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Habitat association, forest cover, and region mediate forest disturbance effects on European bird abundances

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Abstract

Despite the prevalence of forest disturbances, their effects on bird abundance are poorly understood on a continental scale. Near future harvest rates and natural disturbances will likely increase, thus quantifying the influence of disturbances on biodiversity is increasingly important to plan conservation. We studied the influence of forest disturbances on the abundance of 107 bird species across 25 European countries between 2000 and 2022. We explored the response of birds associated with different habitats, the influence of forest cover and time since the disturbance, comparing results at continental and regional scales. 95 species responded significantly to disturbances, mostly negatively. Forest-associated birds responded mostly negatively, while shrub and edge birds showed a higher proportion of positive responses. Open habitat birds had few statistically significant responses with mixed directions. Forest cover negatively influenced the effect of disturbance on abundance. Responses varied among regions, reflecting differences in community composition and landscape characteristics. Importantly, for 21% of species the response direction changed between region and/or forest cover. These findings suggest that forest disturbances, dominated by clear-cut harvesting, exert a mostly negative influence on birds across Europe, requiring adaptive forest management strategies for avian conservation.

Introduction

A key factor shaping forest structure and habitat quality is stand-replacing disturbance (henceforth, disturbance), defined as natural or anthropogenic events causing tree mortality that remove > 70% of trees in a forest (UN FAO Forest definition). The impact of disturbance depends on the disturbance type, which in European forests mostly consist of timber harvesting (82%)[1], windthrow (8% of disturbances), wildfire (4%), and bark beetle outbreaks (3%).[1–3]. In principle, timber harvesting creates more uniform open canopy gaps than natural disturbances, resulting in less habitat complexity and even-aged regeneration[4,5]. While natural disturbances create structural characteristics that are beneficial to biodiversity (e.g. deadwood, tree retention, heterogeneous light conditions), this is frequently offset by salvage logging[1,6–9]. Disturbance is also mediated by regional differences. In southern Europe there is a higher share of large forest fires and lower harvest rates, due to distinct environmental characteristics and management strategies[1,12,13]. In contrast, in northern Europe, landscapes are usually dominated by more intensive harvesting[11,14,15], and thus more anthropogenic disturbances. The area affected by disturbances has been increasing in recent years and is predicted to increase further in the coming decades[1,2,16,17], making it essential to understand how forest disturbances drive biodiversity patterns across European forests.

The novel landscape compositions created by predominantly harvest-dominated disturbance regimes, are likely to have large impacts on biotic communities, including birds[18,19]. Local to regional scale studies demonstrate that disturbances create suitable ecological conditions for bird species associated with open-habitats, shrubland, or edge-habitats, but are detrimental to forest-dependent bird species [5,20]. The effects of disturbances on birds may depend on both species' niche, such as their preferred habitat for breeding and feeding (e.g., open vs closed vegetation), and geographic location. In general, forest bird diversity tends to be higher in northern, Central, and Eastern Europe, whereas edge and shrubland bird diversity are higher in southern Europe[21]. Consequently, geographic variations in both disturbance regimes and bird communities suggest that disturbances will have spatially heterogenous effects on bird communities across the continent,

reflecting differences in ecosystem structure and habitat quality. Therefore, a reasonable hypothesis is that disturbance events create more conservation opportunities for bird communities in southern Europe and more potential threats in northern and Central Europe[22–25]. A continental assessment of bird responses to disturbances and the identification of broad regional patterns are useful to directly inform policy instruments such as the Nature Restoration Regulation, which aims to enhance biodiversity, among other objectives[27,28].

For the first time, a study of bird responses to disturbances at a continental scale is feasible thanks to the recent continent-wide mapping of disturbances, coupled with the increased availability of extensive bird records[3,11,26]. Thus, in this study, we invesitgated how forest canopy gaps resulting from natural and anthropogenic disturbances have affected local abundance of 107 bird species across 25 European countries over 22 years. First, we quantified the effect of forest disturbances of different ages on species-level bird abundance in the entire study area. Second, we studied whether the bird-disturbance relationships differed between the northern, mid, and southern regions of Europe. We expected bird responses to forest disturbance to be more frequently negative in northern latitudes, while more positive in the south. Third, we evaluated whether the direction and magnitude of species-specific responses depended on region and the level of forest cover. We expected that the disturbance effect would change between regions because of differences in habitat characteristics and species ecology, and that disturbances would affect habitat availability at different levels of forest cover. To the best of our knowledge, this is the first study to fully investigate: 1) the relationships between birds and disturbance-induced forest gaps (henceforth, bird-disturbance relationship) at a continental scale, extending knowledge beyond local to national scale where such patterns are better understood[19,20], 2) the interactive effects of latitude, landscape forest cover and time since forest disturbance on the abundance of avian guilds showing different ecological requirements. By explicitly comparing northern, mid, and southern European regions and incorporating landscape context, this study provides insights into large-scale patterns of bird responses to canopy gaps, with direct implications for targeted conservation under global change.

Results

Overall approach

We quantified species-level local abundance responses to forest disturbances by fitting spatiotemporally explicit generalized linear mixed effects models. We used standardized bird counts for 107 species from the Pan European Common Bird Monitoring Scheme[29] on 16,585 sites in 25 European countries between 2000 and 2022 (Fig. 1A). Each species was assigned to a habitat guild by vegetation structure, namely forest (44 species), edge and shrub (30 species), or open vegetation (33 species). Remotely sensed canopy gaps from forest disturbances were obtained from the European Forest Disturbance Atlas (EFDA) and covered the entire study area from 1985 to 2022. We estimated the bird abundance responses to the interaction between the area of forest disturbed at three time intervals after disturbance (i.e., 0–5, 6–11 and 12–17 years) and the forest cover level (i.e., 15%, 50%, and 85%). This relationship was estimated at a continental scale and, regionally (i.e., for southern, mid, and northern latitudes separately). We counted the number of species per habitat guild, level of forest cover, and region with significant positive or negative responses ($p < 0.05$) to disturbances and averaged the statistical effects per group. When we present a range of the percentage of species abundances responding to forest disturbances, this covers the minimum and maximum percentage of species across the different levels of forest cover and times since disturbance.

Effects of canopy gaps on bird abundance across continental Europe

Depending on the surrounding forest cover and the time since disturbance, 49 to 70% (mean = 58%) of species with an acceptable model fit had a significant response to forest canopy gaps, with more species responding negatively than positively (Fig. 2). The average effect of canopy gaps across all species was also negative for all forest cover contexts and disturbance ages (Fig. 3).

Species differed in their responses to forest gaps depending on their main habitat association. Most forest-affiliated species responded negatively to disturbances (54–69%, e.g., *Sitta europaea, Leiopicus medius, Phylloscopus trochiloides*) with the number of species responding significantly varying by forest cover and disturbance age. Only a few forest species had a significant positive response (3–11%, e.g., *Phoenicurus phoenicurus*; Fig. 2; list of all species responses in Supplementary S2). The average effect across the forest species group was also negative (Fig. 3), and the strength of the negative effect increased with forest cover and varied with time since disturbance. Recent forest disturbances usually had the strongest negative relationship with forest bird abundance.

In most cases, species associated with shrubland and edge habitats showed more positive responses (20–60%; Fig. 2; e.g., *Lanius excubitor, Saxicola rubetra*; Supplementary S2) with increases in abundance in response to disturbance (8–28%; Fig. 2; e.g., *Emberiza cirlus*; Supplementary S2). Positive responses of shrubland and edge species abundance to forest disturbance were more common in low forest cover landscapes and for disturbances between 6 and 11 years old, when in most of Europe canopy gaps would be recolonized by shrubby vegetation. Conversely, negative responses were more common for 0-6- and 12-17-year-old disturbances, indicating that canopy gaps only provide brief habitat suitability to species in this group. The average effect of disturbances on this group was non-significant, reflecting the mixed responses of the shrub and edge habitat associated species (Fig. 3).

Finally, when ignoring statistical significance, most open vegetation birds responded positively (Fig. 2). However, only 11–36% of open vegetation birds had a significant positive response to forest disturbances (Supplementary S2) against 11–21% of species with significantly negative responses (e.g., *Sturnus vulgaris*). Positive responses were more common in low forest cover landscapes, where abundances for this group were expected to be higher. The average effect of forest disturbances on species related to open vegetation was generally non-significant (Fig. 3).

Regional effects of canopy gaps on abundance

Similarly to the continental level results, in all three regions, more species responded negatively to disturbances than positively (Figs. 4 and 5). Because of the smaller sample sizes in the northern and southern latitudes regions, model uncertainties were larger for those regions, limiting the possibilities for interpretation. However, there were some notable differences between the regions.

First, in northern latitudes, fewer species are associated with open vegetation and shrub and edge habitat than in the other regions, and the results were dominated by negative effects on forest species in landscapes with intermediate and high forest cover. However, in northern landscapes with low forest cover there were more species positively related to disturbances than in landscapes with more forest cover across all species groups. Second, the mid latitudes largely mirrored the continental patterns. Finally, in the southern latitudes, all but one

significant forest bird-disturbance relationship were negative. For species associated with open vegetation and shrub and edge habitats, the results were comparable to our findings at a continental scale and mid latitudes. However, it should be noted that the species composition of these two habitat groups in the southern latitudes was different from the other regions because some species almost exclusively occurred there (e.g., *Burhinus oedicnemus*, *Clamator glandarius*, and *Galerida theklae*).

The model averaging by habitat association group did not reveal differences between regions and species groups, likely explained by the larger number of species for which regional models were uncertain (Fig. 5). For 21 modeled species, the direction of the bird-disturbance relationship depended on the level of forest cover in the landscape or the region in Europe (Supplementary S2). Specifically, the direction of the bird-disturbance relationship changed between regions for 10 species. For example, *Galerida cristata* abundance increased with higher disturbance in southern latitudes but showed the opposite relationship in mid latitudes. For 11 species, the direction changed depending on both the forest cover level and region. For example, *Perdix perdix* responded negatively in southern latitudes, but positively in low forest cover landscapes in mid latitudes.

Discussion

For the first time, we assessed how local bird abundance is related to forest disturbance rates at a continental-scale, in our case Europe. Our analysis revealed consistent continental-scale effects of disturbances on European birds that were habitat guild dependent, highlighting the distinct sensitivity of species to habitat amount change. Forest disturbance regimes in areas dominated by harvesting and salvage logging[1], are a consistent driver of bird abundance at continental scales. We found that disturbance was consistently important, despite the high degree of diversity in forest composition, habitat quality, and disturbance that exist across Europe, underscoring broad applicability of our results. Forest disturbances had more negative than positive significant effects on species abundances at continental and regional scales, even though positive relationships were not uncommon.

Importantly, disturbance effects on abundance change are strongly influenced by species' habitat association. Forest disturbances were associated with decreased forest bird abundance and had mixed effects on shrub and edge as well as open habitat species. Our findings support the results of a previous study showing that disturbance effects were stronger on forest birds across Germany than on species associated with other habitats[19]. The most obvious mechanism through which forest disturbances drive the patterns that we found is through habitat amount dynamics[30,31], in which disturbances remove forest habitat and subsequent successional processes generate open and shrub habitats. Most of the observed species' responses to canopy gaps were in line with the knowledge about species' habitat niches. For example, *Emberiza citrinella* responded positively to canopy gaps, which is consistent with its association with open habitats for breeding[32,33]. However, some bird-disturbance relationships were not in line with the expectations from our broad habitat associations but were in line with expectations from individual species' ecologies. *Clamator glandarius,* classified as shrub and edge species, had a negative relationship with forest disturbances, in contrast to the expected positive response. However, the species depends on sparse tree cover for its habitat[34] within its southern breeding range, and our forest disturbance data likely included disturbances in such ecosystems.

Land cover was also an important mediator of bird abundance-disturbance relationships. The negative effect of disturbance on forest birds was strongest in high forest cover landscapes. For forest species, any loss of forest cover decreases available habitat and thus forest bird abundance, regardless of the forest cover[35]. The positive relationship between forest cover and the strength of the bird-disturbance relationship is likely due to the positive correlation between habitat availability and abundance[36], which makes habitat removal more impactful in areas with high initial availability. Modified interspecific interactions induced by disturbance could also contribute to the observed patterns if forest disturbances introduce novel species to landscapes and alter community composition[37]. Even though the modelled signal was weak, open vegetation and shrub-and-edge species responded positively to disturbances in landscapes with lower forest cover. This could indicate that colonization of new habitat in landscapes where primary habitat is already present, e.g. clearcuts close to farmlands[38], is easier than in high forest cover landscape, where habitat for such species is limited[31,39]. It is important for future research to investigate how conservation trade-offs between the general loss of forest species abundance and the variable gains for some open, shrub and edge habitat species could be adapted to mitigate negative and increase positive effects.

Even if we did not find a strong effect of time since disturbance on bird species, guild-specific patterns with important conservation implications emerged. On the one hand, forest species were negatively affected by canopy gaps of any age and thus habitat suitability did not recover within the 17-year window considered in this study. The consistently negative effect of disturbances at the three timesteps we studied is likely because the development of mature forests in Europe is much longer than that, often at centennial scales[10]. Considering that we only studied bird species, which are highly mobile compared to many other taxa, the post-disturbance recovery of other forest-affiliated taxa could potentially be even longer, and highly limited by the adjacent landscape context[40]. On the other hand, for edge and shrub species, disturbances of 6-11 years old seemed to have more positive relationships with species abundance than disturbances of other ages. This is likely due to the shrub-like vegetation structure at that age.

The effects of canopy gaps on bird abundance varied among latitudinal regions. Many of these differences were due to changes in bird community composition between the three parts of Europe. In general, the northern latitudes have a richer forest bird community with unique species compared to the other two regions[21,41]. Conversely, the southern latitudes have a richer community of species associated with intermediate and open vegetation, that has been partially shaped by multi-decadal fire cycles over the course of millennia[22,41,42]. Our results did not generally support the hypothesis that the effects of disturbances on birds would be more positive in southern Europe due to the richer community of shrub and edge habitat birds. Nor did results support the hypothesis that disturbance effects would be more negative outside of southern latitudes because of the comparatively richer forest bird community. The lack of more positive results in southern Europe might be because we could not include rarer species with more specialized and stricter habitat requirements. It could also be that the colonization of fire-affected landscapes by species associated with open and shrub habitats is context dependent[43–45]. For example, colonizations of post-fire ecosystems by open habitat birds were found to depend on large scale landscape change while local extinctions could result from landscape changes across small and large scales[46]. Therefore, the potential positive effects of natural disturbances such as fire described in these landscapes may be more specific than the pervasive negative effects of disturbances on forest species[43–45]. Finally, the relative conservation value of species in a landscape varies regionally, thus requiring a

more detailed assessment of how to balance positive and negative spatial effects of disturbances at the community level to achieve regional conservation goals[47,48].

For approximately one-fifth of the species, the direction of species' relationships with forest disturbance differed between regions and / or forest cover. Inter-regional differences in the direction of species' responses to canopy gaps could be explained by inter-regional variation in the landscape characteristics such as forest type and density or landscape mosaic composition. Differences may also be explained by intra-specific trait variation, as local pressures may influence species habitat selection in distinct regions[49]. For example, the Yellowhammer (*Emberiza citrinella*) breeds in lowland farmlands in much of Europe but can be found in forest canopy gaps in northern latitudes and in subalpine open habitats in the Alps and southern Europe[38,50,51]. Changes in the direction of the canopy gap effect between distinct levels of forest cover could be explained by gained or lost habitat complementation in either landscapes dominated by forest or open vegetation[52,53]. For example, if a species nests in forest and feeds in open habitats in a landscape, losing forest cover in a low forest cover landscape implies lost nest sites while in high forest cover landscape it could imply gained feeding opportunities. These context-specific species responses to disturbance are significant for conservation planning, as we cannot expect that functional tradeoffs in the bird community are uniform across contexts, even though general community level patterns seem to indicate that.

Over 80% of disturbances included in this study were either forest clear-cuts or natural disturbances that were subsequently salvage logged, creating clear-cut like ecosystems[1,3,7]. Such canopy gaps from disturbance will likely continue to occur commonly, driven by an increasing demand for timber and an increasing frequency of natural disturbances[54,55]. Under current management of European forest disturbances, our results show limited opportunities for conservation because of the nearly uniformly negative effects of forest disturbance on forest associated bird species and only partially positive results for species associated to shrub and edge habitats or open vegetation. Changing forest and harvest management might provide increased nature conservation benefits as there might be opportunities to improve the impacts of anthropogenic and natural disturbances on bird communities[8,20,56]. For example, increasing the amount of natural post-disturbance vegetation structures, like retained patches of tree or standing and fallen deadwood, could provide significant conservation benefits to a wide variety of species and taxa[6,57,58]. Additionally, more moderate disturbances than those we studied, especially natural ones, can be more beneficial for biodiversity because of the comparably higher potential for structural complexity[5,59,60].

We identify several avenues for future studies to extend the knowledge base we provide here. First, different disturbance causes can lead to different ecosystem responses and impacts on biodiversity[5,61]. Here, we did not investigate the disturbance types to avoid introducing compound uncertainty from both the disturbance mapping and the attribution to disturbance type in the EFDA[3]. We were unable to model the effects of low severity disturbances on bird abundance because the EFDA, by design maps high severity, stand replacing forest disturbances. This is therefore unlikely to record low and medium severity fires in forests where species adaptations facilitate tree survival through most fire events, e.g. epicormic, basal resprouting and high bark thickness. Second, future research should study how habitat suitability can mediate the effects of forest disturbances on biodiversity; i.e., the removal of high-suitability forest habitat might have stronger effects on forest birds than the removal of low-suitability habitat. Future continental availability of forest structural indicators could facilitate the quantification of habitat suitability as a mediator of biodiversity-disturbance

relationships [62,63]. Third, future work could also further refine quantitative estimates using a Before-After-Control-Impact design to assess effect sizes of disturbance regimes[64,65] if continental scale biodiversity data quality challenges could be overcome. Finally, the effects of disturbances on other taxa should also be investigated across large ranges to increase our understanding of the consequences for biodiversity. We focused on birds because of their known sensitivity to vegetation structure and excellent data availability across Europe, but other taxa might have different responses to environmental pressures [66–68].

Our European study reveals that forest disturbance impacts on bird species abundance are neither uniform nor random but follow ecological traits, as well as geographical and landscape patterns, providing important guidance for future assessments. Disturbance effects on forest birds were negative in all contexts and long lasting, while effects on shrub and edge and open vegetation birds were ephemeral, mixed, and context dependent. Therefore, we can confirm for the first time that local patterns often can be extrapolated to much larger scales and can be used as a foundation for conservation planning. The effects varied geographically within and between species, with the main differences in disturbance impacts on species occurring between northern and southern regions, thus conservation-oriented adaptations of forest management should be tailored to bird community composition by region. The mostly negative effects of forest disturbances on bird abundance underscore the need for adaptive and context-specific forest management strategies, such as increased rotation cycles, increased tree retention, reduced salvage logging, and continuous cover forestry on the landscape level. Such management adaptations should carefully consider the changes in abundance of disturbance-sensitive species, particularly under increasing pressure from climate-driven and human-mediated disturbances.

Methods

Study area

The study area comprised 25 European countries for which bird and forest canopy gap data were available (Figure 1A): Austria, Belgium (Wallonia only), Bulgaria, Croatia, Czechia, Denmark, Finland, France, Germany, Hungary, Ireland, Italy, Latvia, Lithuania, Luxembourg, Netherlands, Norway, Poland, Romania, Slovakia, Slovenia, Spain, Sweden, Switzerland, and the United Kingdom. There are large environmental gradients in terms of climate and ecosystem types within the study area. Therefore, we analyzed the effects of forest disturbance on bird community both at continental and regional scales, based on the zones classified in the Environmental Stratification of Europe database[69,70] (EnS). The EnS database distinguishes 13 relatively homogeneous environmental zones based on climate, geomorphology, geology, and soil. To simplify the analysis, we combined the 13 EnS zones into three broad regions that mainly follow a latitudinal gradient (Figure 1A): northern latitudes (comprising Alpine North, Boreal, and Nemoral zones), mid latitudes (comprising Atlantic Central, Atlantic North, Alpine South, Continental, Pannonian zones), and southern latitudes (comprising most of the Iberian and Italian peninsulas, southern France, and parts of the Western Balkans).

Bird abundance data

We used bird count data for the 25 countries from the Pan-European Common Bird Monitoring Scheme[29] (PECBMS; Supplementary S1.1) collected between 2000 and 2022. Survey periods differed slightly among

monitoring schemes[71]:69% of sites have surveys from 2000, 80% from 2001 onwards, and the last year for which data were available was on average 2021 (range: 2020 to 2022).

Survey sites

The survey designs varied among the monitoring schemes included in PECBMS. The exact spatial location and extent of survey points, transects, and areas were not available for the PECBMS dataset, only the centroid of the survey site. Therefore, we extracted all environmental information at the site level in a circular buffer with a radius of 1500 meters around the centroid of the survey site. The buffer equates to a circle encompassing an area of 700 hectares around the centroid of the survey sites which is equal to the median area covered by PECBMS survey sites. Our approach makes the probable assumption that, at the continental scale, the environmental conditions along the actual survey points, transects, and areas are highly correlated with those in the chosen buffers.

We removed 2,051 sites for which the buffer area was mainly urban, i.e., with >50% covered by artificial surfaces according to Corine Land Cover (CLC) 2000, 2006, 2012, or 2018[72–75]. We only included those sites that were visited at least four times in the 23-year sampling period (total sites n = 16,585, from which northern latitudes n = 1,795, mid latitudes n = 12,896, southern latitudes n = 1,894; Figure 1A).

Species selection

To ensure that sufficient data were available for analysis, we retained bird species that were detected in at least 100 sampling events and a total of at least 300 individuals observed in the dataset (n = 316 species). Then, we selected species typically found in open habitats, shrubland and edge habitats, or forests, because those three habitat types (or analogues) occur over time as disturbed forests recover through succession. To this end, we used species associated to agriculture and grassland (n = 56 species), boreal and temperate forest (n = 51 species), and Mediterranean habitats (n = 18 species) according to Tucker and Evans 1997 as also used in the European Breeding Bird Atlas 2 [41,76]. We removed 18 species that are nocturnal, hard to detect using PECBMS methods, or usually observed while flying over and thus not related to local vegetation structure. In addition, we combined data for the closely related species belonging to the subalpine warbler complex, including *Sylvia cantillans*, *S. subalpina,* and *S. iberiae,* so that they were modelled together[77]. The steps in data-processing resulted in 16,506,623 individual bird observations across 107 species for use in this study.

Count metric

We used annual counts of observed individuals or observed territories from the PECBMS dataset as an index of abundance. The annual count is for most schemes the maximum count over the breeding season surveys on sites sampled multiple times per breeding season. We multiplied the number of territories by two, to represent that two individuals occupy a single territory. Non-detections are not explicitly reported to PECBMS, but because in surveys all species are counted, the lack of records means that the species was not observed. Thus, we generated absences (surveys with zero count) in sites where a species had at least one count for all other years in which the site was surveyed, but the species was not recorded. This way, our data represented the sites in which abundance changed or remained stable, removing the sites where the species was never observed.

To account for differences in sampling design among contributing survey schemes, we standardized the count data for each species by dividing counts by the standard deviation of counts across years for each survey scheme and species[78]. We did not subtract the mean, as is common in data standardization, to keep all count data positive and to intepret results like those of usual Poisson models for abundance data. The resulting standardized counts represent relative abundance at the level of each survey scheme.

Bird vegetation-based habitat associations

We assigned species to a habitat association group based on species-specific habitat ecology from AVONET and Birds of the World Online[79,80]. We created three categories of vegetation structure that birds can be associated with (Supplementary S1.2). First, “forest,” which included the species specifically associated with mature forest and woodland vegetation structure (n = 44). Second, “shrubland and edge” (n = 30), which included species associated with shrubs, individual trees, or small woody cover formations in mostly open habitats. Third, “open” (n = 33), which included species associated with purely open vegetation structures with nearly no woody vegetation or only low shrubs (Figure S1).

Canopy gap data

The European Forest Disturbance Atlas V2.1.1[3] has mapped annual stand replacing forest disturbances (>0.5 ha) from 1985 until 2023 at a 30m resolution, based on Landsat satellite imagery. It does not map disturbances that are not stand-replacing, such as drought-induced individual tree mortality. In the EFDA, and our study, forest cover is defined as the maximum extent of forested areas between 1985 and 2023. We used the EFDA data to quantify the annual percentage of forest disturbance area in a 1,500 m radius buffer around the centroid of each PECBMS site (see Survey sites).

Disturbance regimes differ strongly across the study region (Supplementary S1.3). The size of disturbances based on area of canopy gaps is generally larger in Fennoscandia, the British Isles and the Iberian peninsula; whereas the disturbance frequency measured as the number of disturbances per area and year is highest in the west of France and the west of the Iberian peninsula; and the frequency has been increasing in most of Europe[11,13].

We applied two measures to correct potentially wrongly identified canopy gaps. First, because of cloud cover and a limited number of satellite images in certain years, some disturbances were not mapped until several years after the disturbance event. To capture all canopy gaps belonging to a certain year, we defined the percentage of forest affected by disturbance as a three-year rolling sum. A three-year window was chosen because satellite images were rarely missing for more than three consecutive years, ensuring that the data remained both dependable and temporally dynamic. Second, the EFDA classification model can predict false positive forest cover and canopy gaps on wetlands, especially peat bogs in flat areas of Fennoscandia and the Baltic states. To correct these commission errors, we masked out forest canopy gaps in inland marshes, peat bogs, and salt marshes derived from CLC 2000 for canopy gaps from 2002 and earlier, CLC 2006 (for the period 2003–2008), CLC 2012 (2009–2014), and CLC 2018 (2015–2022). To avoid retaining highly unrealistic disturbance estimates, we removed any disturbance records in which the EFDA maps showed more than 500 ha of canopy gaps across the study period, while the CLC showed no forest cover in any available year.

Analysis

All data processing, analysis, and visualization were performed in the statistical software R[81] (v4.1.2).

Species-level models

We fitted a generalized linear mixed model (GLMM) for abundance of each bird species using the *sdmTMB* R-package[82] (v0.7.4; see Supplementary 1.4 for details). Models were fitted with a Tweedie distribution with a log-link function that accommodates non-normal data which includes many zeroes and positive continuous values, which characterized our scaled count data.

We assessed the effect of canopy gaps on changes in species abundance by fitting the following model for each species (1):

$$(1)\ count_{i,t} \sim disturbance\ 0-5_{i,t} * forest\ cover_i + disturbance\ 6-11_{i,t} * forest\ cover_i + disturbance\ 12-17_{i,t} * forest\ cover_i + (1|site_i)$$

The annual (subscript t for year) scaled counts of each species at each site (subscript i for site) were used as the response variable (see *Bird abundance data* section). The area of disturbances (with <6, 6-11, and 12-17 years since disturbance) as a percentage of total buffer area were included as predictors interacting with forest cover as a percentage of the total buffer area. The model also included a spatial random field (modeled as a Gaussian Markov random field over site coordinates) and a spatiotemporal random effect with a first-order autoregressive (AR1) structure across years to control for potential spatial dependence among nearby sites and temporal autocorrelation among years.

To examine responses both at the continental and regional scales, we fitted a maximum of four models per species: one model including all data (i.e., continental scale) and one model for each possible region (northern, mid, and southern latitudes). To ensure sufficient data were available for modelling, we did not fit a model if fewer than 30 records were available for a species in each region (n = 351 models to fit).

After fitting all models, we checked variance inflation factors and confirmed that all were below 5. We excluded all models that had remaining technical issues or explained less than 10% of the deviance (67 models excluded, 284 models remaining for 99 species; Supplementary S1.5).

We then predicted the effects of disturbances of different ages at three levels of the maximum forest extent from the EFDA (15%, 50%, and 85%) and extracted the estimates of the nine predicted effects, along with their standard errors and 95% confidence intervals (Figure S3). Predicted effects were considered significant if the 95% confidence intervals did not overlap zero.

Habitat association trait-group responses

We quantified the average effect of canopy gaps on species abundance, grouping species by their habitat association. First, for each species, we used the slope estimates of the nine predicted effects and their standard errors corresponding to the disturbance effect of the three times since disturbance (0-5, 6-11, and 12-

17 years) and the three levels of forest cover (15%, 50% and 85%). Next, we modeled how the slope estimates of the disturbance effect varied with the time since disturbance and vegetation association group (open, shrubland and edge, and forest vegetation). To do this, we fitted, for each forest cover level, a gaussian linear model with the interaction between species' habitat association and the canopy gap age as predictors:

$$(2)\ \ effect \sim time\ since\ disturbance * habitat\ association$$

To account for uncertainty in the species-level models, we applied a weighted regression using the inverse of the squared standard error of the slopes of the disturbance effects as weights[83]. This approach reduces the influence of highly uncertain slope estimates. We then extracted the marginal effects of species traits and time since disturbance on the disturbance response from the fitted models (see model validation and performance in Supplementary S1.6).

Artificial Intelligence Generated Content

Large Language Models were used for minor text edits to the abstract, to automate the application of the R code for the technical validation across all models, and to generate images of post-disturbance succession and landscape forest cover in figure 1.

Declarations

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Data availability statement

All code and processed environmental data are available on the CORA Research Data Repository from the Consortium of University Services of Catalonia, CSUC (DOI UPON PUBLICATION: https://doi.org/10.34810/data3199). Bird data is available upon request from the PECBMS repository (www.pecbms.info). The European Forest Disturbance Atlas v2.1.1 is publicly available (https://zenodo.org/records/13333034). The AVONET trait database following the Birdlife taxonomy is freely available (https://opentraits.org/datasets/avonet.html). The Environmental Stratification of Europe is publicly available (https://sdi.eea.europa.eu/catalogue/idp/api/records/6ef007ab-1fcd-4c4f-bc96-14e8afbcb688). The Corine Land Cover data is publicly available (https://land.copernicus.eu/en/products/corine-land-cover). European Breeding Bird Atlas species classification is publicly available (https://ico.ams3.digitaloceanspaces.com/ebba2/final_website/docs/EBBA2%20Book%20Appendix%202.xlsx).

Author contributions

TB: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Validation, Writing – Original Draft, Writing – Review and Editing; **LB:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Supervision**,** Writing – Review and Editing; **SR:** Data curation, Formal analysis, Investigation, Methodology, Validation, Writing – Review and Editing; **CF, AVS:** Data curation, Methodology, Writing – Review and Editing; **NS:** Data curation, Formal analysis, Validation, Writing – Review and Editing; **GP:** Formal analysis, Investigation, Methodology, Validation, Writing – Review and Editing; **MM, EPP:** Formal analysis, Investigation, Methodology, Writing – Review and Editing; **YX:** Formal analysis, Validation,Writing – Review and Editing; **AA, MPB, MB, TC, VE, BF, AG, SH, JH, IH, JK, ALe, ALi, DPE, JR, TSz:** Data curation, Writing – Review and Editing; **DPJ, TP, IR, BS, TSa:** Funding acquisition,Writing – Review and Editing

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Figures

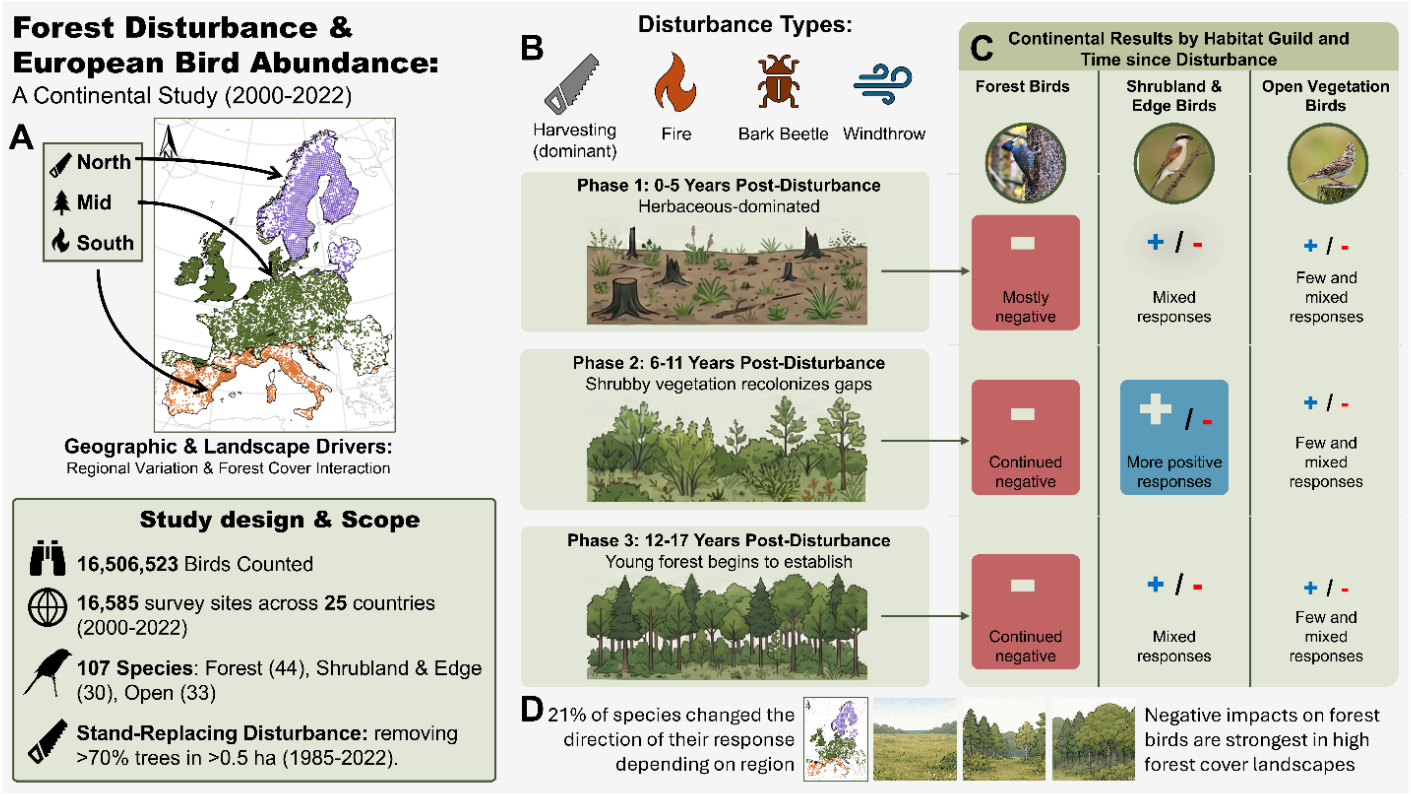


Figure 1

Graphical abstract. This graphical abstract shows the main study design and results of the study. **(A)** the map of the 16,585 study sites and the three regions (North – purple, mid – green, and South - orange). The total study area is indicated by the areas with a black outline in the map. In the bottom left, an overview of the bird and disturbance data used. **(B)** In the center column, the main types of disturbances (the dominant harvest and the natural disturbances fire, bark beetle and windthrow), and the expected analogous ecosystem structure after disturbance. **(C)** a summary of the general patterns in the responses of bird abundance to forest disturbances. **(D)**, the main patterns for different response directions between regions within species and the importance of forest cover in mediating the strength of the effects of disturbance. Bird pictures: *Dryocopus martius* by H. Yamaguchi on Wikimedia Commons CC-BY2.0, *Lanius collurio* by Antonios Tsaknakis on Wikimedia Commons CC-SA4.0, *Alauda arvensis* by Caroline Legg on Wikimedia Commons CC-BY2.0. Ecosystem structure and forest cover drawings generated using AI for this study.

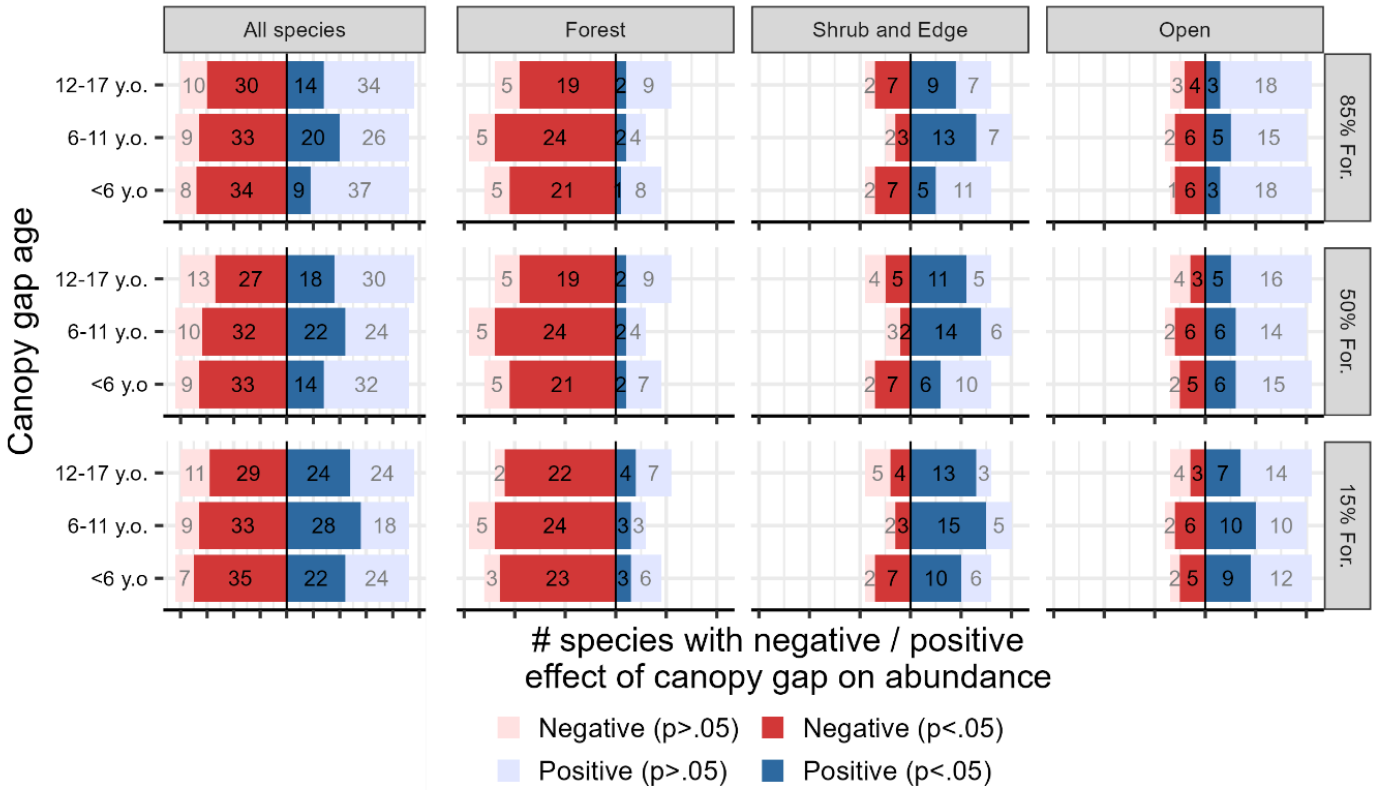


Figure 2

Species responses to canopy gaps. The number of species for which forest canopy gaps had a positive (blue, right of x-axis) or negative effect (red, left of x-axis) on the abundance trend of the species. Dark colors indicate that the effect was significant (with p<0.05) and light colors that the effect was non-significant (with p>0.05). The number of species for each category is written in the respective bar. The y-axis indicates the time since the occurrence of the canopy gap. The facet rows indicate forest cover in the buffer around the site and the facet columns indicate the groups of habitat associations (see Figure S1 for associated vegetation structures).

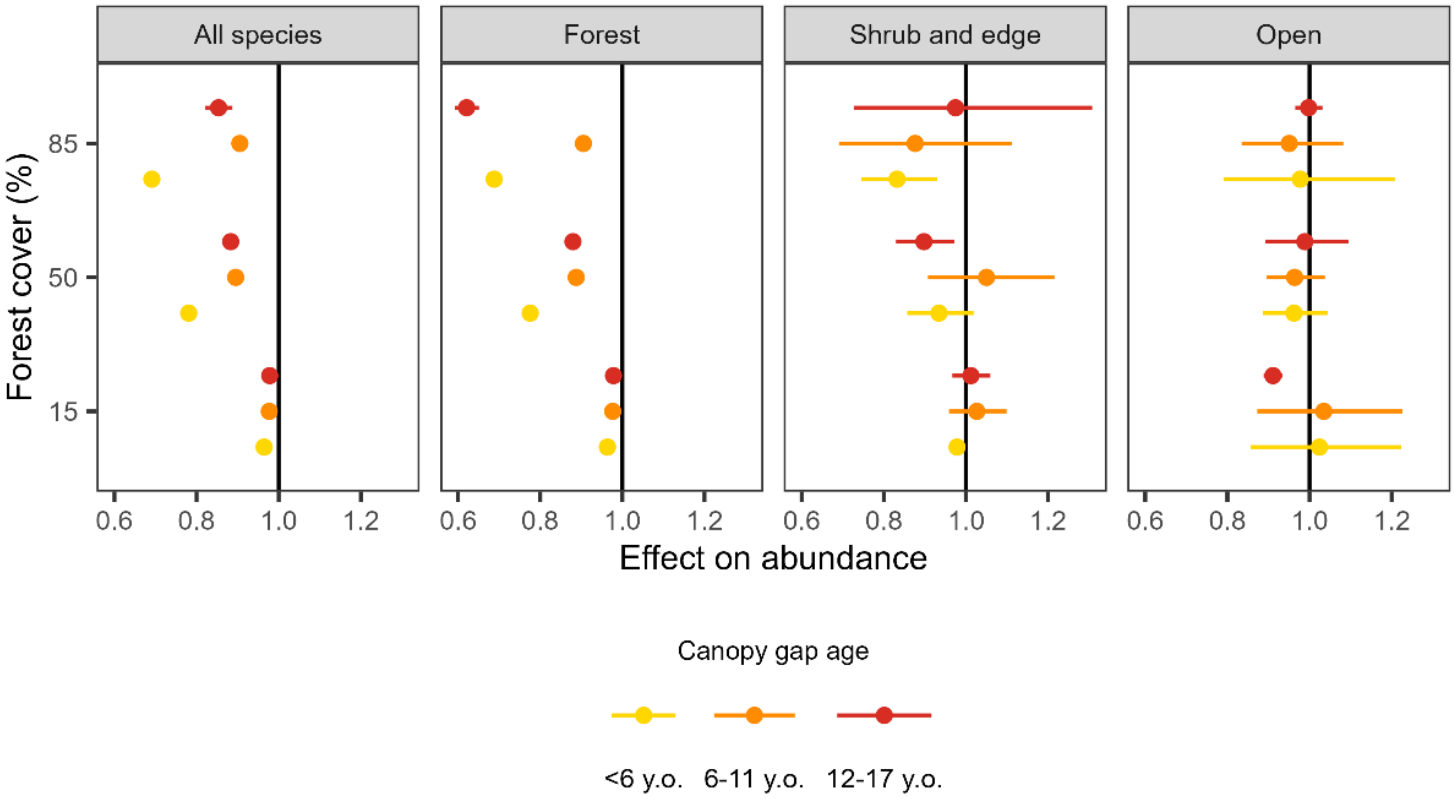


Figure 3

Weighted effects of canopy gaps of different ages on overall and habitat-specific bird abundances. Weighted average and 95% confidence intervals of the effect of canopy gaps of different ages on abundances of all species as well as the species grouped by their habitat association. Points indicate average effect; horizontal lines indicate 95% confidence intervals; colors indicate time since disturbance.

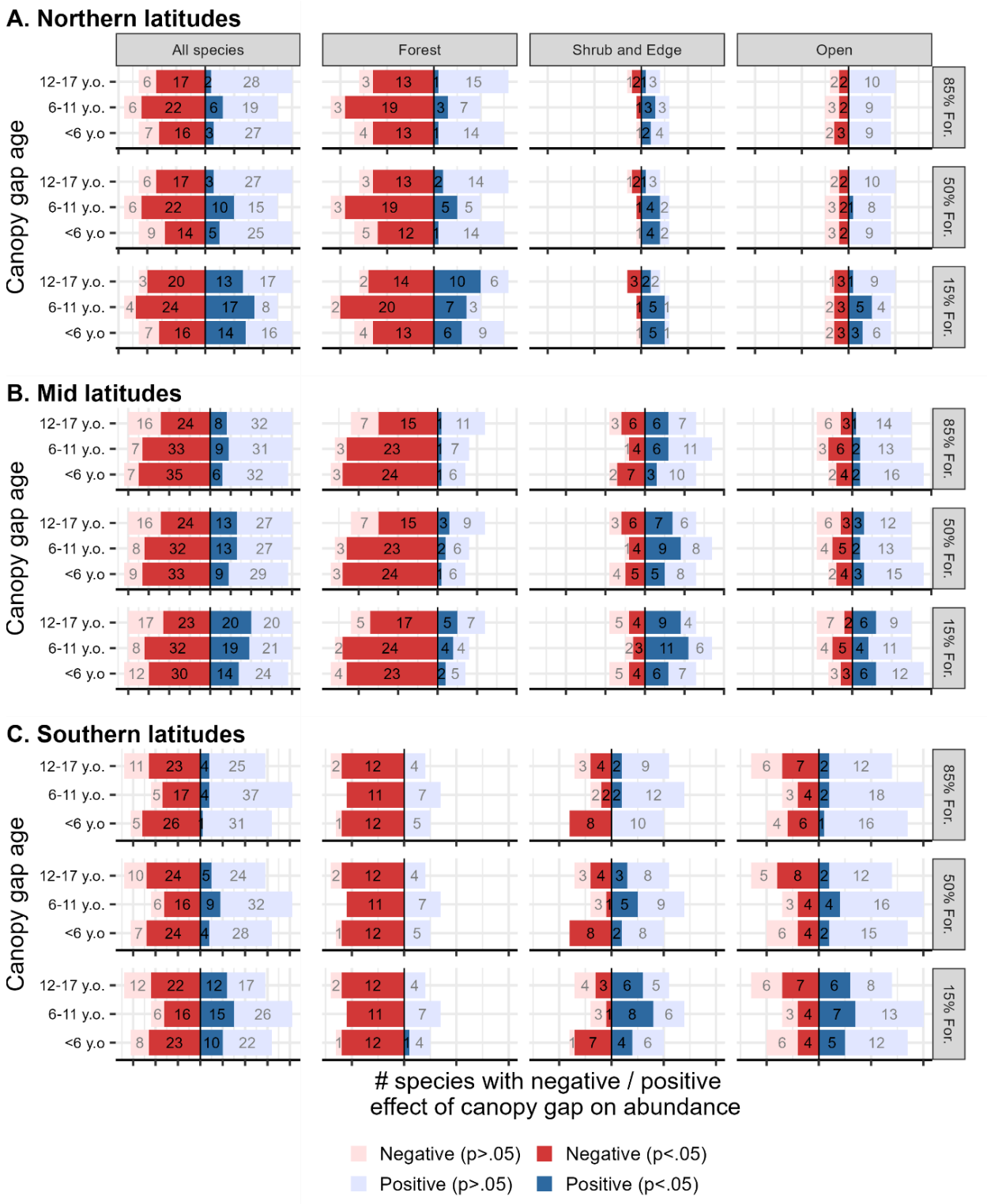


Figure 4

Regional species responses to canopy gaps. (**A-C**) The number of species for which forest canopy gaps had a positive (blue, right of x-axis) or negative effect (red, left of x-axis) on the abundance trend of the species. Dark colors indicate that the effect was significant (with p<0.05) and light colors that the effect was non-significant (with p>0.05). The number of species for each category is written in the respective bar. The y-axis indicates the time since the occurrence of the canopy gap. The facet rows indicate the forest cover in the landscape and the

facet columns indicate the groups of vegetation structure associations (see Figure S1 for associated vegetation structures). (**A**) northern latitudes, (**B**) mid latitudes, (**C**) southern latitudes.

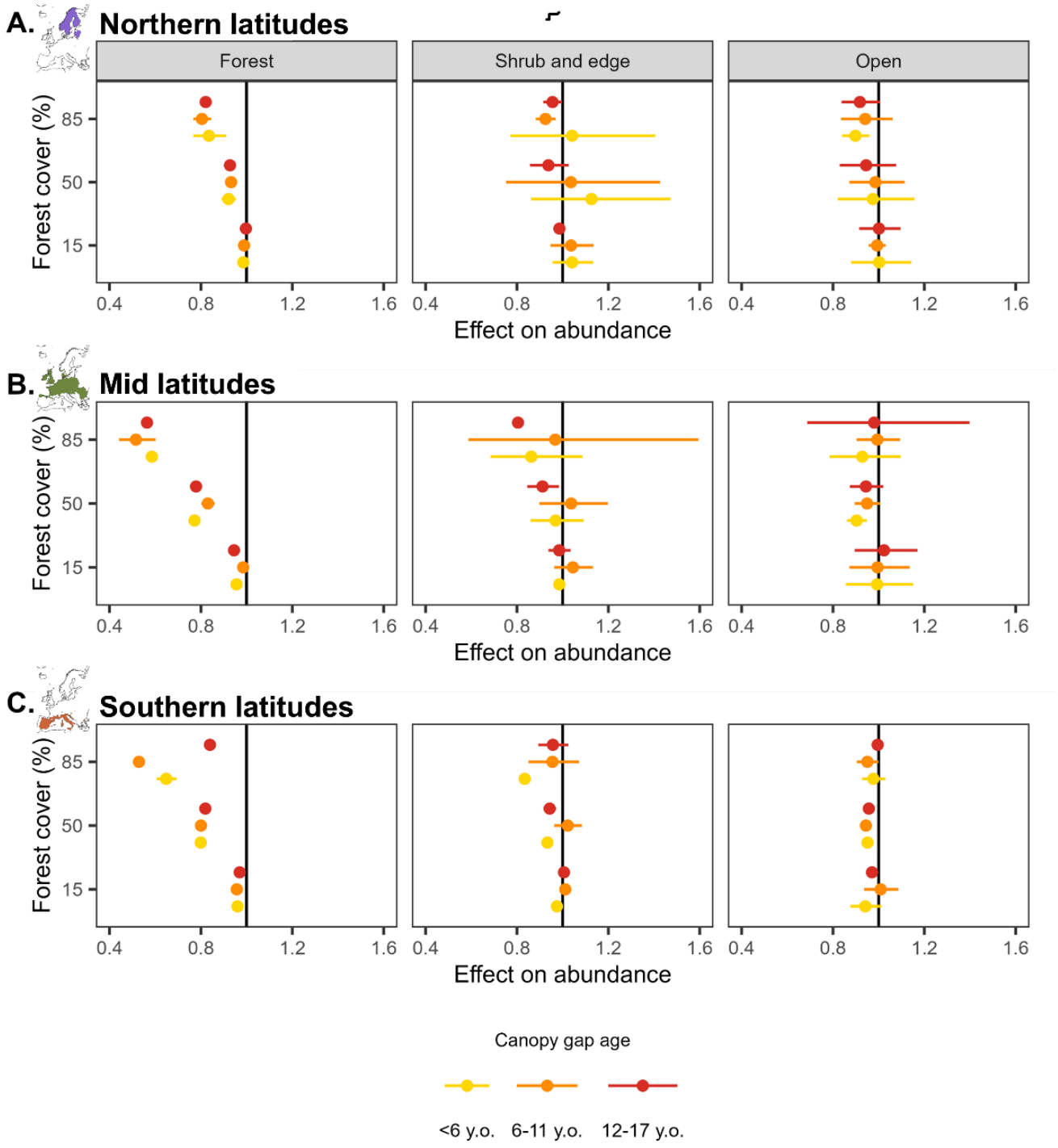


Figure 5

Species responses to canopy gaps by region and vegetation structure guilds. Forest plot of the predicted effect of species vegetation structure association on species relationships with the area of disturbance (Forest cover, %, vertical axes) of different ages (legend color) per region (rows). The species are grouped into three

groups depending on their vegetation preference (columns). Points indicate average estimated effect; horizontal lines indicate 95% confidence intervals.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- ForestDisturbanceeffectsonBirdsSupplementaryS2.xlsx
- ForestDisturbanceEffectsonBirdsSupplementaryS1.docx