CN
Paridae	Coal Tit	Per_ater	*Periparus ater*		R	Conifer	CN
Phylloscopidae	Common Chiffchaff	Phy_coll	*Phylloscopus collybita*		M	Broadleaf	GN
Phylloscopidae	Wood Warbler	Phy_sibi	*Phylloscopus sibilatrix*	NT	M	Broad/Con	GN
Phylloscopidae	Willow Warbler	Phy_troc	*Phylloscopus trochilus*		M	Broadleaf	GN
Paridae	Willow Tit	Poe_mont	*Poecile montanus*	NT	R	Broadleaf	CN
Paridae	Marsh Tit	Poe_palu	*Poecile palustris*	NT	R	Conifer	CN
Prunellidae	Dunnock	Pru_modu	*Prunella modularis*		M	Broad/Con	AG
Fringillidae	Eurasian Bullfinch	Pyr_pyrr	*Pyrrhula pyrrhula*		PM	Broad/Con	AG
Rgulidae	Goldcrest	Reg_regu	*Regulus regulus*		PM	Conifer	AG
Sittidae	Eurasian Nuthatch	Sit_euro	*Sitta europaea*		R	Broadleaf	CN
Sylviidae	Eurasian Blackcap	Syl_arti	*Sylvia atricapilla*		M	Broadleaf	AG
Sylviidae	Garden Warbler	Syl_bori	*Sylvia borin*		M	Broadleaf	AG
Troglodytidae	Eurasian Wren	Tro_trog	*Troglodytes troglodytes*		R	Broad/Con	GN
Turdidae	Redwing	Tur_ilia	*Turdus iliacus*	NT	M	Broad/Con	AG
Turdidae	Common Blackbird	Tur_meru	*Turdus merula*		R	Broad/Con	AG
Turdidae	Song Thrush	Tur_phil	*Turdus philomelos*		M	Broad/Con	AG
Turdidae	Mistle Thrush	Tur_visc	*Turdus viscivorus*		M	Broad/Con	AG

families. With respect to red-listed taxa (Table 2), seven of the bird species encountered are classified as "near threatened" (NT) by the Swedish Red-list (artfakta.se). With one exception (blue tit) all bird species assigned *a priori* to "broadleaf-associated" or "conifer-associated" categories were encountered exclusively or more frequently in broadleaf- or conifer-dominated stands respectively (Fig. 1).

Three dimensions were used in the NMS (Fig. 2), which reached an accepted stress level of 0.15 indicating a stable solution. Five vegetation variables (Tables 3,4) were significantly correlated with the ordination (P = 0.007–0.021, r^2 = 0.30–0.38). From these the basal area of birch (r = -0.98), the percentage of birch (r = -0.99) and variation in the amount of broadleaved tree species (r = 0.85) had the strongest correlation with the first dimension, while the amount of shrubs was correlated to both the first (r = -0.78) and second (r = -0.63) dimensions. The percentage forest cover at the landscape level was correlated with the first (r = 0.72) and third (r = -0.67) dimensions.

The three first components of the PCA (Table 4) together explained 74% of the variation (40%, 21%, 13% respectively) and these compounds of the vegetation variables were used as explanatory variables in the GLMs. The first PC (Table 4) was negatively correlated with spruce basal area (r = -0.94), total basal area (r = -0.70) and variation in the amount of broadleaves in a stand (r = -0.90), while positively correlated to the basal area of birch (r = 0.83), percentage of birch (0.95) and amount of shrubs (r = 0.58). This component thus represents a gradient from high basal area and a large proportion of spruce to low basal area, a large share of birch, and more structurally diverse forest. The second component was negatively correlated to the proportion of old forest on the landscape level (r = -0.82), and positively correlated to the proportion of deciduous forest in the surrounding landscape (r = 0.93). We thus interpret this component as a gradient of landscape composition going from late to early successional forest with more deciduous broadleaf trees. The third component was positively correlated to the amount of dead wood in the stand (r = 0.84), the amount of shrubs (r = 0.60) and forest cover at the landscape level (r = 0.52).

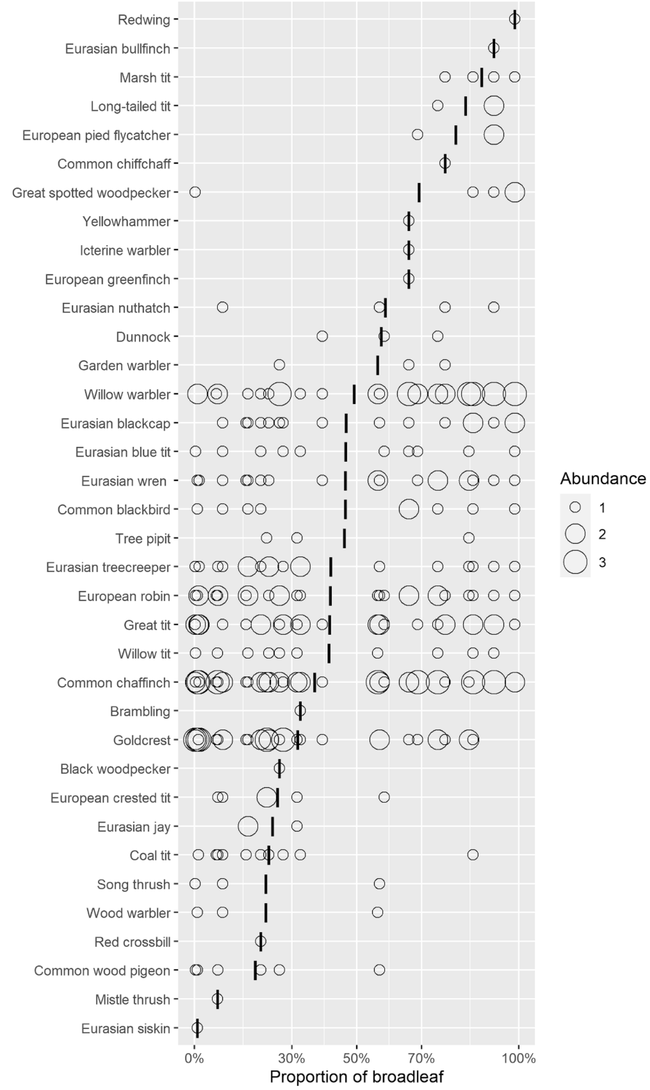

Fig. 1. The 36 bird species observed, ranked on the x-axis according to the mean proportion of deciduous broadleaf trees in stands, with the y-axis ranked according to the mean recorded occurrence of bird species from conifer to broadleaf dominated stands. The size of the circles indicates how many individuals of a species were recorded in a stand while the lines show the mean proportion of deciduous tree species. For image clarity five observations were rounded down to three individuals.

The total species richness, evenness and abundance of bird individuals were significantly higher in stands with a high proportion of birch and lower basal area, as indicated by a positive effect of PC1 (Table 5). The direction of this effect of PC1 was similar in the migrant, broadleaf specialist and ground nesting guilds, but three to four times stronger than on the total abundance (as indicated by the size of the regression coefficients) and did not significantly affect any other guilds (Table 5). The only negative effect of PC1 was on the abundance of conifer specialists (Table 5). There were significant positive effects of PC2 on total abundance, and the abundance of broadleaf specialists and above ground nesters, indicating a higher abundance in stands located in landscapes with a higher proportion of broadleaf and young forest. PC3 had a significant positive effect on the abundance of residents and cavity nesters indicating that there were more of these birds in stands with more dead wood, high levels of forest cover at the landscape level, and more understory shrubs.

The GLM on total abundance, with the lowest AIC, includes the proportion of birch (P = 0.298), PC2 (P = 0.075), PC3 (P = 0.061), and also the second degree polynomial of the proportion of birch (P = 0.044). This indicates an exponential increase in the abundance of birds with increasing birch in the stands (Fig. 3).

4. Discussion

Our results indicate the potential benefits to bird assemblages from the increased prevalence of a broadleaf tree species, as either mixed broadleaf-conifer stands, or broadleaf dominated production forests. First, bird community composition changed with the percentage and basal area of broadleaf trees in the stand. Second, total bird species richness, evenness, and abundance were significantly higher in stands with a higher proportion of birch. Third, bird abundance did not level-off once the mixed species stand threshold was reached (i.e. 70% birch), but continued to improve even into broadleaf-dominated stands. Furthermore, there was a tendency for the total abundance of birds to increase exponentially with the amount of birch in the stand. This relationship is however based on rather few observations at high proportions of birch, and thus must be interpreted with caution. In addition, the diversity and composition of bird assemblages were associated with stand basal area, the amount of shrubs in the understory, and dead wood, as well as landscape scale differences in the age of surrounding forests, and the percentage cover of forest and broadleaved trees. All of these results have implications for how production forest management can be modified to enhance avian diversity, though we emphasize that distinct results may occur with the additional of an even greater diversity of broadleaf tree species, in isolation or in mixtures, than was assessed in this study.

With respect to bird diversity, the occurrence and abundance of bird species and species guilds differed between conifer-dominated, broadleaf-dominated, and mixed species production forest stands. Specifically, bird species classified *a priori* as being associated with broadleaf

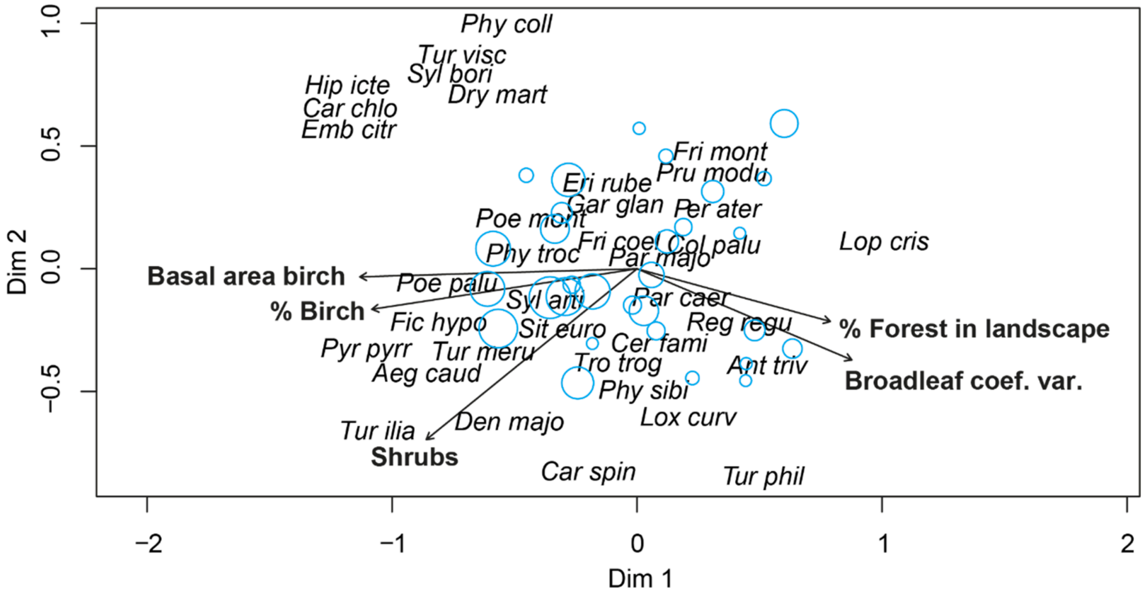

Fig. 2. The two first dimensions (out of three) from the non-metric multidimensional scaling (NMS) of all bird specieś abundances. The arrows show the vegetation variables with a significant ($P < 0.05$) correlation with the ordination (Table 1). Basal area birch = basal area of birch, %birch = proportion of birch, shrubs = number of shrubs (stems ha^{-1}), Broadleaf Coef. Var. = coefficient of variation in the amount of broadleaf trees, % forest in landscape = proportion of forest in the surrounding landscape (radius 1000 m). The circles indicate the proportion of birch in the stands ranging from 0% (smallest circle) to 86% (largest circle).

Table 3

Coefficients of the correlation between the three dimensions from the non-metric multidimensional scaling (NMS) of the bird assemblages and the vegetation variables. The P-values indicate if there is a significant correlative relationship between an individual variable and the bird species composition in the stands.

	Dim1	Dim2	Dim3	r^2	P-value
Spruce BA	0.86	−0.36	0.37	0.24	0.063
Birch BA	−0.98	−0.03	0.17	0.38	**0.009**
Total BA	0.42	−0.67	0.61	0.12	0.336
Birch %	−0.99	−0.15	−0.07	0.34	**0.013**
CWD	0.49	−0.33	−0.81	0.04	0.823
Shrubs	−0.78	−0.63	−0.04	0.35	**0.006**
Old Dec 1 km	0.38	0.89	−0.24	0.07	0.66
Forest 1 km	0.72	−0.2	−0.67	0.34	**0.007**
Dec 1 km	−0.51	0.18	0.84	0.17	0.151
CoV broadleaves	0.85	−0.36	−0.38	0.3	**0.021**

Table 4

Pearson correlation coefficients of vegetation variables and the three first components of Principal Components Analyses.

	PC1	PC2	PC3
Spruce BA	−0.94	0.12	−0.04
Birch BA	0.83	0.3	0.09
Total BA	−0.7	0.35	0.1
Birch	0.95	0.13	0.01
CoV broadleaves	−0.9	−0.1	−0.06
CWD	−0.23	−0.03	0.84
Shrubs	0.58	0.14	0.6
Old Dec 1 km	−0.38	0.39	0.22
Old 1 km	0.13	−0.82	−0.22
Forest 1 km	−0.29	−0.58	0.52
Dec 1 km	−0.11	0.93	−0.1

trees, were significantly more likely to be associated with stands with a higher basal area and proportion of birch, whereas conifer-associated birds showed a significant but less-pronounced aversion to the prevalence of broadleaf trees. For example, broadleaf specialists such as the long-tailed tit and the near-threatened marsh tit (Roberge and Angelstam 2006, Lindbladh et al. 2011) only exhibited breeding behaviour in stands with>70% broadleaf. In contrast, whereas conifer-specialists were (as expected) more prevalent in conifer-dominated stands, species such as the goldcrest, coal tit, and willow tit still exhibited breeding behaviour in stands with as little as 15% conifer. This was despite the facts that the known breeding habitat of the goldcrest in this region is *Picea* dominated forests (Ottosson et al., 2012); while, in northern Europe, the willow tit principally breeds in conifer forest of *Pinus*, *Picea* or *Larix* (Gosler et al., 2019). Our findings thus indicate the complementarity of broadleaf and conifer dominated stands, in terms of the bird assemblages supported (Donald et al., 1998). This complementarity, and its implications for bird diversity, can in turn motivate the use of broadleaf-conifer mixtures to benefit avian diversity in production forests. We found that almost 75% of bird species encountered during our surveys were observed in mixtures, which supported 67% and 80% of the broadleaf and conifer specialists respectively.

If the goal is to enhance the avian diversity of conifer-dominated production forests, then our results lend support to increasing their broadleaf component. This could be achieved using thinning regimes to favour broadleaf trees (primarily birch) that naturally regenerate after clearcutting, resulting in either intimate- (tree species evenly dispersed), or patch scale mixtures (trees clustered by species). Despite their potential importance to bird diversity outcomes, the evidence in support of either approach is limited and contradictory. Whereas some studies advocate the use of intimate broadleaf mixtures to disperse the positive contribution of broadleaf trees (Bibby et al., 1989; Donald et al., 1998); other studies instead advocate concentrating broadleaves into patches to meet the territorial requirements of specialists (French et al., 1986).

Our findings may tentatively provide some indirect support that patch scale spruce-birch mixtures, especially if combined with lower basal area, may improve understory habitats for bird assemblages in this region. Hedwall et al. (2019) found that increasing the prevalence of birch in the overstorey of spruce production stands improves the local coverage and species richness of understory vascular plants for a given stem density, with the highest benefits achieved at a lower basal area. These results indicate that clustering the birch into patches could be used to enhance the prevalence and diversity of understory shrub habitats and resources for bird assemblages. Furthermore, whereas the abundance of both migrants and ground nesting bird species was linked

Table 5

Regression coefficients and P-values from Generalized Linear Models of the effect of three principal components (Table 2) on bird species richness and abundance within different guilds. Regression coefficients with $P < 0.05$ in bold.

		PC1		PC2		PC3	
		coef.	P	coef.	P	coef.	P
Total bird community	Species richness	**0.07**	**0.024**	0.06	0.135	0.05	0.279
	Evenness	**0.02**	**0.019**	0.01	0.158	0.01	0.499
	Abundance	**0.07**	**0.007**	**0.08**	**0.026**	0.07	0.097
Residents	Abundance	0.08	0.078	0.07	0.208	**0.13**	**0.048**
Partial migrants	Abundance	−0.06	0.170	0.03	0.568	0.05	0.527
Migrants	Abundance	**0.22**	**<0.001**	0.10	0.090	0.01	0.879
Broadleaf specialists	Abundance	**0.33**	**<0.001**	**0.18**	**0.009**	0.05	0.491
Generalist (broad and con)	Abundance	0.04	0.232	0.06	0.221	0.08	0.156
Conifer specialists	Abundance	**−0.14**	**0.023**	−0.07	0.442	0.07	0.498
Cavity nesters	Abundance	0.09	0.094	0.02	0.748	**0.16**	**0.035**
Above ground nesters	Abundance	−0.01	0.833	**0.10**	**0.040**	0.04	0.487
Ground nesters	Abundance	**0.20**	**<0.001**	0.06	0.345	0.01	0.884

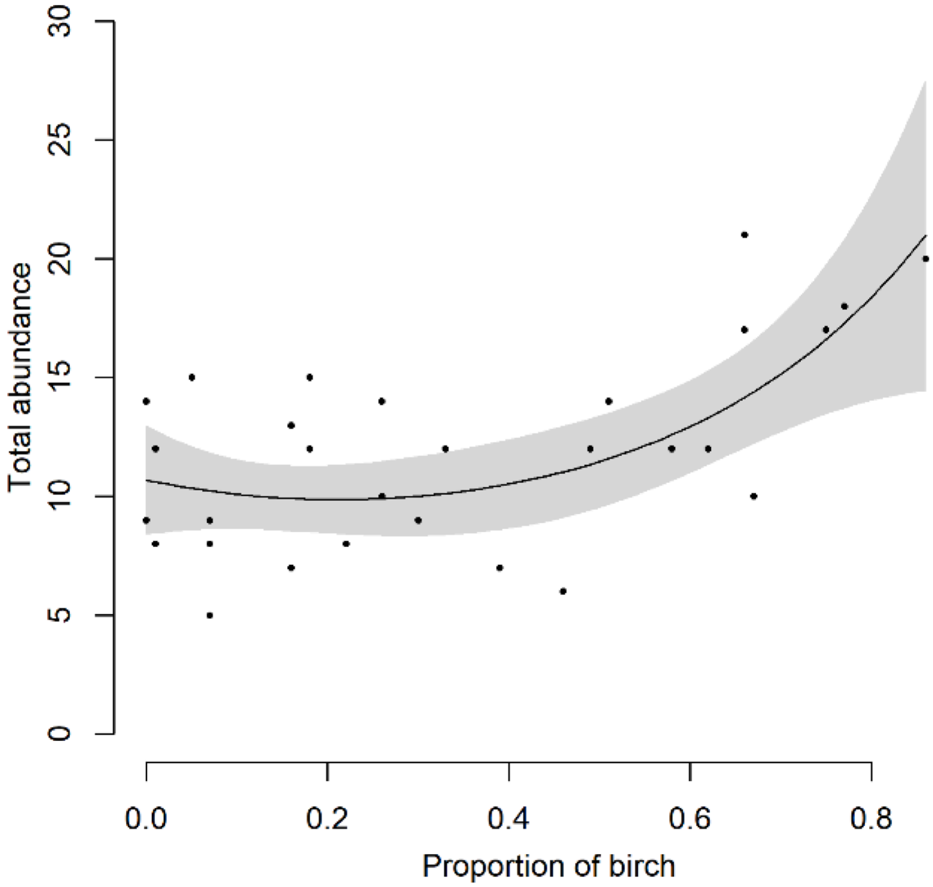

Fig. 3. Predicted abundances (with 95% CI) of all birds, in relation to the proportion of birch, from a Generalized Linear Model (GLM). The model was performed with a log-link but the figure shows the scale of the response variable to facilitate interpretation.

to stands with a higher proportion of birch, the increased prevalence of these groups also likely resulted from the increased coverage of shrubs that occurred in these stands. Many European migratory bird species are associated with open canopy broadleaf forests possessing a high coverage of shrubs (Bibby et al., 1989; Donald et al., 1998; Sweeney et al., 2010). One of the hypothesized explanations is that more open shrub-rich forest environments in Europe are more consistent with the environmental conditions Palearctic migrants have evolved to exploit in their African wintering areas (Bilcke, 1984; Helle and Fuller, 1988). In either regard, many northern European migrants appear to benefit from the diversity of feeding and nesting sites (i.e. ground nesters), as well as protection from predators (Cavard et al., 2011), that a rich understory shrub layer can provide in broadleaf-prevalent production stands.

Just as our results lend support to the use of broadleaf-conifer mixtures to enhance bird diversity, so too can they be used to motivate the use of broadleaf-dominated production forests. As noted previously, bird species richness, total abundance and evenness increased in stands with a higher proportion of broadleaf trees. Most importantly, total bird species abundance continued to improve as the broadleaf component was maximised. This suggests that despite the general loss of conifer trees in the canopy, and what could be inferred as increased biotic homogenization, broadleaf-dominated stands nevertheless appeared to provide better conditions for increasing bird species abundance than either conifer-dominated or even broadleaf-conifer mixtures. Notably, this was despite the fact that these stands were dominated by birch, rather than other native broadleaf tree species known to disproportionately benefit large numbers of red-listed species in Sweden, such as *Quercus* and *Tilia* (Berg et al., 1994; Jonsell et al., 1998; Hultberg et al., 2020). Furthermore, if we consider the few red-listed species (near threatened) that were encountered at least twice during the surveys, then we tentatively suggest that favouring broadleaf-dominated production stands will likely benefit marsh tit and European pied flycatcher, which were only encountered in such stands. Our results do not suggest that the willow tit would be adversely affected by such a shift, though some questions could be made regarding the impact on wood warbler. An additional species of interest that should benefit from more broadleaves, although not red-listed, is long-tailed tit. This resident bird species generally associated with middle-aged to older broadleaf forest (Roberge et al., 2018) that is sensitive to landscape fragmentation and population isolation (Enoksson et al., 1995; Lindbladh et al., 2011). As noted earlier, long-tailed tit was solely encountered in broadleaved-dominated stands during our surveys.

In addition to the tree species grown, there are multiple aspects of production forest management, as well as landscape contexts, that can limit or enhance stand-level biodiversity (Lindenmayer and Franklin, 2002; Brockerhoff et al., 2017). For example, the prevalence of hole nesting birds is necessarily tied to the availability of suitable nesting sites, which in production forests often relies on the retention and prevalence of large old trees and snags (Jokimäki and Huhta, 1996; Lindenmayer and Laurance, 2017). Correspondingly, we found that the abundance of hole-nesting birds was positively associated with stands possessing higher levels of dead wood. In addition, forest characteristics found in the surrounding landscape matrix can influence stand level biodiversity (Donald et al., 1998; Hausner et al., 2002; Wells et al., 2011; Basile et al., 2019), via e.g. spill-over effects (Tscharntke et al., 2012). In this regard, we found that stands situated within landscapes with more broadleaf and young forest, had a greater abundance of birds, as well as more broadleaf specialist and ground nesting bird guilds. However, because of the complex interplay between stand- and landscape-level influences on forest species (Wells et al., 2011), it is difficult to determine the extent to which factors such as the increased abundance of broadleaf forest interacted with the reduced abundance of older forests in surrounding landscapes, to alter the stand level occurrence of individual bird species (Jokimäki and Huhta, 1996). Nevertheless, our results indicate that increasing the prevalence of broadleaf trees at both stand and landscape scales had a positive impact on the diversity of bird assemblages in production forests. Furthermore, efforts to increase the availability of large trees and dead wood, and limit the density of trees per ha in production forest to promote a more diverse and productive understorey vegetation, should likewise enhance the avian assemblages of these stands. Importantly, the adoption of such forest management strategies should provide a range of co-benefits for biodiversity and ecosystem services, from the diversity of understory vascular plants (Hedwall et al., 2019), and saproxylic insects (Lindhe et al., 2005), to the fitness of large game (Felton et al., 2020b) and stand recreational value (Gundersen and Frivold, 2008).

4.1. Conclusion

Our results provide further evidence that silvicultural approaches focused primarily on creating intensively managed conifer-dominated vegetation, are unlikely to capture more than a fraction of the available avian species pool. By increasing the proportion of broadleaf tree species in otherwise conifer-dominated stands, a wider range of bird species is likely to be supported by production forest habitats. In addition, our results highlight the importance of retaining the habitats and resources provided by dead wood, as well as the need to carefully consider the density of the stand and disturbance regimes, to ensure opportunities for the development and retention of a more diverse and structurally complex understory vegetation. If mixed species stands of birch and spruce are to be created, our findings lend indirect support for clustering rather than dispersing birch to help increase light levels in the forest understory. Perhaps most importantly, our results indicate that birch-dominated production stands can be added to the toolbox of means by which production forest habitats can be improved for the benefit of bird assemblages in this region.

CRediT authorship contribution statement

Adam Felton: Conceptualization, Investigation, Methodology, Funding acquisition. **Per-Ola Hedwall:** Conceptualization, Methodology, Formal analysis. **Renats Trubins:** Formal analysis. **Jakob Lagerstedt:** Software. **Annika Felton:** Conceptualization, Funding acquisition. **Matts Lindbladh:** Conceptualization, Investigation, Methodology, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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