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Effects of habitat heterogeneity on bird communities in forests of northeastern Germany

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Abstract

Habitat heterogeneity is a key factor for regulating biodiversity in temperate lowland forests. Specifically, stands associated with late forest development phases provide important habitat structures for many rare and threatened forest bird species. However, how forest stands that differ in their structural complexity, canopy conditions and tree species composition affect forest bird assemblages both at the local and landscape scale remains largely unclear. In a young moraine lake landscape of northeastern Germany, we assessed correlations of bird diversity and bird composition with stand properties. We used data from 48 transects (400 m) established in (1) unmanaged, closed-canopy, mature stands that were dominated by *Fagus sylvatica* (UDS), and (2) diverse managed, mixed coniferous stands with a mosaic of open and closed canopy patches (MCS). We found that bird communities of the UDS strongly differed from those in the MCS, with open habitat species being more frequent in the MCS. By contrast, differences in diversity measures were less distinct. Moreover, we identified nine indicator species for the UDS (*Columba oenas*, *Cyanistes caeruleus*, *Muscicapa striata*, *Leiopicus medius*, *Certhia brachydactyla*, *Ficedula parva*, *Dryobates minor*, *Sturnus vulgaris*, *Ficedula hypoleuca*) and seven indicator species for the MCS (*Periparus ater*, *Pyrrhula pyrrhula*, *Regulus regulus*, *Prunella modularis*, *Lophophanus cristatus*, *Emberiza citronella*, *Anthus trivialis*). Several famous ancient beech forest patches in Müritz National Park and the UNESCO Biosphere Reserve "Schorfheide-Chorin" were found to harbour the set of our UDS indicator species. UDS support bird coenosis typical for old mature broadleaved forests and can be considered as an effective tool for bird conservation. Our results further indicate that the combination of unmanaged and managed stands associated with different habitat complexities would benefit forest bird assemblages at the landscape scale.

Keywords: forest specialist birds; bird conservation; forest nature reserves; old-growth patches; *Ficedula parva*; *Leiopicus medius*; coniferous forest

Introduction

Recent research has shown that habitat heterogeneity is a key factor for regulating the biodiversity in temperate forests (Heidrich et al. 2020, Schall et al. 2021, Eckerter et al. 2022). At the stand level, stand age is closely related to habitat heterogeneity, because as stands mature the abundance, diversity and continuity of habitat structures and their spatial heterogeneity all increase (Fichtner and Härdtle 2021). Specifically, stands associated with late forest development phases provide important habitat structures for many rare and threatened forest bird species, such as a high abundance of old and senescent trees with microhabitats as well as a high amount and diversity of deadwood structures (Moning and Müller 2008, 2009, Rosenvald et al. 2011, Wesołowski et al. 2018). Birds are among the most representative species groups for forest biodiversity (Moning and Müller 2009, Mikusiński et al. 2018, Heidrich et al. 2020), and stand age largely affects bird communities. At the landscape level, there are many criteria affecting habitat heterogeneity that is relevant for the diversity and structure of bird assemblages, such as structure of forest edges, natural canopy gaps, a mosaic of deciduous and coniferous forest patches, gradients from deciduous to conifer dominated stands or a patch mosaic of forest development phases (Wilson et al. 2006, MacKay et al. 2014, Klingbeil and Willig 2016, Terraube et al. 2016, Przepióra et al. 2020, Felton et al. 2021, Lewandowski et al. 2021). It is known that clear-cuts and forest roads in managed forests significantly influence the species richness of other animal groups, like diurnal butterflies or wild bees (Viljur et al. 2020, Eckerter et al. 2022). Landscape mosaics that combine woodlands and open habitats are associated with a high conservational value for bird communities (Terraube et al. 2016). Specifically, forest birds are assumed to benefit from a landscape mosaic due to the availability of habitat patches related to different successional stages and forest edges (cf. Terraube et al. 2016, Fahrig 2020). Moreover, moderate disturbances by low-impact management strategies are also identified as important factors for promoting animal diversity across taxa (Steverding and Leuschner 2002, Terraube et al. 2016, Fartmann et al. 2018, Eckerter et al. 2022, Viljur et al. 2022). Furthermore, mature, naturally regenerating forest patches are important components in intensively managed forest landscapes to maintain diverse forest bird assemblages (MacKey et al. 2014).

Large-scale unmanaged forest areas, such as strictly enforced forest nature reserves, are important habitats where forest biodiversity can be preserved. For maintaining forest biodiversity, the state authorities of Mecklenburg-Western Pomerania established (besides of larger national parks) a number of smaller areas of woodlands with naturally regenerating forests and with varying degrees of protection: local nature conservation areas, Natura 2000 areas and forest reserves. Although the former two are well known in European countries, the forest reserves ("Naturwaldreserate" in German) are 35 areas in Mecklenburg-Western Pomerania of approx. 14–85 hectares (in total approx. 14 km^2) of mainly mature forest patches and autochthonous trees (Engel et al. 2016). A complementary approach is the establishment of several small-scale (e.g., with a minimum of 0.7–1.2 ha in size), unmanaged areas, so called "old-growth islands", within managed stands and forest landscapes (Müller et al. 2012). Such islands can provide essential habitat structures associated with late forest development stages, and therefore specifically contribute to the protection of rare and threatened forest species (MKLLU MV 2002). This conservation approach is assumed to lead to co-benefits from management and conservation, as felling in these unmanaged areas in production forests is minimized, while conservation aspects are optimized. For example, the total number of such old-growth islands in the federal state of Mecklenburg-Western Pomerania amounts to 1.950, which corresponds to a total area of approx. 25 km^2.

We used data from 12 study sites that represent structural differences at the local scale and a broad range of habitat conditions at the landscape scale to assess the importance of habitat heterogeneity in modulating forest bird communities.

Material and methods

Study area and study design

The study was conducted in a heterogenous lake landscape of the young moraine areas in the Mecklenburg Lakeland region of the federal state of Mecklenburg-Western Pomerania in northeastern Germany (Figure 1). In this geomorphologically very young landscape, shaped by glacier expansion and deglaciation processes during the Last Glacial Maximum and Weichselian Late Glacial, the highest elevations are moraine tracts of about 80 to 120 meters above sea level. European beech (*Fagus sylvatica*) forests represent the predominant natural vegetation in the study area. The data were collected in two nature parks, "Sternberger Seenland" as well as "Nossentiner/Schwinzer Heide", and adjacent areas surrounding the city of Schwerin, which mainly represent a topographic pattern typical of this lake landscape (Figure 1). In Germany, a nature park is a large-scale area of approx. 300–600 square kilometres consisting predominantly of protection areas (nature reserves, Natura 2000 areas, landscape protection areas) with high species and habitat richness and a preserved historical cultural landscape characterised by varied usage. Their purpose is to combine nature conservation and integration of humans and their regional identity, as well as sustainable development of tourism and land use.

We used bird data collected at 12 study sites (Figure 1) in two different stand types that represent a broad

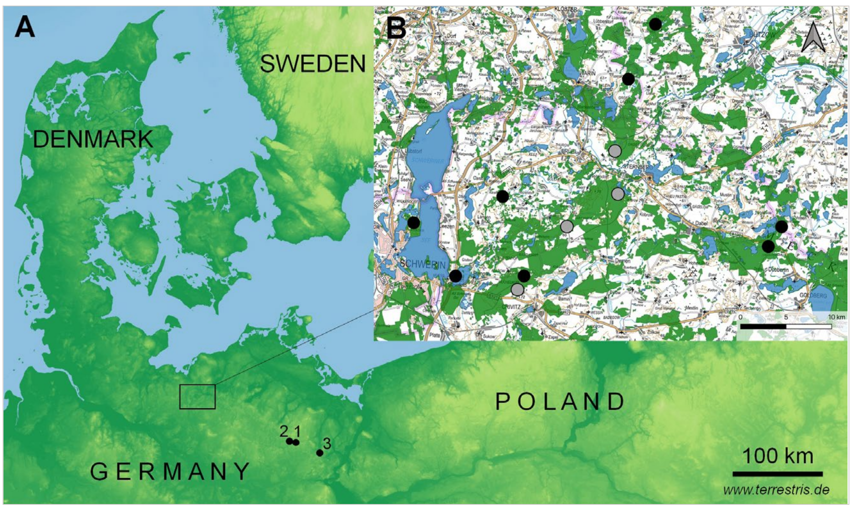

Figure 1. A: Large-scale geographic position of the study area (map: www.terrestris.de) in the European Lowlands and position of old-growth lowland beech forest sites, listed in Table 3 (1 Heilige Hallen, 2 Serrahner Berge, 3 Fauler Ort). B: Small-scale topographic feature of the study area (map: GAIA Atlas M-V) and position of the study sites. Black points designate study sites of unmanaged deciduous-dominated stands (UDS), Light grey points designate managed conifer-dominated stands (MCS)

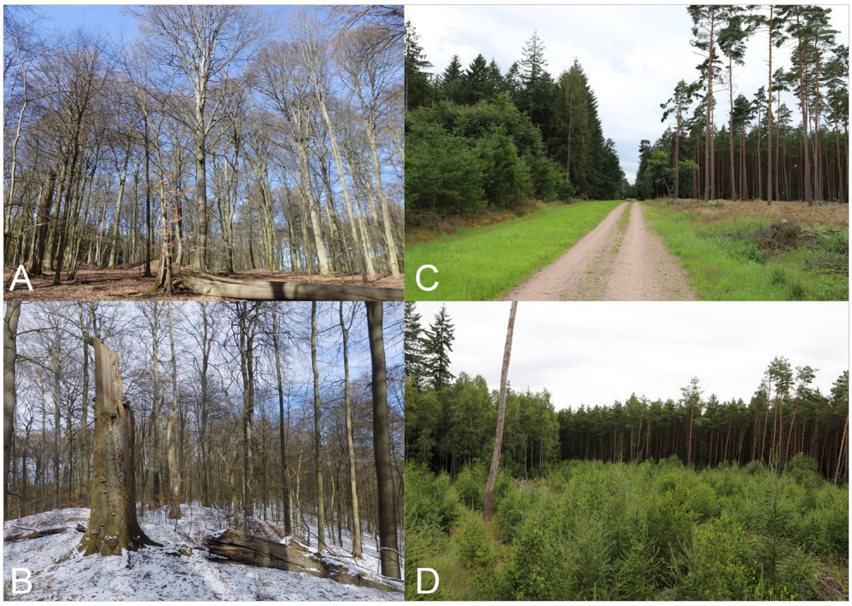

Figure 2. Typical structural features of UDS (unmanaged deciduous-dominated stands) (A, B) and MCS (managed conifer-dominated stands) (C, D)

range of forest habitat conditions at the landscape scale: (1) unmanaged, closed-canopy stands dominated by deciduous trees (especially *Fagus sylvatica*) with a high amount of deadwood and a high abundance of old trees (Figure 2, AB) (hereafter unmanaged deciduous-dominated stands, UDS), and (2) managed, mixed coniferous stands with a mosaic of open and closed canopy patches (Figure 2, CD) hereafter: managed conifer-dominated stands, MCS).

Within each study site, we selected 2–6 transects (*see* bird counting analysis) with a minimum distance of about 300 m resulting in a total of 48 transects (UDS: $n = 24$; MCS: $n = 24$). In our study, all UDS are embedded within managed forests, and can therefore be considered as "old-growth patches" from a landscape ecology perspective (cf. Vandekerkhove et al. 2013). These stands are characterized by a regular occurrence of methuselah trees (> 150 years), as well as a high amount of standing deadwood (Figure 2, AB). The mean stand age is 134.5 years (maximum: 198 years) and the maximum mean diameter at breast height (1.30 m) is 86.6 cm. A further typical feature is the small-scale occurrence of late forest development phases (e.g. terminal and disintegration sensu; Begehold et al. 2015). All transects are dominated by deciduous species (93%) in the upper canopy with *F. sylvatica* being the most abundant tree species. The understorey consists of about 95% of deciduous trees. Most of the UDS are situated in local nature conservation areas or Natura 2000 areas (see Supplementary Table S1).

The MCS are characterised by a mosaic of diverse patches of clearcuts, mixed with conifers and some deciduous trees including younger stages due to harvesting and an additional effect of on average younger trees. Further characteristics are large forest roads between forest plantations and a lack of old-growth attributes (Figure 2, CD). The mean stand age is 76.3 years and the mean diameter at breast height amounts to 47.8 cm, which is almost half compared to those of UDS. The tree species composition of the canopy is 79% dominated by coniferous trees (e.g. Scots pine (*Pinus sylvestris*), common spruce (*Picea abies*) and European larch (*Larix decidua*), whereas the understorey is characterised by 73% deciduous trees (e.g. common oak (*Quercus robur*), red oak (*Quercus rubra*) and European beech (*F. sylvatica*) and conifers (further characteristics are displayed in Supplementary Table S1).

Bird counting and data analysis

Aside from territory mapping, line transect methods (Brotons et al. 2003, Virkkala and Rajasärkkä 2006, Solonen and Kokimäki 2010, Hu et al. 2011, Ibarra et al. 2017, Dylewski and Tobolka 2022) are commonly used in studies on bird diversity. To achieve larger spatial coverage of bird species registration per sampling unit, we used a line transect with four lines (4 × 100 m) in the shape of a square as one local sampling unit. This square with a perimeter of 400 m was passed within 15 minutes per count. All bird species heard or seen within ca. 50 m of the transect were recorded (absence/presence). For each transect, bird species were recorded five times around sunrise between April and June. In total, we sampled 24 transects in the UDS and 24 transects in the MCS (Supplementary Table S1). The bird counting took place between 2016 and 2018 by the first author.

To assess effect of stand type (UDS vs. MCS) on bird species richness and diversity (using Simpson's index), we applied linear mixed-effects models with a Gaussian distribution. Study transects (to account for repeated measures) nested within study site (to account for inter-forest variability) were used as random effects. To test for differences in bird composition between the UDS and MCS, we calculated the Bray-Curtis dissimilarities based on the total abundance of bird species (i.e. sum of all five visits per transect) followed by a multivariate permutational analysis of variation (PERMANOVA). Data were standardized (Wisconsin double standardization) prior to analysis. Stand type-specific bird assemblages were visualized by non-metric multidimensional scaling (NMDS) using two dimensions. Moreover, we performed an indicator species analysis (Dufrêne and Legendre 1997) with 1,000 permutations and allowing for site group combinations based on total abundance of species data to identify those species that were strongly associated with the UDS and MCS. The statistical analyses were performed with R 3.6.3 (R Core Team 2019) using the packages indicspecies (De Cáceres and Legendre 2009), lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2017) and vegan (Oksanen et al. 2019).

Results

A total of 53 bird species were recorded. Chaffinch (*Fringilla coelebs*), wren (*Troglodytes troglodytes*), great tit (*Parus major*), robin (*Erithacus rubecula*), blackbird (*Turdus merula*) and nuthatch (*Sitta europaea*) were the most abundant species in the UDS, as opposed to chaffinch, wren, robin, chiffchaff (*Phylloscopus collybita*), firecrest (*Regulus ignicapilla*), song trush (*Turdus philomelos*) and blackbird in the MCS (Table 1). The most frequent (i.e. those species being present in each of the 24 study transects per stand type) were blackbird, chaffinch, lesser spotted woodpecker (*Dendrocopos major*), stock dove (*Columba oenas*), blackcap (*Sylvia atricapilla*), nuthatch, robin, song trush and wren for the UDS, and blackbird, chaffinch, blackcap, robin, song trush, wren and chiffchaff for the MCS (Table 1). The species pattern shows the most remarkable difference in cavity nesters, where five species (middle spotted woodpecker (*Leiopicus medius*), lesser spotted woodpecker (*Dryobates minor*), jackdaw (*Corvus monedula*), red-breasted flycatcher (*Ficedula parva*) and pied flycatcher (*Ficedula hypoleuca*)) were present in the UDS but completely absent in the MCD (Table 1). There are some conspicuous differences in the presence of birds typical for deciduous forests and coniferous forests, respectively. The short-toed treecreeper (*Certhia brachydactyla*) present in 91.7% of the UDS transects was completely absent in the MCS ones. The crested tit (*Lophophanes cristatus*) and goldcrest (*Regulus regulus*) were present in 46% and 54%, respectively, of the MCS transects, but completely absent in the UDS ones. Species of open forests were much more frequently observed in the MCS (Table 1). Only the tree pipit (*Anthus trivialis*) showed a very scarce presence in the UDS, whereas it was present much more frequently in the MCS. The presence of non-typical forest species was higher in the MCS, and the most remarkable species here was the yellowhammer (*Emberiza citrinella*), recorded in nine MCS transects versus only one UDS transect (Table 1).

Stand type had a marginally significant (F: 3.40, $p = 0.098$) effect on bird species richness (Figure 3a) and a significant effect on species diversity (F: 5.18, $p = 0.047$). Although diversity measures tended to be higher in the UDS than in MCS (Figure 3b), the effects were comparably small. In contrast, compositional difference in bird species between the two stand types was highly significant (PERMANOVA: F: 9.24, $p < 0.001$; Figure 4a). On average, community composition differed by 41% (t: 139.1, $p < 0.001$; Figure 4b). Moreover, the UDS were more similar in their bird species composition compared to the MCS, which is indicated by the lower spread along the NMDS-axes (Figure 4a).

We identified nine indicator species for the UDS and seven for the MCS (Table 2). Stock dove (*Columba oenas*, $p < 0.001$) and short-toed treecreeper (*Certhia brachydactyla*, $p < 0.001$) were most strongly associated with the UDS, while coal tit (*Periparus ater*, $p < 0.001$) was the strongest indicator for the MCS.

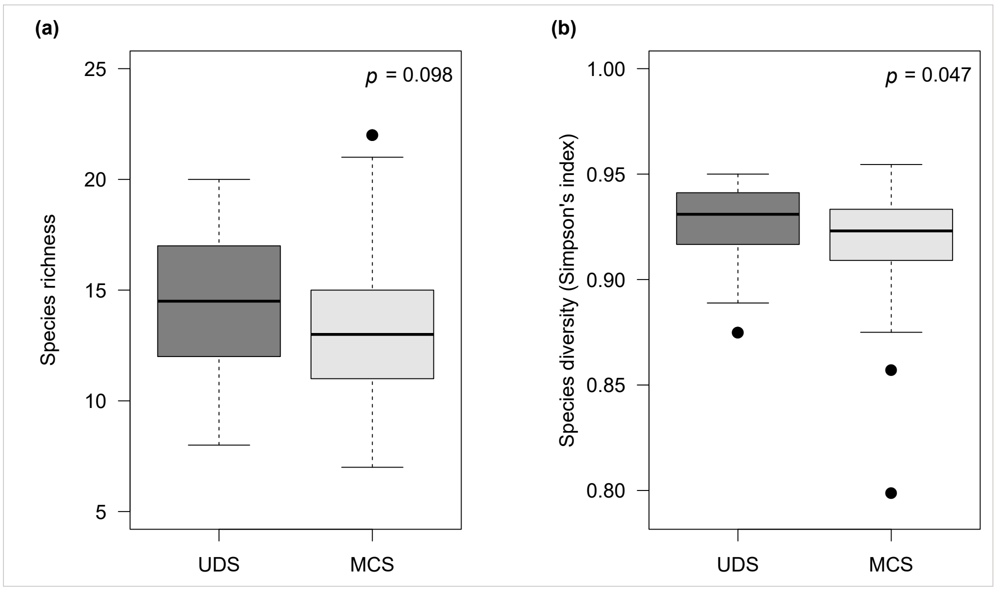

Figure 3. Differences in breeding bird species (a) richness and (b) diversity between the UDS and MCS

Boxplots show observed values; *p*-values were obtained from the linear mixed-effects models. UDS: unmanaged deciduous-dominated stands; MCS: managed conifer-dominated stands.

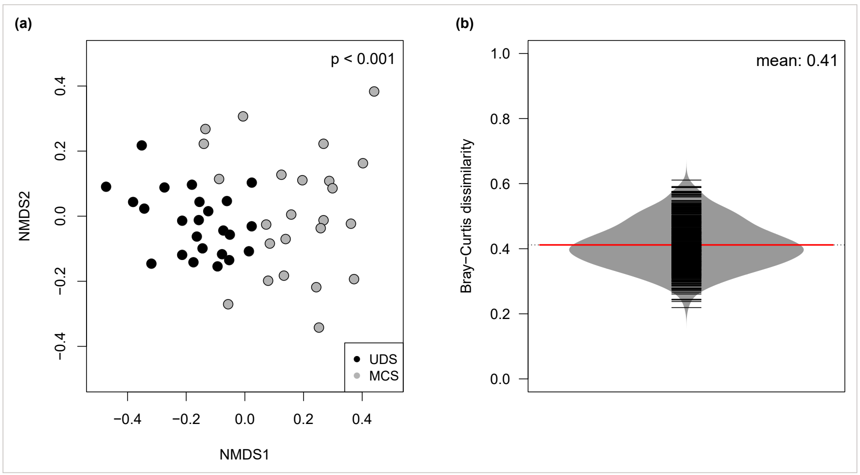

Figure 4. Differences in bird species composition between unmanaged deciduous-dominated stands (UDS) and managed conifer-dominated stands (MCS): (a) Results of a non-metric multidimensional scaling (NMDS) analysis (stress: 0.21); (b) Beanplot for the Bray-Curtis dissimilarity

The small black lines represent individual transect data.

Table 1. Results of bird counts in unmanaged deciduous-dominated and managed conifer-dominated stands

Species preference / guilds	Unmanaged deciduous-dominated stands (UDS)		Managed conifer-dominated stands (MCS)	
	Abundance	Frequency (%)	Abundance	Frequency (%)
Generalist species				
Turdus merula	105	100	75	100
Fringilla coelebs	117	100	116	100
Sylvia atricapilla	80	100	72	100
Troglodytes troglodytes	111	100	112	100
Erithacus rubecula	106	100	93	100
Columba palumbus	53	95.8	65	91.7
Turdus pilaris	2	8.3	5	20.8
Forest birds				
- Coniferous -				
Lophophanes cristatus *	0	0.0	23	45.8
Regulus regulus *	0	0.0	27	54.2
Periparus ater	27	58.3	66	91.7
Pyrrhula pyrrhula	10	41.7	37	75.0
Regulus ignicapilla *	50	75.0	80	95.8
Loxia curvirostra *	6	20.8	10	29.2
- Deciduous -				
Certhia brachydactyla	44	91.7	0	0.0
Aegithalos caudatus	2	8.3	5	20.8
Carduelis spinus *	21	58.3	32	91.7
Phylloscopus trochilus	21	83.3	44	75.0
Poecile palustris *	28	58.3	22	62.5
Garrulus glandarius	21	54.2	26	66.7
Poecile montanus *	34	75.0	20	50.0
Coccothraustes coccothraustes	46	87.5	50	87.5
Turdus iliacus	3	12.5	2	8.3
Oriolus oriolus	6	20.8	5	20.8
- Coniferous / Deciduous -				
Phylloscopus sibilatrix *	67	95.8	52	91.7
Certhia familiaris	59	91.7	40	83.3
Turdus viscivorus	2	8.3	12	41.7
Prunella modularis	2	8.3	26	58.3
Turdus philomelos	90	100	79	100
Phylloscopus collybita *	72	91.7	84	100
Species of open forests				
Lullula arborea	0	0.0	2	4.2
Streptopelia turtur	0	0.0	3	4.2
Anthus trivialis	4	12.5	19	29.2
Obligate cavity nesters				
Leiopicus medius *	22	41.7	0	0.0
Dryobates minor *	7	25.0	0	0.0
Corvus monedula	5	16.7	0	0.0
Ficedula parva *	10	25.0	0	0.0
Ficedula hypoleuca	18	25.0	0	0.0
Dendrocopos major	78	100	58	95.8
Sitta europaea	102	100	57	91.7
Parus major	107	100	70	95.8
Columba oenas	65	100.0	24	37.5
Cyanistes caerulaeus	48	91.7	16	45.8
Sturnus vulgaris	20	45.8	3	8.3
Phoenicurus phoenicurus	9	25.0	3	8.3
Dryacopus martius *	20	58.3	17	37.5
Muscicapa striata	16	45.8	4	16.7
Picus viridis	14	45.8	9	25.0
Non typical forest species [1]				
Saxicola rubicola	0	0.0	2	8.3
Locustella fluviatilis	0	0.0	1	4.2
Carduelis carduelis	0	0.0	4	16.7
Emberiza citrinella	1	4.2	20	37.5
Chloris chloris	6	20.8	4	16.7
Sylvia borin	2	8.3	4	12.5

Note: The 'abundance' indicates the total number of records in all transect per stand type ($n = 120$). The 'frequency' indicates the relative number in how many transects of a specific stand type the species was recorded ($n = 24$, i.e. 24 = 100%). ([1] among others because of larger openings in managed forests, * forest specialist birds after Mikusiński et al. 2018). The association of species with deciduous, coniferous or coniferous/deciduous stands were arranged following Reif et al. (2022) and Felton et al. (2021).

Table 2. Significant indicator species of unmanaged deciduous-dominated ($n = 24$) and managed conifer-dominated stands, $n = 24$) in forests of northeastern Germany on the basis of absence/presence data with indicator species analysis according to Dufrêne and Legendre (1997)

Indicator species	Indicator value	*p*-value
UDS		
Stock dove *Columba oenas*	0.629	< 0.001
Short-toed treecreeper *Certhia brachydactyla*	0.606	< 0.001
Blue tit *Cyanistes caeruleus*	0.548	< 0.001
Middle spotted woodpecker *Leiopicuis medius*	0.428	< 0.001
Pied flycatcher *Ficedula hypoleuca*	0.387	< 0.001
Common starling *Sturnus vulgaris*	0.381	< 0.001
Red-breasted flycatcher *Ficedula parva*	0.289	< 0.01
Spotted flycatcher *Muscicapa striata*	0.327	< 0.05
Lesser spotted woodpecker *Dryobates minor*	0.242	< 0.05
MCS		
Coal tit *Periparus ater*	0.625	< 0.001
Bullfinch *Pyrrhula pyrrhula*	0.493	< 0.001
Goldcrest *Regulus regulus*	0.474	< 0.001
Dunnock *Prunella modularis*	0.449	< 0.001
Crested tit *Lophophanes cristatus*	0.438	< 0.001
Yellowhammer *Emberiza citrinella*	0.398	< 0.001
Tree pipit *Anthus trivialis*	0.362	< 0.01

Note: For location of the sites, see Figure 1. The indicator value ranges between 0 (no indication) and 1 (perfect indication).

Discussion

Our data show that local species richness in the unmanaged deciduous-dominated stands with closed canopies and a high amount of deadwood and a high abundance of old trees is not considerably higher compared to the managed conifer-dominated stands with open and closed canopy conditions (only one species more on average in the UDS). Given that birds are highly mobile organisms, adverse management effects on habitat structures can be masked by new opportunities caused by management (open sites, younger stages etc.) and therefore result in ambiguous outcomes with respect to species diversity (Paillet et al. 2010). Moreover, Lešo et al. (2019) and Bonica (2000) showed that the bird species composition and the occurrence of rare species and forest specialists rather than species diversity characterize the main differences between managed and natural/unmanaged forest stands. This is in line with our finding of large differences in species composition, but not in species diversity between the UDS and MCS. We show that a heterogenous landscape composed of a managed, coniferous dominated forest contains similar species richness/diversity as a comparatively near natural, deciduous dominated stand. Caused by a considerable patch heterogeneity of open sites, clearcuts, monospecific patches including young coniferous and deciduous stands, embedded in a mesh of large, often very broad forest roads (Figure 2, CD), the MCS offers species of open forests, coniferous specialists and non-typical forest species such as the yellowhammer additional niches. This compensates for the lack of several specialised cavity nesters or deciduous specialists, which we found to be completely absent in the MCS. This interpretation is also supported by Fahrig (2020), who concluded that the availability of habitat patches of different successional stages (as is the case for the MCS) may support higher biodiversity levels. Interestingly, the absence/presence patterns of indicator species in our study, also reflecting structural differences in both stand types, are in accordance with those of the ancient beech forest patches in Müritz National Park (Figure 1, No. 1–3) and the UNESCO Biosphere Reserve "Schorfheide-Chorin" (Figure 1, No. 4). The absence/presence patterns of bird species from these sites (data source: Müritz National Park: S. Rannow; Schorfheide-Chorin (site "Fauler Ort"): Schumacher 2006) show that nearly the complete subset of our identified indicator species for the UDS is also present in those forests (*see* Table 3). Conversely, the indicator species of the MCS are, with the exception of the coal tit, largely absent in those ancient forests (Table 3). Even though the bird counting methods

Table 3. Comparison of indicator species identified in this study with species absence/presence data of old-growth lowland beech forests in northeastern Germany

Indicator species	This study		Ancient beech forests of northeastern Germany		
			1	2	3
	UDS	MCS	300 years Heilige Hallen (25 ha)	200 years Ser-rahner Berge (75 ha)	250 years Fauler Ort (13 ha)
UDS					
Columba oenas ***	X	X	X	X	X
Certhia brachydactyla ***	X		X	X	X
Cyanistes caeruleus ***	X	X	X	X	X
Leiopicus medius ***	X		X	X	X
Ficedula hypoleuca ***	X		X	X	X
Sturnus vulgaris ***	X		X		X
Ficedula parva **	X		X	X	
Muscicapa striata *	X	X	X	X	X
Dryobates minor *	X		X	X	X
MCS					
Periparus ater ***	X	X	X	X	X
Pyrrhula pyrrhula ***	X	X			
Regulus regulus ***		X			
Prunella modularis ***	X	X			
Lophophanes cristatus ***		X			
Emberiza citrinella ***	X	X			
Anthus trivialis **	X	X			

Note: For location of sites 1–4, see Figure 1a. The mean stand age is given in the table header. Significance levels: $p < 0.001$***, $p < 0.01$**, $p < 0.05$*. Data source for site 1 and 3: Schumacher (2006), data source for site 2: unpublished database of the Müritz National Park (Department for Research and Monitoring). UDS: unmanaged deciduous-dominated stands; MCS: managed conifer-dominated stand.

from the mentioned sites differ from our study, the species occurrence is highly indicative for entire species presence (or absence) at those sites.

Several "indicator species" of the UDS represent their preferences for typical old-growth attributes of mature forests like standing deadwood, veteran trees, increasing tree-microhabitat diversity or diversity of forest development phases.

First of all, *Ficedula parva* is suggested to be the best indicator for forest biodiversity in birds, because it represents forest with the highest complexity of old-growth attributes (Pakkala et al. 2014). Next to nesting holes/niches, this also includes steep ground profile, high stand age as well as high tree age (Moning et al. 2011, Moning and Müller 2008). Moreover, *Leiopicus medius* is recommended as an excellent indicator for forest bird diversity and mature and structured broadleaved stands, as well as old and closed woods (Müller and Hothorn 2004, Kosiński 2006, Walczak et al. 2013, Lehikoinen and Virkkala 2018). Both *Ficedula hypoleuca* and *Cyanistes caeruleus* are known to reach high densities in cavernous forest stands (Wesołowski and Martin 2018) and we explain the highly significant indicator value of both species for the UDS with a much higher density of cavernous tree-related microhabitats in contrast to the MCS. Other species from our indicator species list such as *Dryobates minor*, *Columba oenas*, and *Certhia brachydactyla* are generally associated with mature and old-growth temperate forests (Wesołowski et al. 2018) and, along with *Muscicapa striata,* have been suggested as indicator species for lowland beech forests by Schumacher (2006).

The partially open character of the managed conifer-dominated stands (*see* Figure 2, CD) supports their colonization by several typical open habitat species such as yellowhammer (*Emberiza citrinella*) or tree pipit (*Anthus trivialis*) in the set of indicator species. Whereas the first species is atypical and rare in natural forests, the presence of *A. trivialis* in forests depends on the degree of canopy openness and will not be found in stands with more than 40% canopy coverage (Müller and Hothorn 2004). The inclusion of *Prunella modularis*, with its preference for young open and bushy spruce stands as breeding sites (Tuomenpuro 1989), in our list of indicator species for the MCS can be explained by the dominance of patchy conifer plantations including younger stages in the MCS sites. Other indicator species for the MCS such as *Pyrrhula pyrrhula*, *Lophophanes cristatus*, *Regulus regulus* or *Parus ater*, all of which are associated with coniferous trees (cf. Wesołowski et al. 2018) are likely to be attracted by dense pinewood stands characteristic of the managed forests. Given that *Ficedula parva* and *Leiopicus medius* were identified as indicator species for the UDS in our study, we suggest that the UDS, identified as old-growth islands in forestry and nature conservation in northeastern Germany, support bird coenosis typical for mature broadleaved forests (cf. Wesołowski et al. 2018) and can be considered an effective tool for bird conservation within managed forests.

Moreover, the distinct compositional difference in bird species assemblages between the two stand types (UDS and MCS) has consequences for biodiversity conservation at the landscape scale. The UDS investigated here are single patches, embedded within or at the margin of larger managed forests (typically similar to the selected MCS). We therefore assume that the composition of such adjacent patches with different species compositions is an important requirement to enhance bird diversity at the landscape scale (i.e. gamma diversity). We conclude that a combination of unmanaged deciduous-dominated forests and managed coniferous-dominated forests would benefit both local and regional bird communities in forest landscapes.

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Supplements

Table S1. Forest structure data of the investigated study stands

Transect ID	Mean stand age (canopy layer)	Mean diameter at breast height	Mean tree height	Mean standing volume (per hectare)	Percentage of deciduous trees (canopy / understory)	Max. diameter at breast height (1.30 m)
			UDS			
1 **	-	-	-	-	-	-
2 **	-	-	-	-	-	-
3 **	-	-	-	-	-	-
4 *	191 years	75 cm	36 m	334 Vfm	100 %	89 cm
5 *	186 years	71 cm	35 m	382 Vfm	100 %	90 cm
6 ***	-	-	-	-	-	-
7 ***	-	-	-	-	-	-

Table S1 (continued)

Transect ID	Mean stand age (canopy layer)	Mean diameter at breast height	Mean tree height	Mean standing volume (per hectare)	Percentage of deciduous trees (canopy / understory)	Max. diameter at breast height (1.30 m)
8 ***	-	-	-	-	-	-
9 **	129 years	55 cm	31.8 m	606 Vfm	100% / 100%	100 cm
10 **	129 years	55 cm	31.8 m	606 Vfm	100% / 100%	100 cm
11 **	169 years	67 cm	34.2 m	374 Vfm	98% / 100%	100 cm
12 **	169 years	67 cm	34.2 m	374 Vfm	98% / 100%	100 cm
13 *	-	-	-	-	-	-
14 *	-	-	-	-	-	-
15	81 years	31 cm	23 m	182 Vfm	61% / 80%	86 cm
16	81 years	31 cm	23 m	182 Vfm	61% / 80%	86 cm
17	112 years	39 cm	27 m	218 Vfm	79% / 100%	70 cm
18	198 years	78 cm	32.5 m	-	100% / 100%	-
19	172 years	70 cm	34 m	-	100% / 90%	-
20	165 years	60 cm	36 m	438 Vfm	100% / 100%	98 cm
21**	80 years	40 cm	28 m	250 Vfm	100%	80 cm
22**	80 years	40 cm	28 m	250 Vfm	100%	80 cm
23**	65 years	45 cm	25 m	290 Vfm	100%	70 cm
24**	145 years	65 cm	36 m	350 Vfm	95%	70 cm
			MCS			
25	83 years	32 cm	26.8 m	386 Vfm	55% / 80%	-
26	83 years	32 cm	26.8 m	372 Vfm	55% / 80%	-
27	83 years	32 cm	26.8 m	416 Vfm	55% / 80%	-
28	90 years	-	27.3 m	337 Vfm	5% / 75%	-
29	60 years	41 cm	30.6 m	450 Vfm	0% / 0%	-
30	85 years	39 cm	26.6 m	359 Vfm	5% / 60%	-
31	129 years	44 cm	32 m	530 Vfm	0% / 100%	50 cm
32	52 years	27 cm	25 m	224 Vfm	0% / 70%	-
33	95 years	33 cm	30 m	470 Vfm	5% / 100%	44 cm
34	139 years	45 cm	36 m	425 Vfm	0% / 100%	60 cm
35	58 years	26 cm	27 m	425 Vfm	0% / 98%	33 cm
36	65 years	29 cm	30 m	450 Vfm	0% / 100%	35 cm
37	51 years	22 cm	18 m	98 Vfm	21% / 100 %	45 cm
38	48 years	23 cm	19 m	106 Vfm	32% / 100%	46 cm
39	60 years	30 cm	21 m	295 Vfm	92% / 100%	71 cm
40	63 years	29 cm	24 m	243 Vfm	23% / 79%	50 cm
41	73 years	29 cm	26 m	208 Vfm	17% / 0%	52 cm
42	56 years	25 cm	23 m	278 Vfm	3% / 0%	40 cm
43	96 years	38 cm	28 m	390 Vfm	67% / no data	62 cm
44	60 years	22 cm	23 m	218 Vfm	94% / no data	51 cm
45	45 years	19 cm	21 m	291 Vfm	88% / no data	23 cm
46	96 years	38 cm	28 m	390 Vfm	67% / no data	62 cm
47	52 years	19 cm	22 m	240 Vfm	81% / no data	56 cm
48	45 years	19 cm	21 m	291 Vfm	88% / no data	23 cm

Note: * regional nature reserve, ** nature forest reserve, *** Natura 2000 area. The bird counting in different transects was carried out in 2016 (transect 25–48), 2017 (transect 15–24) and 2018 (transect 1–14).