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RESEARCH ARTICLE

Impacts of clearcut accumulation on boreal forest bird communities: Defining a safe operating space at the landscape level

Rémi Duflot[1,2] | Jenna Rönttinen[1] | Aleksi Lehikoinen[3] | Mikko Mönkkönen[1,2] | Jérémy Cours[1,2,4]

[1]Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland

[2]School of Resource Wisdom, University of Jyväskylä, Jyväskylä, Finland

[3]LUOMUS Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland

[4]Unité de Recherche de Zoologie Forestière (URZF), INRAE, Orléans, France

Correspondence
Rémi Duflot
Email: remi.r.duflot@jyu.fi

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Abstract

1. Intensive management based on clearcut harvesting is a major threat to forest biodiversity globally. However, it remains unclear how the long-term accumulation of clearcuts at the landscape level affects biodiversity and what the maximum level of clearcutting that forest species can tolerate is, that is the safe operating space. We aim to evaluate the impact of the accumulation of clearcutting areas over time on bird communities in the intensively used forest landscapes of southern Finland and to define an ecological boundary for forest species in this region.
2. Based on the Finnish bird monitoring line transects (2006–2020), we related species richness and the abundance of the overall community and of species groups based on habitat affinity and Red List status with the accumulated area and mean size of clearcuts in the 5 and 20 years prior to bird observations. A trend analysis was conducted on a subset of transects with sufficient data to define a threshold of clearcut accumulation below which the abundance of forest species does not decline.
3. Clearcuts benefited open-habitat species, including common farmland and mire threatened species. However, the 20-year accumulation of clearcuts had negative impacts on common forest species and old-growth forest specialists. The analyses of temporal trends showed that a maximum of 9.6% of the landscape should be clearcut in 10 years to maintain or allow the recovery of old-growth forest specialists. Such a safe threshold corresponds to a rotation time of 91 years and indicates that at least 20% of forest areas should not be used in clearcutting management.
4. *Synthesis and applications.* Although clearcuts can benefit open-habitat species, they should be limited to avoid declines in mature- and old-forest species. By defining a safe limit in clearcut areas, we provide a readable target for ecologically sustainable forest use and a methodology that translates to other regions globally. However, such thresholds should be applied critically, as they are potentially context-dependent and would require validation with multi-taxa analyses.

KEYWORDS
avian community, biodiversity, ecological ceiling, Fennoscandia, forestry, silviculture, sustainable forest management, sustainable harvesting rate

1 | INTRODUCTION

Forest ecosystems and the biodiversity they host are threatened by human exploitation and climate change. While deforestation dominates in South America and Asia and wildfires concentrate in northern Canada and Siberia, forestry is the main cause of forest loss in Europe and North America (Curtis et al., 2018; Masek et al., 2011; Seidl & Senf, 2024). In such production landscapes, forest cover remained relatively stable (and might even have slightly increased in some areas), as losses are compensated by gains from forest regrowth and afforestation (Hansen et al., 2013). In these regions, the forestry sector follows the principles of economically sustainable forest use to ensure the renewal of the natural resource and the continued long-term wood supply (Rytteri et al., 2016). Yet, in these landscapes, human activities (i.e. forest management) have replaced natural disturbances as a driver of landscape dynamics, shaping forest ecosystems to forestry needs by homogenizing forest structure, modifying tree species composition and altering the distribution of forest age classes (e.g. Kuuluvainen & Gauthier, 2018). These widespread modifications to forest ecosystems have consequences for biodiversity. For instance, forest bird abundance and their habitats significantly declined in boreal Europe and eastern Canada (Betts et al., 2022; Lehikoinen & Virkkala, 2018). Such forest degradation will likely continue or even accelerate as global timber demand increases due to the development of the bioeconomy (FAO, 2024; Subramanian et al., 2025).

Increasing demand for timber will likely result in the expansion of forestry into still relatively well-preserved areas—particularly within the boreal biome, which hosts most of the remaining intact forests globally (Watson et al., 2016)—or in the intensification of already managed forests. However, in Europe and North America, most of the productive forest lands are already used for timber production or protected (Gustafsson et al., 2025; Marsik et al., 2018; Nagel et al., 2024). Therefore, there is a high risk that intensive forest management based on clearcutting (aka rotation or even-aged forestry) and the planting of fast-growing tree species will expand.

Since the 1950s, clearcutting has been a dominant silvicultural system in many European and North American regions, such as Fennoscandia, eastern Canada, northwestern and southeastern United States (Boucher et al., 2009; Marsik et al., 2018; Mönkkönen et al., 2018; Phalan et al., 2019), and elsewhere, including Australia (Lindenmayer, 2016). However, regions such as Central Europe have used a combination of clearcutting and various forms of continuous cover forestry (e.g. selection cutting, uneven-aged forestry), while mountainous areas often avoid clearcutting (Marsik et al., 2018; Nagel et al., 2024; Suvanto et al., 2025).

Clearcutting is a harvesting method where (nearly) all trees are felled at the same time, causing an abrupt change in the forest ecosystem that may have both short- and long-term and local- and landscape-level impacts on biodiversity (Lunde et al., 2025). By creating openings in the canopy, clearcutting alters local microclimatic conditions within the forest, affecting temperature, humidity, wind, and the physical and chemical compositions of soils, thus causing cascading effects on species at the local level (Landmann et al., 2023; Lunde et al., 2025; Zellweger et al., 2019). For instance, in boreal forests, temperatures remained warmer in summer after clearcutting for an average of 30 years compared with non-cleared forests (Starck et al., 2025). Consequently, a combination of clearcuts and warming summers caused forest bird populations to decline in a southern boreal landscape (Virkkala et al., 2023). Canopy gaps allow more sunlight to penetrate to the forest floor, stimulating the growth of understorey plants; in turn, these resources may attract animals, such as butterflies, various pollinators, farmland birds and other herbivores (Hilmers et al., 2018; Ram et al., 2020; Rodríguez & Kouki, 2017; van Halder et al., 2011). However, forests regenerating after clearcutting (often planted) are significantly different from those resulting from natural disturbances, for example a lack of deadwood and large old habitat trees, which are needed by many saproxylic species, among others (Heikkala et al., 2016; Nonaka et al., 2007). Furthermore, the even-aged forest structure following clearcutting is more homogenous than naturally regenerating forest (including understorey plant communities) and lacks the habitat complexity needed to support ecological diversity, including reduced and modified tree species composition and little variation in tree age and size (Boucher et al., 2009; Lunde et al., 2025; Mönkkönen et al., 2022; Scheller & Mladenoff, 2002).

At the landscape level, clearcutting modifies habitat composition and configuration. First, when applied widely in a landscape, clearcutting reduces the area of old forests and replaces them with managed young forests lacking natural post-disturbance structural legacies (Betts et al., 2022; Kuuluvainen & Gauthier, 2018; Lunde et al., 2025). The loss and fragmentation of old forests negatively affects many species that depend on them, such as fungi, lichens, bryophytes, insects and birds, especially endangered species (Aune et al., 2005; Lunde et al., 2025). Second, clearcutting also affects species communities in nearby forests through edge effects, for as long as 50 years (Lunde et al., 2025; Ruete et al., 2016). By modifying light and the microclimate up to 200 m within adjacent forests (Landmann et al., 2023), edges substantially reduce the area of core forest habitats (Aune et al., 2005). For instance, Määttänen et al. (2023) found that higher levels of logging around protected areas increase the temperature index of their bird community, showing that the local effects of clearcuts on the microclimate translate to a larger scale and aggravate the effect of climate change. The

edge effect might be particularly significant as management usually generates patchier landscape mosaics compared with unmanaged landscapes—that is clearcutting creates many sharp edges between small forest management units (Kuuluvainen & Gauthier, 2018).

It is still not clear how the accumulation of clearcuts in space and time affects overall forest species communities at the landscape level (Landmann et al., 2023; Lunde et al., 2025). The dual effect of clearcutting on habitat heterogeneity—that is increased early successional stages to the detriment of old and complex forests—leads to contrasting effects on species communities with different habitat requirements (Savilaakso et al., 2021). There is evidence that clearcutting reduces the local species richness and affects the species composition of many taxa in the long term (e.g. see the review of Lunde et al., 2025 and the meta-analysis in Landmann et al., 2023). Clearcutting rotation time (RT) is usually (much) shorter than the return intervals of natural disturbances; therefore, repeated clearcutting hinders the recovery of most key habitat features (Berglund & Kuuluvainen, 2021; Schütz et al., 2016; Venier et al., 2014). However, these effects have so far been mostly evaluated at the local level. Moderate areas of clearcuts in a landscape may enhance habitat heterogeneity and overall landscape-level (gamma-) biodiversity, while an excessively large area may be detrimental to species associated with complex, mature and old forests.

Defining the maximum accumulated area of clearcuts that forest ecosystems and species can tolerate in a landscape would provide an important guideline for the ecologically sustainable use of forests. Such a limit to timber resource use would set a practical and accountable policy target and apply the principles of planetary boundary and safe operating space to forestry (Mönkkönen et al., 2025). Planetary boundaries represent ecological limits below which the impacts of human activities on key Earth system processes remain low, thereby maintaining a 'safe operating space' for humanity (Rockström et al., 2009; Steffen et al., 2015). By contrast, overshooting boundaries corresponds to a high risk of destabilizing ecosystems, their functions and their contribution to human well-being. Biodiversity loss (or biosphere integrity) is one of the boundaries. However, this boundary is difficult to set because biodiversity loss is a slow process that does not readily scale up or down from local to global (Mace et al., 2014). It has been suggested that the concept be operationalized to ecological limits for specific human activities and geographic areas, for example the forestry sector in boreal Europe (Mönkkönen et al., 2025). Due to their fundamental impacts on forest ecosystems and species, we considered the area of clearcuts in a landscape as a relevant control variable (sensu Mace et al., 2014; Steffen et al., 2015) for biodiversity loss in boreal production forest landscapes.

The purpose of this study was to evaluate the impacts of clearcutting area accumulation over time on bird communities in the intensively used forest landscapes of southern Finland. Due to its long history of clearcutting, the Nordic countries are an ideal region to test the effects of clearcuts on forest ecosystems. Since the 1950s, even-aged forestry, based on clearcutting, thinning and replanting, has been the dominant form of forest management on a substantial proportion of productive forest land in these countries, with negative consequences for biodiversity (Gustafsson et al., 2025; Mönkkönen et al., 2018). For instance, in Finland, over 75% of forest habitat types are threatened (Kouki et al., 2019) and forests are the primary habitat for 31% of threatened species (Hyvärinen et al., 2019). We focus on bird species because, although common forest birds have remained relatively stable in Europe (Gregory et al., 2019), populations of forest specialists have declined, especially in the boreal zone (Cours et al., 2025). In addition, some birds associated with open habitats (e.g. farmland birds are declining in Europe [Rigal et al., 2023]) may benefit from clearcuts (e.g. Bakx et al., 2020). Forest birds are also good indicators of the dynamics of forest landscape mosaics, being sensitive to changes and reacting quickly to them (Harris & Betts, 2021). Finally, long time series with many replicates are available, allowing us to study the impact of clearcuts on long periods.

We used two analytical approaches: (i) a static approach (yearly bird observations) analysing the influence of landscape metrics describing the effect of land cover and clearcut accumulation on the richness and abundance of different bird guilds, (ii) a trend analysis (time series of bird observations) where we focused on the rate of changes in biodiversity over time and on defining safe thresholds of accumulated clearcut area for forest species. More specifically, we aimed to answer the following questions:

1. How do the accumulated area and spatial pattern of clearcuts affect bird communities beyond the influence of overall landscape composition?
2. Does the response vary between groups of species with different habitat preferences, Red List status and specialization levels?
3. Is there a threshold of accumulated areas of clearcuts in a landscape above which forest species abundance starts declining?

2 | MATERIALS AND METHODS

2.1 | Study area and forestry in Finland

Due to its long history of intensive forest management, Finland provides a good opportunity to study the effects of the accumulation of clearcuts over time on biodiversity. In particular, the southern parts of Finland have a long history of intensive forest management (Mönkkönen et al., 2022). Therefore, we focused our study on the hemiboreal and southern boreal vegetation zones (Figure 1). Forests cover 65% of the total land area in the region. Since the 1950s, even-aged forestry with clearcuts and plantations has been the dominant management system, involving a rotation cycle of 60–90 years with one to three thinning operations (depending on soil fertility; Äijälä et al., 2019; Mönkkönen et al., 2018). Despite legal reforms in 2014 allowing greater variation in management systems, over 90% of commercial forests are still managed with even-aged rotation forestry (Kulju et al., 2023).

2.2 | Biodiversity data and response variables

The bird observation data came from Finnish bird monitoring conducted on standardized line transects in Finland since 2006 (Virkkala & Lehikoinen, 2014). As we used existing data, this study did not require animal ethics approval, and no fieldwork were conducted. The method consists of a one-visit census in late May to mid-June in southern Finland, early morning (usually from 4 to 9 AM), where all pairs of birds are counted along a transect with a typical length of 6 km. The line of the transect is a preset loop following a rectangle shape of 2 km (south–north orientation)×1 km (east–west orientation), although the exact shape varies depending on geographical features, such as lakes or urban areas. Along each transect, all pairs of birds are counted within the first 25 m on each side of the line transect—that is the main belt—and beyond 25 m, as far as it is possible to identify a bird species—that is the supplementary belt. We used the combination of both belts in our present study—that is the survey belt.

The monitoring programme uses 566 transects systematically distributed across the country at about 25 km apart from each other (Lindström et al., 2019; Virkkala & Lehikoinen, 2014). Not all transects are visited every year. We selected the transects located in the hemiboreal and southern boreal zones (Figure 1), so that the bird communities would be comparable across the study area. In addition, to control for the overall landscape composition, we focused on forest-dominated landscapes by selecting transects surrounded by at least 60% forest cover (based on the three spatial scales analysed; see landscape metrics below). As a result, we used bird observation data from 858 visits across 144 transects (i.e. ~6 revisits per transect on average; Figure 1).

We calculated species richness and abundance of the overall community (i.e. all terrestrial species, excluding marine and coastal bird species) and of species groups based on habitat affinity and Red List threat status (see the list of species and associated traits in Table S1). We calculated the abundances of common breeding farmland (13 species), mire (16 species) and forest (33 species) birds using the list of indicator species for Finland (Fraixedas et al., 2017; Lehikoinen, Auvinen, et al., 2024; Table S1), as well as the richness and abundance of old-growth forest specialists (26 species; Fraixedas et al., 2015; Mönkkönen et al., 2014). We also measured the richness of threatened open-habitat, wetland and forest species, totalling 26, 32 and 11 species, respectively, including species classified as Near Threatened, Vulnerable, Endangered and Critically Endangered on the Red List (Hyvärinen et al., 2019). We used the habitat preference classification from Tobias et al. (2022). Finally, we calculated the community-weighted mean (CWM) of the species human tolerance index developed by Marjakangas et al. (2024) and of the species habitat specialization index developed by Le Viol et al. (2012). Abundances were calculated as the number of breeding pairs along each transect. Species bird abundances were corrected for differences in detectability using species-specific correction coefficients (Virkkala & Lehikoinen, 2014). Correction coefficients are based on the distance of sampling, using the proportion of bird observations made inside the main survey belt (<25 m on both sides of the transect lines) relative to the total number of observations. Therefore, the correction coefficient applies a penalty for species that can be detected from a greater distance than other species (Järvinen & Väisänen, 1983). The mean values and range of variation of the biodiversity variables are presented in Figure S2.1.

In addition to the approach based on yearly biodiversity surveys (hereafter static)—that is biodiversity level in a specific year—we performed a trend analysis based on biodiversity changes over time. A trend approach better represents the dynamic response of bird communities to landscape changes. It also provides readable measures of biodiversity change, whereby positive and negative trends can be directly interpreted as being within the safe or high-risk zone of change, respectively (sensu planetary boundaries; Steffen et al., 2015).

We used the *ptrend* and *change* function from the package *poptrend* (Knape, 2023) in R (version 4.5.1; R Core Team, 2025) to calculate biodiversity trends over time for the 96 transects with at least five revisits (5 years of bird observations) spanning at least 10 years between 2006 and 2020 (i.e. time series). We focused on measuring the annual rate of change, that is the overall percentage change over the whole time series divided by the number of years. We evaluate the rate of change in the abundance of common farmland, mire and forest species, as well as the abundance and species richness of old-growth forest specialists and richness of threatened farmland, wetland and forest species. The *ptrend* function uses GAM, including time (i.e. year in our study) as fixed and random variables. We applied a quasipoisson data distribution for both abundance and species richness metrics. From the GAM, the *change* R function estimates the percentage change (and it 95% CI) in the biodiversity variable between two given time points (i.e. the first and last year of revisits in the time series for a given transect), which we divided by the number of years of the time series, as they varied slightly across transects.

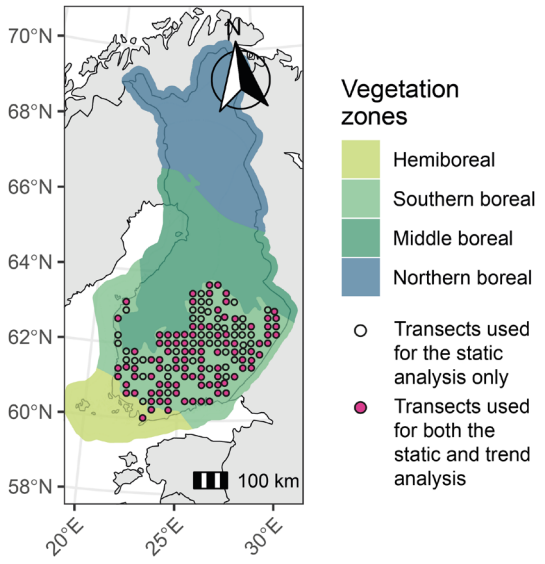

FIGURE 1 The 144 transects included in the study (circles), located in the hemiboreal and southern boreal vegetation zones in Finland. Pink-filled circles represent the 96 transects selected for trend analysis.

2.3 | Landscape metrics: Clearcuts and land cover

Landscape metrics of accumulated clearcuts and land covers were calculated for all transects at buffer distances of 100, 500 and 2000 m (hereafter, landscape scales). For a 6-km-long transect, these distances correspond to landscapes of about 1.2, 5.8 and 26 km^2, respectively. We used the *landscapemetric* package in R, along with parallelization in the supercomputer facility of the IT Center for Science (CSC; csc.fi), to speed up the calculations.

Clearcuts were identified using the European map of disturbances by Senf and Seidl (2021a, 2021b), which is based on Landsat satellite imagery from 1986 to 2020. The map characterizes disturbances through forest disturbance type (i.e. biotic or abiotic), year of occurrence and severity (percentage of damage), using changes in Normalized Difference Vegetation Index (NDVI) at a pixel resolution of 30 m. Biotic disturbances strongly dominate in Finland and reflect human-induced disturbances, mostly representing clearcuts (Määttänen et al., 2022; Seidl & Senf, 2024; Senf & Seidl, 2021b).

We extracted the pixels corresponding to biotic disturbances with damage severity greater than 80%, thereby excluding thinning operations but including clearcutting with green tree retention, and measured their accumulated areas at different spatial (landscape) and temporal scales. Clearcut pixels were accumulated over the 5, 10, 15 and 20 years preceding the bird observation data, representing short-, mid- and long-term impacts. Accumulating clearcuts over time is relevant because species respond to long-term habitat changes, not single-year events and clearcuts have effects beyond the time of occurrence (Virkkala et al., 2025). Metrics of clearcut accumulation are equivalent to measures of the current area of forests that are less than 5–20 years old, respectively. For each accumulation period, adjacent pixels were merged into patches through a raster-to-shapefile transformation. To obtain more cohesive clearcut patches with smoother edges, we performed a dilation–erosion process, aka morphological closing (Soille, 2004). First, patches were expanded by 30 m (buffer), that is the size of one pixel, to merge patches separated by only one pixel and fill in small gaps (non-clearcut pixels surrounded by clearcut pixels). Second, patches were reduced by 30 m (negative buffer). In addition, any patches of less than three pixels (i.e. patches <0.27 ha) were deleted, as such small forest losses may not be considered as clearcuts but part of gaps of partial logging.

For the static analyses, we calculated the accumulated proportion of clearcut area and the average size of clearcut patches for each transect, landscape scale, time period (5, 10, 15 and 20 years preceding the bird observation data) and bird observation years (Figure 2). For the trend analysis, the same method as for the static analyses was used. However, we calculated only the 10-year accumulation of clearcuts finishing in the year of the last revisit of the time series, corresponding to the period for which the rates of change in biodiversity variables were evaluated.

To reflect the general landscape context, basic land-cover metrics were calculated, in addition to the clearcut measurements (Figure 2). We used the COoRdination of INformation on the Environment (CORINE) land-cover raster layers from 2006, 2012 and 2018 (Source: SYKE, Finnish Environment Institute), assigning bird observation data to the closest year available. We used classification level 1: water, urban area, cropland, wetland, grass and moorland, forest and woodland scrub. Forest and woodland scrub were later combined as an overall forest area because, in Finland, the

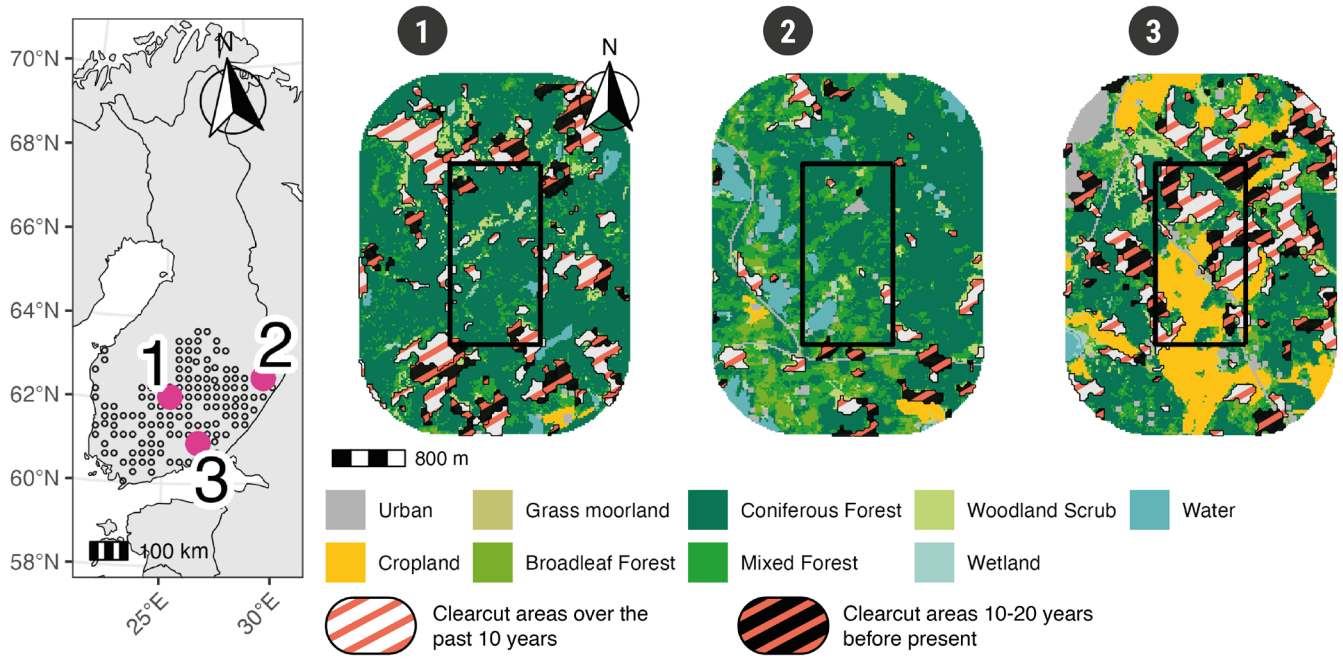

FIGURE 2 Map of clearcuts and land covers for three landscapes with: (1) high threat (i.e. low abundance and negative trend), (2) suitable (i.e. high abundance and positive trend) for old-growth forest specialists and (3) suitable for common farmland bird species (i.e. high abundance and positive trend). The black squares represent the line transects.

woodland scrub category represents the early succession stages of forest. Land-cover type proportions, as well as the Shannon diversity index based on these proportions, were calculated for each transect and landscape scale. We also removed the proportion of grass and moorland from the analyses since their values were very low—that is a maximum 7% area around a transect at the 500 m scale.

Ultimately, we inspected correlations across landscape metrics within each spatial scale to select only independent, uncorrelated ones for statistical modelling. For pairs or groups of landscape metrics with correlations equal to or greater than 0.7 (Spearman correlation index), only one was selected, keeping in priority the metric of interest for the research questions (see Figure S2.2). For example, clearcut accumulation and the average size over the past 10 and 15 years and the Shannon diversity index at all scales were excluded to keep clearcut accumulation metrics at 5 and 20 years and the different land-cover proportions.

2.4 | Analyses

The relationships between bird community response variables and landscape metrics were analysed through generalized linear mixed models (GLMMs; Brooks et al., 2024). Landscape metrics were centred and scaled, that is subtracting to mean and dividing by their standard deviation, allowing direct comparison of model coefficients (effect size) across landscape metrics with different units and ranges of values. The models included the species richness or abundance of a bird ecological group as a response variable, all landscape metrics, an offset component to account for variations in transect lengths (mean = 6022 m; min = 2498 m; and max = 6988 m), the interaction of geographic coordinates to account for spatial autocorrelation and both transect ID and year of observation as random variables. Random variables were added because of the repeated visits in the same transects across years and across several transects in the same year, making bird observation data non-independent. We used the Poisson distribution for species richness and the negative binomial or tweedie distribution for abundance. Poisson was chosen for species richness because it is better suited for discrete count data with low variability. The negative binomial distribution is adapted to count data with overdispersion, which is often the case with abundance data since their variability is greater. A negative binomial distribution was used as a standard, but when overdispersion was still detected, the tweedie distribution was used. We checked for overdispersion and residual normality in all final models using the *performance* R-package (Lüdecke et al., 2020).

Statistical models were created for each response variable of the static and trend approaches in two steps: (i) selecting the best model at each spatial scale (i.e. the 100, 500 and 2000 m buffers) and (ii) combining the three scales into a single model. At each scale, the dredge function from the *MuMIn* R-package (Bartoń, 2020) was used to generate models for all possible combinations of the fixed variables, that is the landscape metrics, and including all the covariables and random factors. For each response variable, the best-performing and parsimonious model was identified at each scale, that is the model with the lowest Akaike Information Criterion (AIC) and with the minimum number of variables across the models within the ΔAIC <2 compared with the best model. Then, the variables of the best models at each scale were put together in a multiscale model, which was also subject to the dredge process. To illustrate the results of the best-performing models, predicted response curves were produced using the *ggeffects* R-package, which estimates the expected values of the response variable across the range of a selected landscape metric while keeping other metrics at their mean value (Lüdecke, 2018). Predictions were plotted with confidence intervals to account for model uncertainty.

In the trend analysis, we defined the threshold for the safe operating space and the high-risk zone (sensu Steffen et al., 2015) as the accumulated clearcut area below which and above which the annual rate of change of bird abundance is positive or negative, considering the model uncertainty (95% confidence interval). We also defined the uncertainty zone between the two thresholds, that is the range in which the confidence interval of the model includes 0. We focused the threshold analysis on the effects of clearcut accumulation on forest specialists, that is common forest birds and old-growth forest birds. Following the obtained results of the trend analysis, we also calculated thresholds for the effects of mean clearcut size on common farmland birds.

The accumulation of clearcuts over 10 years expressed as a proportion of landscape area can be translated into clearcut RT (i.e. return interval, Equation 1; Virkkala et al., 2023), provided that the average forest area in the studied landscapes at the 100 m scale is 87%. The RT indicates the number of years after which the threshold value of the accumulated clearcut area led to the entire forest being cut once. It is also possible to calculate the area of forest that can be used under clearcutting if a particular RT is kept, while maintaining the same accumulated clearcut area over 10 years (Equation 2). We calculated how large proportion of the forest can be managed under clearcutting with a RT of 80 years (i.e. current recommendation for southern Finland; Äijälä et al., 2019) and close to the age at final harvest in 2017 (Kniivilä et al., 2020).

$$RT = \frac{1}{Pcc / Pforest} \times ACCt, \quad (1)$$

$$MaxPccforest = \frac{Pcc}{Pforest} \times \frac{RTref}{ACCt} \times 100. \quad (2)$$

RT is calculated based on the threshold proportion of clearcut in a landscape (Pcc, %), the average proportion of forests in the studied landscapes (Pforest, %) and the accumulation time used to measure the proportion of clearcuts (ACCt, year). The maximum proportion of clearcut relative to the forest area (MaxPccforest, %) is calculated based on the proportion of clearcut in a landscape (Pcc, %), the average proportion of forests in the studied landscapes (Pforest, %), the reference RT (RTref, %) and the accumulation time used to measure the proportion of clearcuts (years).

To evaluate the impact of the uncertainty associated with estimating the annual rate of change, we performed a bootstrap analysis (1000 repetitions) by resampling the rates of change within the 95%

confidence interval provided by the GAMs and repeated the threshold evaluation process for each repetition. In both the static and trend approaches, we checked for spatial autocorrelation of residuals in all the final models, which was always nonsignificant (*DHARMa* R-package; Table S2.3a,b).

3 | RESULTS

3.1 | Joint effect of clearcuts and land cover on bird communities

Total abundance and species richness decreased with the proportion of forests and increased with the proportion of cropland (Figure 3). This result reflects the response of common farmland and common mire species, as well as threatened open-habitat and wetland species. Some of these guilds also increased with the proportion of wetlands. Urban areas were associated with a narrow range of human-tolerant species. By contrast, forest species were unaffected by the proportion of forest or cropland (which never exceeded 30% in our data) and avoided urban areas. Overall, latitude had a negative effect on most of the biodiversity response variables; however, we found that the abundance of common mire species and the richness of threatened wetland species increased northwards (Figure 3).

Regarding forest clearcuts, we found that their short-term (i.e. 5 years) accumulation was associated with increasing overall species richness, as well as the abundance of common mire species and the richness of threatened wetland species (Figure 3). Long-term clearcut accumulation (i.e. 20 years) was linked with an increase in richness of threatened open-habitat species and human-tolerant species (Figure 2). By contrast, we found that long-term clearcut accumulation was negatively associated with the abundances of common forest species, old-growth forest specialists and the community specialization index (Figures 3 and 4a,b). Moreover, we found that the mean size of clearcuts accumulated over 20 years was positively associated with common farmland species (Figures 3 and 4c).

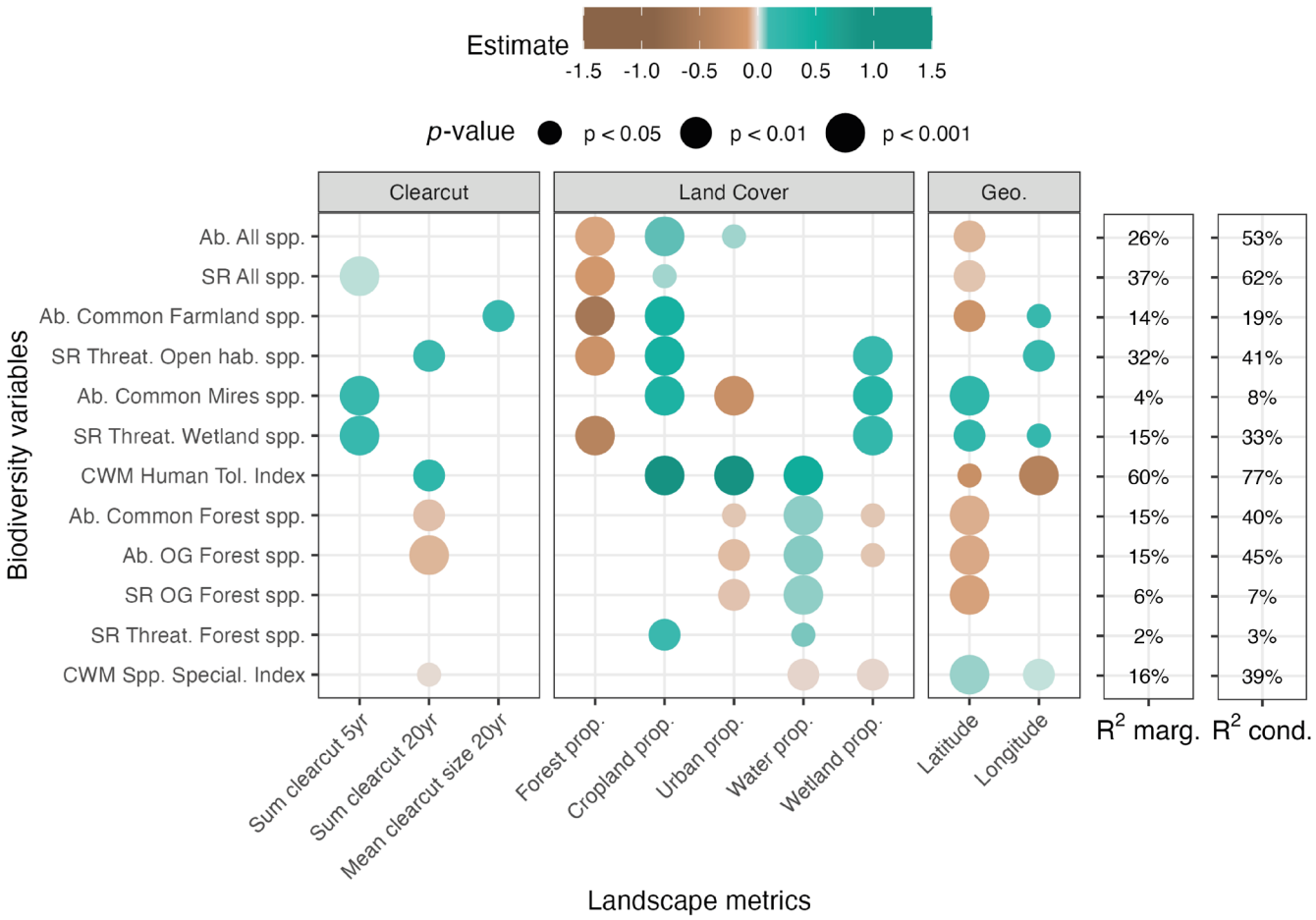

FIGURE 3 Results from the static analyses showing the relationship between biodiversity variables and landscape metrics and geographic coordinates. Point sizes and colours denote the model estimate and *p*-value, respectively. GLMM were fitted using bird observation data from 858 visits across 144 transects, spanning from 2006 to 2020. Marginal and conditional R^2 represent the variance explained by the fixed effects and the total variance explained by the fixed and random effects, respectively. Ab, abundance; CWM, community-weighted mean; Geo., geographic coordinates; OG, old-growth; SR, species richness. The landscape scales of the detected effects and of all the studied biodiversity variables are presented in Figure S2.4.

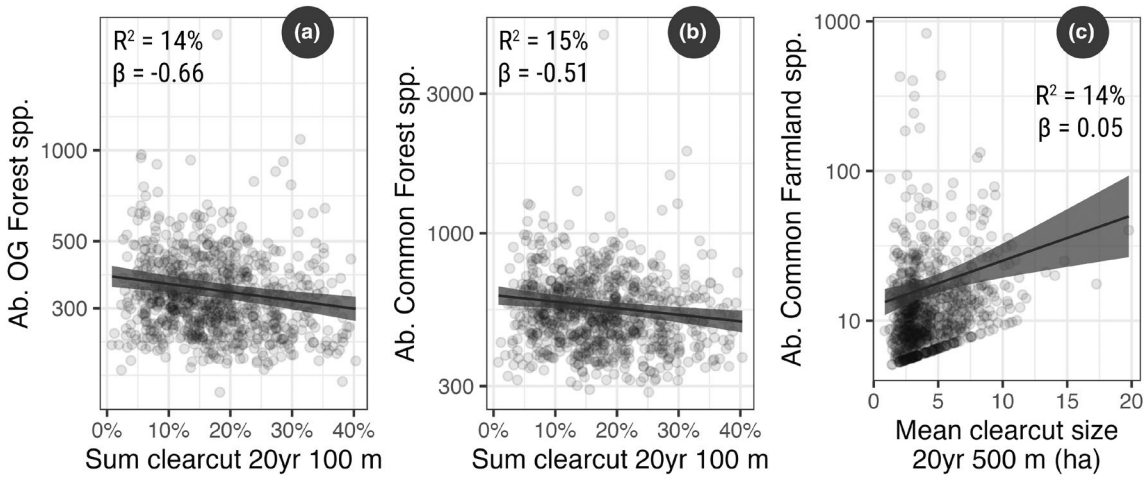

FIGURE 4 Three examples of predicted relationships between the clearcut accumulation at the 100 m scale over 20 years and bird species abundance (number of breeding pairs): (a) old-growth forest specialists, (b) common forest species and (c) between the mean clearcut size accumulated at the 100 m scale over 20 years and common farmland species. Points are the partial residuals from the fitted models (see all the results in Figure 3). Solid lines and grey ribbons are the predicted curves and 95% confidence intervals (estimated from models with *ggeffect*). R^2 are marginal—that is they only reflect the variance explained by the fixed factors. β-values are the estimates from models without scaling the landscape metrics; note the exponential link with the response variables.

3.2 | Trend analysis and safe thresholds for forest species

Land cover in the landscapes influenced the general biodiversity trends in a similar fashion as in the static analyses. High proportions of forests were linked with a declining abundance of common farmland birds, richness of threatened wetland species and a reduction in the community human tolerance index (Figure 5). By contrast, higher proportions of cropland areas supported the richness of threatened open-habitat species (Figure 5). Furthermore, the proportion of water bodies positively affected the abundance of common mire species and the richness of both threatened open-habitat and old-growth forest specialists (Figure 5). All biodiversity variables in the trend analyses showed a greater decline when the initial abundance, richness or CWM were higher (Figure 5). The geographical gradient was not as strong as in the static analyses. However, we also found negative trends for common forest and old-growth forest specialists northwards (Figure 5).

Regarding forest clearcutting, the accumulated area of clearcuts over the analysed 10-year time series was associated with an increase in the abundance of common mire species but a decrease in the abundances of common forest and old-growth forest specialists (Figures 5 and 6). We also found that a greater mean size of clearcuts over the 10-year time series was associated with an increase in the abundance of common farmland species and a decrease in the abundance of common mire species (Figure 5). Specifically, a mean clearcut size above the threshold of 1.8 ha should lead to an increasing abundance of common farmland birds (Figure S2.6).

The trend analysis shows that the safe maximum of the 10-year accumulated clearcut area for old-growth forest specialists is 9.6% of the overall landscape (Figure 6a) and 7.8% for the common forest species (Figure 6b). These safe thresholds correspond to RTs of 91 and 112 years, respectively, for the two species groups, meaning that at these clearcutting rates, the whole forest area will be cut once during that time. In other terms, to keep these safe thresholds, only 88% or 72% of the forest can be managed with clearcutting if a RT of 80 years is maintained. Meanwhile, the high-risk zones, indicating collapsing abundances, were reached at 18.4% and 24.5% for old-growth forest specialists and common forest birds, respectively. The stricter threshold for common forest birds than for old-growth forest birds is the result of greater uncertainty of model estimates rather than a stronger effect of clearcuts. Indeed, the accumulation of clearcuts along the 10-year time series had a similar effect size on the two groups (estimate = −0.16 and −0.21 respectively; Figure 6).

The bootstrap analysis exploring the effect of the uncertainties associated with the rate of change estimation on the threshold showed that the true threshold values for the safe maximum of 10-year accumulated clearcut area are likely lower, that is 8.5% and 6.5% for old-growth forest specialists and common forest birds, respectively (Figure S2.7). This corresponds to RTs of 102 and 134 years, respectively.

4 | DISCUSSION

4.1 | Clearcut areas, substitutes for semi-natural open habitats?

Clearcut accumulation in forested landscapes fostered open-habitat birds, including farmland species, as observed in previous works (Bakx et al., 2020; Lindbladh et al., 2017; Ram et al., 2020; Żmihorski, 2008), but also mire, wetland and human-tolerant species. The accumulation of clearcuts even promoted the presence of open-habitat and wetland threatened species. While mire and wetland birds benefited from

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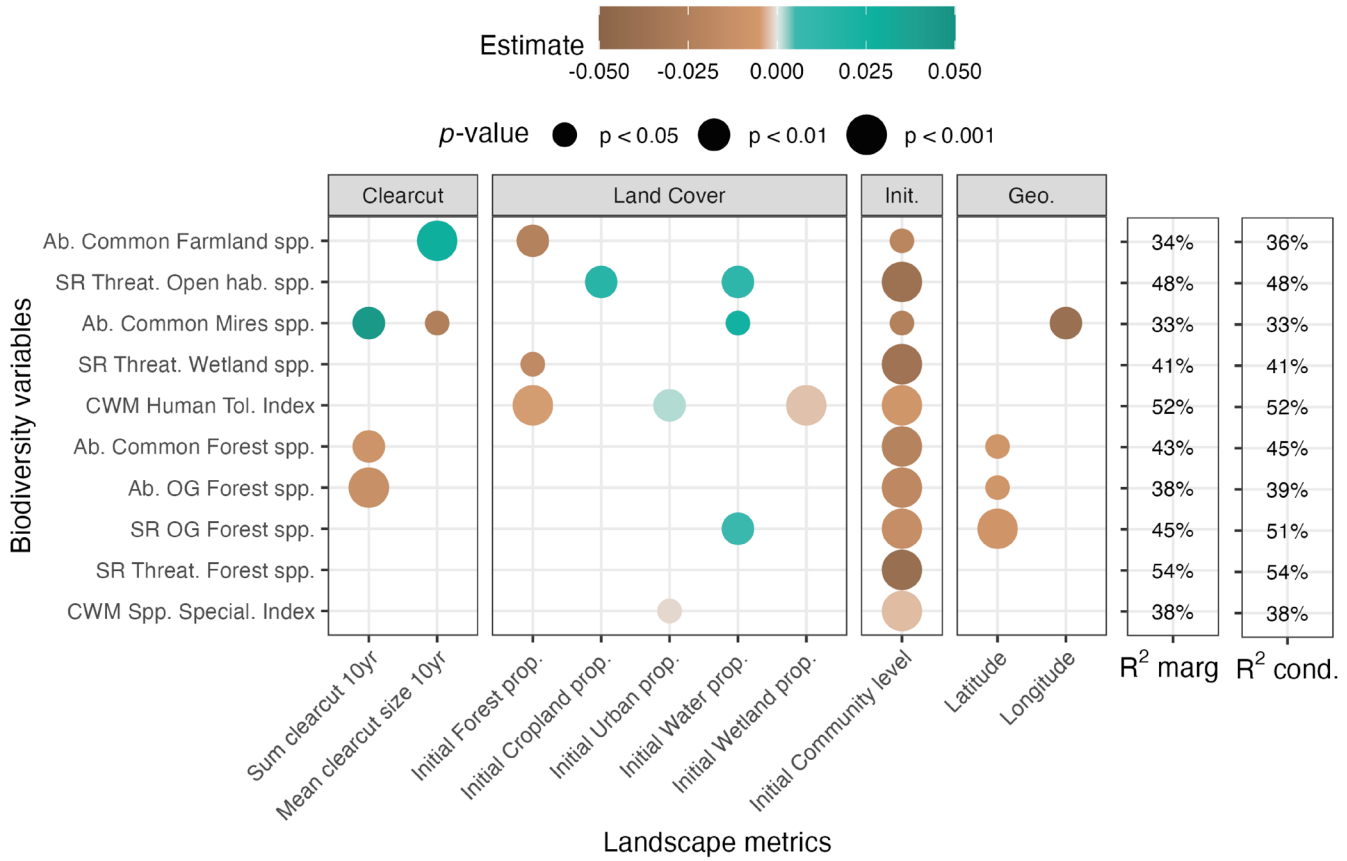

FIGURE 5 Results from the trend analyses showing the relationship between biodiversity variables and landscape metrics, initial biodiversity value and geographic coordinates. Point sizes and colours denote the model estimate and *p*-value, respectively. GLMM were fitted using 96 transects with at least five revisits over 10 years. Time series were analysed in GAMs to estimate the annual rate of change. Marginal and conditional R^2 represent the variance explained by the fixed effects and the total variance explained by the fixed and random effects, respectively. Ab, abundance; CWM, community-weighted mean; Geo., geographic coordinates; OG, old-growth; SR, species richness. Init., initial community level, that is the value of the biodiversity variable in the first year of the time series. The landscape scales of the detected effects are presented in Figure S2.5.

clearcuts only in the short term (5-year accumulation), farmland birds were positively associated with the long-term (20-year) accumulation of clearcuts. This result is congruent with earlier research showing that some farmland and shrubland species can use clearcuts up to 10 years after the harvest has occurred (George et al., 2019; Ram et al., 2020; Zhao et al., 2013; Żmihorski, 2008). Farmland and wetland bird species have dramatically declined over the last 40 years in Europe, and conservation measures are still needed (Rigal et al., 2023). Finland is no exception, and both farmland and mire bird species have been continuously declining since the 1980s due to the intensification of agricultural practices and habitat degradation (Fraixedas et al., 2017; Lehikoinen, Auvinen, et al., 2024). On average, nearly 16% of our landscapes at the 2000 m scale were covered by open habitats in 2018 (i.e. cropland, wetland and grassland; from CORINE Land Cover), while the clearcut accumulation over 20 years represented nearly 15%. Therefore, considering our results, clearcuts may provide a substantial amount of habitats to maintain those declining species. In landscapes with greater proportions of non-forest lands, the benefits of clearcuts to open-habitat species may be lower, depending on how intensively managed they are (e.g. natural grassland vs. cropland).

Current Finnish landscapes are more forested than 100 years ago (Mönkkönen et al., 2022), adding extra pressure on species associated with open habitats. Fire-suppression management and the drainage and afforestation of millions of hectares of peatlands have led to the depletion of natural open habitats (Elo et al., 2025; Mönkkönen et al., 2022). In Finnish forest-dominated landscapes, the presence of croplands and wetlands increases habitat heterogeneity, which enriches the bird communities with species associated with farmlands, mires and wetlands. Such changes in species composition across different landscape contexts concur with the results of a recent literature review on the effects of landscape heterogeneity on forest bird communities (Cours & Duflot, 2025). Threatened open-habitat and wetland species were both promoted by the proportion of wetlands, and their disappearance certainly led to the decline of these species (Fraixedas et al., 2017). Therefore, clearcut areas seem to be used as substitutes for these historical natural habitats (e.g. Helle, 1985).

Nonetheless, despite its positive effects, the widespread use of clearcutting in Finland has not maintained the population levels of open-habitat species, which have been continuously declining, suggesting that conservation actions are needed. It is good to keep in

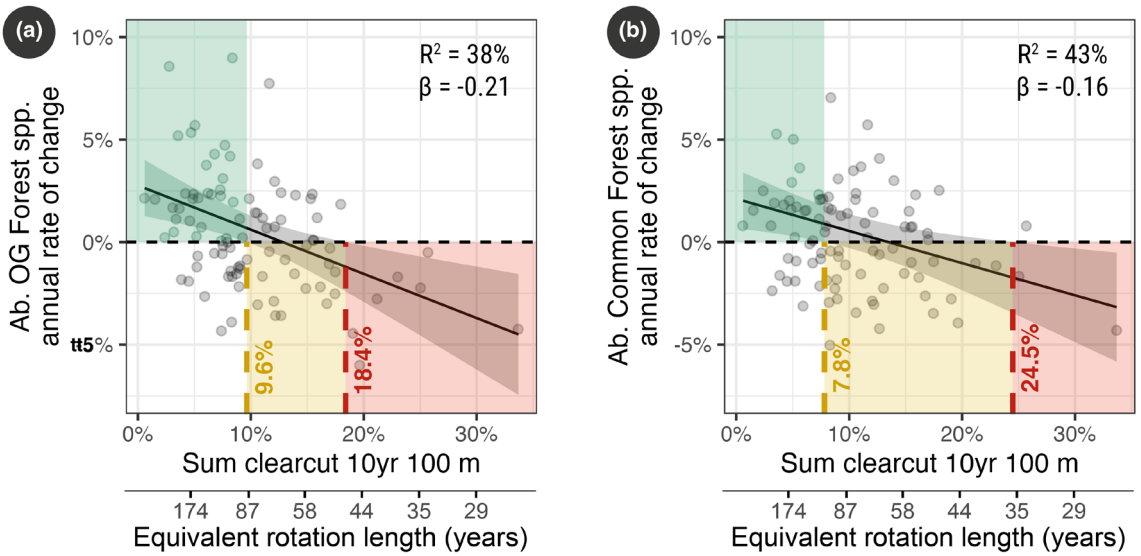

FIGURE 6 Predicted relationship between clearcut accumulation over 10 years along the time series at the 100 m scale and the estimated annual rate of change of (a) old-growth forest specialists and (b) common forest species abundance (number of breeding pairs). The equivalent rotation length translates the 10-year accumulated proportion area of clearcuts into a clearcut return interval (year) on forest lands. The green, yellow and red areas represent the safe operating space (bird population recovery with positive annual change), the uncertain zones, where the lower and upper 95% CI crossed 0, and the high-risk zone (with negative annual change), respectively; sensu Steffen et al. (2015). Solid lines and grey ribbons are the predicted curves and 95% confidence intervals (estimated from models with *ggeffect*). Points are the partial residuals from the fitted models, representing the 96 transects with at least five revisits over 10 years. β-values are the estimates from models without scaling the landscape metrics; note the exponential link with the response variables.

mind that densities of open-habitat species are typically smaller in clearcuts than their traditional breeding habitats in peatlands, farmlands or naturally disturbed areas, and that many mire and farmland species do not breed in clearcuts (A.L., unpublished line transect data). A recent study conducted in Norwegian boreal landscapes found that only a subset of farmland bird species can use forest clearcuts and that they reproduce poorly in them (Dale, 2026). Therefore, the best solution to enhance the conservation status of these threatened guilds might be to restore their farmland and natural habitats—for example peatlands or burned areas (Kellett et al., 2023). For instance, post-fire open areas host more species and a different species assemblage than clearcuts for as long as 10 years post disturbance (Frank et al., 2025). Based on our results, restoration should aim to create patches of open habitats of at least 1.8 ha on average, as common farmland bird species showed a positive trend above that threshold (Figure S2.6). Indeed, farmland and shrubland species often prefer large open areas and avoid edges, up to 200 m from them (George et al., 2019; Lehikoinen, Bosco, et al., 2024; Pithon et al., 2021; Żmihorski, 2008).

4.2 | Clearcuts are driving habitat loss for common and specialist forest species

Our results showed long-lasting negative effects of clearcuts on forest bird communities in southern Finland, including the threatened forest species, consistent with earlier studies that found that the landscape-level area of clearcuts is a stronger predictor of mature-forest birds than local structural attributes (Jansson & Andrén, 2003; Zhao et al., 2013). The main mechanism is the loss of suitable habitats, as clearcutting abruptly converts older forests into an early developmental stage (Lunde et al., 2025; Virkkala, 2016). Accumulation of clearcuts in the landscape considerably reduces the area and connectivity of mature and old-growth forests, especially when compared to pre-exploitation landscape conditions; clearcut return intervals are much shorter than those of natural disturbances (Figure 2; e.g. Berglund & Kuuluvainen, 2021; Linder & Östlund, 1998). These local- and landscape-level effects lead to the broader decline in forest bird populations in northern Europe (Lehikoinen & Virkkala, 2018) and particularly of species associated with late successional forest habitats (Fraixedas et al., 2015). Contrary to our expectations, we did not detect any negative effects of clearcut size on forest birds, suggesting that edge effects and a lack of interior habitats are not important drivers for birds in the highly forested landscapes we studied (see also Drapeau et al., 2000, in a Canadian context).

We defined safe and high-risk levels of clearcut accumulation, that is threshold values below which forest species thrive and above which they continue to decline, respectively. If less than 9.6% of the landscapes are being clearcut over 10 years, that is if the rotation length is longer than 91 years, the abundance of old-growth forest specialists should not decrease. The thresholds assessed with a subset of transects were confirmed with the whole dataset, as we found in complementary analyses that the estimated overall population of old-growth forest species was increasing and

decreasing, respectively, when selecting landscapes below the safe threshold (41% of 144 transects) and above the high-risk threshold (20% of the transects; see Figure S2.8). Rotation length in southern Finland has shortened since 2010 from about 90 to 83 years in 2017 (Kniivilä et al., 2020), that is it is shorter than the safe ecological threshold and might have become even shorter since (e.g. 73 years in Virkkala, 2016; see also Kortesalmi et al., 2025). Given the already degraded state of forests in southern Finland, the defined values should be considered the minimum objective at which the abundances of old-growth forest specialists start to recover.

The overshoot of the ecological ceiling is more evident if the uncertainty associated with estimating the rate of change in individual transects is accounted for. Then, the safe threshold for clearcut accumulation is 8.5% of the landscapes over 10 years, corresponding to a safe rotation length longer than 102 years (see Figure S2.7). We focused on the old-growth forest species to define the safe operating space, as the analyses of common forest birds led to much higher uncertainty. Indeed, common forest birds include a broader group of species with various degrees of habitat specialization and sensitivity. Hence, this group includes species with more diverse responses to clearcuts, producing greater unexplained variability in the data. However, our results show that the effect size of clearcut accumulation on common forest birds is only slightly lower than on old-growth forest specialists. Given the greater uncertainty, the safe operating threshold needs to be more restrictive than for old-growth forest birds.

We argue that the safe zone represents the conditions allowing for the recovery of forest bird communities, which saw a 25% decline in European boreal forests during 1980–2012 (Lehikoinen & Virkkala, 2018). Meanwhile, harvesting levels within the uncertainty zone likely maintain a degraded forest state and the high-risk zone worsens it, which will likely result in further declines. Earlier research has shown that excessively high rates of clearcutting prevent the recovery of forest communities. In a systematic review, Lunde et al. (2025) suggest that RTs of up to 80 years are not sufficient for the recovery of boreal forest communities for many taxa due to long-term legacy effects of clearcutting. Theoretically, forest regeneration should offer new habitats; however, the long recovery of forest communities based on slow recolonization cannot compensate for the losses in bird populations caused by too many new clearcuts (Virkkala et al., 2023). Because of the long time needed for recovery and recolonization, the use of a longer-rotation length may not be sufficient by itself (Zhao et al., 2013). This suggests that it would be more efficient for forest bird conservation to leave a proportion of forest landscapes without clearcutting management, instead of delaying clearcutting (longer rotation) on the whole forest area. The safe threshold analyses suggest that at least 20% of the forest should then be excluded from clearcutting operations.

In Finland, reducing the forest area under clearcutting would necessarily rely on both expanding protected areas and adopting non-clearcutting harvesting methods, that is continuous cover forestry practices. Currently, about 5% of the forest land in southern Finland is protected; consequently, the objective of 10% strict protection from the EU biodiversity strategy (European Commission, 2021) is not met in the region. Existing and new protected areas could be surrounded with buffers without clearcutting to reduce their landscape-level impacts on protected sites (Määttänen et al., 2023). However, it is not yet clear whether various forms of continuous cover forestry can better support old-growth forest species than clearcutting (but see Savilaakso et al., 2021), as continuous cover forestry (or uneven-aged management) may have limited deadwood volume, number of large, old trees and structural variation, and, therefore, may contribute little to forest species across taxa (Duflot et al., 2025; Schall et al., 2018). As the practice of continuous cover forestry has remained very limited in boreal Europe, it was not included in our study. Therefore, we cannot conclude on the respective ideal proportion of unmanaged versus non-clearcutting management in landscapes. To improve their efficiency, the expansion of protected area and continuous cover forestry should be guided towards forests with high biodiversity value (Mikkonen et al., 2023), which are harvested at the same rate as any other forests in Finland (Kortesalmi et al., 2025). Finally, it might be efficient to concentrate clearcuts in proximity to open habitats, such as farmlands, which would act as sources for transient clearcut habitats (Żmihorski, 2008) and preserve forest interiors (Figure 2).

4.3 | Generalization of the method and result

We present a reproductible, data-driven, statistical method to operationalize the concept of planetary boundaries to regional forestry sectors, applicable to other land-use-based human activities. At the crossroads between landscape ecology focusing on spatial patterns (e.g. habitat amount and edge effect) and disturbance ecology focusing on temporal processes (e.g. legacy effects and recovery time), we introduce the accumulation of clearcut areas as a control variable for biodiversity loss in forest production landscapes. Indeed, in these landscapes, harvests and regrowth are the main drivers of the habitat dynamics. Similar metrics of land-use intensity, for example proportion of semi-natural habitats in agricultural landscapes, could be used similarly. We make a statistical interpretation of the safe, uncertain and high-risk zone of the planetary boundary framework (Steffen et al., 2015). We argue that the metrics of biodiversity trends using time series are more suitable than static biodiversity observations for defining ecological limits because positive and negative rates of biodiversity change are straightforward indicators of ecological sustainability, indicating biodiversity recovery or loss. By contrast, richness or abundance values raise discussions about which adequate viable levels should be targeted. In addition, we emphasize that observations of landscape-level gamma diversity are needed to assess the overall local- and landscape-level effects of clearcuts on multiple habitats, allowing the balancing of their antagonistic influence on various species groups.

The choice of indicator species for biodiversity loss is an important aspect to consider. Our results show that the accumulation of clearcuts over time at the landscape level is an important driver of bird communities, with contrasting responses of open-habitat versus forest species. These

results also likely extend to other taxa (Lunde et al., 2025). However, we defined ecological limits for common and old-growth forest birds, while the specific responses of uncommon old-growth forest specialists should also be studied. The exact threshold values of the safe operating space are likely variable, and other taxa sensitive to forest management should be investigated (e.g. lichens; Gustafsson et al., 2025). Ultimately, the most restrictive value should be considered.

Finally, as clearcutting is a global phenomenon, we argue that the accumulation of clearcut areas is a suitable variable for defining ecologically sustainable management in regions other than southern Fennoscandia. However, the threshold values obtained for southern Finland may not translate well into other contexts, let alone other biomes. In our study region, harvesting happens in forests that have a long management history, with large areas of mature forest facing a second cycle of clearcutting. While some regions in North America and Europe share a similar silvicultural history, there are large areas at northern latitudes, mountain ranges or in the temperate zone where the history of forest use is different (Lunde et al., 2025; Marsik et al., 2018; Suvanto et al., 2025). For instance, in the northern boreal zone in Finland, intensive forestry is more recent (Mönkkönen et al., 2022). In addition, the forest is growing slower at high latitude, so the RT would be naturally longer. Because the forests that re-establish after clearcutting are usually not similar to the original ones, clearcutting might have a greater impact in regions with more intact forests or where selective cutting has been dominant. However, selective cutting may also lead to severe forest habitat degradation (e.g. Schall et al., 2018). One may expect lower safe thresholds for accumulated areas of clearcuts in such contexts. Furthermore, in some regions, the effect of clearcuts might need to be considered jointly with other biodiversity threats, such as climate change. For instance, clearcut accumulation in conjunction with increased fires may lead to a landscape trap where both phenomena are positively linked, resulting in a self-maintained degraded state and ultimately ecosystem collapse (Lindenmayer, 2016).

To conclude, we argue that defining maximum clearcut areas can provide a readable minimum target for ecologically sustainable forest use; however, such thresholds should be applied critically, as they are potentially context-dependent and would require validation with multi-taxa analyses.

AUTHOR CONTRIBUTIONS

Rémi Duflot: Conceptualization, methodology, writing—original draft, writing—review and editing; **Jenna Rönttinen**: Methodology, formal analysis, writing—original draft, writing—review and editing, supervision, funding acquisition; **Aleksi Lehikoinen**: Data curation, writing—review and editing; **Mikko Mönkkönen**: Conceptualization, writing—review and editing; **Jérémy Cours**: Conceptualization, data curation, methodology, formal analysis, visualization, writing—original draft, writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data and code used in the study are available from Zenodo (https://zenodo.org/records/21823296; Cours et al., 2026). The original complete data are available in FINBIF (laji.fi, 'Luomus monitoring schemes—Line transect censuses of breeding birds').

ORCID

Rémi Duflot https://orcid.org/0000-0002-5070-903X
Aleksi Lehikoinen https://orcid.org/0000-0002-1989-277X
Mikko Mönkkönen https://orcid.org/0000-0001-8897-3314
Jérémy Cours https://orcid.org/0000-0003-4179-2350

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. List of species found in studied transects and associated traits.

Figure S2.1. Mean values ± standard deviation (bold line) and minimum and maximum values (thin line) for each biodiversity metrics: (a) abundance metrics, (b) species richness metrics and (c) CWM metrics.

Figure S2.2. Correlations between all the landscape metrics prior selection due to high correlation.

Table S2.3a. Measure of residual spatial autocorrelation in models of the static analyses.

Table S2.3a. Measure of residual spatial autocorrelation in models of the trend analyses.

Figure S2.4. Results from all the models of the static analyses and the landscape scales of the effects.

Figure S2.5. Results from the trend analyses, including the scales of the effects.

Figure S2.6. Predicted relationship (and 95% confidence interval) between clearcut size over 10 years along the time series at the 100 m scale and the estimated annual rate of change of common farmland species abundance.

Figure S2.7. Density of the lower threshold (left) and higher threshold (right) of the safe operating space and the dangerous zones for old-growth forest specialists (top) and common forest species (bottom) from the 1000 bootstrap iterations.

Figure S2.8. Results of TRIM analysis applied on the abundance of old-growth forests over the 144 transects in Southern Finland.

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