

Determining factors of habitat in dynamic forest ecosystems.

An explorative approach to habitat preferences of birds in a naturally disturbed forest.



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1 Abstract

Bark beetle outbreaks alter forest habitats significantly and thus habitat availability and biodiversity. A recent outbreak in Białowieża Primeval Forest (Poland, Belarus) and consequential management provided an opportunity to analyse the effects of the resulting mosaic of forest habitats on local bird species. Within the mosaic of habitats, we recorded species-specific bird sounds to find the presence of birds. Through optimal model selection, we compared the effect of canopy openness with a set of four habitat types, resulting from bark beetle outbreaks. We found that six species were affected by canopy openness, nine were affected by at least one of the habitat types, and two were affected by a combination of the variables. These results show the impact of habitat alterations through natural disturbances and forestry management on forest ecosystems, and we advocate against the practice of salvage logging, as it replaces important forest habitats.

2 Introduction

Bark beetle outbreaks are events that can cause large-scale tree mortality, leading to the creation of large gaps in the otherwise closed canopy of a mature forest (Lindenmayer, Burton, & Franklin, 2012a). This process can be seen as part of the life cycle of forest ecosystems, increasing habitat heterogeneity and biodiversity on a landscape scale, although also temporarily affecting some ecosystem services locally, such as soil quality and the regulation of water conditions (Leverkus et al., 2020; Shorohova, Kneeshaw, Kuuluvainen, & Gauthier, 2011). The most impactful bark beetle species in Europe is the European spruce bark beetle (*Ips typographus*), causing considerable damage to forestry each year (Hlásny et al., 2021; Schelhaas, Nabuurs, & Schuck, 2003).

One of the most impactful effects of spruce bark beetle outbreaks on forest habitats is a significant reduction in canopy cover, due to high tree mortality (Kamińska, Lisiewicz, Kraszewski, & Stereńczak, 2021; Mikusiński et al., 2018; Senf et al., 2018). The canopy closure shapes the microclimate of the undergrowth, as it affects, among other things, light intensity, moisture, and temperature (De Frenne et al., 2019; Kovács, Tinya, & Ódor, 2017). As a result, a closed canopy cover benefits shade-tolerant heterotrophic species, detritivores and saprophytes favouring high soil humidity and species benefitting from the cooler microclimate (Bramer et al., 2018; Franklin et al., 2002; Geiger, Aron, & Todhunter, 2009). Contrastingly, an opening in the canopy cover creates a hotter and drier microclimate where sunlight can reach the understory (De Frenne et al., 2019; Kovács et al., 2017). This benefits light-demanding pioneer species, such as birches, flowering herbs, and shrubby vegetation, and species benefitting from the hotter and drier microclimate, such as reptiles (Hlásny et al., 2021; Swanson et al., 2011). Lastly, the amount of canopy cover also provides different habitat niches on a structural level, for example for birds. On one hand, a closed canopy allows for tree canopy foraging or gleaning, and it provides shelter, for example from predators flying above the canopy level. On the other hand, an open canopy allows for open field foraging, such as hawkking for invertebrates and it is less restricted in space, making flight easier for less manoeuvrable birds (Hoyo, Elliott, Sargatal, & Christie, 1992; Pigot et al., 2020).

Increased canopy openness after spruce bark beetle outbreaks depends on forest characteristics before the disturbance. One of the most important drivers is the density of target tree species, the Norway spruce (*Picea abies*) (Hlásny et al., 2021). Spruce monocultures are more susceptible to outbreaks than mixed forest habitats, which are more resistant as the density of spruces is lower. Mixed forests provide a variety of ecological niches, which can support higher biodiversity as compared to forest monocultures (Lindenmayer, Margules, & Botkin, 2000; Spiecker, 2003). Typical for spruce-dominated plantations is a high density of trees and low diversity in tree species, attracting birds typical for conifer forests, such as breeding goldcrests (*Regulus regulus*) and crested tits (*Lophophanes cristatus*) (Hoyo et al., 1992; Klimo, Hager, & Kulhavý, 2000; Lindbladh, Lindström, Hedwall, & Felton, 2017; Spiecker, 2003).

The habitat characteristics of bark-beetle-induced forest gaps also vary greatly. The choice of management after a bark beetle outbreak largely determines the characteristics of the resulting open habitat and thus the related biodiversity (Hlásny et al., 2021; Leverkus et al., 2020; Lindenmayer et al., 2012a; Swanson et al., 2011; Thorn et al., 2018). One of the most commonly practised management is the removal of dead, affected or even nearby living trees, known as “salvage logging” (Lindenmayer, Burton, & Franklin, 2012b; Thorn et al., 2018). Salvage logging is usually aimed at curbing the spread of the current outbreak, accelerating the regeneration processes of the new age stand, capturing some of the economic value in dead and damaged trees that would otherwise be lost or ensuring public safety by

removing hazardous weakened trees (Lindenmayer et al., 2012b). Salvage logging results in a homogenised, open habitat, with much of the structural heterogeneity, typical to naturally disturbed forests, removed. It leads to an overall decrease in biodiversity due to the removal of natural disturbance legacies and habitat simplification (Swanson et al., 2011; Thorn et al., 2018). However, salvage-logged areas may serve as a surrogate farmland habitat, hosting typical farmland bird species, some of them protected in Europe (Bakx et al., 2020; Žmihorski, Berg, & Pärt, 2016). On the other hand, non-interference management, where very little to no management is applied after a natural disturbance, leads to a large accumulation of standing and lying deadwood, which often increases biodiversity due to the resulting distinctive foraging and habitat niches formed by soft, decaying wood (Leverkus et al., 2020; Swanson et al., 2011). The resulting habitats of both of these management choices are relatively open, suggesting a comparable canopy cover.

Białowieża Primeval Forest (Poland, Belarus) recently experienced the largest known outbreak (2012-2019) of the European spruce bark beetle (*Ips typographus*), killing approximately 40% of the Norway spruce (*Picea abies*) population in the forest (Grodzki, 2016; Kamińska et al., 2021). Salvage logging was performed in parts of the forest, while other parts were left without any intervention. Nevertheless, the bark beetle did not affect the whole forest uniformly. Numerous spruce-dominated stands and mixed forest stands (ranging from dominated by conifers to dominated by deciduous trees) survived the outbreak relatively undisturbed. This has created the opportunity to examine the impact of a bark beetle outbreak on species preferences in a mosaic of forest habitats, including two types of disturbed forest stands: salvage-logged and non-intervention.

To assess the habitat preferences of animals in the mosaic of forest habitats, birds are often used as they are relatively easy to identify and reliably surveyed (Gregory et al., 2005). Therefore, we chose to focus on bird species as an indicative measure of biodiversity in the novel and preexisting habitats of the Białowieża forest. Canopy openness has a significant effect on bird species' habitat preferences in this context (Žmihorski et al., 2016). However, other characteristics, such as the amount of deadwood and tree species composition, also affect habitat preferences of bird species for example through food base alterations (Cours et al., 2023; Viljur et al., 2022) or nest site availability (Basile et al., 2023). To make informed decisions in the management of pre- and post-disturbed forests, it is crucial to recognise the magnitude of which it impacts habitat availability and thus biodiversity. In this explorative research, we aim to answer which bird species are more accurately predicted simply by habitat openness as opposed to other habitat variables to gain insight into the determining factors of habitat availability in the context of a naturally disturbed forest ecosystem.

We hypothesise that canopy openness is a good predictor of the occurrence of typical farmland species, such as yellowhammer (*Emberiza citrinella*) as described in Bakx et al. (2020) and Žmihorski et al. (2016, 2019). Contrastingly, we expect that canopy openness is also a good predictor of the occurrence of some closed-canopy species, such as firecrest (*Regulus ignicapilla*), as they may avoid large openings in forest structures (Ram, Axelsson, Green, Smith, & Lindström, 2017). While canopy openness might predict the occurrence of typical farmland or closed-canopy species, we hypothesise that the other habitat characteristics (such as those induced by post-disturbance management) are better for predicting the occurrence of the majority of birds. For example, species mainly foraging in conifer forests, such as crested tit (*Lophophanes cristatus*) and willow tit (*Poecile montanus*) may strongly prefer spruce-dominated stands over closed-canopy mixed forests. On the other hand, species modifying wood for foraging, nesting or habitat (e.g., Eurasian treecreeper (*Certhia familiaris*) and woodpeckers) can be

expected to prefer deadwood-abundant sites, such as non-intervention disturbed areas or old-growth mixed forests (Hoyo et al., 1992; Swanson et al., 2011), as the softer wood of deadwood is easier to modify. Lastly, we hypothesise that some species preferences are best predicted by a combination of both canopy openness and habitat type: for example, those preferring closed-canopy conifer, such as goldcrest (*Regulus regulus*) or species that forage in open habitat, but rely on disturbance legacies, that are removed due to salvage logging (fallen and standing deadwood, shrubs), such as dunnoek (*Prunella modularisor*) (Hoyo et al., 1992).

3 Methods

3.1 Study area

Białowieża forest is one of the oldest remaining old-growth forest ecosystems in Europe, with a continuous vegetation history since the last glaciation (about 11-12 thousand years ago), located on the border between Poland and Belarus (Samojlik, Fedotova, Daszkiewicz, & Rotherham, 2020) (figure 1.B). It covers a total area of 150,582 ha, of which 41% is in Poland and additionally our research area. Dominating tree species are pedunculate oak (*Quercus robur*), 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 (*Picea abies*) (Drozdowski, Buraczyk, & Brzeziecki, 2017). Both the Polish and Belarusian parts of Białowieża Forest are UNESCO World Heritage Site (UNESCO The World Heritage Committee, 2012). In addition, the Polish part is a Natura 2000 site (Puszcza Białowieska, PLC200004), which makes it a protected landscape area and a Biosphere Reserve. Besides the international designations, there are several national designation levels, which are Białowieża National Park, with well-preserved old-growth stands (17% of the Polish part of the forest), nature reserves including well-preserved old-growth stands and the most valuable forest stands outside the reserves (together 20%) and the remaining stands (63%), which are managed by the State Forests Holding, where logging and wood extraction is allowed (UNESCO The World Heritage Committee, 2012).

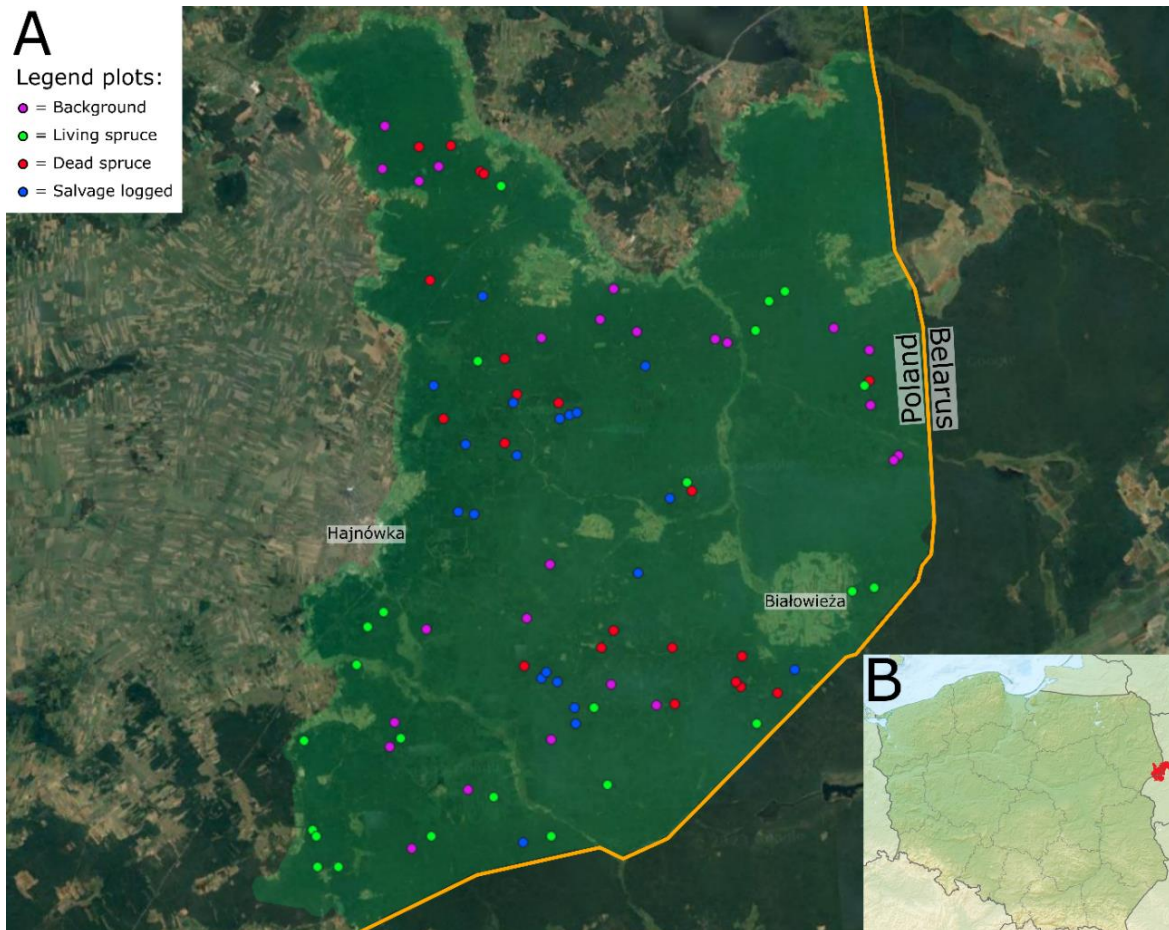


Figure 1: Location of the study site and recording locations. A: Satellite view of the Polish part of Białowieża Forest, with the study area highlighted in green and the recording locations, colour-coded per habitat. B: map of Poland and in red: Range of Białowieża Forest in Poland and Belarus (Based on: Marcin Koziel. Protection of natural and landscape values in the Polish-Belarusian borderland on the example of the Białowieża Primeval Forest. "Problems of Landscape Ecology". Vol. XXVI, pp. 271-284. 2010, and maps of the Natura 2000 area "Puszcza Białowieska" (PLC200004)).

3.2 Habitat classification

After the bark beetle outbreak and consequential management, we divided the forest into compartments or “plots”, classified to represent one of the four habitats, and randomly selected 25 plots per habitat, with the total area partly determining the probability of their choice, as larger plots serve as more representative habitats. Plots were at least 500m apart to reduce spatial auto-correlation and overrepresentation of recorded individuals. Both the salvage logging and tree die-off due to the outbreak in our study plots transpired mostly between 2015 and 2018, therefore the disturbed plots were assumed to have a similar tree regeneration time. After visual inspections in the field, plots that did not match our criteria (e.g., partial salvage logging on dead spruce plots, logging without removal of dead wood on salvage-logged plots) were replaced. These plots had to adhere to the following criteria (tree species data from Forest Research Institute, 2021, post-outbreak classification by Sentinel-2 data from Mikusiński et al. (2018)):

Habitat	Hereafter called	# of recorded plots	Criteria
Salvage-logged forest (figure 2.A)	Salvage-logged plots (LOG)	20	>30% of trees present are Norway spruce, of which a majority died during the outbreak and >2000m ² was salvage-logged in response between 07-2015 and 06-2018.
Non-intervened dead forest (figure 2.B)	Dead spruce plots (DEAD)	21	>30% of trees present are Norway spruce, of which >80% died during the outbreak and were not removed.
Spruce-dominated forest (figure 2.C)	Living spruce plots (LIV)	23	>30% of trees present are Norway spruce, of which >80% were alive in 2019.
Mixed species forest (figure 2.D)	Background plots (BG)	25	<30% of trees present are Norway spruce.

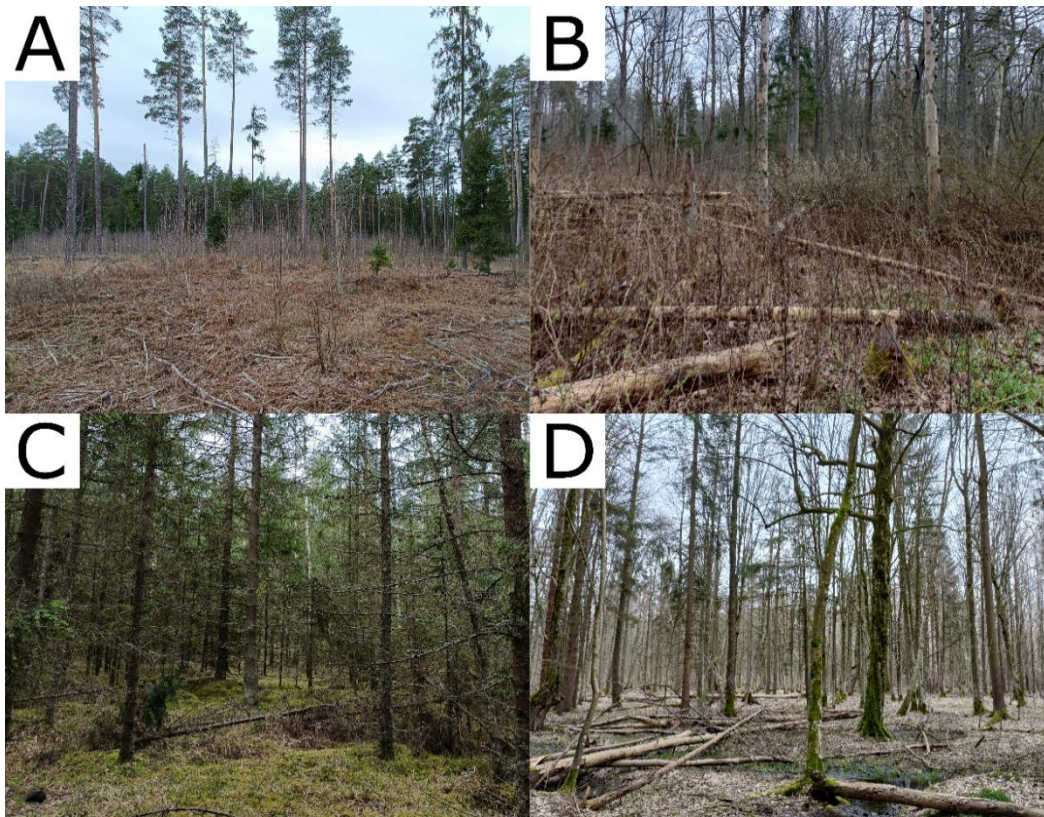


Figure 2: Visual representation of each habitat. Plots classified as salvage-logged (A), dead spruce (B), living spruce (C) and background (D).

3.3 Bird inventories

To detect bird species, we selected a specific tree within the plots to hang audio recorders on (figure 1.B), facing them towards the correct habitat classification, and, if possible, east to avoid wind disruption. We used custom-made Autonomous Recording Units (ARU) to record all bird sounds in early spring on the 8th and 9th of April 2022 (both resident species and wintering or breeding species for the area). A recording lasted four hours, from 1h before sunrise, to 3h after sunrise. In each recording, 1 minute was selected every 20 minutes, except the first hour after sunrise, during peak bird activity, where 1 minute every 10 minutes was selected. This resulted in a total of 15 selected minutes (i.e., respectively per hour: 3+6+3+3 minutes) per recording per night. After this extraction, each recorded minute was checked for the occurrence of a species, recognised by species-specific sounds (e.g., song, calls and woodpecker drumming) and summarised as the presence or absence of each species during the recorded timeframe per plot. This was done for sound recordings in a total of 89 plots, without information about the habitat classification of the ARU location. Due to complications during recordings (e.g., waterlogged ARUs or too much noise from wind or machinery), some recordings could not be checked, resulting in respectively 20, 21, 23 and 25 recordings in salvage-logged, dead spruce, living spruce and background plots.

3.4 Analysis

All analyses were performed using R Statistical Software (v4.2.3; R Core Team 2023)

3.4.1 Canopy openness

The canopy openness is determined by calculating the proportion of 2.5 by 2.5-meter pixels with canopy/foilage lower than two meters, extracted from the Sentinel-2 data of Mikusiński et al. (2018), within a 50-meter radius area around the ARU locations (figure 1.A). This results in a continuous value between 0 and 1 per plot, with 0 representing a fully closed mature canopy and 1 representing a completely open canopy, with shrubs, fallen trees and saplings possibly present (lower than two meters).

3.4.2 Model selection

To find the best predictor between habitat classification and canopy openness, we ran four different generalised linear models (glm function from the stats package (R Core Team, 2023)) per bird species, including 1) no predicting variables (intercept-only model), 2) habitat classification as predicting variable (habitat classification model), 3) canopy openness as predicting variable (canopy openness model) and 4) an interactive model (habitat classification*canopy openness), including both variables as predictors (combined model). We chose bird species presence as the response variable with a binomial distribution (i.e., present, or absent). Per species, each model records an Akaike information criterion (AIC) value (dredge function from the MuMIn package (Bartoń, 2023)) that ranks the four competing models on the explanatory power of their respective response values. The lowest value between the four models explains the most variance and this model is selected as the optimal model. However, models that have a difference in AIC values (deltaAIC) of less than two are assumed to be explaining equal variance, in which case the model was selected with the least amount of variables, as this would be the least complex model, or simply the lowest deltaAIC between the habitat classification model and canopy openness model was selected as optimal model (Symonds & Moussalli, 2011). Lastly, with the selected models, we ran generalised linear models (glm function from the stats package (R Core Team, 2023)) for each species that had one or both of the two predicting variables in their optimal model, to show the predicted effect of this variable or combination of variables on the presence of the species, according to our measured species presences.

4 Results

4.1 Species occurrences

We recorded a total of 8139 species occurrences and a total of 84 distinct species. We filtered out species that were recorded in more than 95% of the plots and less than 8% of the plots, as the models were unable to run with these amounts (supp. materials for unselected species). This resulted in the following 38 analysed species, with the percentage of plots a species was recorded in:

English name	Latin name	% of plots present
Great spotted woodpecker	<i>Dendrocopos major</i>	94.38
Great tit	<i>Parus major</i>	93.26
Eurasian wren	<i>Troglodytes troglodytes</i>	80.90
Black woodpecker	<i>Dryocopus martius</i>	77.53
Common chiffchaff	<i>Phylloscopus collybita</i>	76.40
Eurasian treecreeper	<i>Certhia familiaris</i>	70.79
Hawfinch	<i>Coccothraustes coccothraustes</i>	66.29
Eurasian blue tit	<i>Cyanistes caeruleus</i>	65.17
Eurasian jay	<i>Garrulus glandarius</i>	62.92
Marsh tit	<i>Poecile palustris</i>	60.67
Lesser spotted woodpecker	<i>Dryobates minor</i>	55.06
Eurasian nuthatch	<i>Sitta europaea</i>	44.94
Common crane	<i>Grus grus</i>	43.82
Tawny owl	<i>Strix aluco</i>	40.45
Eurasian blackcap	<i>Sylvia atricapilla</i>	34.83
Crested tit	<i>Lophophanes cristatus</i>	32.58
Willow tit	<i>Poecile montanus</i>	31.46
Eurasian Siskin	<i>Spinus spinus</i>	30.34
Dunnock	<i>Prunella modularis</i>	29.21
Stock dove	<i>Columba oenas</i>	28.09
White-backed woodpecker	<i>Dendrocopos leucotos</i>	28.09
Eurasian three-toed woodpecker	<i>Picoides tridactylus</i>	24.72
Goldcrest	<i>Regulus regulus</i>	22.47
Coal tit	<i>Periparus ater</i>	21.35
Mistle thrush	<i>Turdus viscivorus</i>	20.22
Yellowhammer	<i>Emberiza citrinella</i>	20.22
Grey-headed woodpecker	<i>Picus canus</i>	19.10
Tree pipit	<i>Anthus trivialis</i>	19.10
Common starling	<i>Sturnus vulgaris</i>	17.98
Redwing	<i>Turdus iliacus</i>	17.98
Common firecrest	<i>Regulus ignicapilla</i>	15.73
Green sandpiper	<i>Tringa ochropus</i>	15.73
Middle spotted woodpecker	<i>Dendrocoptes medius</i>	15.73
Common raven	<i>Corvus corax</i>	14.61
Eurasian woodcock	<i>Scolopax rusticola</i>	11.24
Hazel grouse	<i>Tetrastes bonasia</i>	11.24
European green woodpecker	<i>Picus viridis</i>	8.99
Hooded crow	<i>Corvus cornix</i>	8.99

4.2 Canopy openness per habitat classification

When comparing the canopy openness of each habitat classification (figure 3), salvage-logged plots are shown to have significantly more open canopy than all of the other habitat classes ($p < 0.001$). Dead spruce plots showed a higher variation of canopy openness compared to background plots and living spruce plots, but the difference is not significant.

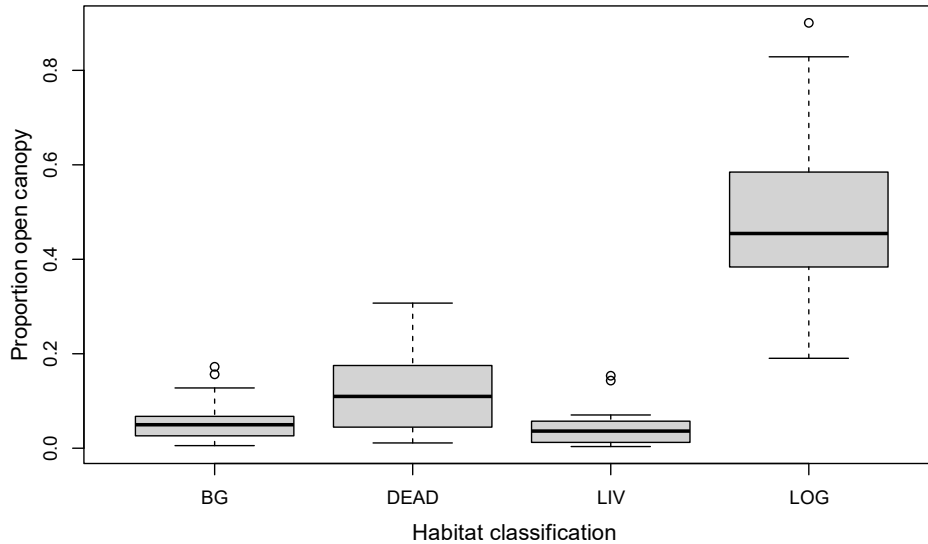


Figure 3: Boxplot of the proportion open canopy (y-axis) per habitat classification (x-axis). BG = background plots, DEAD = dead spruce plots, LIV = living spruce plots, LOG = salvage-logged plots.

4.3 Model selection

To predict the presence of most (21) species per plot, intercept-only was the optimal model (figure 4.A). For most of these species, the explanatory power of the other models ranked similarly, with the canopy openness model ranking second and the combined model ranking last. All but one species (hazel grouse) scored below the threshold value of ΔAIC in the canopy openness model, showing equal explanatory power, while all but three species (hazel grouse, three-toed woodpecker, and redwing) scored above the threshold in the combined model, showing less explanatory power. In the case of the habitat classification model, only seven species (crane, great tit, hazel grouse, nuthatch, raven, redwing, and white-backed woodpecker) scored below the threshold and showed equal explanatory power. For six species the optimal model had canopy openness as the predictor variable (figure 4.B). Between these species, only one species (firecrest) scored below the threshold with other models, namely the habitat classification and combined models, thus being the only models that did not show less explanatory power than the canopy openness model. For nine species the optimal model had habitat classification as the predictor variable (figure 4.C). All of these species showed equal explanatory power of the combined model, as all values are below the threshold, but only one species (Eurasian treecreeper) showed this for another model as well, namely the canopy openness model, as all of the other model predictions showed less explanatory power. Lastly, two species had the combined model with both predictor variables canopy openness and habitat classification included as the optimal model (figure 4.D). Due to the optimal model selection process, the other models for these species do not show ΔAIC values below the threshold, as this model would then be the less complex and thus the optimal model for the species. For both

species, however, the habitat classification model shows much lower deltaAIC values, compared to the other non-optimal models, as it is bordering the threshold value.

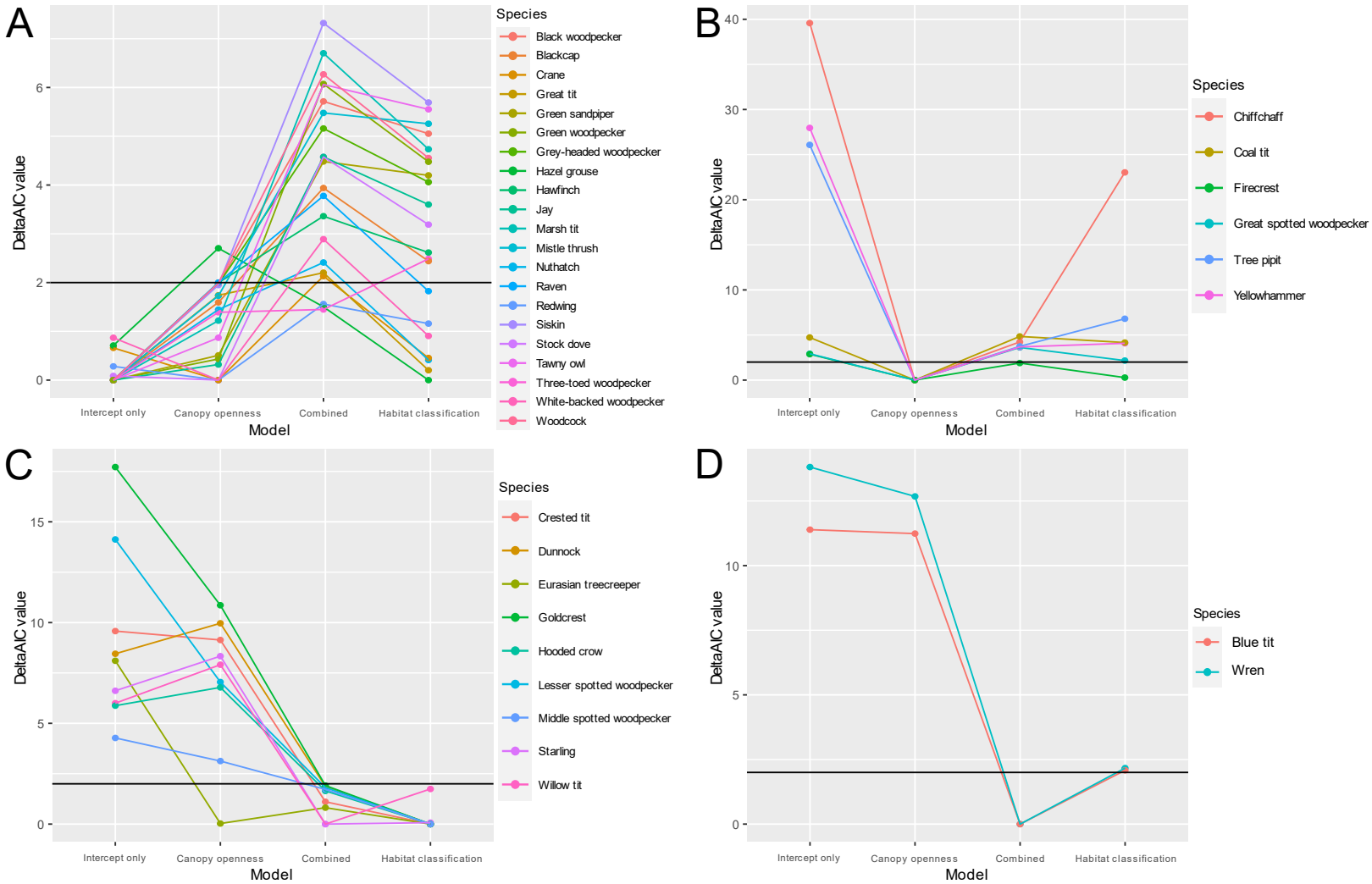


Figure 4: DeltaAIC value (on the y-axis) per model (on the x-axis) of each analysed species, divided in separate graphs with species that have the same optimal model: A) intercept-only, B) canopy openness, C) habitat classification and D) combined. The black line indicates the deltaAIC threshold value of two. Note that y-axes are not equal.

4.4 Canopy openness model

Out of the six species where the canopy openness model was the optimal model, chiffchaff ($p < 0.001$), great spotted woodpecker ($p > 0.1$), tree pipit ($p < 0.001$) and yellowhammer ($p < 0.001$) were positively affected by canopy openness, while coal tit ($p < 0.1$) and firecrest ($p < 0.1$) were negatively affected by canopy openness (figure 5).

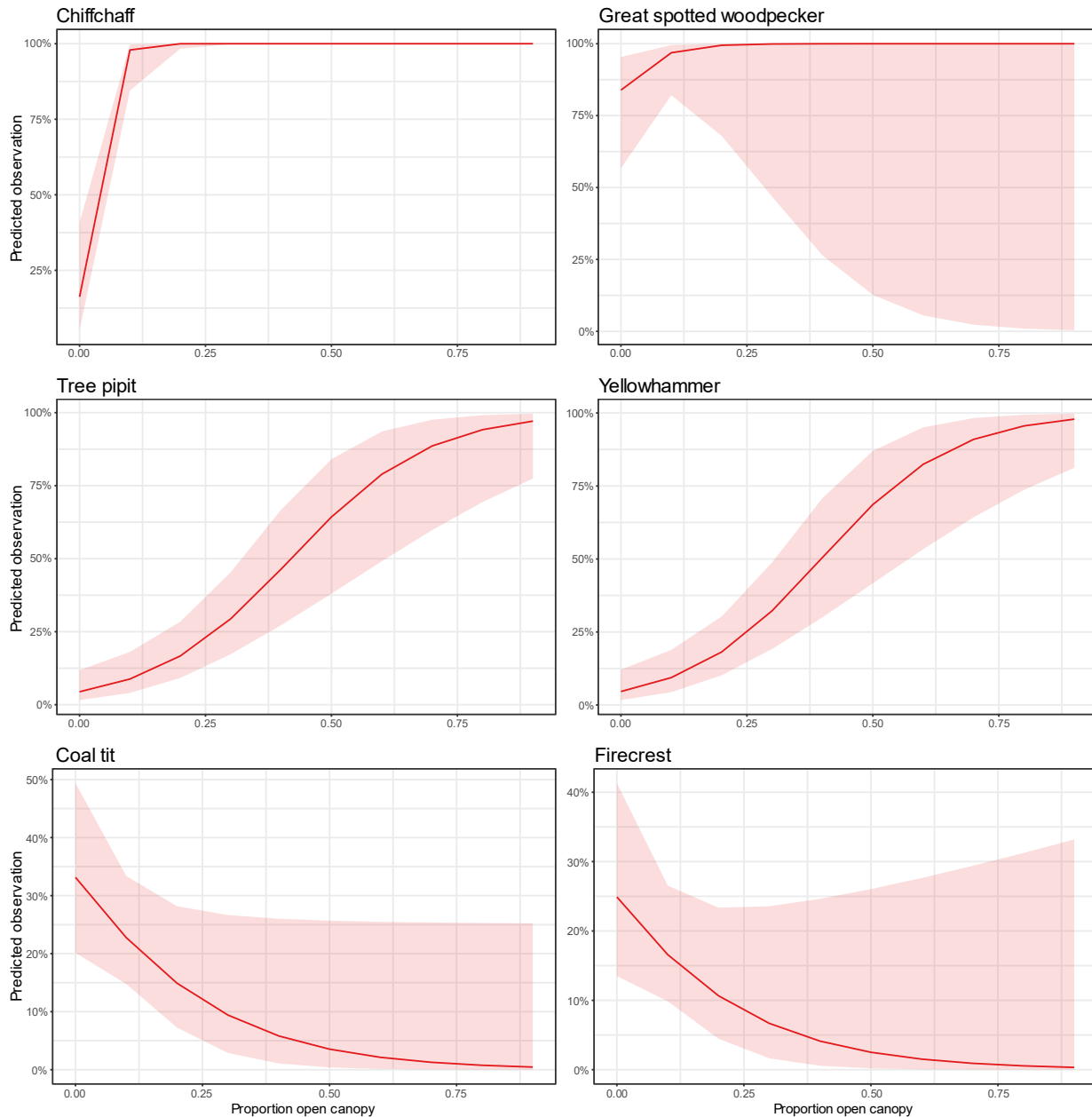


Figure 5: The predicted observation in percentages (y-axis) per species plotted against the proportion of open canopy (x-axis) with error margins. Shown are the six species of which the canopy openness model was the optimal model. Note that y-axes are not equal.

4.5 Habitat classification model

For the nine species that had the habitat classification model as the optimal model, Starling and hooded crow showed the highest predicted presence in background plots, Eurasian treecreeper and dunnock showed the highest predicted presence in dead spruce plots, crested tit, willow tit and goldcrest showed the highest predicted presence in living spruce plots and lesser spotted woodpecker and middle spotted woodpecker showed the highest predicted presence in salvage-logged plots (figure 6).

Willow tit showed the lowest predicted presence in background plots and crested tit showed a relatively low predicted presence here. For the dead spruce plots, hooded crow and goldcrest showed the lowest predicted presence and middle spotted woodpecker showed a relatively low predicted presence here. Starling and hooded crow showed the lowest predicted presence in living spruce plots and dunnock, lesser spotted woodpecker and middle spotted woodpecker showed relatively low predicted presence here. Lastly, goldcrest showed the lowest predicted presence in salvage-logged plots and Eurasian treecreeper, crested tit and willow tit showed relatively low predicted presence here.

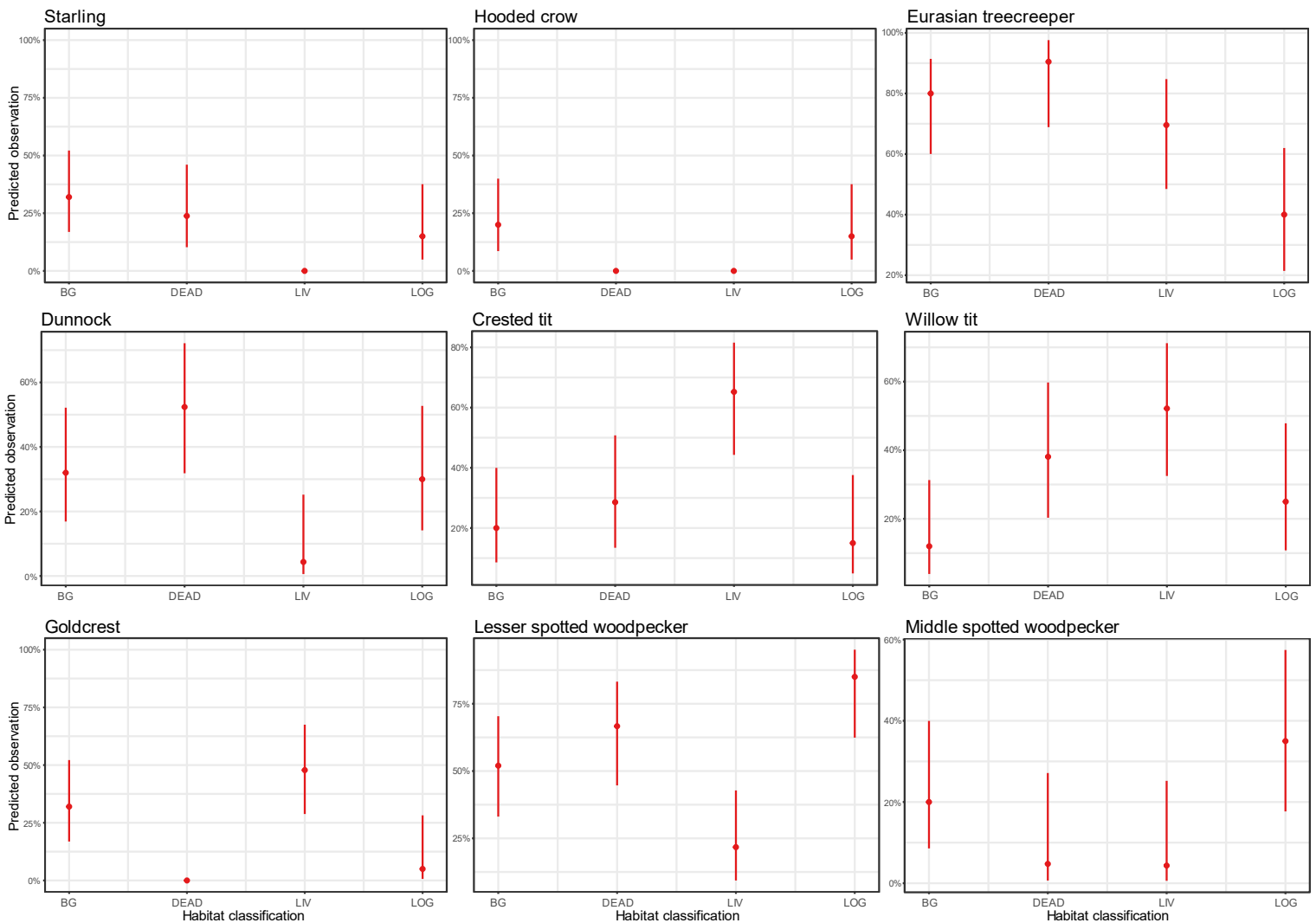


Figure 6: The predicted observation in percentages (y-axis) per species per habitat classification (x-axis) with error bars (no error bar means no sounds were recorded for the species in that habitat class): BG = background plots, DEAD = dead spruce plots, LIV = living spruce plots, LOG = salvage-logged plots. Shown are the nine species of which the habitat classification model was the optimal model. Note that y-axes are not equal.

4.6 Combined model

For both species that had the combined model as the optimal model, blue tit and wren, we found a negative effect of canopy openness on the predicted presence in a plot (both $p < 0.1$) and similar predicted presences were found for these species per habitat classification: relatively high predicted presence in dead spruce plots and salvage-logged plots and relatively low predicted presence in living spruce plots (figure 7).

We also ran the canopy openness model for each of the habitat classifications separately to disentangle the interaction between the two explanatory variables in this combined model (figures 8 and 9). Here we found no clear trends in the background plots for both species and in the dead spruce plots for the wren, as it was present in all dead spruce plots. We do find a positive trend of canopy openness in the living spruce plots for both species ($p < 0.2$). We also find negative effects of canopy openness in the salvage-logged plots for both blue tit ($p < 0.1$) and wren ($p < 0.05$) and the dead spruce plots for the blue tit ($p < 0.1$).

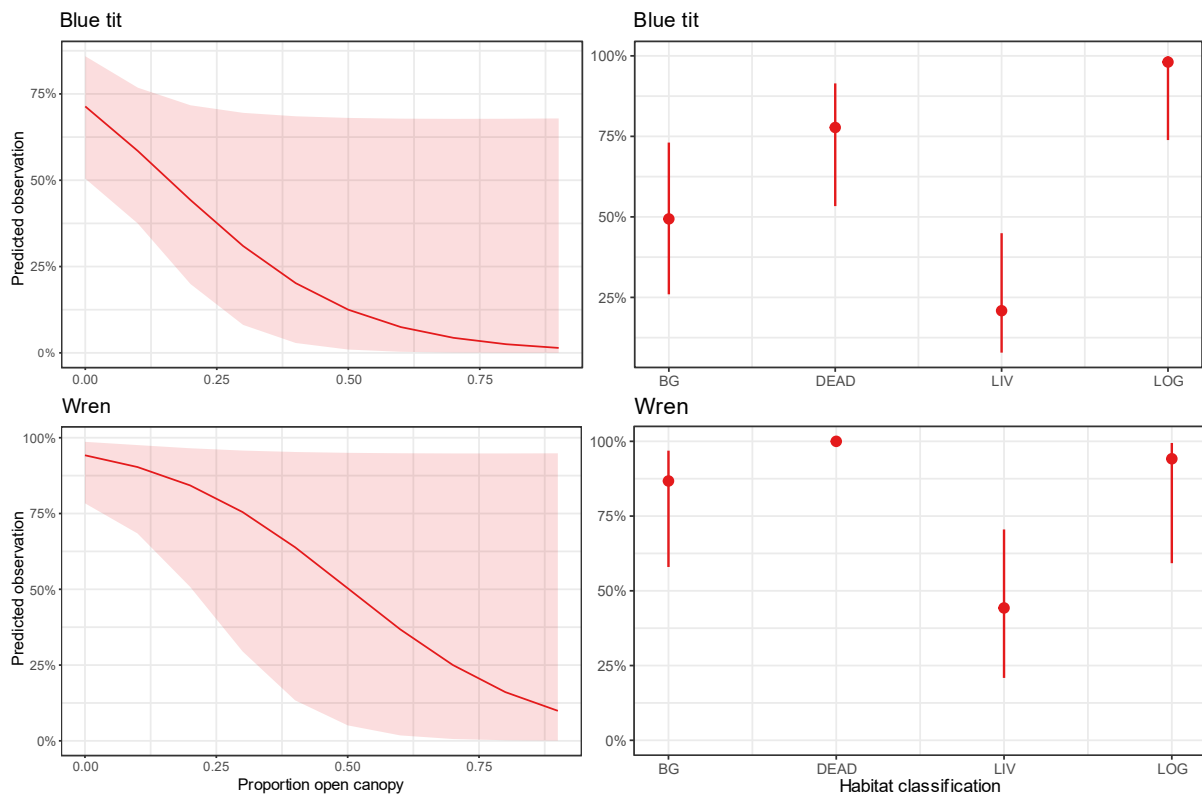


Figure 7: The predicted observation in percentages (y-axis) per species, on the left: plotted against the proportion of open canopy (x-axis) with error margins and on the right: per habitat classification (x-axis) with error bars (no error bar means sounds were recorded for the species in all plots of that habitat class): BG = background plots, DEAD = dead spruce plots, LIV = living spruce plots, LOG = salvage-logged plots. Shown are the two species of which the combined model was the optimal model. Note that y-axes are not equal.

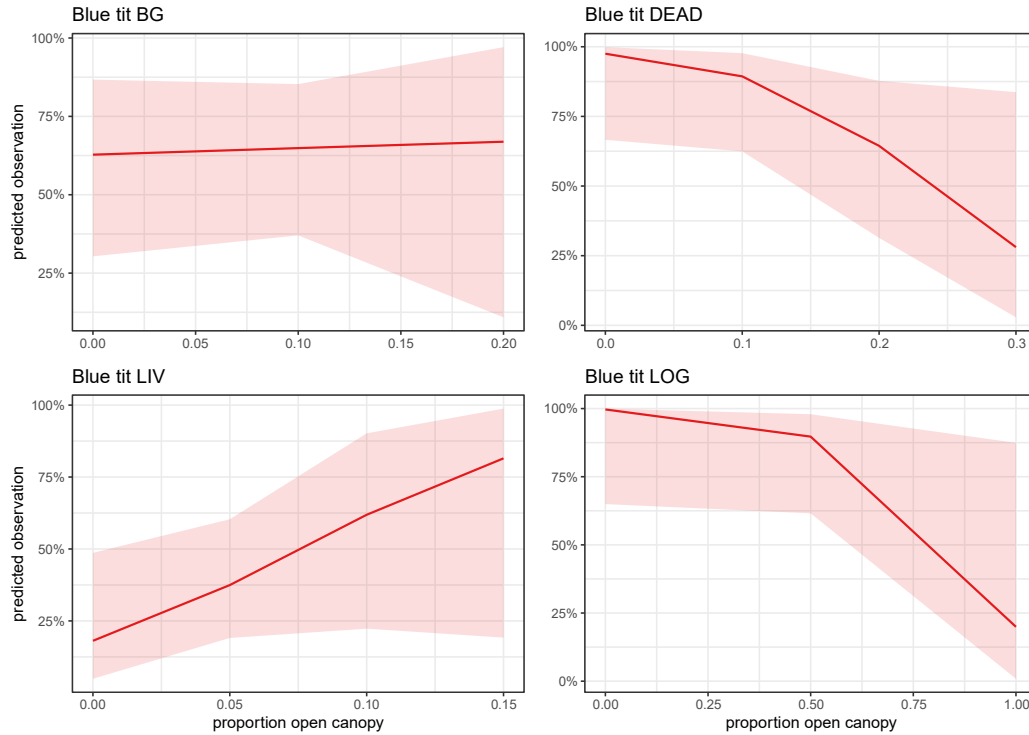


Figure 8: The predicted observation of blue tits in percentages (y-axis) per habitat classification (BG = background plots, DEAD = dead spruce plots, LIV = living spruce plots, LOG = salvage-logged plots) plotted against the proportion of open canopy (x-axis) with error margins. Note that x-axes are not equal.

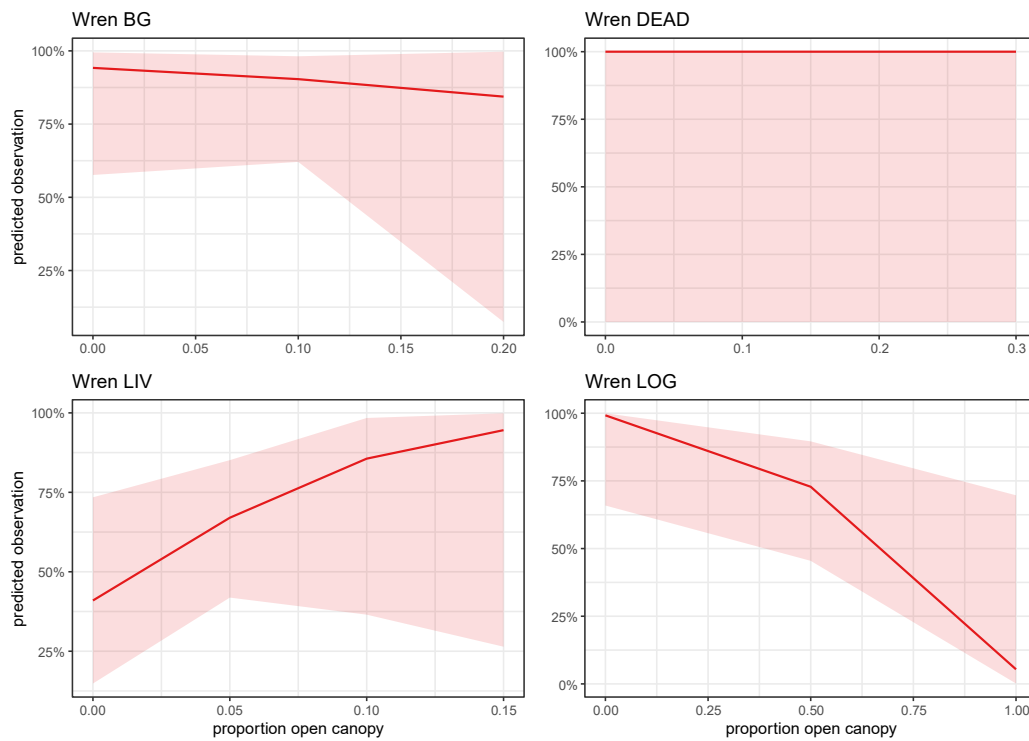


Figure 9: The predicted observation of wrens in percentages (y-axis) per habitat classification (BG = background plots, DEAD = dead spruce plots, LIV = living spruce plots, LOG = salvage-logged plots) plotted against the proportion of open canopy (x-axis) with error margins. Note that x-axes are not equal.

5 Discussion

In this research, we assessed in what way specific habitats and canopy cover shape the habitat preferences of 38 forest bird species in a partially disturbed forest ecosystem. With optimal model selection, we aimed to find if these specific variables, connected to both bark beetle disturbance and subsequent human management or the absence thereof, could predict bird species presence better than an intercept-only model. If this was the case for a species, we determined respectively for canopy openness and habitat classification, if the effect was positive or negative and the relative effect sizes of each habitat class on the predicted presence.

An important consideration in the interpretation of our results is that the canopy openness per habitat classification did not follow our expectations, as the dead spruce plots did not have significantly more open canopy compared to non-disturbed plots, while the salvage-logged plots did. This has led to collinearity between canopy openness and the salvage-logged habitat classification, which masks the effects of habitat specifics that are typical for salvage-logged habitat besides the canopy openness, compared to the other disturbed and assumed relatively open habitat classification, the dead spruce plots, such as the pioneering vegetation differences. It also disrupts the combined model, as any effect of canopy openness is overrepresented in this model, in both the canopy openness and the salvage-logged habitat classification as predicting variables. The discussion will be held with this in mind.

For six species (chiffchaff, great spotted woodpecker, tree pipit, yellowhammer, coal tit and firecrest), we found that the canopy openness model was the optimal model to predict their presence in a plot. This is an indication that canopy openness affects the habitat choices of these species. However, the effect of canopy openness on the presence of great spotted woodpeckers proved to be minimal, with only a slightly lower presence than 100% at low canopy openness. The chiffchaff, tree pipit and yellowhammer did show significantly higher presences with higher canopy openness. Only at less than ~10% canopy openness, we find a sharp decline of presence for the case of chiffchaff, while they were recorded in all plots with a canopy openness higher than ~20%. This result suggests that the chiffchaff avoids a more closed-canopy forest while being abundant in the rest of the forest. This is explained by the chiffchaff's preference for more sparse or disturbed forests and forest edges (Hoyo et al., 1992). For tree pipit and yellowhammer, however, there was a more or less constant increase of presence with increasing canopy openness, suggesting a preference for open woodlands. Tree pipits are highly related to disturbed areas, as they forage primarily on the ground in open woodlands and make use of coppice and perch structures. They breed on the ground amongst grass or heather tussocks (Hoyo et al., 1992). Yellowhammers prefer similar habits, although they commonly use low shrubbery for nesting. They are also mainly foraging from the ground on grasses, herbs and invertebrates related to grasslands (Hoyo et al., 1992). All of the behaviours and preferences mentioned above are highly related to open canopy habitats within a disturbed forest context, which explains the constant relation of the canopy openness and their presence, without the need for any habitat classification.

The coal tit and firecrest both showed a more or less constant decrease of presence with increasing canopy openness. These species are highly connected to closed canopy forest ecosystems during breeding season. In the case of coal tits, they are mainly found breeding in dense coniferous woods like spruce plantations, but also often in more deciduous or mixed forests, in birches (*Betula*) and alders (*Alnus*) for example (Hagemeyer et al., 1997). The common denominator in preference seems to be a relatively closed canopy forest, while it is indifferent to the type of forest, as shown by our results that

canopy openness is a better explanatory variable than habitat classification. In our results, the firecrest showed similar closed canopy preferences as the coal tit, with the main difference being that firecrest presence could also be explained by the habitat classification model. This could be the result of its breeding preference being primarily in broadleaf and mixed forests and less in spruce-dominated forests (Hoyo et al., 1992).

When looking at our results of the species presences predicted by habitat classification, some species show more pronounced effects than other species. For starlings and hooded crows, the model did not show pronounced effects and it is difficult to conclude the background class is the most preferred habitat here because this habitat is highly diverse. Both species are omnivorous and opportunistic (Hoyo et al., 1992; Pigot et al., 2020), which could explain their presence in the diverse habitat class. They both also appeared in the salvage-logged plots and starling in dead spruce plots, which can be explained by their additional preferences for open habitats (Kosicki & Chylarecki, 2014; Żmihorski et al., 2016).

The dead spruce plots benefitted some species, such as the Eurasian treecreeper. It showed the highest predicted presence in the dead spruce plots, while also relatively present in the other habitat classes, apart from the relatively low presence in salvage-logged plots. This result can be explained by its pronounced preference for old-growth forest as a habitat (Suorsa et al., 2005). Specifically, dead wood accumulation and large, preferably spruce, tree stems are key components for this bird, which explains its relative absence in the salvage-logged plots. We also found dunnocks to prefer dead wood plots, which is possibly due to their foraging niche of being an invertivore on the ground and their preference for shrubbery (Table 3, Hoyo et al., 1992; Pigot et al., 2020). In the dead wood plots, under the protective cover of fallen trees, it is possible to forage safely for invertebrates and the plots were often covered in *Rubus* shrubbery.

The species that we found mostly present in the living spruce plots, crested tit, willow tit and goldcrest, all show a high preference for Norway spruces as a habitat tree species (Hagemeijer et al., 1997), which explains their specific habitat preference. Additionally, willow tits also prefer shrubby vegetation, similar to the dunnock (Hoyo et al., 1992), and are therefore also expected more in the dead wood plots, as we also found.

The lesser and middle spotted woodpecker both show relatively high presences in the salvage-logged plots. The lesser spotted woodpecker is, as shown by this result, highly related to open forest habitat, but also to softwood, which is their preferred foraging substrate, which explains why they also show a high predicted presence in the dead wood plots that contain substantial amounts of dead softwood (Hagemeijer et al., 1997). The middle spotted woodpecker is more difficult to explain, as the main habitat preference of this species is old-growth deciduous forest, mainly foraging on large oak (*Quercus*) and hornbeam (*Carpinus*) (Hoyo et al., 1992), therefore the expected highest presence would be in the background habitat class, not in the salvage-logged plots. Possibly a high amount of so-called habitat trees (trees left alive in an otherwise empty salvage-logged plot) are mature oaks or hornbeams, which has attracted this species in these plots. Another possibility is that both of these species are actually mainly found in the relatively closed canopy salvage-logged plots because the canopy openness model explained less variance of their presence, while they apparently prefer the highly open salvage-logged habitats. In other words, the collinearity of these two variables could have interfered with these results.

We found that for the majority of the analysed species, the intercept-only model best predicts their presence. This is an indication that most species are not significantly affected by differences in canopy

openness and there are no significant differences between each of the habitat classes for these species. Explanations for this result can be specific for each species. Some species can occupy a wide range of habitats, as we see in species like the great tit (Hoyo et al., 1992), which could explain its non-specific presence. Species in this group mostly occupy omnivorous trophic levels or niches, compared to other trophic levels or niches, according to Pigot et al. (2020), which could also explain their non-specific presence. There were also species recorded with trophic niches that could be less related to canopy openness or the investigated habitat classes, but more related to for example prey (tawny owl) or water (green sandpiper) availability (Pigot et al., 2020). Another explanation could be that certain species are significantly louder than others, like the black woodpecker and the crane, which means that the sounds of these species could have been recorded from outside of the relevant range and therefore their non-specific presence could be the result of imprecise measurements. For other species, the sample size could have been too low to show an effect, like the green woodpecker, hazel grouse, and woodcock. These species may be present in a specific habitat but behave relatively silent (Hoyo et al., 1992). Lastly, it is possible that these variables did affect certain species, but only significantly in the context of a more specific or a more complex set of ecological variables. Often in ecological or behavioural research, it is impossible to recreate the perfect model due to the complexity of these natural systems (Hegyí & Garamszegi, 2011; Symonds & Moussalli, 2011).

For the blue tit and wren, a combined model seemed to be the optimal model. However, a combination of the models proved to be problematic during the analysis, due to the significant collinearity of canopy openness and the salvage-logged habitat classification. This has masked the results in such a manner that it is unclear how to interpret the combined model. Both species showed a negative effect on the presence of canopy openness in salvage-logged plots and blue tit showed the same in the dead spruce plots, while both species also showed a positive trend (not significant) of canopy openness in the living spruce plots. Given the average canopy cover of each habitat classification (figure 3), these results disentangle the problem with the combined model. It shows a higher presence in the relatively closed canopy plots of the otherwise open salvage-logged plots (and the dead spruce plots in the case of blue tits) and vice versa for the dense living spruce plots, meaning that these species seem to prefer forest habitat that is not too open and not too dense. The collinearity seems to be caused by the prediction of high presences in salvage-logged plots with highly closed canopies (up to fully closed canopy), while the proportion of canopy openness in these plots averages around 0.5 and none below 0.2 (figure 3), which leads to an overrepresentation of canopy openness as an explanatory variable in the salvage-logged habitat classification.

For future research, we suggest increasing the dataset by measuring in different seasons, as we could not measure the effects on many migratory species as they are not yet present in early April and the canopy cover is much more pronounced later in the year, as deciduous trees did not grow their leaves yet. We also suggest additional point counts with distance sampling at ARU locations to increase the precision of the dataset and aid with some downsides of ARU usage (fewer overall detections and unknown distances of bird sounds) (Buckland et al., 2001; Shonfield & Bayne, 2017). This could provide an additional density measure of species besides the presence/absence data that we used. It also informs us about species-specific sound reach as it is important to know from what distance a sound could be recorded by the ARUs in the habitat preference context. An improvement of the canopy openness quantification is also needed, as we expect significant differences in canopy openness if we change the 50m radius range and 2m foliage height threshold we used. On visual inspection, we found that the salvage-logged plots were

more open in a specific area (meticulously logged areas), while in the dead spruce plots, the canopy opened up in a more chaotic, spread-out manner, possibly interfering with the method we used of qualifying a 2.5m by 2.5m plot as open or closed. Model selection as a method has shown to be useful in analysing the effect of habitat variables on specific species, but we suggest increasing this scope with more elaborate measurements of habitat-defining variables, such as ground coverage of deadwood or a ground vegetation inventory. We also suggest building on this research with an analysis of connectivity between the plots, which could give more context to species presence, as species presence in a habitat is influenced by the level of isolation of this plot, as per the island theory (Simberloff, 1974).

Although our method had certain limitations connected to bias in estimating canopy openness and the resulting collinearity of variables, our results give important insights into a complex ecological situation that arose from the bark beetle outbreak in the Białowieża forest and its effects on local bird species. Through model selection, we found that the resulting mosaic of habitats and canopy cover attracts distinct species, aiding in sustaining the biodiversity of this important old-growth forest ecosystem. However, we suggest limiting the human interactions in this process, specifically salvage logging management, as we suspect that much of the habitat characteristics that are typical for dynamic forest habitats are removed in these plots, leading to habitat simplification (Swanson et al., 2011; Thorn et al., 2018) and overall largest diversion from a natural forest ecosystem. Our results support this claim with lower presences of typical forest species in salvage logged habitat, as shown by Eurasian treecreeper, goldcrest, and crested tit and with higher canopy openness, which we found to be highly related to salvage logging in this forest, as shown by firecrest and coal tit. Contrastingly, we found an increased presence of typically open habitat species, yellowhammer, and tree pipit, with increasing canopy openness, further supporting the deteriorating effect on forest habitat. As typical forest species were replaced by typical open habitat species due to salvage logging management, we argue that a forest ecosystem should serve as a habitat for the former species group.

6 References

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7 Supplementary materials

English and Latin names of species that were recorded but not included in the analysis due to the count of plots these species were present, which is given in the third column:

English name	Latin name	# plots present (out of 89)
Common blackbird	<i>Turdus merula</i>	89
Common chaffinch	<i>Fringilla coelebs</i>	89
Common wood pigeon	<i>Columba palumbus</i>	87
European robin	<i>Erithacus rubecula</i>	87
Song thrush	<i>Turdus philomelos</i>	87
Common snipe	<i>Gallinago gallinago</i>	6
Eurasian pygmy owl	<i>Glaucidium passerinum</i>	6
Whooper swan	<i>Cygnus cygnus</i>	6
Common cuckoo	<i>Cuculus canorus</i>	5
Eurasian bullfinch	<i>Pyrrhula pyrrhula</i>	4
Eurasian skylark	<i>Alauda arvensis</i>	4
European goldfinch	<i>Carduelis carduelis</i>	4
Fieldfare	<i>Turdus pilaris</i>	3
Spotted nutcracker	<i>Nucifraga caryocatactes</i>	3
Wood warbler	<i>Phylloscopus sibilatrix</i>	3
Northern goshawk	<i>Accipiter gentilis</i>	2
Red-breasted flycatcher	<i>Ficedula parva</i>	2
Willow warbler	<i>Phylloscopus trochilus</i>	2
Woodlark	<i>Lullula arborea</i>	2
Boreal owl	<i>Aegolius funereus</i>	1
Collared flycatcher	<i>Ficedula albicollis</i>	1
Common rosefinch	<i>Carpodacus erythrinus</i>	1
Eurasian magpie	<i>Pica pica</i>	1
Eurasian wryneck	<i>Jynx torquilla</i>	1
European turtle dove	<i>Streptopelia turtur</i>	1
Grey heron	<i>Ardea cinerea</i>	1
Long-tailed tit	<i>Aegithalos caudatus</i>	1
Mallard	<i>Anas platyrhynchos</i>	1
Northern lapwing	<i>Vanellus vanellus</i>	1
Spotted flycatcher	<i>Muscicapa striata</i>	1