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Bird response to small- and large-scale natural disturbances in mountain spruce forests in Central Europe

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Abstract:	Although more frequent and severe natural disturbances are likely to increase as a result of climate change, we have little evidence of the disturbance severity effect on species diversity. We aimed to compare the effect of small- and large-scale natural disturbances on the bird species composition in the non-intervention area of Šumava National Park, CR. For this purpose, we surveyed bird communities in 1) small- and 2) large-scale disturbance, 3) enclaves of live trees in large-scale disturbance areas and 4) non-disturbed forests. Furthermore, we used habitat characteristic to determine structural factors affecting the species composition of bird communities. Birds were sampled using the point count method in breeding season 2021 and analysed using linear models (LMs). Additionally, we use the principal component analysis (PCA) to characterise habitat types using habitat characteristics. The most important habitat characteristics for bird communities are structural complexity, live tree density and understory cover. Small-scale disturbances increase the structural complexity of a forest and have a generally positive effect on birds. Both small- and large-scale disturbances supported species nesting on the ground and shrub layer. In contrast, large-scale disturbances negatively affected canopy nesting and specialist species. The likely reason is a reduction of small-scale habitat heterogeneity with increasing disturbance severity. High severity disturbance changes the structurally rich forests to rather uniform open-canopy habitats that are temporally unsuitable for closed canopy birds. On the other hand, low severity disturbance enhances large-scale habitat heterogeneity and maintains suitable habitat for species of closed canopy forest, including some specialist species.
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	Natural disturbances, Sustainable forest management

Dear Editors,

Natural disturbances are currently a much-discussed topic, especially in protected areas with non-intervention management, where they divide society into two opposite camps. The recent increasing frequency and magnitude of disturbances affect mountainous spruce forests but also spruce dominated monocultures of production forests. Understanding the ecology of natural disturbances that are suppressed in production forests is therefore important for further forest management planning practices and conservation of biodiversity in forests. For this purpose, birds were selected as a model group that well reflects current environmental conditions. Furthermore, we divided birds into nesting guilds and habitat specialization groups, which have very different requirements and indicate various environmental characteristics.

We chose your journal because the results of the research could be beneficial for the Forest Ecology and Management journal. The research deals with the issue of insect pests of forest stands associated with global climate change, management in forest stands of protected areas and conservation biology. The thematic suitability of the research also results from a significant number of cited articles from the Forest Ecology and Management journal.

Our results show that small-scale disturbances increase the heterogeneity of spruce forests and increase the diversity of many bird groups. In case of large-scale disturbances, the habitat is completely transformed which results in a loss of canopy nesting species common in non-disturbed closed forests. However, on the contrary, there are suitable conditions for open habitat and shrub layer species. When we compare small- and large-scale disturbances, we found lower total, generalists and ground or shrub nesting species abundance in large-scale disturbances. This suggests that large-scale disturbances are less suitable than small-scale. However, still provides suitable conditions for generalists and ground or shrub nesters compared to non-disturbed forests. Moreover, the remaining live mature trees in large-scale disturbances provide suitable conditions for canopy nesting and specialist species. Both magnitude levels disturbances brig valuable elements which are missing or in limited quantities in non-disturbed stands.

We declare the originality of the submitted research carried out by the listed authors. All authors agree with the contents of the manuscript and its submission to the Forest Ecology and Management journal. No part of the research has been published in any form elsewhere and the manuscript is not being considered for publication elsewhere while it is being considered for publication in the Forest Ecology and Management journal. All sources of funding are acknowledged in the manuscript.

Best regards

Dominik Kebrle

Highlights

Small-scale disturbances host higher total and generalist abundance than large-scale

Rest of mature trees in large-scale disturbances are refuge for closed canopy species

Ground/shrub nesters and generalists are disturbance winners, canopy nesters losers

Specialists react negatively to large- but more neutrally to small-scale disturbances

Bird response to small- and large-scale natural disturbances in mountain spruce forests in Central Europe

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KEYWORDS

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Abstract

Although more frequent and severe natural disturbances are likely to increase as a result of climate change, we have little evidence of the disturbance severity effect on species diversity. We aimed to compare the effect of small- and large-scale natural disturbances on the bird species composition in the non-intervention area of Šumava National Park, CR. For this purpose, we surveyed bird communities in 1) small- and 2) large-scale disturbance, 3) enclaves of live trees in large-scale disturbance areas and 4) non-disturbed forests. Furthermore, we used habitat characteristic to determine structural factors affecting the species composition of bird communities. Birds were sampled using the point count method in breeding season 2021 and analysed using linear models (LMs). Additionally, we use the principal component analysis (PCA) to characterise habitat types using habitat characteristics. The most important habitat characteristics for bird communities are structural complexity, live tree density and understory cover. Small-scale disturbances increase the structural complexity of a forest and have a generally positive effect on birds. Both small- and large-scale disturbances supported species nesting on the ground and shrub layer. In contrast, large-scale disturbances negatively affected canopy nesting and specialist species. The likely reason is a reduction of small-scale habitat heterogeneity with increasing disturbance severity. High severity disturbance changes the structurally rich forests to rather uniform open-canopy habitats that are temporally unsuitable for closed canopy birds. On the other hand, low severity disturbance enhances large-scale habitat heterogeneity and maintains suitable habitat for species of closed canopy forest, including some specialist species.

1 Introduction

Extreme weather events such as severe windstorms and drought are likely to increase in frequency globally as a result of climate change (Rahmstorf and Coumou, 2011). The canopy mortality increase in 35 European countries from 1985 to 2018 (Senf et al., 2021) and the wind and insect disturbances are ones of the main factors damaged forest in Central Europe (FOREST EUROPE, 2020). Considering these, the more frequent and severe bark beetle (*Ips typographus*) outbreaks, typically triggered by windstorms and supported by drought weakened trees will probably lead to high severity forest disturbances (FOREST EUROPE, 2020; Senf and Seidl, 2018). However, windstorms and bark beetle outbreaks are part of the natural cycle of mountain coniferous forests (Čada et al., 2016; Svoboda et al., 2012). These disturbances are important for many taxa, for example, beetles (Kozák et al., 2020), birds (Kortmann et al., 2018; Repel et al., 2020), fungi (Veselá et al., 2019) and lichens (Langbehn et al., 2021). Natural disturbances are a source of biological legacies such as snags, canopy openness, forest-floor deadwood, increase in shrub layer or ground disruption (Burris and Haney, 2005), which are key elements of forest structural complexity (Kozák et al., 2020). Windstorms usually cause tree stems to break or topple, while trees killed by bark beetle remain as standing deadwood. Deadwood is important for cavity nesting birds, bats and saproxylic insects (Bouvet et al., 2016; Saab et al., 2014; Scherzinger, 2006). However, dead stems are a particularly valuable habitat element for birds when they are standing upright (Augustynczik et al., 2019). Lying deadwood may still offer food for woodpeckers but does not serve as a resource for birds nesting in cavities (Mollet et al., 2013). Furthermore, the severity of the disturbance turns out to be a very important factor. The increasing disturbance severity increased the amount of dead wood (Kortmann et al., 2021), decreased the mean diameter of remaining trees and increased canopy openness (Peterson et al., 2013). Compared with non-disturbed forests, the light penetration in disturbances of similar severity is twice higher if disturbances are distributed and four times if are aggregated (Vogel et al., 2020). This increase in light close to the forest floor is associated with a warmer and drier microclimate in a forest (Thom et al., 2020). However, the exposure of the deadwood to the sun can be beneficial to the number of saproxylic insects or fungi (Vogel et al., 2020).

Forest disturbance events are usually classified based on the spatial extent, severity, and frequency into three broad categories, low-severity (gap-scale), moderate-severity, and catastrophic disturbance (Hart and Kleinman, 2018; Reyes et al., 2010). Low-severity natural disturbances in the closed forests should increase the abundance and richness of bird species, for example, foraging or nesting on bare ground (Fuller, 2000), insectivorous and cavity nesting (Przepióra et al., 2020). These disturbances, in the form of small gaps of a few trees killed by bark beetle or felled down by the wind in an otherwise healthy forest, can increase stand heterogeneity and significantly increase bird abundance in many stand types (Gharehaghaji et al., 2012; Lewandowski et al., 2021; Przepióra et al., 2020). Conversely, high-severity disturbances caused great changes in bird species composition (Kamp et al., 2020; Moning and Müller, 2008; Thorn et al., 2016b) with a decrease of canopy layer birds (Saab et al., 2014; Scherzinger, 2006). Additionally, in the high-severity disturbed forest, many bird species tended to be more abundant in areas less damaged by disturbance with remaining live trees (Kameniar et al., 2021).

The bird assemblage composition is changing continuously with the ongoing succession of disturbed forests (Scherzinger, 2006; Zmihorski, 2012). Moreover, the highest diversity is in the early and late successional stages (Hilmers et al., 2018). Generally, in the early succession stages most habitat specialized and threatened bird species appeared (Drapeau et al., 2000; Reif et al., 2013). However, other taxa may respond differently to the progressive succession of disturbed stands. For example, the number of red-listed lichen species increases with the increasing age of disturbance (Langbehn et al., 2021). In the case of birds, the assemblage composition changes every year and stop about 10 years after a high-severity disturbance event (Scherzinger, 2006).

With regard global climate change and the increasing frequency and severity of natural disturbances, there is a growing need to understand the ecological processes of these events. Many studies have found the importance of both, gap-level (Fuller, 2000; Przepióra et al., 2020) and high-severity disturbances (Scherzinger, 2006; Żmihorski, 2010). However, studies usually investigate each disturbance size type separately and generally found a positive effect of increasing disturbance size, especially for saproxylic insects (Kortmann et al., 2021), often reflecting increasing amounts of dead wood. Furthermore, the effect of disturbance size is sometimes in contrast for various species groups (Gharehaghaji et al., 2012). Here we compared small-scale (low-severity) and large-scale (high-severity) natural forest disturbances and compared them with non-disturbed stands. Moreover, we aimed to identify the critical structure attributes of disturbed forests and compared these attributes between various size disturbances and non-disturbed stands. For this purpose, we use birds as good bioindicators with a rapid response to environmental changes. The study is located in the non-intervention area of the Šumava National Park, which lies in the central part of the Bohemian Forest, historically affected by wind and bark beetle disturbances of various severity (Čada et al., 2016; Svoboda et al., 2012).

2 Material and methods

2.1 Study area and design

The study is located in Šumava National Park, which lies in the southwest of the Czech Republic, along the state border with Germany (Bavaria) and Austria in the central part of the Bohemian Forest. The Šumava NP together with the neighbouring Bavarian Forest National Park forms the largest cross-border protected area in Central Europe. The Šumava NP was established in 1991 and covers the app. 685 km^2. The study area is mainly forested by Norway spruce (*Picea abies* L. Karst), which replaced the original beech (*Fagus sylvatica)* and fir (*Abies alba* Mill.) in lower altitudes (Brůna et al., 2013). The highest peak of Šumava NP is Plechý 1 379 m a.s.l., the mean annual temperature varies from 3°C to 6°C and the mean annual precipitation between ca 1 000 and 1 400 mm $year^{-1}$ (Tolasz et al., 2007). Forests in the study area have been affected by several recent events in consecutive episodes. One of the most significant was the storm Kyrill in 2007, which caused large-scale windthrow mainly in the higher parts of the Šumava NP. One year after this storm, the bark beetle spread mainly around the forest damaged in the previous year, and the area of disturbances continued to increase until 2011 (Janík and Romportl, 2018). At present, the disturbed forest covered app. 25% of the total forested area of Šumava NP. The largest continuum of damaged forest area is located along the state border between apps 888 to 1 373 m a. s. l. and reaches up to 25 km in length (Fig. 1).

We located 48 sampling points in non-disturbed forest = NDF (766 to 1 231, mean 1 017 m a. s. l.) - mature stand with a predominance of vital tree cover. The proportion of disturbances in the area within the radius of 300 m from the sampling point does not generally exceeded 30% of the area. Furthermore, 37 points in small-scale (low- to moderate-severity) disturbed forest = SSD (818 to 1 188, mean 971 m a. s. l.) - damage of minor dimensions in the matrix of an otherwise healthy stand. The area of disturbance in the 300 m surrounding the sampling point does not generally exceeded <50% of the area. 34 points in large-scale (high-severity) disturbed forest = LSD (1 036 to 1 355, mean 1 201 m a. s. l.) - large areas of damaged stands, where the area of disturbance within 300 m around the sampling point usually exceeded >50% of the area. Additionally, we located 22 points to enclaves of living trees of various sizes lying in areas of large-scale disturbances = ELT (1 007 to 1 243, mean 1 140 m a. s. l.). An example of habitat types is shown in Fig. 2.

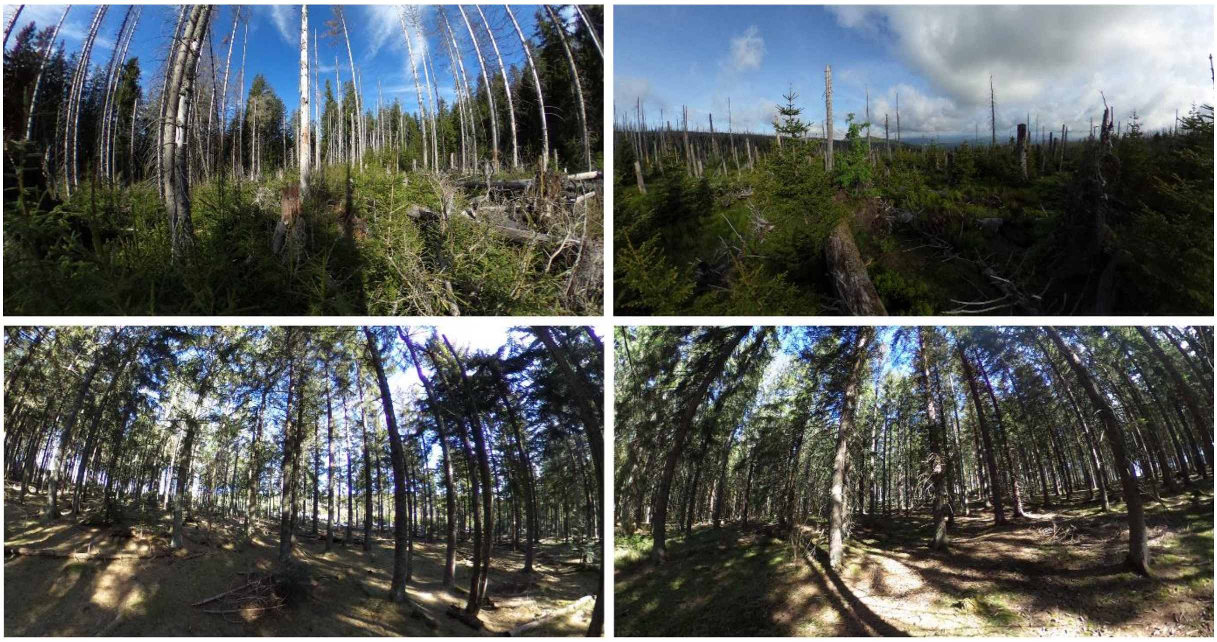

Fig. 2: Example of survey points in four different habitat types: “SSD” = “Small-scale disturbance” (top-left), “LSD” = “Large-scale disturbance” (top-right), “ELT” = “Enclaves of live trees in large-scale disturbance areas” (bottom-left) and “NDF” = “Non-disturbed forest” (bottom-right).

From 100 m surrounding of survey points, the proportion of disturbed forest was 93.9% for LSD (windthrow 22.9, bark beetle 55.2, salvage logging 15.8%), 62.4% for SSD (windthrow 4.4, bark beetle 40.9, salvage logging 17.1%), for ELT 42.1% (windthrow 1.7, bark beetle 20.6, salvage logging 19.8%), and for NDF 9.4% (windthrow 0.1, bark beetle 2.5, salvage logging 6.8%). Salvage logging in the study area was applied before 2007 in two regimes, with the retention of timber for thinning (40.1%) and clearing of all timber (59.9%). Additionally, plots located in SSDs and LSDs were covered by similarly aged disturbances. In total, 141 plots were selected across Šumava NP. Each of the plots was spaced at least 300 m apart and at least 100 m from the nearest road to avoid the edge effect (Šálek et al., 2010). Additionally, we studied disturbances in the spruce forests. Therefore, we avoided the broadleaved stands and scattered old broadleaved trees which may affect bird numbers in spruce stands (Kebrle et al., 2021).

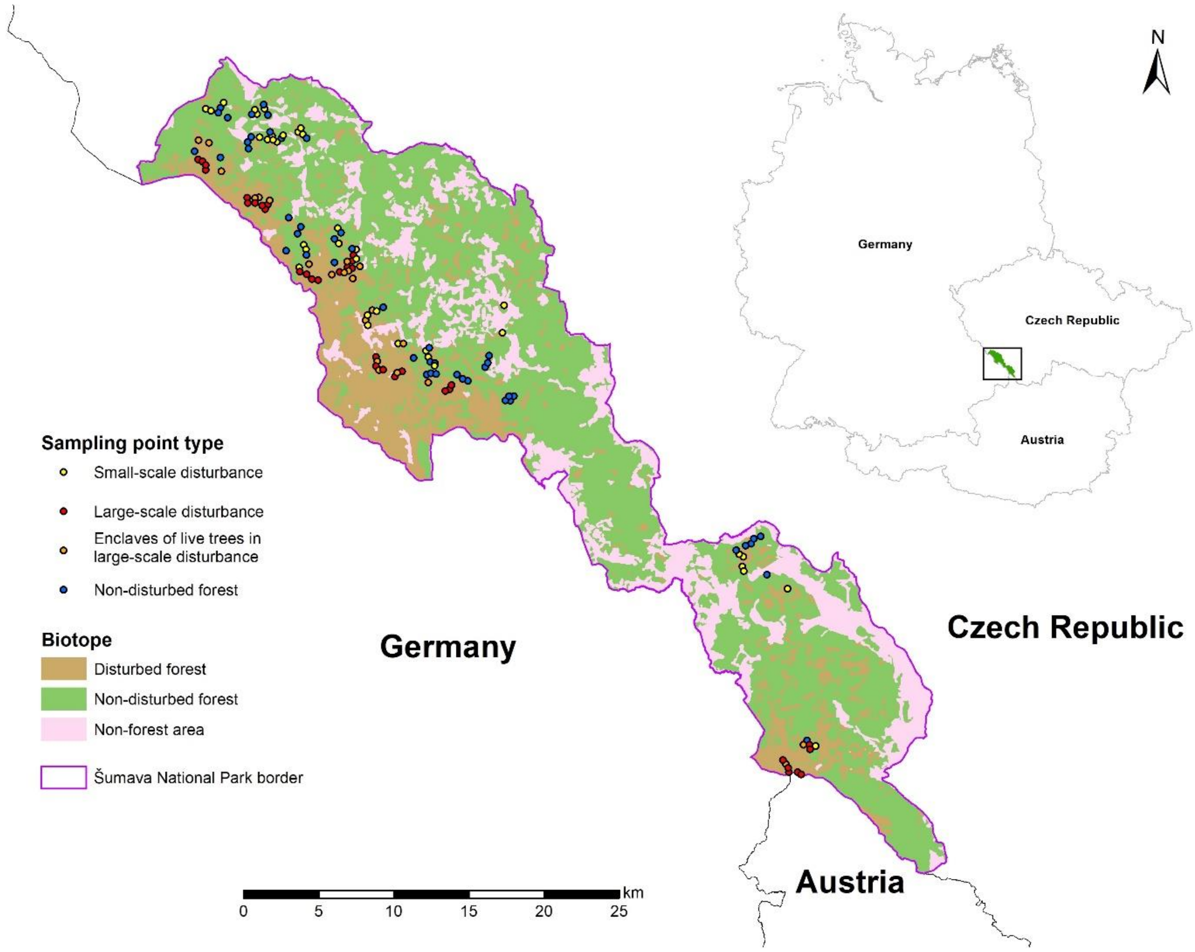

Fig. 1: Location of the study area and localization of sampling points in 4 different habitat types.

2.2 Bird survey

Bird survey was carried out in 2021 by the point count method (Bibby et al. 2000). Each point was surveyed twice the year, in April-May for early nesters and May-June for late nesters (Bouvet et al., 2016). Intervals between consecutive visits exceeded two weeks. Surveys were conducted within 4 h of sunrise and were restricted to good weather conditions (Bibby et al., 2000). All individuals heard or seen within 50 m of the survey point were recorded. Owls and raptors (<0.1% of the birds recorded) were excluded from our analyses as the point count method is inappropriate for them (Bouvet et al., 2016).

Bird species were classified into three nesting guilds [1) cavity, 2) canopy and 3) ground or shrub nesters] according to national literature (Šťastný and Hudec, 2011). We also classified bird species according to the threat status listed in the Red List of the Czech Republic (Chobot and Němec, 2017) as Red List species. Furthermore, we adopted the attributes regarding bird species habitat specialization (generalist and specialist species) relevant in the CZ as reported by (Reif et al., 2010). Additionally, we used a species rarity index showing the scarcity of each species. The index was calculated based on large-scale quadrat mapping of birds across the CR during 2014 to 2017 (Šťastný et al., 2021) using the calculation method according to the Šálek (2012).

2.3 Spatial and environmental variables

We used four habitat types (1. NDF = non-disturbed forest, 2. SSD = small-scaled disturbance, 3. ELT = enclave of living trees in large-scale disturbance and 4. LSD = large-scale disturbance) to assess effect of various severity disturbances. To describe habitat characteristics, we used digitized forest cover layer (current as of autumn 2020) to analyse proportion of windfalls and total biological legacy (all stands disturbed by bark beetle or wind). Furthermore, we used LiDAR (Light Detection and Ranging) derived individual tree detection layer (ITD) to determine live tree density, and digital elevation model (DEM) to extract the elevation of the survey point. ITD layer was current for 2017, therefore newly dead trees as of 2020 were updated according to the current digitization layer and aerial photographs. Digitized forest cover layer and LiDAR derived data were provided by the administration of the Šumava NP. All analyses were done in 100 m surrounding of survey points using a geographic information system (ArcGIS 10.4). Additionally, we took a 360° field of view picture using a spherical camera (RICOH Theta S) at a representative location of each survey point. Using these pictures, we estimated understory cover (%) represents rejuvenation and bushes from 0.5 to 4 m of high, and forest stand structural complexity. Structural complexity was based on the occurrence of large live trees, standing dead trees or snags, laying deadwood or uproot trees, and spruce regeneration within 50 m surrounding. All survey points were evaluated by the same person using a 10-point scale, with 1 indicating very low and 10 very high complexity (Fig. 3).

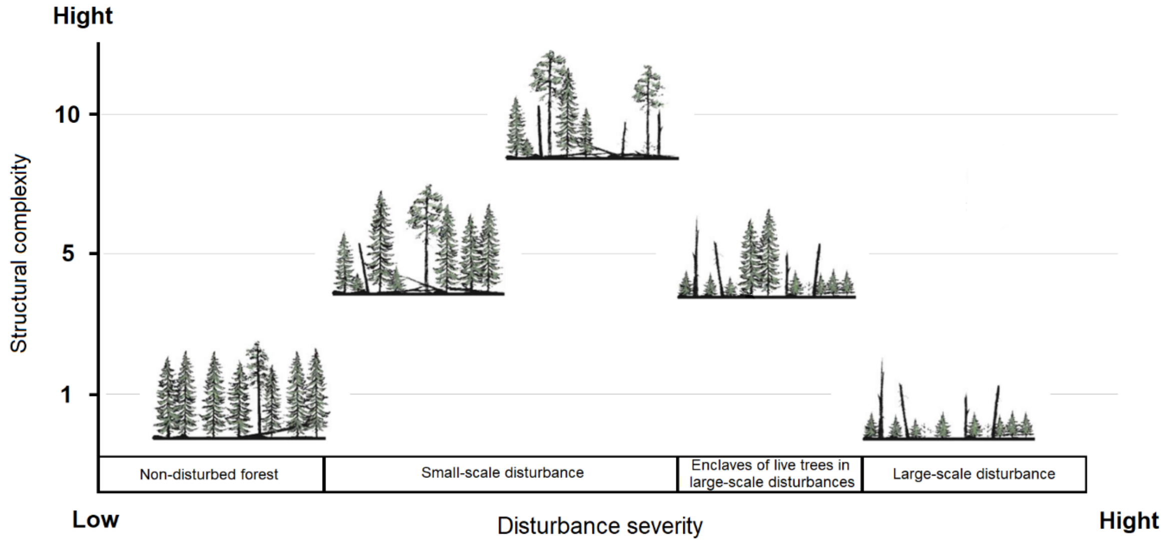

Fig. 3: Schematic representation of forest stand structural complexity classification (a 10-point scale, with 1 indicating very low complexity = homogeneous habitat with a low richness of structural objects and 10 indicating very high complexity = both live and dead standing trees, snags, lying dead wood and undergrowth present) and disturbance severity scale with the corresponding classified habitat types (1. non-disturbed forest, 2. small-scaled disturbance, 3. enclaves of living trees in large-scale disturbances and 4. large-scale disturbance). Schemes of forest cohorts were adopted from Kuuluvainen (2016) and modified.

2.4 Statistical analysis

To assess the effect of disturbance type on the species richness, abundance, and conservation status, we used linear models with species richness/abundance as a response, habitat type as a categorical predictor, and elevation as a covariate. Elevation was included to control for a possible effect of an uneven altitudinal distribution of habitat types. We fitted a separate model for the following categories of species: all species; specialists; generalists; canopy nesters; cavity nesters; ground/shrub nesters; Red List species and Rarity index. In combination with either species richness or abundance, this resulted in 14 separate models, to which we added another model with species rarity index as a response. Although for responses like richness or abundance, the natural choice of model would be Poisson GLM, we found linear models to be performing better for our data (lower AIC), with diagnostic plots showing good parameters, and hence we adopted them (the same applies for all linear models we fitted in this study).

To assess the effect of more specific habitat characteristics on the species richness, abundance, and conservation status (Red List species and Rarity index), we fitted other 15 linear models with the same responses as previously, but with the following candidate predictors: elevation (m a. s. l.); structural complexity (score 1 - 10); live trees density (trees/ha); understory cover (%); biological legacy cover (%); and windfalls cover (%). Because the biological legacy cover was highly correlated with the live tree density (r = -0.89), and windfalls cover showed a medium correlation with understory cover (r = 0.51), we excluded these two variables from the list of candidate predictors. For each model, we then performed a backward model selection based on AIC (function step in R).

Finally, we tried to characterise the four habitat types using the habitat characteristics listed in the previous paragraph. First, we performed the principal component analysis (PCA) with all the habitat characteristics (rescaled to a common scale) and displayed the observations from different disturbance types in the principal component space [package factoextra in R; (Kassambara and Mundt, 2020)]. Then, we used random forest classification (package ranger in R; (Wright and Ziegler, 2017) to see the level to which the habitat characteristics can be used as predictors of habitat type. The classification was performed separately with the original habitat variables and with the PCA variables, each time using 500 classification trees, with variable importance assessed using the impurity measure, and with otherwise default settings. For each habitat type, the classification performance was assessed by sensitivity (i.e., the fraction of true presences that were correctly identified), specificity (i.e., the fraction of true absences that were correctly identified), and balanced accuracy (i.e., the average of sensitivity and specificity), using package caret for R (Kuhn, 2022).

All statistical analysis was done using R statistical software version 4.1.2(R Core Team, 2021). The plots were produced by package ggplot2 (Wickham, 2016). Data and code of the analysis are available at https://github.com/vojta-bartak/Disturbance.

3 Results

In total, we recorded 40 bird species and 1 543 individuals of which were 23 generalists (1 026), 17 specialists (517); 14 canopy nesting (504), 12 cavity nesting (359), 12 ground or shrub nesting (675) and 2 unclassified (5) (nesting parasite *Cuculus canorus* and non-nesting in CZ *Fringilla montifringilla*). We recorded six red-listed species: *Tetrao urogallus* (CR; 6 individuals), *Picoides tridactylus* (EN; 13), *Turdus torquatus* (EN; 4), *Tetrastes bonasia* (VU; 8), *Nucifraga caryocatactes* (VU; 1) and *Acanthis flammea* (NT; 1).

3.1 Effect of habitat type on the species richness, abundance and conservation status

Generally, we found a positive effect of small-scale disturbance (SSD) on species richness and abundance of bird communities, whereas non-disturbed closed-canopy forests (NDF) and enclaves of alive trees in disturbed areas (ELT) had species poorer and less abundant bird communities (Table S3 and Fig. 4). The richness of generalist species was significantly higher in both types of disturbed forest (SSD and LSD) compared to NDF while the abundance of generalist species was significantly higher in SSD compared to all other classes. Conversely, we found significantly lower species richness and abundance of specialist species in LSD compared to NDF and ELT. The richness and abundance of canopy nesting birds were reduced in habitats subjected to large-scale disturbance (LSD) both disturbance types (SSD and LSD) supported ground/shrub nesting birds. Occurrences of red-listed species were scarce and the models provided only non-significant results (also for rarity index).

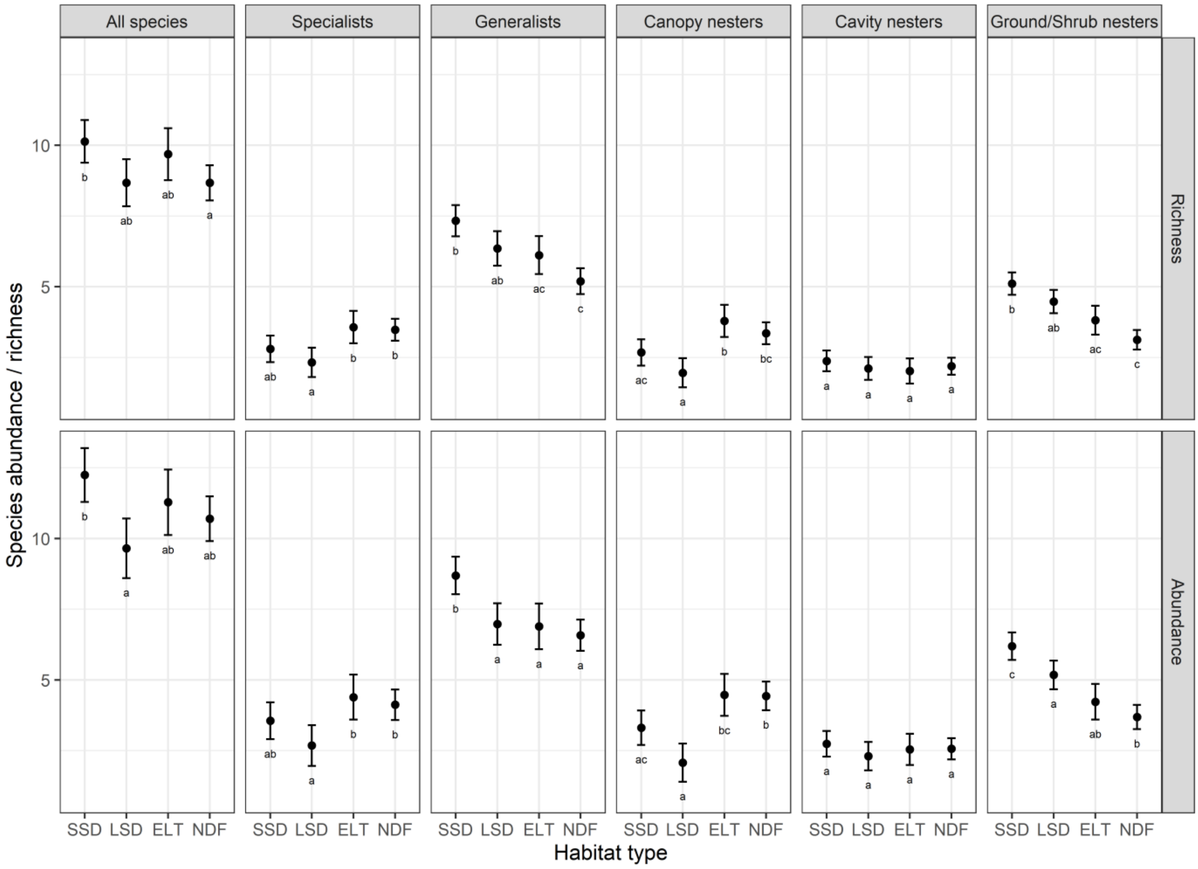

Fig. 4. Effect of habitat type on species richness/abundance for different groups of bird species, estimated by linear models. “SSD”, “LSD”, “NDF”, and “ELT” stand for “Small-scale disturbance”, “Large-scale disturbance”, “Non-disturbed forest”, and “Enclaves of live trees in large-scale disturbance areas”, respectively. The points and whiskers represent the predicted mean together with 95% confidence intervals.

3.2 Effect of habitat characteristics on the species richness and abundance

Structural variables combined in PCA explained well the habitat type differences, with the first four principal components explaining 93.7% of the variance (Fig. S1). The highest contribution (over 35%) showed biological legacy, live tree density (20%) and elevation (18%), see Table S5 and Fig. S2.

Using LMs, structural complexity, live tree density, understory cover and elevation were the only significant predictors of bird species richness and abundance (Fig. 5 and Fig. 6). Structural complexity had a positive effect on the richness and abundance of all bird species, generalists and cavity nesters and also the abundance of specialists. Live tree density had a significant positive effect on total abundance, specialists and canopy nesters abundance and richness while a negative effect on ground/shrub nesting species. The understory cover had significant positive effect on generalists and ground/shrub nesting species. Additionally, elevation negatively affected the richness and abundance of the bird communities.

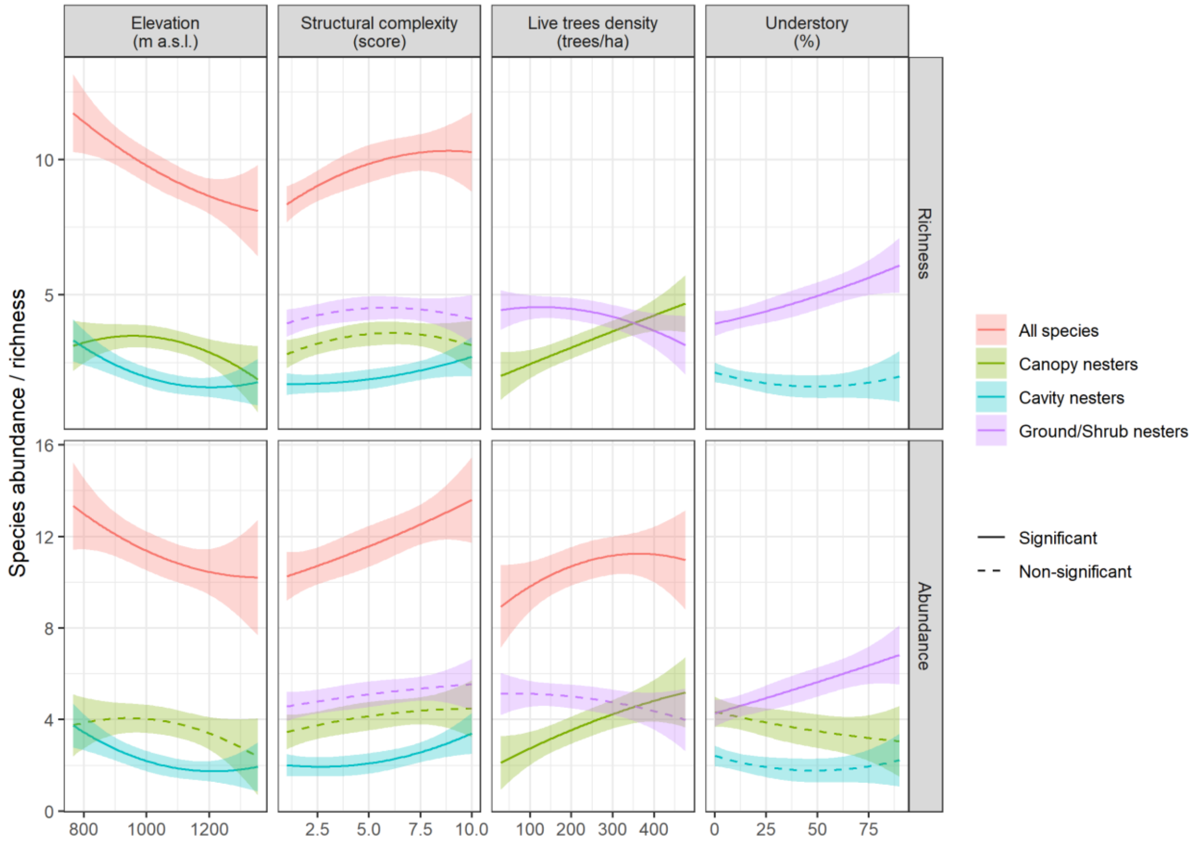

Fig. 5. Effects of elevation, structural complexity, live tree density, and proportion of understory on the species richness and abundance of all bird species as well as specific nesting guilds, estimated by linear models. Quadratic relationships were considered for all model terms.

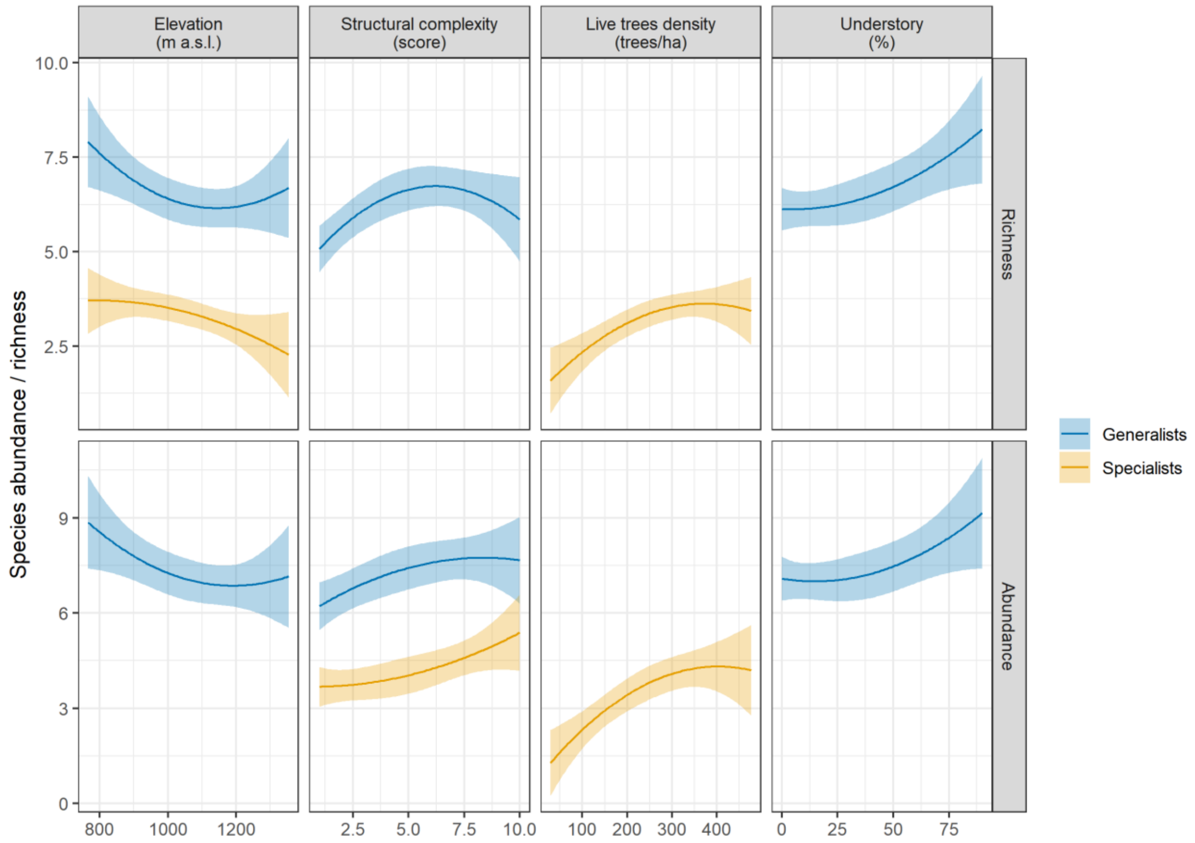

Fig. 6. Effects of elevation, structural complexity, live tree density, and proportion of understory cover on the species richness and abundance of all bird species as well as generalists and specialists, estimated by linear models. Quadratic relationships were considered for all model terms. Only significant effects are displayed.

4 Discussion

4.1 Effect of disturbances and habitat characteristics on bird communities

In this study, we documented the generally positive effect of disturbance on species richness and abundance of bird communities, ground/shrub nesters, and particularly generalist birds. Generalists are linked to more diverse habitats (Devictor et al., 2008b; Richmond et al., 2005), with high structural complexity that represents small-scale disturbances in our study. In general, with habitat heterogeneity increases the number of different microhabitats (Tews et al., 2004) which is reflected by the high number of species. However, quite equally low abundances between LSD, ELT and NDF, indicating that in large-scale disturbances, generalist species, although higher in the number of species, are not more abundant than in the non-disturbed forests. A positive effect of small gaps on total bird richness found also Gharehaghaji et al., (2012), for species nesting on the ground Fuller (2000) and also on cavity-nesting species (Przepióra et al., 2020). However, the cavity nesting birds surprisingly did not differ between habitat types in our study, which was found also in the Bavarian forest (Thorn et al., 2016b). Possible explanations could be the large territory of some cavity nesting species (e.g. *Picoides tridactylus* or *Dendrocopos major*) including surrounding stands with sufficient occurrence of dead trees and thus nesting opportunities. The second possible explanation is the higher age of the large proportion of disturbances (more than 10 years) which are now in the advanced succession stage defined by the complete decay of the dead trees (only broken tree trunks remained standing). Birds may prefer deadwood in specific decay stages. For example, the *Picoides tridactylus* mainly profit from trees freshly infested with bark beetle and its abundance decreases again once the desiccation of trees (Scherzinger, 2006; Zielewska-Büttner et al., 2018). Additionally, cavity nesting birds can use dead trees for nesting if are staying upright (Augustynczik et al., 2019; Mollet et al., 2013). Interestingly, cavity-nesting birds show a positive association with structural complexity, although the numbers of these species did not differ between four habitat types. They are probably also influenced by disturbances, including the very small ones, which increased habitat heterogeneity even in non-disturbed forest stands.

Conversely, the negative effect of large-scale disturbances was found for canopy nesters and habitat specialists. As expected, canopy nesting birds (and also specialists) closely coincided with live tree density. This reflected the very strong association (specialism) of these species to the living tree layer (Benedetti et al., 2022). The decrease of canopy nesting birds in LSD correspond with a finding of other authors (Scherzinger, 2006; Thorn et al., 2016b). On the other hand, small-scale disturbance in otherwise non-disturbed closed canopy forests had a positive effect on canopy nesting birds in most studies (Fuller, 2000; Gharehaghaji et al., 2012; Lewandowski et al., 2021; Przepióra et al., 2020). In our case, the negative effect on canopy nesting species may be due to the relatively large size of small-scale disturbances, which follows from its definition (disturbed areas in matrices of non-disturbed with non-limited size). In the case of enclaves of live trees in large-scale disturbances, we assumed that these stands would be inhabited by species associated with the surrounding disturbed areas and enriched with species of live canopy layer. Also, other studies found that in high-severity disturbances many bird species are more abundant in forests less damaged by disturbance (Kameniar et al., 2021). However, the richness and abundance between enclaves of live trees and non-disturbed stands were quite similar for most of the guilds, including canopy nesting species. This suggests that these rests of live forests in large areas of disturbed stands are still sufficient for typically closed forest birds probably due to their relatively large size (the minimum size was defined by 50 m surrounding for bird census). Moreover, the interior of these plots is similar to non-disturbed stands (low amount of understory and high density of live trees), and are still not suitable for species of open habitats and shrub layers. For example, the ground/shrub nesting species showed similarly lowest and conversely canopy nesting and habitat specialized bird highest occurrences in NDF and ELT.

Habitat specialists inhabit narrow niche ranges and utilize limited habitat resources and thus are more likely to be susceptible to extinction (Devictor et al., 2008b; Richmond et al., 2005). Consequently, species with higher levels of specialization had more negative population trends in Europe (Morelli et al., 2020, Gregory et al. 2007) and may be more susceptible to habitat fragmentation and disturbance (Devictor et al., 2008b; Devictor and Robert, 2009; Terraube et al., 2016). Disturbances generally caused a shift in habitat specialisation from specialised to more generalised assemblages (Devictor et al., 2008a). Moreover, specialised bird species tend to become more generalist over time, which leads to functional homogenization of bird community (Barnagaud et al., 2011). Our results support a negative effect of large-scale disturbances on specialists. On the other hand, we did not find a significant negative effect of small-scale disturbances on specialists and the specialist species numbers in enclaves of live trees in large-scale disturbed areas are quite similar to in the non-disturbed forest. This suggests that the negative disturbance effect on specialist is modulated by disturbance severity and a number of survived mature trees.

4.2 The spatial aspect of the disturbance effect on bird communities

In comparison with small-scale, large-scale disturbances correspond more with high values of wind-felled trees. From total disturbed forest by Kyrill and bark beetle outbreaks, the rate of forest damaged by wind is app. 10% in small- and app. 30% in large-scale disturbances. Large-scale disturbances are located primarily in higher elevations where are unfavourable weather conditions and less productive soils (Fuller, 2008). Considering these, the cover and growth of seedlings in large-scale disturbances may be lower than in small-scale disturbances where rejuvenation is protected by surrounding trees. Moreover, the occurred live trees can be seed source for recolonization of disturbed areas (Seidl et al., 2014).

The forest structure is quite similar in non-disturbed forests (NDF) and enclaves of live trees in large-scale disturbances (ELT). Although ELT represents blocks of uniform forest stand with low small-scale heterogeneity, they considerably enhance heterogeneity at the landscape level. The landscape perspective is also ecologically important (Mikoláš et al., 2021) but it is beyond the scope of our study.

4.3 The temporal aspect of the disturbance effect on bird communities

The composition of many taxa is changing continuously with time since the disturbance event (Thorn et al., 2016a) and the differences between disturbed and non-disturbed stands may become more significant over time (Thorn et al., 2016b). The bird assemblage composition changes every year and the species turnover reach its saturation about 10 years after the disturbance event (Scherzinger, 2006). In the early years species richness is quite similar between disturbed and non-disturbed forests (Repel et al., 2020). However, after app. 5-10 years, the species richness increase and the difference between disturbed and non-disturbed forests is well-marked in favour of the non-disturbed plots (Repel et al., 2020; Thorn et al., 2016b). In our study, the damaged forest stands were in most cases more than 10 years after the disturbance event (from 100 m surrounding 67% for SSD and 81% for LSD). Hence, we suppose that species composition and abundances in our study reflect well the effect of disturbances on the bird communities at the local scale. Moreover, there are rare species for which a certain stage of succession is more important. For example, fresh bark beetle infestation stage for *Picoides tridactylus* (Zielewska-Büttner et al., 2018) or 10 to 15 years after disturbance for *Tetrao urogallus* and *Tetrastes bonasia* (Kortmann et al., 2018).

5 Conclusion

The monitoring of bird communities in mountain spruce forests affected by small- and large-scale natural disturbances revealed the guild-specific effect and identified key structural elements for bird communities. Natural disturbances were characterised by a high proportion of biological legacies of disturbances (e. g. lying dead wood, standing dead trees, and uprooted trees). Especially small-scale disturbances were followed by high values of structural complexity and understory cover at the local scale. Structural complexity was important for most bird guilds studied (except ground and shrub nesting species), with a generally positive effect. Furthermore, live tree density had a positive effect on the canopy and conversely a negative on ground and shrub nesting species. Disturbances (regardless of intensity) generally supported the ground or shrub nesting species and habitat generalists (disturbance winners). In contrast, large-scale disturbances had a negative effect on canopy nesting species and habitat specialists (disturbance losers). However, even enclaves of remnant living stands in large-scale disturbances may provide refuge for closed canopy species and thus maintain a still high diversity at a wider spatial scale. When we compared small- and large-scale disturbances, we found a higher abundance of all species, generalists and ground or shrub nesters in small-scale disturbances. Moreover, habitat specialists were relatively tolerant to small- compared to large-scale disturbances. Increasing frequency of small-scale disturbances likely had a generally positive effect due to the increasing heterogeneity of forest stands. The increasing severity of natural disturbances completely changes the habitat and causes local loss of typically closed forest species. On the other hand, lower severity of disturbances maintains suitable habitat even for forest specialists.

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6 References

Augustynczik, A.L.D., Asbeck, T., Basile, M., Bauhus, J., Storch, I., Mikusiński, G., Yousefpour, R., Hanewinkel, M., 2019. Diversification of forest management regimes secures tree microhabitats and bird abundance under climate change. Sci. Total Environ. 650, 2717–2730. https://doi.org/10.1016/j.scitotenv.2018.09.366

Barnagaud, J.Y., Devictor, V., Jiguet, F., Archaux, F., 2011. When species become generalists: on-going large-scale changes in bird habitat specialization. Glob. Ecol. Biogeogr. 20, 630–640. https://doi.org/10.1111/j.1466-8238.2010.00629.x

Benedetti, Y., Morelli, F., Callaghan, C.T., Fuller, R., 2022. Distribution and protection of avian specialization in Europe. Glob. Ecol. Biogeogr. 31, 10–24. https://doi.org/10.1111/geb.13405

Bibby, C.J., Burgess, N.D., Hill, D.A., Mustoe, S.H., 2000. Bird Census Techniques, 2. ed.

Bouvet, A., Paillet, Y., Archaux, F., Tillon, L., Denis, P., Gilg, O., Gosselin, F., 2016. Effects of forest structure, management and landscape on bird and bat communities. Environ. Conserv. 43, 148–160. https://doi.org/10.1017/S0376892915000363

Brůna, J., Wild, J., Svoboda, M., Heurich, M., Müllerová, J., 2013. Impacts and underlying factors of landscape-scale, historical disturbance of mountain forest identified using archival documents. For. Ecol. Manage. 305, 294–306. https://doi.org/10.1016/j.foreco.2013.06.017

Burris, J.M., Haney, A.W., 2005. Bird communities after blowdown in a late-successional Great Lakes spruce-fir forest. Wilson Bull. 117, 341–352. https://doi.org/10.1676/04-104.1

Čada, V., Morrissey, R.C., Michalová, Z., Bače, R., Janda, P., Svoboda, M., 2016. Frequent severe natural disturbances and non-equilibrium landscape dynamics shaped the mountain spruce forest in central Europe. For. Ecol. Manage. 363, 169–178. https://doi.org/10.1016/j.foreco.2015.12.023

Chobot, K., Němec, M. (Eds.), 2017. Red List of Threatened Species of the Czech Republic. Vertebrates., 34th ed. Příroda, PRAHA.

Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A., Couvet, D., 2008a. Functional biotic homogenization of bird communities in disturbed landscapes. Glob. Ecol. Biogeogr. 17, 252–261. https://doi.org/10.1111/j.1466-8238.2007.00364.x

Devictor, V., Julliard, R., Jiguet, F., 2008b. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 0, 080211051304426–0. https://doi.org/10.1111/j.2008.0030-1299.16215.x

Devictor, V., Robert, A., 2009. Measuring community responses to large-scale disturbance in conservation biogeography. Divers. Distrib. 15, 122–130. https://doi.org/10.1111/j.1472-4642.2008.00510.x

Drapeau, P., Leduc, A., Giroux, J., Savard, J.L., Vickery, W.L., 2000. Landscape-Scale Disturbances and Changes in Bird Communities of Boreal Mixed-Wood Forests Bergeron and William L . Vickery Published by : Wiley on behalf of the Ecological Society of America Stable URL : http://www.jstor.org/stable/2657210 JSTOR is a not- 70, 423–444. https://doi.org/Doi 10.1021/Ct3004645

FOREST EUROPE, 2020. State of Europe’s Forests 2020. Ministerial Conference on the Protection of Forests in Europe FOREST, Liaison Unit Bratislava.

Fuller, R.J., 2008. Bird Life of Woodland and Forest. Cambridge University Press.

Fuller, R.J., 2000. Influence of Treefall Gaps on Distributions of Breeding Birds within Interior Old-Growth Stands in Białowieża Forest, Poland. Condor 102, 267–274. https://doi.org/10.2307/1369637

Gharehaghaji, M., Shabani, A.A., Feghhi, J., Danehkar, A., Kaboli, M., Ashrafi, S., 2012. Effects of landscape context on bird species abundance of tree fall gaps in a temperate deciduous forest of Northern Iran. For. Ecol. Manage. 267, 182–189. https://doi.org/10.1016/j.foreco.2011.12.001

Hart, J.L., Kleinman, J.S., 2018. What are intermediate-severity forest disturbances and why are they important? Forests 9. https://doi.org/10.3390/f9090579

Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., Müller, J., 2018. Biodiversity along temperate forest succession. J. Appl. Ecol. 55, 2756–2766. https://doi.org/10.1111/1365-2664.13238

Hlásny, T., König, L., Krokene, P., Lindner, M., Montagné-Huck, C., Müller, J., Qin, H., Raffa, K.F., Schelhaas, M.-J., Svoboda, M., Viiri, H., Seidl, R., 2021. Bark beetle outbreaks in Europe: State of knowledge and ways forward for management. Curr. For. Reports - Accept. Manuscr.

Janík, T., Romportl, D., 2018. Recent land cover change after the Kyrill windstorm in the Šumava NP. Appl. Geogr. 97, 196–211. https://doi.org/10.1016/j.apgeog.2018.06.006

Kameniar, O., Baláž, M., Svitok, M., Reif, J., Mikoláš, M., Pettit, J.L., Keeton, W.S., Pettit, J.M., Vostarek, O., Langbehn, T., Trotsiuk, V., Morelli, F., Frankovič, M., Kozák, D., Janda, P., Čada, V., Ferenčík, M., Málek, J., Begovič, K.,... Svoboda, M., 2021. Historical natural disturbances shape spruce primary forest structure and indirectly influence bird assemblage composition. For. Ecol. Manage. 481. https://doi.org/10.1016/j.foreco.2020.118647

Kamp, J., Trappe, J., Dübbers, L., Funke, S., 2020. Impacts of windstorm-induced forest loss and variable reforestation on bird communities. For. Ecol. Manage. 478, 118504. https://doi.org/10.1016/j.foreco.2020.118504

Kassambara, A., Mundt, F., 2020. factoextra: Extract and Visualize the Results of Multivariate Data Analyses.

Kebrle, D., Zasadil, P., Hošek, J., Barták, V., Šťastný, K., 2021. Large trees as a key factor for bird diversity in spruce-dominated production forests: Implications for conservation management. For. Ecol. Manage. 496. https://doi.org/10.1016/j.foreco.2021.119460

Kortmann, M., Heurich, M., Latifi, H., Rösner, S., Seidl, R., Müller, J., Thorn, S., 2018. Forest structure following natural disturbances and early succession provides habitat for two avian flagship species, capercaillie (Tetrao urogallus) and hazel grouse (Tetrastes bonasia). Biol. Conserv. 226, 81–91. https://doi.org/10.1016/j.biocon.2018.07.014

Kortmann, M., Müller, J.C., Baier, R., Bässler, C., Buse, J., Cholewińska, O., Förschler, M.I., Georgiev, K.B., Hilszczański, J., Jaroszewicz, B., Jaworski, T., Kaufmann, S., Kuijper, D., Lorz, J., Lotz, A., Łubek, A., Mayer, M., Mayerhofer, S., Meyer, S.,... Thorn, S., 2021. Ecology versus society: Impacts of bark beetle infestations on biodiversity and restorativeness in protected areas of Central Europe. Biol. Conserv. 254. https://doi.org/10.1016/j.biocon.2020.108931

Kozák, D., Svitok, M., Wiezik, M., Mikoláš, M., Thorn, S., Buechling, A., Hofmeister, J., Matula, R., Trotsiuk, V., Bače, R., Begovič, K., Čada, V., Dušátko, M., Frankovič, M., Horák, J., Janda, P., Kameniar, O., Nagel, T.A., Pettit,... Svoboda, M., 2020. Historical Disturbances Determine Current Taxonomic, Functional and Phylogenetic Diversity of Saproxylic Beetle Communities in Temperate Primary Forests. Ecosystems. https://doi.org/10.1007/s10021-020-00502-x

Kuhn, M., 2022. caret: Classification and Regression Training.

Kuuluvainen, T., 2016. Conceptual models of forest dynamics in environmental education and management: keep it as simple as possible, but no simpler. For. Ecosyst. 3. https://doi.org/10.1186/s40663-016-0075-6

Langbehn, T., Hofmeister, J., Svitok, M., Mikoláš, M., Matula, R., Halda, J., Svobodová, K., Pouska, V., Kameniar, O., Kozák, D., Janda, P., Čada, V., Bače, R., Frankovič, M., Vostarek, O., Gloor, R., Svoboda, M., 2021. The impact of natural disturbance dynamics on lichen diversity and composition in primary mountain spruce forests. J. Veg. Sci. 32, 0–11. https://doi.org/10.1111/jvs.13087

Lewandowski, P., Przepióra, F., Ciach, M., 2021. Single dead trees matter: Small-scale canopy gaps increase the species richness, diversity and abundance of birds breeding in a temperate deciduous forest. For. Ecol. Manage. 481. https://doi.org/10.1016/j.foreco.2020.118693

Meigs, G.W., Morrissey, R.C., Bače, R., Chaskovskyy, O., Čada, V., Després, T., Donato, D.C., Janda, P., Lábusová, J., Seedre, M., Mikoláš, M., Nagel, T.A., Schurman, J.S., Synek, M., Teodosiu, M., Trotsiuk, V., Vítková, L., Svoboda, M., 2017. More ways than one: Mixed-severity disturbance regimes foster structural complexity via multiple developmental pathways. For. Ecol. Manage. 406, 410–426. https://doi.org/10.1016/j.foreco.2017.07.051

Mikoláš, M., Svitok, M., Bače, R., Meigs, G.W., Keeton, W.S., Keith, H., Buechling, A., Trotsiuk, V., Kozák, D., Bollmann, K., Begovič, K., Čada, V., Chaskovskyy, O., Ralhan, D., Dušátko, M., Ferenčík, M., Frankovič, M., Gloor, R., Hofmeister, J.,... Svoboda, M., 2021. Natural disturbance impacts on trade-offs and co-benefits of forest biodiversity and carbon. Proc. R. Soc. B Biol. Sci. 288. https://doi.org/10.1098/rspb.2021.1631

Mollet, P., Birrer, S., Pasinelli, G., 2013. Forest birds and their habitat requirements, in: Kraus, D., Krumm, F. (Eds.), Integrative Approaches as an Opportunity for the Conservation of Forest Biodiversity. European Forest Institute, p. 284.

Moning, C., Müller, J., 2008. Environmental key factors and their thresholds for the avifauna of temperate montane forests. For. Ecol. Manage. 256, 1198–1208. https://doi.org/10.1016/j.foreco.2008.06.018

Morelli, F., Benedetti, Y., Callaghan, C.T., 2020. Ecological specialization and population trends in European breeding birds. Glob. Ecol. Conserv. 22, e00996. https://doi.org/10.1016/j.gecco.2020.e00996

Peterson, C.J., Krueger, L.M., Royo, A.A., Stark, S., Carson, W.P., 2013. Disturbance size and severity covary in small and mid-size wind disturbances in Pennsylvania northern hardwoods forests. For. Ecol. Manage. 302, 273–279. https://doi.org/10.1016/j.foreco.2013.03.045

Przepióra, F., Loch, J., Ciach, M., 2020. Bark beetle infestation spots as biodiversity hotspots: Canopy gaps resulting from insect outbreaks enhance the species richness, diversity and abundance of birds breeding in coniferous forests. For. Ecol. Manage. 473. https://doi.org/10.1016/j.foreco.2020.118280

R Core Team, 2021. R: A language and environment for statistical computing.

Rahmstorf, S., Coumou, D., 2011. Increase of extreme events in a warming world. PNAS 108, 17905–17909. https://doi.org/10.1073/pnas.1201491109

Reif, J., Jiguet, F., Šťastný, K., 2010. Habitat specialization of birds in the Czech Republic: Comparison of objective measures with expert opinion. Bird Study 57, 197–212. https://doi.org/10.1080/00063650903477046

Reif, J., Marhoul, P., Koptík, J., 2013. Bird communities in habitats along a successional gradient: Divergent patterns of species richness, specialization and threat. Basic Appl. Ecol. 14, 423–431. https://doi.org/10.1016/j.baae.2013.05.007

Repel, M., Zámečník, M., Jarčuška, B., 2020. Temporal changes in bird communities of wind-affected coniferous mountain forest in differently disturbed stands (High Tatra Mts., Slovakia). Biologia (Bratisl). 75, 1931–1943. https://doi.org/10.2478/s11756-020-00455-5

Reyes, G.P., Kneeshaw, D., De Grandpré, L., Leduc, A., 2010. Changes in woody vegetation abundance and diversity after natural disturbances causing different levels of mortality. J. Veg. Sci. 21, 406–417. https://doi.org/10.1111/j.1654-1103.2009.01152.x

Richmond, C.E., Breitburg, D.L., Rose, K.A., 2005. The role of environmental generalist species in ecosystem function. Ecol. Modell. 188, 279–295. https://doi.org/10.1016/j.ecolmodel.2005.03.002

Saab, V.A., Latif, Q.S., Rowland, M.M., Johnson, T.N., Chalfoun, A.D., Buskirk, S.W., Heyward, J.E., Dresser, M.A., 2014. Ecological consequences of mountain pine beetle outbreaks for wildlife in Western North American forests. For. Sci. 60, 539–559. https://doi.org/10.5849/forsci.13-022

Šálek, M., 2012. Spontaneous succession on opencast mining sites: Implications for bird biodiversity. J. Appl. Ecol. 49, 1417–1425. https://doi.org/10.1111/j.1365-2664.2012.02215.x

Šálek, M., Svobodová, J., Zasadil, P., 2010. Edge effect of low-traffic forest roads on bird communities in secondary production forests in central Europe. Landsc. Ecol. 25, 1113–1124. https://doi.org/10.1007/s10980-010-9487-9

Scherzinger, W., 2006. Reaktionen der Vogelwelt auf den großflächigen Bestandeszusammenbruch des montanen Nadelwaldes im Inneren Bayerischen Wald. Vogelwelt 127, 209–263.

Seidl, R., Rammer, W., Spies, T.A., 2014. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. Ecol. Appl. 24, 2063–2077. https://doi.org/10.1890/14-0255.1

Senf, C., Sebald, J., Seidl, R., 2021. Increasing canopy mortality affects the future demographic structure of Europe's forests. One Earth 4, 749–755. https://doi.org/10.1016/j.oneear.2021.04.008

Senf, C., Seidl, R., 2018. Natural disturbances are spatially diverse but temporally synchronized across temperate forest landscapes in Europe. Glob. Chang. Biol. 24, 1201–1211. https://doi.org/10.1111/gcb.13897

Šťastný, K., Bejček, V., Mikuláš, I., Telecký, T., 2021. Atlas hnízdního rozšíření ptáků v České republice 2014 - 2017, I. ed. Aventinum.

Šťastný, K., Hudec, K. (Eds.), 2011. Fauna ČR. Ptáci 3/I, 3/II., II. ed. Academia, Prague.

Svoboda, M., Janda, P., Nagel, T.A., Fraver, S., Rejzek, J., Bače, R., 2012. Disturbance history of an old-growth sub-alpine Picea abies stand in the Bohemian Forest, Czech Republic. J. Veg. Sci. 23, 86–97. https://doi.org/10.1111/j.1654-1103.2011.01329.x

Terraube, J., Archaux, F., Deconchat, M., van Halder, I., Jactel, H., Barbaro, L., 2016. Forest edges have high conservation value for bird communities in mosaic landscapes. Ecol. Evol. 6, 5178–5189. https://doi.org/10.1002/ece3.2273

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. J. Biogeogr. 31, 79–92. https://doi.org/10.1046/j.0305-0270.2003.00994.x

Thom, D., Keeton, W.S., 2020. Disturbance-based silviculture for habitat diversification: Effects on forest structure, dynamics, and carbon storage. For. Ecol. Manage. 469, 118132. https://doi.org/10.1016/j.foreco.2020.118132

Thom, D., Sommerfeld, A., Sebald, J., Hagge, J., Müller, J., Seidl, R., 2020. Effects of disturbance patterns and deadwood on the microclimate in European beech forests. Agric. For. Meteorol. 291, 108066. https://doi.org/10.1016/j.agrformet.2020.108066

Thorn, S., Bässler, C., Bernhardt-Römermann, M., Cadotte, M., Heibl, C., Schäfer, H., Seibold, S., Müller, J., 2016a. Changes in the dominant assembly mechanism drive species loss caused by declining resources. Ecol. Lett. 19, 163–170. https://doi.org/10.1111/ele.12548

Thorn, S., Werner, S.A.B., Wohlfahrt, J., Bässler, C., Seibold, S., Quillfeldt, P., Müller, J., 2016b. Response of bird assemblages to windstorm and salvage logging - Insights from analyses of functional guild and indicator species. Ecol. Indic. 65, 142–148. https://doi.org/10.1016/j.ecolind.2015.06.033

Tolasz, R., Míková, T., Valeriánová, A., Voženílek, V., 2007. Atlas podnebí Česka: Climate atlas of Czechia. Český hydrometeorologický ústav, Praha.

Veselá, P., Vašutová, M., Edwards-Jonášová, M., Cudlín, P., 2019. Soil fungal community in Norway spruce forests under bark beetle attack. Forests 10, 1–14. https://doi.org/10.3390/f10020109

Vogel, S., Gossner, M.M., Mergner, U., Müller, J., Thorn, S., 2020. Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: An experimental approach. J. Appl. Ecol. 57, 2075–2085. https://doi.org/10.1111/1365-2664.13648

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Wright, M.N., Ziegler, A., 2017. ranger: A Fast Implementation of Random Forests for High Dimensional Data in C++ and R. J. Stat. Softw. 77, 1–17. https://doi.org/10.18637/jss.v077.i01

Zielewska-Büttner, K., Heurich, M., Müller, J., Braunisch, V., 2018. Remotely sensed single tree data enable the determination of habitat thresholds for the three-toed woodpecker (Picoides tridactylus). Remote Sens. 10. https://doi.org/10.3390/rs10121972

Żmihorski, M., 2012. The effects of anthropogenic and natural disturbances on breeding birds of managed Scots pine forests in northern Poland. Ornis Fenn. 89, 63–73.

Żmihorski, M., 2010. The effect of windthrow and its management on breeding bird communities in a managed forest. Biodivers. Conserv. 19, 1871–1882. https://doi.org/10.1007/s10531-010-9809-x

7 Supplementary material

Table S1. F tests assessing significance of individual predictors in linear models of species richness/abundance on habitat type and elevation. Significant values are bold.

	All species		*Specialists*		*Generalists*		*Canopy sp.*		*Cavity sp.*		*Ground/shrub sp.*	
Term	*F*	*p value*	*F*	*p value*	*F*	*p value*	*F*	*p value*	*F*	*p value*	*F*	*p value*
Species richness												
Habitat type	**4.11**	**0.008**	**6.17**	**<0.001**	**13.24**	**<0.001**	**10.73**	**<0.001**	0.48	0.696	**19.97**	**<0.001**
Elev	**15.20**	**<0.001**	**7.87**	**0.006**	**8.51**	**0.004**	**7.45**	**0.007**	**12.34**	**<0.001**	0.40	0.526
Abundance												
Habitat type	**4.33**	**0.006**	**4.85**	**0.003**	**8.94**	**<0.001**	**13.22**	**<0.001**	0.46	0.714	**20.67**	**<0.001**
Elev	**7.83**	**0.006**	**4.19**	**0.043**	**4.04**	**0.046**	2.54	0.113	**10.42**	**0.002**	0.07	0.799

Table S2. Table of coefficients for linear models of species richness/abundances on habitat type and elevation. “SSD”, “LSD”, “NDF”, and “ELT” stand for “Small-scale disturbance”, “Large-scale disturbance”, “Non-disturbed forest”, and “Enclaves of live trees in large-scale disturbance areas”, respectively. Significant values are bold.

	All species			*Specialists sp.*			*Generalists sp.*			*Canopy nesters*			*Cavity nesters*			*Ground/shrub nesters*		
Term	*Estimate*	*SE*	*p value*	*Estimate*	*SE*	*p value*	*Estimate*	*SE*	*p value*	*Estimate*	*SE*	*p value*	*Estimate*	*SE*	*p value*	*Estimate*	*SE*	*p value*
Species richness																		
(Intercept)	**16.960**	**1.629**	**<0.001**	**5.868**	**1.017**	**<0.001**	**11.092**	**1.196**	**<0.001**	**5.642**	**1.012**	**<0.001**	**5.373**	**0.794**	**<0.001**	**5.692**	**0.93**	**<0.001**
Habitat: LSD	**-1.462**	**0.630**	**0.022**	-0.479	0.393	0.226	**-0.983**	**0.463**	**0.035**	-0.718	0.391	0.069	-0.267	0.307	0.386	-0.499	0.36	0.172
Habitat: ELT	-0.450	0.635	0.481	0.768	0.397	0.055	**-1.217**	**0.467**	**0.010**	**1.115**	**0.395**	**0.005**	-0.356	0.310	0.252	**-1.188**	**0.36**	**0.002**
Habitat: NDF	**-1.464**	**0.471**	**0.002**	**0.676**	**0.294**	**0.023**	**-2.139**	**0.346**	**<0.001**	**0.682**	**0.292**	**0.021**	-0.187	0.229	0.418	**-1.956**	**0.27**	**<0.001**
Elev	**-0.006**	**0.002**	**<0.001**	**-0.003**	**0.001**	**0.006**	**-0.004**	**0.001**	**0.004**	**-0.003**	**0.001**	**0.007**	**-0.003**	**0.001**	**<0.001**	0.000	0.00	0.526
Abundance																		
(Intercept)	**18.450**	**2.063**	**<0.001**	**6.659**	**1.412**	**<0.001**	**11.789**	**1.434**	**<0.001**	**5.568**	**1.319**	**<0.001**	**6.149**	**0.981**	**<0.001**	**6.479**	**1.15**	**<0.001**
Habitat: LSD	**-2.591**	**0.798**	**0.002**	-0.874	0.546	0.112	**-1.717**	**0.555**	**0.002**	**-1.232**	**0.510**	**0.017**	-0.438	0.380	0.251	**-0.944**	**0.44**	**0.037**
Habitat: ELT	-0.966	0.804	0.232	0.835	0.551	0.132	**-1.801**	**0.559**	**0.002**	**1.162**	**0.514**	**0.025**	-0.197	0.383	0.608	**-1.912**	**0.45**	**<0.001**
Habitat: NDF	**-1.544**	**0.596**	**0.011**	0.566	0.408	0.167	**-2.111**	**0.414**	**<0.001**	**1.125**	**0.381**	**0.004**	-0.179	0.284	0.530	**-2.488**	**0.33**	**<0.001**
Elev	**-0.006**	**0.002**	**0.006**	**-0.003**	**0.001**	**0.043**	**-0.003**	**0.001**	**0.046**	-0.002	0.001	0.113	**-0.003**	**0.001**	**0.002**	0.001	0.00	0.799

Table S3. Post-hoc pairwise multiple comparisons of habitat type differences in species richness and abundance. “SSD”, “LSD”, “NDF”, and “ELT” stand for “Small-scale disturbance”, “Large-scale disturbance”, “Non-disturbed forest”, and “Enclaves of live trees in large-scale disturbance areas”, respectively. Significant values are bold.

	All species			*Specialists sp.*			*Generalists sp.*			*Canopy nesters*			*Cavity nesters*			*Ground/shrub nesters*		
Pair	*Diff*	*SE*	*p*	*Diff*	*SE*	*p*	*Diff*	*SE*	*p*	*Diff*	*SE*	*p*	*Diff*	*SE*	*p*	*Diff*	*SE*	*p*
Species richness																		
LSD - SSD	-1.462	0.630	0.096	-0.479	0.393	0.612	-0.983	0.463	0.148	-0.718	0.391	0.257	-0.267	0.307	0.818	-0.638	0.290	0.128
ELT - SSD	-0.449	0.635	0.892	0.768	0.397	0.215	**-1.217**	**0.467**	**0.048**	**1.115**	**0.395**	**0.027**	-0.356	0.310	0.655	**-1.290**	**0.329**	**0.001**
NDF - SSD	-1.464	0.471	0.012	0.676	0.294	0.101	**-2.139**	**0.346**	**<0.001**	0.682	0.292	0.094	-0.187	0.229	0.846	**-1.983**	**0.267**	**<0.001**
ELT - LSD	1.013	0.590	0.314	**1.247**	**0.368**	**0.005**	-0.234	0.433	0.948	**1.833**	**0.366**	**<0.001**	-0.089	0.288	0.990	-0.652	0.334	0.210
NDF - LSD	-0.002	0.564	1.000	**1.155**	**0.352**	**0.007**	**-1.156**	**0.414**	**0.030**	**1.400**	**0.350**	**<0.001**	0.081	0.275	0.991	**-1.346**	**0.274**	**<0.001**
NDF - ELT	-1.014	0.583	0.302	-0.092	0.364	0.994	-0.922	0.428	0.139	-0.433	0.362	0.626	0.170	0.284	0.932	-0.693	0.315	0.126
Abundance																		
LSD - SSD	**-2.591**	**0.798**	**0.008**	-0.874	0.546	0.377	**-1.717**	**0.555**	**0.012**	-1.232	0.510	0.077	-0.438	0.380	0.653	**-1.013**	**0.358**	**0.027**
ELT - SSD	-0.966	0.804	0.623	0.835	0.551	0.425	**-1.801**	**0.559**	**0.008**	1.162	0.514	0.111	-0.197	0.383	0.955	**-1.962**	**0.405**	**<0.001**
NDF - SSD	-1.544	0.596	0.050	0.566	0.408	0.504	**-2.111**	**0.414**	**<0.001**	**1.125**	**0.381**	**0.019**	-0.179	0.284	0.921	**-2.502**	**0.330**	**<0.001**
ELT - LSD	1.626	0.747	0.132	**1.710**	**0.511**	**0.006**	-0.084	0.519	0.998	**2.395**	**0.477**	**<0.001**	0.241	0.355	0.904	-0.949	0.412	0.101
NDF - LSD	1.047	0.714	0.456	**1.441**	**0.489**	**0.019**	-0.394	0.496	0.855	**2.357**	**0.457**	**<0.001**	0.259	0.340	0.869	**-1.489**	**0.338**	**<0.001**
NDF - ELT	-0.579	0.738	0.859	-0.269	0.505	0.950	-0.310	0.513	0.929	-0.037	0.472	0.400	0.018	0.351	1.000	-0.540	0.338	0.504

Table S4. F tests assessing the significance of individual predictors in linear models of species richness/abundance on habitat characteristics (Complexity = structural complexity, LiveTrees = density of live trees, Understory = understory cover) and elevation (Elev). Significant values are bold.

	All species		*Specialists*		*Generalists*		*Canopy sp.*		*Cavity sp.*		*Ground/shrub sp.*	
Predictor	*F*	*p value*	*F*	*p value*	*F*	*p value*	*F*	*p value*	*F*	*p value*	*F*	*p value*
Species richness												
Complexity	**9.03**	**<0.001**			**10.78**	**<0.001**	3.02	0.052	**3.71**	**0.027**	1.98	0.142
LiveTrees			**11.33**	**<0.001**			**16.08**	**<0.001**			**4.14**	**0.018**
Understory					**5.87**	**0.004**			2.21	0.114	**12.83**	**<0.001**
Elev	**12.50**	**<0.001**	**4.03**	**0.020**	**4.67**	**0.011**	**3.24**	**0.042**	**12.49**	**<0.001**		
Abundance												
Complexity	**8.24**	**<0.001**	**4.27**	**0.016**	**5.76**	**0.004**	2.61	0.078	**4.44**	**0.014**	2.52	0.084
LiveTrees	**3.33**	**0.039**	**17.33**	**<0.001**			**11.47**	**<0.001**			1.94	0.148
Understory					**3.52**	**0.032**	2.86	0.061	2.20	0.115	**12.12**	**<0.001**

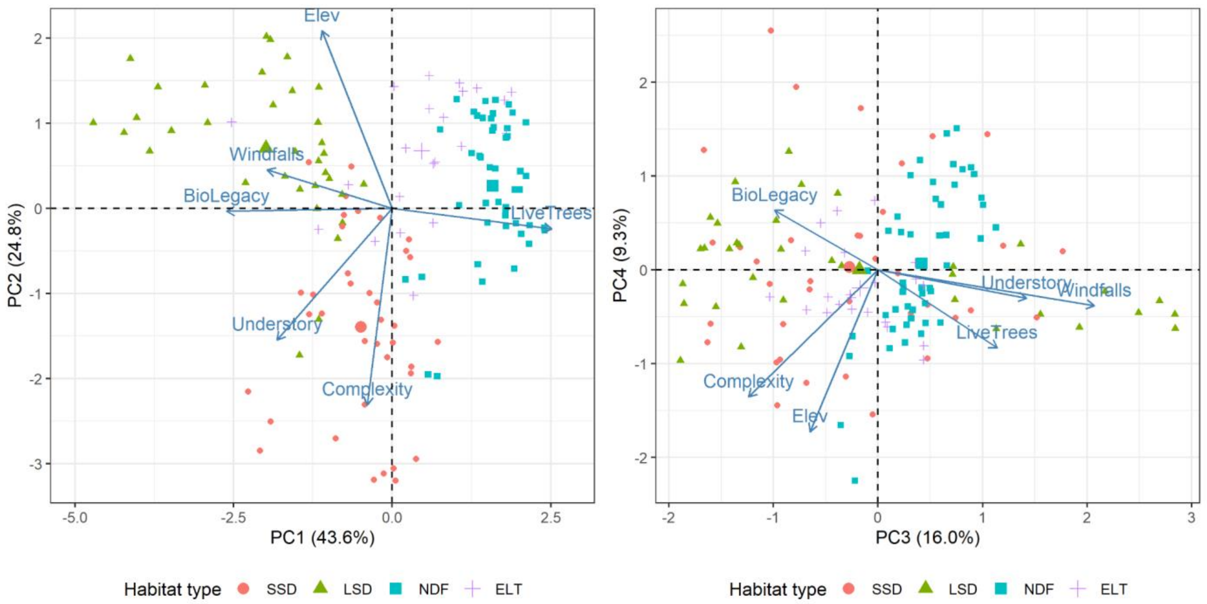

Fig. S1. Biplots of the first and second (left) and the third and fourth (right) principal components, with the corresponding percentage of explained variance in parentheses. Observations belonging to different habitat types are depicted by different symbol shapes and colours, and the original variables describing the habitat characteristics are depicted as arrows. “SSD”, “LSD”, “NDF”, and “ELT” stand for “Small-scale disturbance”, “Large-scale disturbance”, “Non-disturbed forest”, and “Enclaves of live trees in large-scale disturbance areas”, respectively. Complexity = structural complexity, LiveTrees = density of live trees, Understory = understory cover, Windfalls = proportion of wind disturbed area, BioLegacy = total proportion of disturbed forest.

Table S5. Performance metrics for classification of habitat types based on habitat characteristics using random forest models. “SSD”, “LSD”, “NDF”, and “ELT” stand for “Small-scale disturbance”, “Large-scale disturbance”, “Non-disturbed forest”, and “Enclaves of live trees in large-scale disturbance areas”, respectively.

	Original variables				*PCA variables*			
Metric	*SSD*	*LSD*	*ELT*	*NDF*	*SSD*	*LSD*	*ELT*	*NDF*
Sensitivity	0.865	0.882	0.273	0.958	0.892	0.853	0.455	0.875
Specificity	0.904	0.944	0.983	0.903	0.875	0.953	0.975	0.935
Prevalence	0.262	0.241	0.156	0.340	0.262	0.241	0.156	0.340
Detection Rate	0.227	0.213	0.043	0.326	0.234	0.206	0.071	0.298
Balanced Accuracy	0.884	0.913	0.628	0.931	0.883	0.903	0.715	0.905

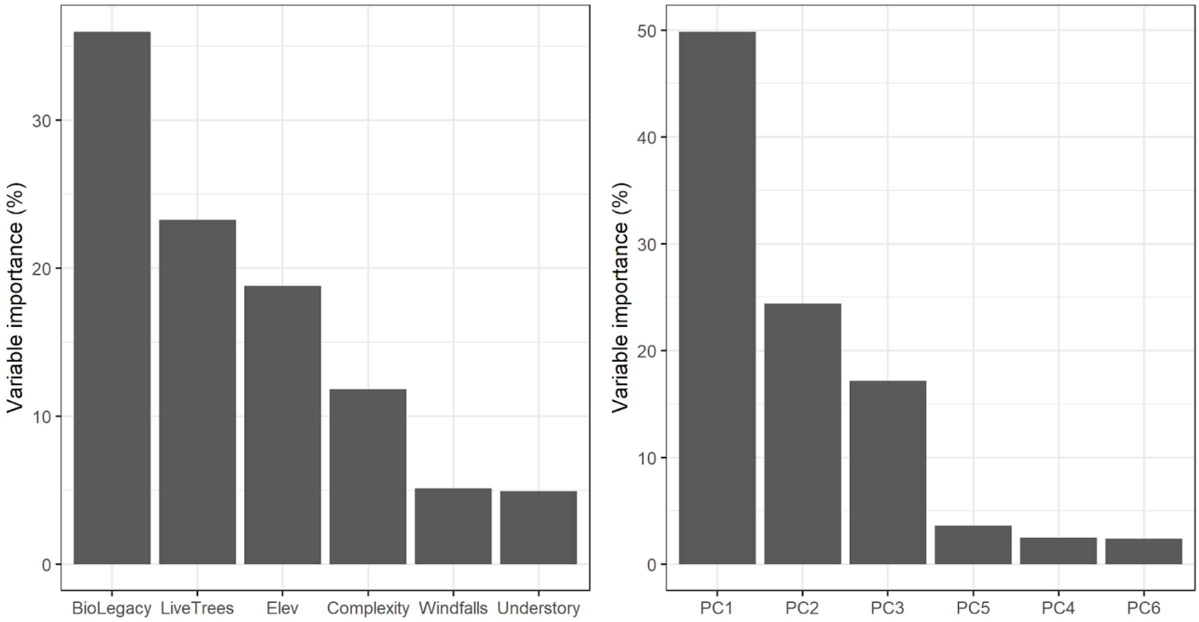

Fig. S2. The relative importance of individual variables (left) and principal components (right) in the classification of habitat types using random forest models. Variable importance is assessed by the corrected impurity measure, rescaled so that the importance values for all variables sum up to 100. Complexity = structural complexity, LiveTrees = density of live trees, Understory = understory cover, Windfalls = proportion of wind disturbed area, BioLegacy = total proportion of disturbed forest.

Table S6: List of species recorded, their abundance (Abun), frequency (Freq), habitat specialization (Spec) as generalist (G) or specialist (S), nesting guild classification (Nest site) and Red-List classification (Red List)

Species	Abun	Freq	Spec	Nest site	Red List
Erithacus rubecula	200	94,3	G	Ground/Shrub	LC
Fringilla coelebs	172	81,6	G	Canopy	LC
Periparus ater	156	83,7	S	Cavity	LC
Prunella modularis	103	66,7	G	Ground/Shrub	LC
Troglodytes troglodytes	85	57,4	G	Ground/Shrub	LC
Sylvia atricapilla	83	55,3	G	Ground/Shrub	LC
Certhia familiaris	76	51,1	S	Cavity	LC
Regulus regulus	63	40,4	S	Canopy	LC
Turdus merula	63	44,7	G	Ground/Shrub	LC
Turdus philomelos	52	35,5	G	Canopy	LC
Spinus spinus	49	24,1	S	Canopy	LC
Phylloscopus trochilus	46	31,9	G	Ground/Shrub	LC
Phylloscopus collybita	45	29,8	G	Ground/Shrub	LC
Regulus ignicapilla	34	21,3	S	Canopy	LC
Columba palumbus	34	21,3	G	Canopy	LC
Dendrocopos major	33	22,0	G	Cavity	LC
Pyrrhula pyrrhula	31	19,1	S	Canopy	LC
Anthus trivialis	26	14,2	G	Ground/Shrub	LC
Loxia curvirostra	25	12,8	S	Canopy	LC
Turdus viscivorus	22	13,5	S	Canopy	LC
Parus major	20	14,2	G	Cavity	LC
Sitta europaea	18	10,6	G	Cavity	LC
Garrulus glandarius	16	9,9	G	Canopy	LC
Phoenicurus phoenicurus	14	9,9	G	Cavity	LC
Picoides tridactylus	13	9,2	S	Cavity	EN
Dryocopus martius	12	8,5	S	Cavity	LC
Poecile montanus	8	4,3	S	Cavity	LC
Tetrastes bonasia	8	3,5	S	Ground/Shrub	VU
Tetrao urogallus	6	2,8	S	Ground/Shrub	CR
Lophophanes cristatus	6	3,5	S	Cavity	LC
Phylloscopus sibilatrix	6	4,3	S	Ground/Shrub	LC
Turdus torquatus	4	2,8	G	Ground/Shrub	EN
Turdus pilaris	3	2,1	G	Canopy	LC
Cuculus canorus	3	2,1	G	unclassified	LC
Fringilla montifringilla	2	1,4	G	unclassified	LC
Muscicapa striata	2	1,4	G	Cavity	LC
Acanthis flammea	1	0,7	S	Canopy	NT
Nucifraga caryocatactes	1	0,7	S	Canopy	VU
Cyanistes caeruleus	1	0,7	G	Cavity	LC
Coccothraustes coccothraustes	1	0,7	G	Canopy	LC

Declaration of interests

☒ 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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

CRediT authorship contribution statement

Dominik Kebrle: Conceptualization, Data curation, Writing - original draft, Investigation, Writing - review & editing, Methodology, Project administration, Resources. **Petr Zasadil:** Conceptualization, Validation, Writing - review & editing. **Vojtěch Bartá**k: Formal analysis, Visualization**, Jeňýk Hofmeister**: Writing - review & editing