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Seasonal patterns of habitat use of resident birds in Białowieża Forest and its links to post-disturbance management

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ABSTRACT

Resident bird species staying in the same area year-round may face very different habitat conditions between seasons in temperate forests. This may cause resident forest birds to use different habitats during winter and spring. Furthermore, habitat use and their seasonal shifts could be additionally affected by large scale forest disturbances (e.g. outbreaks of bark beetles) and post-disturbance management, as they likely affect the availability of crucial resources for reproduction and survival. We investigated the impact of the European spruce bark beetle (*Ips typographus*) outbreak and post-outbreak management on winter and spring habitat use of 18 resident bird species in Białowieża Forest, Eastern Poland. We showed differences in habitat use of resident birds in winter and spring, at the level of species, community and three foraging guilds (i.e. invertivore bark foragers, invertivore arboreal gleaners and omnivores). First, bird species richness and bird abundance recorded at 111 sites in winter were not related or even showed a negative relationship with richness and abundance in spring, indicating that winter and spring bird diversity hotspots did not spatially overlap. Second, the wintering community as a whole, and the invertivore arboreal gleaners in specific, shifted their density towards more coniferous sites and increased their density at moderately salvage-logged sites, while decreasing their density at strongly salvage-logged sites. The wintering invertivore bark foragers shifted towards more outbreak sites (i.e. both salvage-logged and natural regeneration) and distributed more evenly along the natural regeneration – salvage-logged gradient. The distributions of habitat use were species-specific and there was no single habitat or level of disturbance preferred or avoided by all species or groups in spring or winter. This study highlights the importance of considering habitat use outside of the breeding season, when assessing habitat requirements of resident forest bird communities to evaluate the impact of post-disturbance management. In addition, it shows the significance of maintaining the heterogeneity of forest habitats to the wintering resident bird community, especially when deciding on post-disturbance management actions.

1. Introduction

Forest bird communities in boreal and temperate regions are profoundly affected by ecosystem disturbances like fire, windstorms or outbreaks of invertebrates (Brawn et al., 2001; Drapeau et al., 2000; Mikusiński et al., 2018b). Natural forest disturbances may increase habitat complexity and enhance the amount of dead wood, and can therefore enrich bird communities (Beudert et al., 2015; Przepióra et al., 2020). Following a forest disturbance, there are generally two options regarding post-disturbance management: to not intervene and let the forest regenerate naturally (Thorn et al., 2018) or to perform salvage-logging, i.e. to remove dead and dying trees. Generally, naturally regenerating habitat and salvaged habitat differ in terms of food availability, possible nest sites and structural heterogeneity (Swanson et al., 2011). The ample amounts of snags, lying dead wood and woody debris in naturally regenerating stands provide habitat for prey (e.g. saproxylic beetles), nest sites for excavating bird species and secondary cavity nesters and create a high variety of local microclimates (Basile et al., 2023; Norvez et al., 2013; Thorn et al., 2018). In salvaged habitat, little to no structural heterogeneity is left, leading to increased exposure

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to sunlight, more extreme temperatures (ground and air), higher wind velocities, and lower levels of relative humidity and moisture in litter and surface soil (Swanson et al., 2011). These circumstances benefit especially open-habitat specialists, such as carabid beetles and epigeal spiders and bird species that are typically linked to farm- or shrublands (Thorn et al., 2018; Żmihorski et al., 2019). Hence, salvage-logging is known to have generally negative effects on forest biodiversity (Lindenmayer and Noss, 2006; Müller et al., 2019; Thorn et al., 2018) and may reduce habitat suitability for some forest specialists, including forest birds (e.g. Żmihorski et al., 2019; Basile et al., 2023). Nevertheless, salvage-logging remains one of the most common post-disturbance management practices even in protected forests where normally no logging would occur (Thorn et al., 2018). Therefore, as climate change increases both the frequency and severity of forest disturbances (Diffenbaugh and Field, 2013; Machado Nunes Romeiro et al., 2022; Patacca et al., 2023) with potentially far-reaching consequences for the associated bird communities, a better understanding of the relationship between increasingly important post-disturbance forest dynamics (Raffa et al., 2008), post-disturbance management and forest bird communities is needed.

Among forest birds, resident species in the highly seasonal conditions of the temperate biomes may be especially prone to forest dynamics linked to disturbances and post-disturbance management, due to their dependence on the same area year-round (Latimer and Zuckerberg, 2021). Since these species face very different environmental conditions and challenges in each season, both habitat requirements and suitability are likely to be season-dependent, leading to seasonal changes in habitat use (examples of drivers of habitat use are summarised in Fig. 1 and its caption) (Alatalo, 1981; Lundquist and Manuwal, 1990; Morrison et al., 1986). Hence, the use of post-disturbance habitat is likely to differ between seasons as well. Moreover, since winter mortality is the limiting factor in shaping the population dynamics of many resident birds (Jansson et al., 1981; McNamara and Houston, 1990; Nilsson 1987), the availability of suitable winter habitat will affect the fitness of resident birds as much as – or even more than – the availability of suitable spring and summer habitat (Jansson et al., 1981; Sæther et al., 2004; Siriwardena et al., 2000). Therefore, to understand the impacts of forest disturbances and post-disturbance management on forest bird communities, it is of particular importance to evaluate the effects on habitat use of the resident bird community in both spring and winter. However, the question how forest disturbances and post-disturbance management shape resident bird species richness and abundance during both the breeding and wintering season remains greatly understudied (Elsen et al., 2020; Fraixedas et al., 2020; Gudex-Cross et al., 2022).

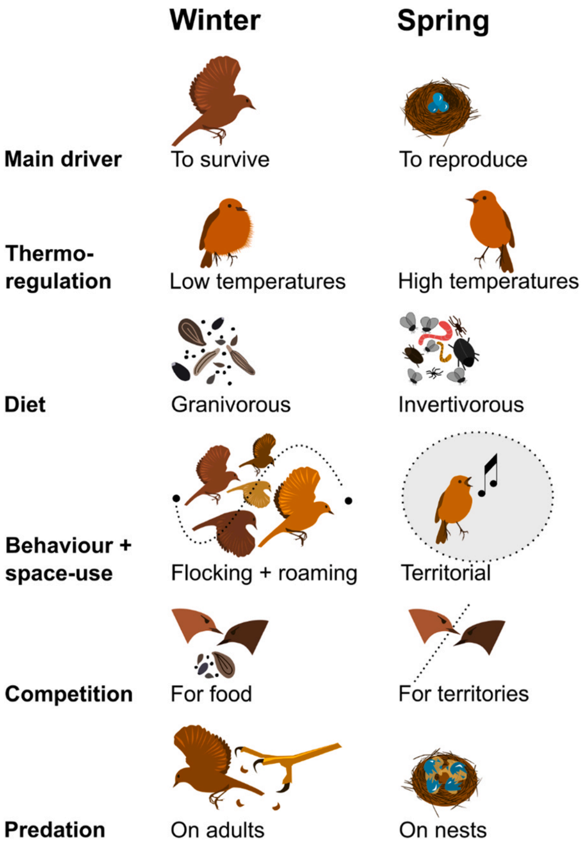

Fig. 1. Examples of different drivers of habitat use of resident birds in winter and spring in temperate forests. Differences regarding main drivers of habitat suitability in terms of survival and reproduction are shown. These drivers may be related to weather conditions, diet (preferences or seasonal shifts in diet from more granivorous in winter to more invertivorous in spring), behaviour and space-use (from multi species flocks moving over large areas in winter to territories in spring, competition and predation pressure (from predation on adults in winter to nest predation during the breeding season.

In this study we analyse the distribution across the post-disturbance habitat gradient of 18 resident forest birds and three trophic groups (i.e. invertivore bark foragers, invertivore arboreal gleaners and omnivores; (Pigot et al., 2020)) in both spring and winter in Białowieża Forest, Poland. The European spruce bark beetle (*Ips typographus*) outbreak of 2015 – 2019, caused the wide-spread die-off of Norway spruces (*Picea abies*) in the Polish part of the Białowieża Forest (Kamińska et al., 2021). The resulting forest mosaic of naturally regenerating, salvage-logged and unaffected stands and stands of various tree species compositions (e.g. forest stands ranging from dominated by conifers to dominated by deciduous trees), offers an excellent chance to study the effects of natural disturbance and post-disturbance management on the winter and spring distributions of the resident bird community across different habitat gradients. Based on the drivers of the habitat use of resident birds presented above (see also Fig. 1) we hypothesize that: (1) the local breeding and wintering species richness and abundance of resident birds is only weakly correlated or unrelated, (2) the wintering and breeding bird community is distributed differently across habitat gradients that reflect the forest mosaic of more coniferous to deciduous habitat and of more unaffected to more post-disturbance habitat (i.e. natural regeneration and/or salvage-logged habitat), with a shift towards more coniferous and naturally regenerating areas in winter and 3) the difference in distribution across habitat gradients in winter and spring will be specific for the three trophic groups, as species from different trophic groups are expected to utilize different habitats (de Groot et al., 2016).

2. Methods

2.1. Study area

The study was performed in the Białowieża Forest, a contiguous forest complex bordering Poland and Belarus (Fig. 2). The forest covers a total area of 150,582 ha, of which 41% is located in Poland. It is perceived as the best-preserved fragment of lowland temperate forest that once covered the European Plains (Faliński, 1986; Jaroszewicz et al., 2019; Samojlik et al., 2013). Dominating tree species are pedunculate oak (*Quercus robur*), common hornbeam (*Carpinus betulus*), small-leaved lime (*Tilia cordata*), black alder (*Alnus glutinosa*), birches (*Betula pendula* and *Betula pubescens*), Scots pine (*Pinus sylvestris*) and Norway spruce (Drozdowski et al., 2017). The forest covers a broad variety of habitat types, ranging from planted coniferous forest stands, dominated by Scots pine and Norway spruce (Tomiałojć and Wesołowski, 2004; Wesołowski, 2005), up to close-to-primeval mixed stands with high share of deciduous trees and also Norway spruce (Drozdowski et al., 2017). The Białowieża Forest (both the Polish and Belarusian parts) is a UNESCO World Heritage Site (UNESCO The World Heritage Committee, 2012). In addition, the Polish part is a Natura 2000 site (Puszcza Białowieska, PLC200004), a protected landscape area and a

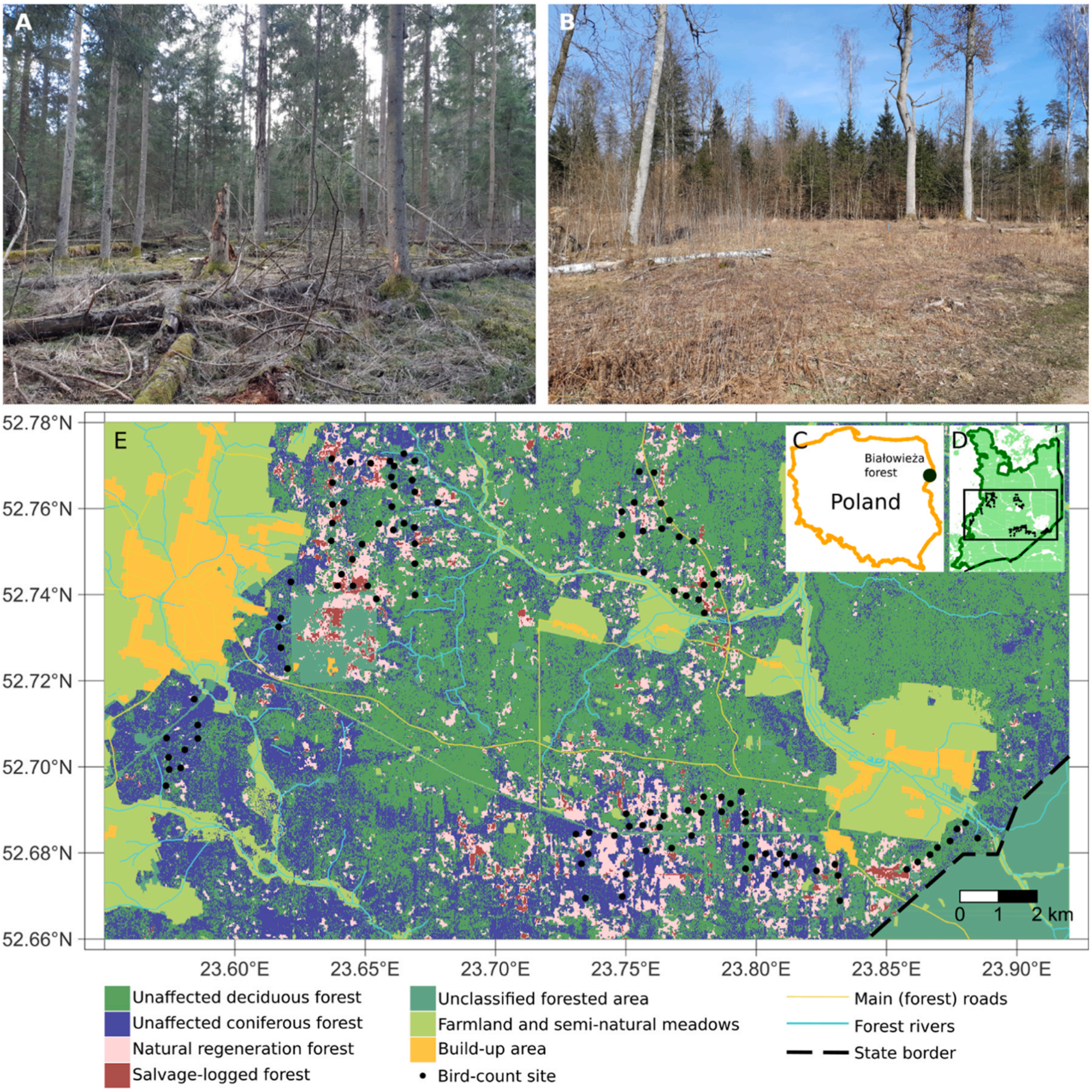

Fig. 2. Example of (A) a natural regeneration patch, with standing and lying dead wood and several remaining living spruces and (B) a salvage-logged patch, with some living deciduous trees remaining, bordered by a patch of living spruces. March 2023. In addition, the location and overview of the study area, showing (C) the location of Białowieża Forest in Poland; (D) the location of the study area in Białowieża Forest, and (E) The forest mosaic in relation to the 111 bird-count sites indicated by the black dots (resolution: 2x2m for tree stand composition (Modzelewska, 2022) and 10x10m^2 for forest management (Mikusiński et al., 2018a).

Biosphere Reserve. These international designations overlap with several national levels of protection and use, ranging from Białowieża National Park with well-preserved old-growth stands (17% of Polish part of the forest) through nature reserves including well-preserved old growth stands and the most valuable forest stands outside the reserves (together 20%) to the remaining stands (63%), managed by the State Forests Holding, where logging and wood extraction is occasionally allowed (UNESCO The World Heritage Committee, 2012).

In 2015–2019 a European spruce bark beetle outbreak led to the widespread die-off of Norway spruce; in total 39% of all Norway spruces in the canopy layer died during the outbreak (Kamińska et al., 2021). The State Forests Holding that manages the greater part of Polish part of Białowieża Forest, decided to salvage-log, creating clear-cuts that amounted to 675 ha (1.16% of the total forest cover), including 229 ha of old-growth stands, despite their alleged exclusion from forest management (Mikusiński et al., 2018a). However, single clear-cuts were small; when disregarding cuts smaller than 0.25 ha, Mikusiński et al. (2018a) found their average size being slightly more than one hectare. As a result of the outbreak and salvage-logging, two distinct new forest habitats were created: (1) affected forest left for natural regeneration (i.e. the majority of dead wood was left on the site and barely or no management took place; Figs. 2A) and (2) salvage-logged areas (i.e. patches where nearly all large-scale dead wood was collected and the majority of dead standing trees were removed; Fig. 2B). Both types of disturbed habitats were spread unevenly over the forest, as stands dominated by Norway spruce are widespread, but at the same time clustered in space (Fig. 2E).

3. Bird-count site selection

We selected 111 bird-count sites (Fig. 2E) in the managed parts of the forest that was most affected by European spruce bark beetle outbreak, based on visual cues and (Mikusiński et al., 2018a), to capture a habitat gradient from highly disturbed to unaffected forest stands (Fig. 2A), covering both naturally regenerating (Fig. 2A) and salvage-logged stands (Fig. 2B), as well as the gradient of coniferous and deciduous area (Fig. 2E). For each bird-count site we assessed the habitat characteristics within a 100 m radius from the point from where the count was conducted. We used satellite and hyperspectral data for deriving these habitat characteristics (see section 3.4 on habitat description).

3.1. Bird counts

In all 111 sites, 10-minute bird point counts were conducted, one time in winter and two times in spring by 2 expert field ornithologists, except one site with one visit in spring and two in winter. During each visit all seen and heard individuals of all bird species (except individuals flying over tree tops) were recorded within the 100 m radius from the bird-count point. Counts were performed only in good weather conditions, i.e. without heavy rain/snowfall, strong wind or fog. In spring counts were completed before 10:00 am, in winter counts were carried out throughout the whole day. Maximum spring count per location for each species was selected for further analyses.

Bird counts were performed during the winter (20th January 2018 – 10th March 2018) and spring (21st April 2018 – 29th June 2018). The winter of 2018 was slightly colder (e.g. −4.6 ± 0.82 ℃ on average in February 2018, compared to a long-term average of −0.24 ± 0.24 ℃ in 2013–2023), and had less snow cover compared to the average (1.38 ± 0.16 cm in February 2018, compared to 10.57 ± 0.82 cm in February 2013–2023). The spring of 2018 was warmer than average (16.72 ± 0.47 ℃ in May 2018, compared to 13.09 ± 0.21 ℃ in May 2013–2023) and the amount of precipitation was similar to the average (1.01 ± 0.51 mm in May 2018, compared to 2.4 ± 0.37 mm in May 2013–2023) (presented values are based on daily averages collected by a weather station in Białystok, station ID: GHCND:PLM00012295, *rnoaa* package (Chamberlain, 2021), Fig. A1 and A2).

3.1.1. Trophic groups

Trophic groups within the observed bird species community were assigned based on the foraging niches (invertivore bark foragers and invertivore arboreal gleaners) and food niches (omnivores) utilized during breeding season, as classified by (Pigot et al., 2020) (Table 1). Each species was assigned to one group only (Table 1). Since coal tit (*Periparus ater,* generalist) and Eurasian siskin (*Spinus spinus,* granivore arboreal) both were the only representatives of their trophic group, they were excluded from this part of the analysis (Table 1) (Pigot et al., 2020). Note that omnivores consist of an ecologically very diverse group of species.

3.2. Habitat description

We used two environmental variables to describe the habitat within a buffer of 100 m around the bird-count sites: (1) the amount of salvage-logged, natural regenerating or unaffected area (in m^2) and (2) the amount of coniferous or deciduous canopy cover (in m^2) (using *raster-*, *terra-* and *sf*-packages (Hijmans, 2023a, 2023b; Pebesma, 2018)). To quantify the area covered by salvage-logged, natural regeneration and unaffected patches, we used Sentinel-2 data from (Mikusiński et al., 2018a) (Fig. 2E). Salvage-logged patches were defined as patches with forest loss due to logging that happened between 2015 to 2017. Natural regeneration patches were unlogged and defoliated patches, as in the case of Białowieża Forest, defoliation in the period of 2015 – 2017 was primarily caused by the European spruce bark beetle outbreak affecting spruce trees. All forest area that was not classified as salvage-logged or natural regeneration was classified as unaffected. For details on this method, see (Mikusiński et al., 2018a). The area (in m^2) within the buffer that was covered by either coniferous or deciduous trees was calculated using data obtained from (Modzelewska, 2022), based on hyperspectral images acquired in August and September 2019 (resolution: 2x2m^2, in which each pixel represents one of 8 classes of tree species, i.e. "birch", "oak", "hornbeam", "lime", "alder" and "other deciduous"; grouped as "deciduous" and "pine" and "spruce"; grouped as "coniferous") (Fig. 2E). For details on this method, see (Modzelewska, 2022).

Table 1
Trophic groups based on the foraging niches (invertivore bark foragers, invertivore arboreal gleaners, generalist and arboreal granivores) and trophic niches (omnivores) as classified by (Pigot et al., 2020).

Species (English)	Species	Trophic group
Coal tit	*Periparus ater*	Generalist
Eurasian siskin	*Spinus spinus*	Arboreal granivore
Black woodpecker	*Dryocopus martius*	Invertivore bark foragers
Lesser spotted woodpecker	*Dryobates minor*	
Middle spotted woodpecker	*Dendrocoptes medius*	
Eurasian nuthatch	*Sitta europaea*	
Eurasian treecreeper	*Certhia familiaris*	
Eurasian blue tit	*Cyanistes caeruleus*	Invertivore arboreal gleaners
Crested tit	*Lophophanes cristatus*	
Goldcrest	*Regulus regulus*	
Great tit	*Parus major*	
Long-tailed tit	*Aegithalos caudatus*	
Marsh tit	*Poecile palustris*	
Willow tit	*Poecile montanus*	
Eurasian bullfinch	*Pyrrhula pyrrhula*	Omnivores
Great spotted woodpecker	*Dendrocopos major*	
Eurasian jay	*Garrulus glandarius*	
Common raven	*Corvus corax*	

3.3. Analyses

All analyses were performed in R version 4.2.2 and 4.3.0 (R Core Team, 2023).

3.3.1. Species richness and abundance in winter and spring (GLMM)

To test how spring species richness was related with winter richness in each point, we used a GLM with a Poisson-distribution (i.e. log-link), using spring bird species richness (i.e. the total number of species counted per point) as predictor variable and winter bird richness as response variable. To determine to what extent spring abundance of resident species (i.e. the total number of individuals counted per point) was related with winter abundance in one point, we created a GLMM (*nlme* package (Pinheiro et al., 2023)) with a Poisson-distribution (i.e. log-link), with total winter abundance as the response variable, total spring abundance as the predictor variable and with species as a random effect. In addition, we modelled winter abundance with spring abundance at the species level, using a GLM with a Poisson-distribution (glm function from the *stats* package (R Core Team, 2023)). To estimate the goodness of fit of all our models we calculated the likelihood-ratio based pseudo R^2, which allows comparison between GLMM and GLM results (R_p^2, r.squaredGLMM function from the *MuMIn* package, (Bartoń, 202)).

3.3.2. Habitat use (principal component analysis)

To assess what habitat resident birds used in winter and spring, we first performed PCA (rda function from the *vegan*-package (Oksanen et al., 2022)) on the two environmental variables describing the habitat gradient of the 111 bird-count sites. We selected the principal components for further analyses based on the cumulative proportion of the variance explained and eigenvalues (i.e. we used all components until a steep drop was observed in proportion of the variance explained). We interpreted the ecological meaning of principal components (i.e. what habitat gradient was described by this component) based on their loadings.

Subsequently, we checked whether birds change their environmental niche (summarized by the PC values) between winter and spring. Therefore, we assigned the PC values corresponding to a specific bird-count site to each bird observation in that site. More specifically, we treated each bird observation independently and tested whether birds distributed differently along the habitat gradients as represented by PC1, PC2 and PC3 in spring and winter for the total community, for the trophic groups and for each species. We therefore used a density comparison (a permutation test of equality, 1000 permutations, sm.density.

compare function from the *sm*-package (Bowman and Azzalini, 2021)), which tests whether the density distribution along the habitat gradient, as determined by the respective PCs, could be significantly different, even if the means are the same (i.e. the H_0 is that the density distributions observed in both seasons originate from the same distribution).

Data visualisation was done using ggplot2 (Wickham, 2016).

4. Results

In total, 18 resident bird species were observed (Table 2) and 613 and 734 individuals were counted in winter and spring, respectively. In winter, crested tit and goldcrest were most abundant (i.e. $n = 85$ and 149, respectively, Table 2). In spring, goldcrest (*Regulus regulus*) and great tit (*Parus major*) were most abundant (i.e. $n = 84$ and 131, respectively, Table 2). Mean species richness in winter and spring was 2.47 ± 0.21 SE and 4.41 ± 0.17 SE, respectively. Mean total abundance (uncorrected for species) was 5.52 ± 0.59 SE and 6.61 ± 0.31 SE in winter and spring, respectively.

4.1. Species richness and species abundance in winter and spring

At the local level of sites ($n = 111$ sites), species richness in spring was not related with winter species richness ($R_p^2 = 0.012$, $p = 0.276$, GLM, Fig. 3A), while species spring abundance was negatively related with its local winter abundance (spring effect on winter abundance: -0.315 ± 0.051 SE, $p < 0.001$, $R_p^2 = 0.48$, GLMM with log-link, Fig. 3B, i.e. sites with a high abundance in spring did not have a high abundance in the winter). A total of 12 species showed a significant negative relationship between winter and spring abundance while the others showed no clear associations (i.e. only the great spotted woodpecker (*Dendrocopos major*) showed a marginally significant positive effect, meaning that sites with high abundance in spring also had high abundance in the winter; effect = 0.156, $p = 0.079$, Table 2, GLM, Fig. A3).

Table 2

Summary of generalized linear models estimating the effects of spring abundances on winter abundances for 18 resident bird species in Białowieża Forest. For each species the parameter estimates (Spring effect, in log-link) ± the SE, the significance of this estimate (p-value), the goodness of fit (R_p^2) are given. Winter abundance (n_{winter}) and maximum abundance out of two spring visits (n_{spring}) are also shown. Bolds indicate species with a significant effect ($p < 0.05$, Fig. A3).

Species	Spring effect ± SE (log-link)		p-value	R_p^2	n_{winter}	n_{spring}
Black woodpecker	**-2.111**	**± 1.019**	**0.038**	**0.726**	**12**	**7**
Eurasian blue tit	-0.443	± 0.267	0.098	0.215	21	61
Eurasian bullfinch	-21.872	± 13.113	0.999	0.998	9	5
Coal tit	**-2.620**	**± 0.788**	**0.001**	**0.472**	**6**	**62**
Crested tit	**-0.880**	**± 0.274**	**0.001**	**0.381**	**85**	**14**
Goldcrest	**-0.247**	**± 0.094**	**0.009**	**0.135**	**149**	**84**
Great spotted woodpecker	0.156	± 0.089	0.079	0.040	77	131
Great tit	**-0.636**	**± 0.273**	**0.020**	**0.195**	**25**	**131**
Eurasian jay	**-1.100**	**± 0.365**	**0.003**	**0.431**	**23**	**31**
Lesser spotted woodpecker	**-2.639**	**± 1.080**	**0.015**	**0.647**	**7**	**7**
Long-tailed tit	**-2.260**	**± 0.701**	**0.001**	**0.927**	**11**	**23**
Marsh tit	-0.488	± 0.260	0.061	0.200	26	34
Middle spotted woodpecker	**-2.662**	**± 1.140**	**0.020**	**0.527**	**4**	**18**
Eurasian nuthatch	**-0.795**	**± 0.251**	**0.002**	**0.323**	**46**	**43**
Common raven	-21.433	± 14.125	0.999	0.996	5	5
Eurasian siskin	0.136	± 0.093	0.141	0.196	35	12
Eurasian treecreeper	**-1.227**	**± 0.318**	**< 0.001**	**0.524**	**29**	**45**
Willow tit	**-0.785**	**± 0.278**	**0.005**	**0.326**	**43**	**21**

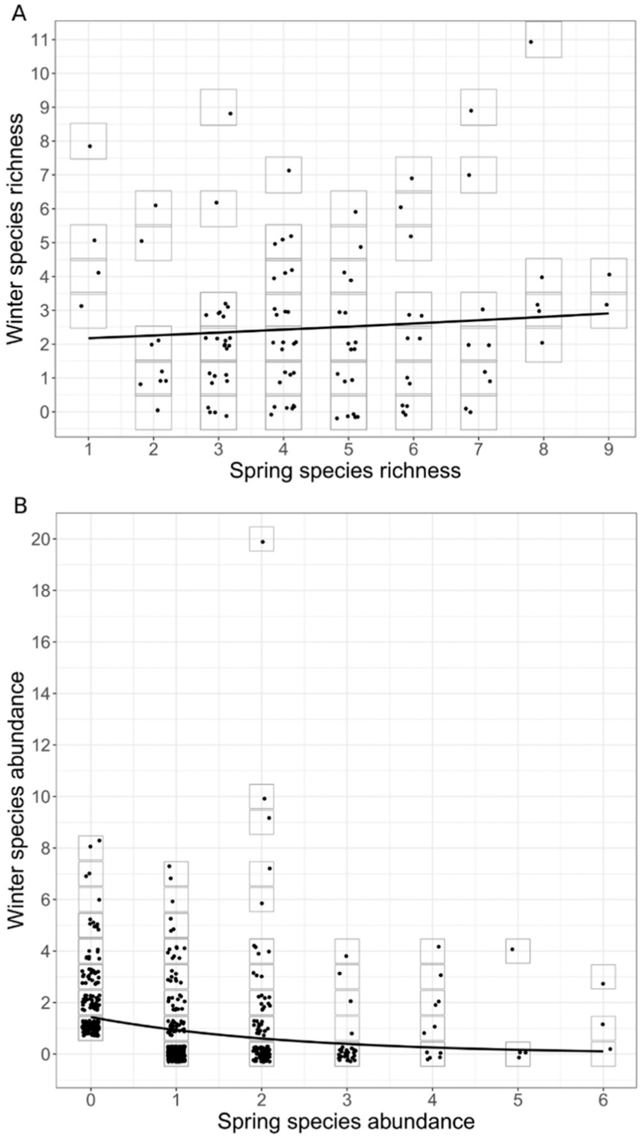

Fig. 3. The relationship between spring and winter bird species richness and species abundance at 111 count sites in Białowieża Forest. A: Each point represents the species richness in one location in winter and spring. The black line indicates the association as predicted by the fitted GLM ($p = 0.276$, $R_p^2 = 0.012$). B: Each point represents the total abundance of one species in one location in winter and spring (NOTE: points represent abundances of individual species, despite the use of a single point colour and shape). The black line indicates association as predicted by the fitted GLMM ($p < 0.001$, $R_p^2 = 0.48$). Jittering was added along both axes to reduce symbol over plotting. Squares indicate points with the same richness (A) or abundance (B).

4.2. Distribution in winter and spring

Of the 5 principal components, we selected principal component 1 to 3, with a cumulative proportion of the variance explained of 0.98 (Table A1, Fig. 4A). Each selected principal component described one aspect of the habitat gradient present in our study; i.e. showing the gradient from more outbreak-area to more unaffected area (PC1), from more coniferous to predominantly deciduous sites (PC2) and from naturally regenerating area to more salvage-logged area (PC3, Table A1). Table 3.

Based on these components, wintering resident birds as compared to breeding resident birds distributed differently across the coniferous-deciduous habitat gradient (PC2, $p = 0.001$) and across the post-

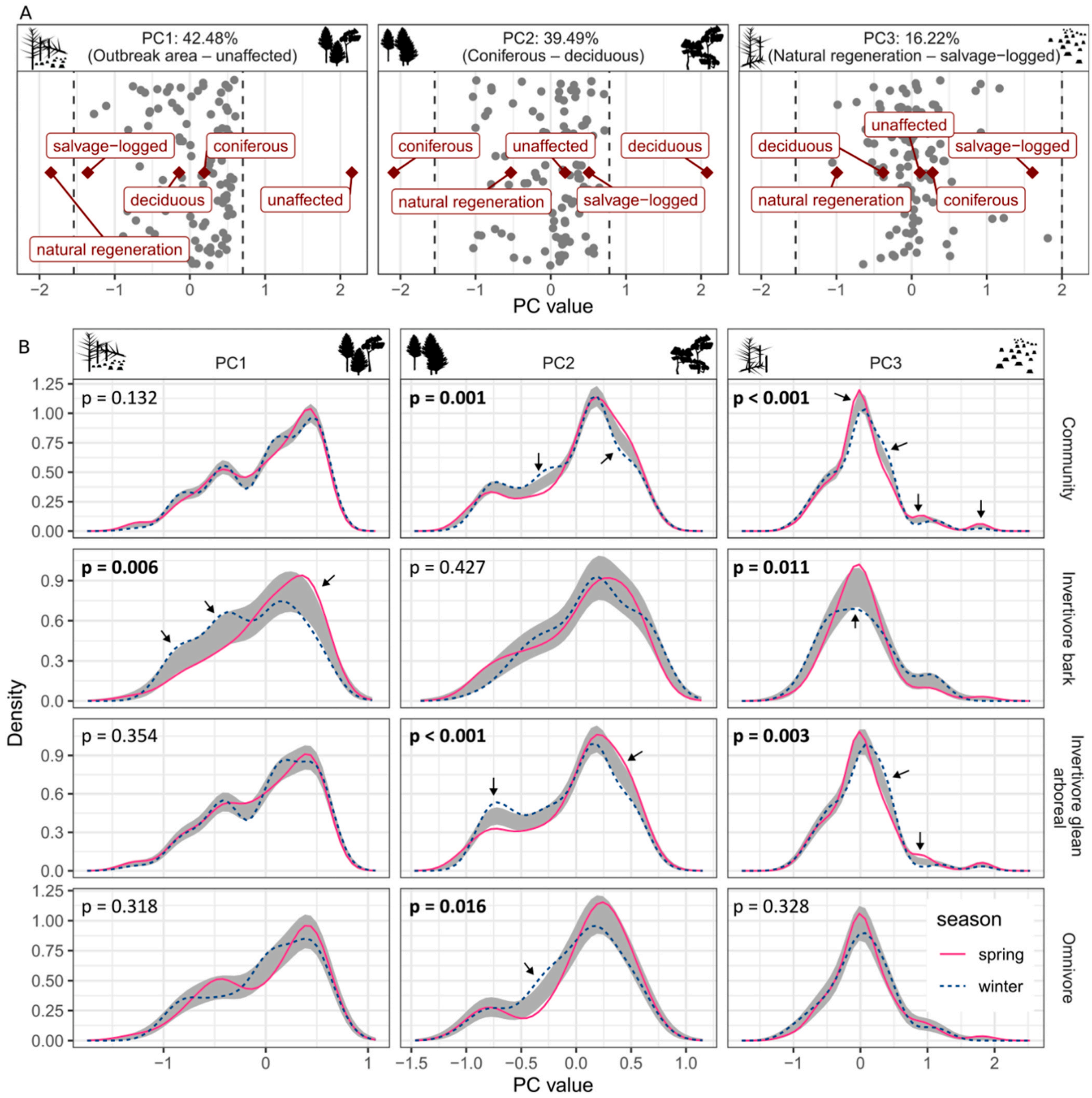

Fig. 4. A: Principal component analyses. PC 1, 2 and 3 respectively, with the 111 study sites in light grey and the five environmental variables as red diamonds. To promote their visibility, random noise was added to the points along the y-axis. The dashed lines show the extent of the graphs in B, respectively. Plot titles show the PC, the percentage of the variance explained and a description of the meaning of the PC, to facilitate the interpretation of the results. B: Spring (pink) and winter (blue) distributions of the community and the trophic groups along the habitat gradients described by PC1, 2 and 3 (more details about how to interpret PC1, 2 and 3 can be found in the plot titles of A). Grey areas indicate confidence bands for the two compared seasons pooled. Results of the permutation test is given for each comparison (i.e. the p-values) and significant differences are marked in bold. Arrows indicate parts of the plot where winter and spring distributions are significantly different (i.e. the distributions extent beyond the confidence band). For species specific results of the permutation test, see Table 3 and Fig. A4.

disturbance habitat gradient (PC3, $p < 0.001$; Fig. 4B). The wintering community as a whole slightly shifted its density towards more coniferous sites (PC2). Although the distributions were statistically different, the response to PC3 was rather ambiguous, as the wintering community appeared to increase its density towards moderately salvage-logged sites, but this was combined with a slight decrease in density at more strongly salvage-logged sites (PC3, Fig. 4B).

In addition, all trophic groups distributed differently along the habitat gradients in winter compared to spring. The wintering invertivore bark forager density was higher in outbreak compared to undisturbed sites (PC1, $p = 0.006$). The wintering invertivore arboreal gleaner density as well as omnivore density was higher in coniferous as compared to deciduous sites (PC2, $p < 0.001$ and $p = 0.016$, respectively). Both the invertivore arboreal gleaners and the invertivore bark foragers distributed significantly different across the natural regeneration – salvage-logged gradient in winter and spring (PC3, $p = 0.003$ and $p = 0.011$, respectively), however the preference for/avoidance of either natural regeneration or salvage-logged sites was ambiguous for

Table 3
Species specific results (i.e. p-values) from the permutation test comparing winter and spring distributions (density comparison analysis) along the habitat gradient as represented by PC1, PC2 and PC3. Bolds indicate significantly or marginally insignificantly different winter compared to spring distributions ($p < 0.1$).

Species (English)	PC1	PC2	PC3
Black woodpecker	0.343	0.256	0.077
Eurasian blue tit	0.613	0.887	0.897
Eurasian bullfinch	0.529	**0.048**	0.583
Coal tit	0.416	0.267	0.600
Crested tit	**0.041**	0.464	0.570
Goldcrest	0.570	0.627	0.602
Great spotted woodpecker	0.580	0.315	0.870
Great tit	0.758	0.475	0.531
Eurasian jay	0.500	0.181	0.328
Lesser spotted woodpecker	0.356	0.762	**0.017**
Long-tailed tit	**0.015**	0.064	0.549
Marsh tit	0.500	0.268	**0.014**
Middle spotted woodpecker	0.833	0.642	0.826
Eurasian nuthatch	**0.011**	0.209	**0.012**
Common raven	0.155	0.923	0.355
Eurasian siskin	**0.005**	0.096	0.101
Eurasian treecreeper	0.538	0.539	0.633
Willow tit	0.111	0.080	0.327

both groups. The wintering invertivore bark forager density was more spread out along the habitat gradient as indicated by a reduced density around the median (PC3, Fig. 4B). The wintering invertivore arboreal gleaners increased its density at moderately salvage-logged sites, but this was combined with a slight decrease in density at strongly salvage-logged sites (PC3, Fig. 4B).

Changes in distributions across habitat gradients between winter and spring were species-specific. In total, nine of the studied species distributed significantly different across the forest habitat in winter and spring ($p < 0.05$) or tended to distribute differently ($p < 0.10$) (Table 3 and Fig. A4). In spring, both Eurasian siskin and long-tailed tit (*Aegithalos caudatus*) increased in density in sites with less unaffected area ($p = 0.005$ and 0.015, respectively, PC1, Fig. A4). Along the coniferous – deciduous gradient (PC2), only Eurasian bullfinch (*Pyrrhula pyrrhula*) significantly increased its winter density at more coniferous sites ($p = 0.048$, Fig. A4). Lesser spotted woodpeckers (*Dryobates minor*) and Eurasian nuthatches (*Sitta europaea*) both distributed differently along the natural regeneration – salvage-logged gradient in winter compared to spring (PC3, Table 3). While lesser spotted woodpeckers shifted towards more natural regeneration sites in winter ($p = 0.017$), Eurasian nuthatches did not shift but spread out more along the habitat gradient due to a reduced density around the median ($p = 0.012$, Fig. A4).

Four species that significantly distributed differently in winter compared to spring (Table 3) correspondingly showed a significantly negative relation between winter and spring abundances per location (i.e. crested tit (*Lophophanes cristatus*), lesser spotted woodpecker, long-tailed tit and Eurasian nuthatch; Table 2). However, eight species that had a significantly negative relation between winter and spring abundances (Table 2), did not distribute significantly different in winter and spring (i.e. black woodpecker (*Dryocopus martius*), coal tit, goldcrest (*Regulus regulus*), great tit (*Parus major*), Eurasian jay (*Garrulus glandarius*), middle spotted woodpecker (*Dendrocoptes medius*), Eurasian treecreeper (*Certhia familiaris*) and willow tit (*Poecile montanus*); Table 3).

5. Discussion

Our results show that wintering and breeding resident birds in Białowieża Forest were distributed differently across post-disturbance forest landscape, both at the level of the community, the level of the three trophic groups and the species level. First of all, in accordance with our first hypothesis, the use of wintering habitat was unrelated or even negatively related with the use of breeding habitat. In addition, partly in contrast with our second hypothesis, the resident community indeed distributed differently in winter and spring, as the density of the wintering community as compared to the breeding community was elevated in more coniferous sites and was distributed differently along the gradient of natural regeneration to salvaged sites, although no clear directional shift could be observed for the latter gradient. Lastly, in accordance with our third hypothesis, all trophic groups distributed differently along the habitat gradients in winter compared to spring. The observed changes in the distribution of the community as a whole, as well as for the trophic groups were small, but significant, even though habitat use in different seasons was highly species specific and species often shifted in opposing directions. This means that, despite obvious differences among resident bird species and their trophic groups, still some distribution patterns regarding habitat use in winter and spring exist at the level of the community. Moreover, it highlights the need for a heterogenic forest habitat gradient to support a vital and rich resident bird community during the whole year.

Key processes enhancing heterogeneity of forested landscapes are local forest disturbances, such as the European spruce bark beetle outbreak in this study, which often increases habitat complexity in otherwise closed-canopy stands and enhance the amount of dead wood (Swanson et al., 2011; Thorn et al., 2018), and can therefore enrich the bird community (Beudert et al., 2015; Przepióra et al., 2020). Indeed, in our study area, the outbreak and the following post-disturbance management (i.e. natural regeneration or salvage-logging) created a heterogenic forest habitat mosaic (Mikusiński et al., 2018a). Our results show that the resident bird community as a whole as well as the invertivore bark foragers and the invertivore arboreal gleaners distributed differently along the gradient between natural regeneration and salvaged sites, although no clear directional distribution shift along this gradient could be observed for any of these groups. The absence of a clear habitat shift between seasons, while the distributions are different in each season, may be due to species-specific distribution changes of the birds within the community and within the trophic groups. For example, of the invertivore bark foragers, Eurasian nuthatches, lesser spotted woodpeckers and black woodpeckers all distributed differently along the natural regeneration – savage-logged gradient in winter compared to spring. Firstly, wintering lesser spotted woodpeckers shifted towards more natural regeneration sites. This shift could be explained by the enhanced food availability (e.g. invertebrates) that is provided due to the increased amount of standing and downed dead trees (Bouget and Duelli, 2004) and is known to especially attract woodpeckers (Askeyev et al., 2022) such as wintering lesser spotted woodpeckers (Hogstad, 2010). Secondly, wintering black woodpeckers tended to shift towards more salvaged sites, which may be due to the tree stumps left after logging that are often colonized by ants (Włodarczyk et al., 2009) and hence are used as a foraging microhabitat by black woodpeckers (Mikusiński, 1997) as well as other woodpeckers (Aszalós et al., 2020). Simultaneously, nuthatches did not shift into a certain direction at all, but rather spread out more along the gradient, which may reflect the movement behaviour of mixed species flocks in winter (Alatalo, 1982; Lee and Jabłoński, 2006; Tellería and Santos, 1995). These species-specific distribution changes between seasons could explain the broader distribution of the wintering invertivore bark foragers and its narrower distribution in spring, when distributions of these species are relatively more similar. Moreover, this illustrates how species-specific distributions in winter and spring may result in different density distributions in winter compared to spring, without a clear habitat shift, as observed in this study for the community as a whole and the invertivore arboreal gleaners and bark invertivores. Hence, the presence of a broad disturbance habitat gradient, linked to the European spruce bark beetle outbreak, appears to be especially important to support a rich resident forest bird community year-round. Salvage logging creates a small-scaled mosaic of open habitats in the forest habitat. As most species home ranges (in summer and winter) cover both forest and salvage logged patches it is difficult to point to which species suffers more than others from salvage logging. In contrary, less mobile organisms like herbs, show much clearer local impact of disturbances (Orczewska et al., 2019).

Undisturbed forest can provide a diverse forest habitat mosaic (Drozdowski et al., 2017), that could affect the distribution of the resident forest bird across the forest in winter and spring. Indeed, our results show that the resident bird community as a whole as well as the invertivore arboreal gleaners, the omnivores and Eurasian bullfinches shifted towards more coniferous sites in winter as compared to more deciduous sites in spring. On the one hand, the presence of foliage in coniferous stands in winter may attract certain residents, as it provides foraging substrate and shelter against predation (Carrascal and Alonso, 2006; Rodríguez et al., 2001) and harsh weather conditions (Elsen et al., 2021; Jansson et al., 1981; McNamara and Houston, 1990). On the other hand, resident birds may be attracted to deciduous stands in spring, due to several reasons. Firstly, arthropods, especially larvae of leaf-eating insects that are an important food-source of nestlings (Wesołowski and Rowiński, 2014; Wesołowski and Tomiałojć, 1997) – mostly occur at deciduous trees (Pedley et al., 2014) and their spring abundance on deciduous trees is the key factor triggering start of breeding of forest invertivores (e.g. (Hinks et al., 2015). In addition, in the case of Białowieża Forest, a higher share of hornbeam, lime and poplars benefit (secondary) cavity nesters due to their provision of cavities and tree hollows (Czeszczewik and Walankiewicz, 2003; Walankiewicz et al., 2007). Notably, 13 out of 18 species in our study rely on cavities both for nesting and roosting. Hence, the importance of a heterogenic forest mosaic to support all habitat requirements of a rich resident bird community during the whole year.

In highly seasonal forests, such as the Białowieża Forest, it can be expected that habitat suitability for resident birds differs greatly between seasons (Fuller, 2012). For example, a study on lesser spotted woodpecker in Southern Sweden demonstrated an enormous difference in its seasonal home-range; as it declined from on average 742 ha in winter to 42 ha during nesting period (Wiktander et al., 2001). Indeed, our results show that forest habitat suitability in one season may not be mirrored in other seasons. This is of particular importance, as most studies of habitat suitability are done during the breeding season (Fuller, 2012), and may therefore be incomplete or underestimate the ecological niche of the resident bird population. Winter conditions may be critical for the population dynamics of many resident birds, as the effects of winter conditions may carry-over to other seasons or parts of their life-history (Robb et al., 2008). Moreover, mortality often peaks in this season (Jansson et al., 1981; Rogers, 1991; Tompa, 1971) and annual survival of adults and/or juveniles is often of greater importance to the population dynamics than other parts of their life-history, such as fecundity (Arcese et al., 1992; Crone, 2001; Germain et al., 2018; Sæther and Bakke, 2000; Siriwardena et al., 1998). As a result, the availability of suitable wintering habitat could be a very important driver for the population dynamics and species distribution of resident birds in the temperate forest biomes. In addition, habitat suitability may be different also during periods of for example fledging (summer) or post-natal dispersal (autumn). Thus, when only assessing habitat use in the breeding season, the year-round range of the habitat used by the resident bird population will likely be seriously underestimated.

Winter conditions in temperate forests may differ a lot between the years and within a particular season concerning temperatures and snow conditions. These differences have large influence on resident bird population fluctuations (survival) and on their behaviour. For example, Rolstad and Rolstad (1995) found in southern Norway that when snow or frost prohibited ground feeding in grey woodpeckers (*Picus canus*), birds were instead feeding on bark-dwelling insects in old pine and dead trees and enlarged their home-range up to 100 times. Periods with very low temperatures and snow conditions clearly affected activity of forest resident birds in forests of south-western Germany, but responses varied between species (Renner et al., 2012). Therefore, we expect that results concerning the patterns of winter habitat use by birds in Białowieża Forest may be also influenced by harshness of winter. However, assessment of this influence would require a long-term winter studies.

When comparing winter counts with spring counts, possible but unknown differences in detectability of certain bird species between seasons may be a problem. These differences could arise from differences in vocalisation (i.e. most studied birds are highly vocal in the breeding season, and much less in winter (Gil and Llusia, 2020)), visibility (e.g. due to the absence/presence of foliage on deciduous trees) and the behaviour and space-use of birds (e.g. territorial or roaming mixed species flocks (Alatalo, 1982; Alatalo et al., 1980; Krams et al., 2020)). Low detection.

probability is likely to increase the chance of underestimating the proportion of the area occupied (Clement et al., 2016), which could have affected our results. Nevertheless, we did not see such an effect on our results. Indeed, as wintering birds are less vocal, they would be expected to be detected less, especially in densely foliated coniferous stands, leading to lower winter compared to spring counts and lower bird abundances in coniferous stands in winter. However, although slightly fewer birds have been counted in winter compared to spring, we simultaneously observed an increased density of the wintering community in coniferous stands, rather than a decrease. Hence, while we were not able to investigate nor correct for the difference in detectability between seasons, we assume that the effect of detectability on our results is limited.

5.1. Implications for conservation management

Our study suggests the importance of keeping a broad range of forest habitats for promoting a high diversity of resident bird species in the temperate boreal zone, by increasing their prospects of survival and reproduction during the whole year. Many species displayed different distributions across the available habitats in winter compared to spring. Therefore, when assessing the value of, or managing, forest areas for high resident bird diversity, one needs to realize that habitat suitability is season-dependent and that many species therefore express multiple habitat requirements. This means that a one-season approach (i.e. during breeding season) to identify valuable areas for management and protection may lead to the wrong conclusions concerning key habitats for bird diversity maintenance. Also, when selecting sites for protection or restorations on the basis of a single season only, habitats central for the survival of birds outside of that season may be overlooked.

However, the great majority of studies into bird-habitat relations are conducted only in the breeding season, and derive management implications without regarding other seasons (e.g. the studies on the effects of salvage-logging on birds reviewed by (Thorn et al., 2018) and the studies on habitat suitability in Natura 2000 areas reviewed by (Portaccio et al., 2023)). Since there is general scarcity of evidence (Fuller, 2012) (but see (Caula et al., 2014)), we suggest that more studies investigate the use of different forest habitats by resident birds outside the breeding season. In cases of managing bark beetle outbreaks, that are most often salvaged, we suggest to leave at least some damaged sites for natural regeneration as that would increase forest heterogeneity and thus most likely forest biodiversity as well.

Bird surveys in seasons other than spring, and in particular in winter are more difficult to perform and interpret, due to detectability issues mentioned above and logistic problems created by weather conditions (e.g. the inaccessibility of bird-count sites due to heavy snowfall or wet field conditions). Hence, we point at bioacoustics studies as a promising path to achieve such knowledge (Shaw et al., 2021). However, more research and data is needed to assess the reliability of bioacoustics in describing winter bird assemblages in different forest types, regions and parts of winter season.

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CRediT authorship contribution statement

RM: Conceptualization, Validation, Methodology, Software, Formal analysis, Writing – original draft, Visualization. MŻ: Conceptualization, Writing – original draft, Funding acquisition. TP: Writing – original draft, Funding acquisition. MW: Validation, Writing - review & editing. GM: Conceptualization, Writing – original draft, Supervision.

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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.

Data Availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2023.121669.

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