Importance of climate-induced tree species composition changes in forecasting the amount of reachable habitat for forest birds

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Abstract

Aim: Bird and tree species distributions will shift along with future climatic conditions through direct effects related to species responses to bioclimatic variables. In addition, tree species composition changes should indirectly drive changes in forest bird habitats. Here, we predicted the effects of climate changes on the amount of reachable habitat for forest birds and teased apart the role of the indirect effects.

Location: France.

Methods: We projected tree and bird species distributions (2020 and 2050) using generalized additive models which accounted for climatic conditions at a large scale (France) and local environmental conditions at regional scale. The projections combined two scenarios of climate changes (RCP 2.6 and 8.5) and two scenarios of forest management (increase in either deciduous or coniferous stands). We modelled the amount of reachable habitat with landscape graphs and the equivalent connectivity index (EC) for five birds associated to the main forest types of the study area. To differentiate the sources of EC change between 2020 and 2050, we compared two future landscape graphs including only the indirect effect, or the direct and indirect effects of climate changes.

Results: For birds with low and intermediate thermal maxima, climate-based distributions were nearly stable over time (absence of direct effects), EC change was only attributed to indirect effects. In contrast, for bird species with high thermal maximum, EC change was mostly driven by direct effects (more favourable climatic conditions) and little by indirect effects.

Main conclusions: Using an innovative modelling framework that bind species distribution and connectivity models with climate and land use changes in forest, we showed that EC dynamics could be completely due to climate-driven changes in tree species composition. Our results highlight the importance of accounting for the indirect effects of climate changes, especially in forests where major shifts in tree species composition are expected.
1 INTRODUCTION

Climate changes drive species distribution through direct impacts related to species responses to climatic variations that constrain fitness and metapopulation processes (De Kort et al., 2020; Möller et al., 2010). Species’ responses depend on their sensitivity to climatic conditions, which is exacerbated at range distribution limits (Devictor et al., 2008; Morin et al., 2007; Vissault et al., 2020). For example, thermal maximum or the temperature at the hot edge of the climate envelope was used as an indicator of birds’ sensitivity to climate changes (Jiguet et al., 2007, 2010). Sharp population declines have been observed for species with low thermal maximum, that is an affinity for cold temperatures (Jiguet et al., 2010). Therefore, the consequences of climate changes on a species are often seen through the lens of shifts in the species range distribution (e.g. Barbet-Massin et al., 2012). However, regional-scale species distribution can be impacted even within species range distribution because climatic changes can modify the distribution of ecosystems and thus alter species habitat availability and landscape connectivity (Ay et al., 2014; De Kort et al., 2020). Landscape connectivity is defined as the degree to which the landscape facilitates or impedes species movements between habitats (Taylor et al., 1993). To understand these mechanisms, we need to account for land use change, understand how climate indirectly drives the distribution of dominant vegetation and clearly identify the cascading effects of climate changes on species dynamics (He et al., 2019). For example, our future climate will drive changes in tree species biogeographical distribution, local environmental conditions and forest management, and these processes will in turn drive changes in habitat availability and connectivity for forest-dwelling species (De Kort et al., 2020). Accounting for climatic and land use changes in modeling habitat availability and connectivity should enable us to understand the consequences of climate changes on metapopulations via direct effects (bird responses to bioclimatic variables through the direct occurrence-climate relationship) and indirect effects (climate-induced changes in tree species composition and their cascading effects on birds).

Tree species distributions are predicted to shift under future climatic conditions (Hanewinkel et al., 2013). A projection of the climatic envelop of European tree species have identified “winner” and “loser” species (Dyderski et al., 2018). However, large-scale predictions of the future distribution of individual tree species do not give enough information to forecast the spatial rearrangement of tree species when climatic conditions remain suitable (within species distribution range) for several tree species at the same location. For that purpose, it is necessary to account for local environmental conditions (soil, topography) and management trajectories related to socio-economic factors (Houballah et al., 2020). Even if options for forest management are constrained by climate changes in the temperate continental regions, several trajectories remain possible, such as favouring deciduous or coniferous trees (Lindner et al., 2010). Further investigations are needed to understand how climate-driven changes would translate into future forest stand composition. Studying a combination of climate change scenarios and land use change scenarios related to contrasted trajectories of forest management could fill this knowledge gap.

Climate-induced land use change could indirectly drive forest species distribution via changes in forest stand composition and structure (Ay et al., 2014). In the context of global changes, bird population trends are strongly correlated to habitat use, especially for specialist species, which can decline very rapidly when their habitat is degrading (Jiguet et al., 2007). Studies that forecast the future distribution of birds recognize the importance of accounting for dispersal but generally overlooked habitat connectivity, notably because the spatial scale of analysis is too large (Barbet-Massin et al., 2012; Devictor et al., 2008; Triviño et al., 2011). Indeed, species distribution models do not incorporate habitat connectivity, which depends on the area, quality and spatial configuration of the suitable habitats embedded in a more or less unsuitable environment, the so-called landscape matrix, which facilitates or impedes species dispersal among populations (Riva & Nielsen, 2020). To fill this gap, we need new methodological frameworks that integrate climate changes into landscape connectivity approaches (Costanza et al., 2019; De Kort et al., 2020; Keeley et al., 2018; Littlefield et al., 2019). To tackle this issue, species distribution models and landscape graphs could be combined (Duflot et al., 2018; Keeley et al., 2016). A landscape graph is a conceptual representation of a landscape where pairs of suitable habitats are connected by paths depicted in the landscape matrix. Paths represent potential movements of individuals or gene fluxes between habitats (Urban et al., 2009). For example, they can be depicted by least-cost paths that minimize both Euclidean distance between habitats and matrix resistance to movements (Adriaensen et al., 2003). Matrix resistance can be derived from habitat suitability, using, for example a negative exponential transformation of suitability to strengthen the barrier effect of the least favourable areas (Keeley et al., 2016). While species distribution models only quantifies the amount of potential habitat, the amount of reachable habitat accounts for habitat area, quality (or mean suitability) and spatial configuration, matrix resistance and species dispersal distance into a single graph-based metric (Saura et al., 2011; Saura & Pascual-Hortal, 2007).

In this study, we evaluated how the future climate in 2050 combined with forest management trajectories would drive the
amount of reachable habitat and isolated the specific role of climate-driven tree species composition change within the global effects of climate changes. More precisely, we combined two contrasted climate change scenarios (RCP 2.6 and 8.5) and two forest management scenarios (coniferous increase or deciduous increase), in a forest area with high compositional heterogeneity (662 km²). We selected five bird species with diverse ecological requirements in terms of tree species composition (Regulus regulus, Sitta europaea, Dendrocopos major, Certhia brachydactyla and Phylloscopus collybita).

First, we applied species distribution models to relate current focal bird and tree species occurrences to climatic variables at the national scale (France), which was largely enough to prevent spurious extrapolation when assessing future conditions at the regional scale.

Second, using other databases on bird and tree species available at the regional scale, we applied species distribution models to the same focal bird and tree species at this regional scale in order to account for topography and soil for trees and landscape compositional heterogeneity for birds (including forest land use, i.e. tree species composition).

Third, for trees, we combined national-scale and regional-scale distribution models to build future scenarios of tree species composition for all forest stands present in our study area. For birds, we combined national-scale and regional-scale models to quantify the amount of reachable habitat for birds through landscape graphs and equivalent connectivity EC (Saura et al., 2011).

Using the above modelling framework, our objectives were to (1) examine the direct, indirect and global effects of climate changes on birds using EC variations, and relate these effects to bird thermal maximum; (2) identify whether alternate forest management scenarios could mitigate the impact of climate changes on birds and thereby meet bird conservation objectives.

### Methods

#### 2.1 Study area and model species

The study area (662 km²) was located in the northern part of the French central massif (latitude: 46.0022°, longitude: 3.8319°) and was composed of forests (57%), agricultural lands (37%), urban areas (5%), and streams and water bodies (1%; see Appendix S1). Altitude ranged from 298 to 1286 m and the forests were composed of coniferous stands (Pseudotsuga menziesii and Abies alba), deciduous stands (Fagus sylvatica and Quercus spp.) and mixed stands (A. alba and F. sylvatica or Quercus spp.; Table 1; see Appendix S1). Tree species composition of the stands was extracted from the attribute table of the vector layer BD Forêt® v.2 map (2006) produced by the French National Institute of Geographic and Forest Information from orthophotos. The polygon composition specifies the dominant tree species if a single species occupies over 75% of the canopy cover (two oak species are grouped, i.e. Quercus spp. = Quercus petraea and Quercus robur), or indicates the tree species mixture if at least two species occupy over 25% of the canopy cover. We considered 77% of the forested area to be dynamic in our future projections, and excluded mixed-deciduous stands (for which the exact tree species composition was unknown) and other dominant trees that comprised less than 1% of the forested area. Non-forest areas (agricultural lands, urban areas, streams and water bodies) were considered stable over time.

We extracted bird data from the French Bird Protection League database for the year 2019. This database includes either presence-only bird points or bird abundance on 100 m-radius plots inventoried using songs and visual contacts. We used abundance data to calculate the degree of association between forest birds and five forest stand types according to an indicator value index (indval, Dufrêne & Legendre, 1997). We then selected four species—R. regulus, S. europaea, D. major and C. brachydactyla—as model species for forest stands dominated

| Tree species composition | 2020 Current | 2020 DEC 2.6 | 2020 CON 2.6 | 2020 DEC 8.5 | 2020 CON 8.5 |
|--------------------------|--------------|--------------|--------------|--------------|--------------|
| Pseudotsuga menziesii    | 7595 ha 26%  | 10099 ha 36% | 16373 ha 58% | 1315 ha 5%   | 1384 ha 5%   |
| Abies alba               | 6573 ha 23%  | 1945 ha 7%   | 1996 ha 7%   | 1339 ha 5%   | 1431 ha 5%   |
| Mixed forest             | 5682 ha 20%  | 1441 ha 5%   | 1441 ha 5%   | 1229 ha 4%   | 1229 ha 4%   |
| Fagus sylvatica          | 2910 ha 10%  | 8000 ha 28%  | 2450 ha 8%   | 4793 ha 17%  | 4640 ha 17%  |
| Quercus spp.             | 1051 ha 4%   | 2672 ha 9%   | 1897 ha 7%   | 3322 ha 11%  | 3314 ha 11%  |
| Degraded forest          | 4779 ha 17%  | 4434 ha 15%  | 4433 ha 15%  | 16591 ha 58% | 16591 ha 58% |
respectively by A. alba, F. sylvatica, Quercus spp. and mixed deciduous-coniferous forests. These birds were selected because they had the highest indicator values for one type of forest stand dominated by the above-mentioned tree species (Dufrene & Legendre, 1997). The model species had affinities for one forest stand type but were not specialists (low indicator values: indval index >0.20, \( p < .001 \)). No association was detected between any birds and stands dominated by P. menziesii. Beyond the responses of birds associated with specific tree species, we also aimed to study a generalist species and included P. collybita as a fifth model species. The indicator value showed no preferential association between this bird and specific tree species.

2.2 | National data

At the national scale, the occurrences of the tree species, previously described, were extracted from the data collected between 2005 and 2015 in 1-km squares by the French National Forest Inventory (Vidal et al., 2007), and occurrences of the five bird species models were extracted from the French National Atlas of Breeding Birds (2009–2013) in a regular grid of 10-km squares (Issa & Muller, 2015). We used the national scale to totally avoid spurious extrapolation when we predicted species response to 2050 climatic conditions currently inexistent in our study area.

2.3 | Species distribution models

The modelling framework that links species distribution and connectivity models to climate and land use changes is summarized in Figure 1. Species distribution models were fitted for each tree and bird species with generalized additive models (GAM; Wood, 2017). Smoothing splines were limited to three degrees of freedom to avoid overfitting. Models were validated with the area under the curve (AUC) when using occurrence data, and AUC and the Continuous Boyce Index (CBI) when using presence-only data (Fielding & Bell, 1997; Hirzel et al., 2006). These indices were averaged over 20 replicates of a bootstrap cross-validation (80% and 20% partitioning for calibration and validation, respectively).

First, we related tree and bird species occurrence to climatic variables at the national scale to project species response according to 2050 climatic conditions. We selected four bioclimatic variables (1 km resolution at the equator), extracted from the Chelsa database (Table 2; Karger et al., 2017), that were not too much correlated to each other (Spearman correlation coefficient \( <0.7 \); Dormann et al., 2013). Bird occurrences in the 10-km squares were related to bioclimatic variables averaged over the 10-km squares (Table 2; Issa & Muller, 2015). However, we then used this model to predict bird occurrences at the original resolution of the climatic data (1 km) under the hypothesis that the bird occurrence-climate relationship would not change between the two scales (1 km and 10 km). This assumption is reasonable for studying the variation in equivalent connectivity with time, but could lead to a loss of accuracy in the predictions of occurrence probability for each date.

Second, we fitted regional-scale models to account for local environmental conditions. We related tree species occurrences to topography and soil acidity, both of which were considered stable over time (Table 2). Tree species occurrences were extracted for each polygon of the BD Forêt® v.2 map and related to mean topographic conditions and soil acidity for each polygon. The distributions of Quercus petraea and Quercus robur were merged at the regional scale because we did not know which of the two species was present; the BD Forêt® v.2 map only informs on the presence of Quercus spp. For birds, we extracted presence-only data from the database of the French Bird Protection League. Additional details are provided in the Supporting Information (see Appendix S2) for sampling bias correction and pseudo-absence selection. Bird occurrence was related to the proportion of each land use class at a 5-m resolution (including forest land use based on tree species composition). These landscape metrics were calculated in moving windows within a radius of 100 m in accordance with species home-range size (Table 2; see Appendix S2).

Finally, for birds, the national and the regional-scale GAM were used to predict species occurrences in 2020, using an occurrence probability threshold following Liu et al. (2013). Species distribution models and GIS manipulations were performed with R software v.3.6.2 (R Core Team, 2021).

2.4 | Projection of future tree species composition

Following Sanderson et al. (2015), we averaged the predictions for the bioclimatic variables from five contrasted global climate models (CESM1-CAM5, FIO-ESM, IPSL-CM5A-MR, MIROC5 and MPI-ESM-MR). We used two scenarios, RCP 2.6 and RCP 8.5, which...
(a) Species distribution models for trees

(b) Species distribution models and landscape graph for birds

(c) Comparison of the amount of reachable habitat for birds

(d) Isolating the indirect effects of climate changes on bird (due to changes in tree species composition)
**TABLE 2** Description of variables used to relate tree and bird species with climate at the national scale, and topography and soil acidity (for trees) or landscape factors (for birds) at the regional scale

| Scale of analysis (main aim)          | Data type | Data base or source | Resolution or area | Variable                                                                 | Biological model concerned |
|---------------------------------------|-----------|---------------------|--------------------|--------------------------------------------------------------------------|-----------------------------|
| Regional (equivalent connectivity estimate) | Birds     | French Bird Protection League database | 100 m              | Presence-only                                                            | -                           |
|                                       | Trees     | IGN (BD Forêt® database) Mean area = 11.3 ha (±76.8 SD) | Occurrence per polygon | -                                                                        |                            |
|                                       | Land use and land cover | IGN (BD Forêt® database) Mean area = 11.3 ha (±76.8 SD) | Occurrence per polygon | Bird species                                                             |                            |
|                                       | Landscape descriptors | IGN (BD TOPO® database) 5 m Land cover | -                  | -                                                                        |                            |
|                                       |           | IGN (RPG® database) 5 m Agricultural lands | -                  | -                                                                        |                            |
|                                       | Topography | IGN (BD Atri® database) 25 m Proportion of each land use and land cover calculated in sliding windows within a radius of 100 m | -                  | Bird species                                                             |                            |
|                                       | Soil      | SoilGrids (Hengl et al., 2017) 250 m pH | -                  | Tree species                                                             |                            |
| National (species-climate relationships) | Birds     | French Breeding Bird Atlas (Issa & Muller, 2015) 10 km | Occurrence per mesh | -                                                                        |                            |
|                                       | Trees     | National Forest Inventory 1 km | Occurrence per mesh | -                                                                        | Tree and bird species      |
|                                       | Climate   | Chelsa (Karger et al., 2017) 1 km | Annual mean temperature (Bio 1) Temperature seasonality (Bio 4a) Annual precipitation (Bio 12) Precipitation seasonality (Bio 15) | -                           |                            |

IGN, French National Institute of Geographic and Forest Information; SD, standard deviation.
respectively predict an increase of 1.1°C and 2.1°C in mean annual temperature by 2050 in the study area. In addition, we tested two different forest management scenarios, which predict overall changes in tree species composition in 2050 but no change in total forest area. The "coniferous" scenario predicts an increase in the share of pure coniferous stands and reflects intensive management devoted to the production of construction and industrial wood. The "deciduous" scenario predicts an increase in the share of pure deciduous stands and foresees an adaptation of the wood sector towards wood energy and a decrease in the introduced species _P. menziesii_. In both scenarios, the current mixed coniferous-deciduous stands were considered to be stable over time, as long as it was consistent with the future tree species distributions. We combined the two climate scenarios with the two forest management scenarios and compared them to the current situation. We labelled the scenarios by merging climate and management scenario codes (e.g. "deciduous 2.6"). We also considered an additional third scenario that consisted in increasing mixed coniferous-deciduous stands as a continuation of the historical change in tree species composition over the past 30 years. The results related to this scenario are provided only in the Supporting Information because environmental and climatic constraints in our study area mostly precluded an additional increase in mixed stands in 2050 (see Appendix S3).

For all scenarios, we considered that the tree species composition of a polygon had changed (between 2020 and 2050) if the polygon was no longer entirely included in the projected distribution of the dominant tree species (or the mixture of co-dominant tree species) that originally defined its composition. In this case, the new composition depended on the forest management scenario, which defined priorities for deciduous or coniferous trees. More precisely, the new composition was determined by the coniferous (or deciduous) species with the highest occurrence probability in the coniferous (or deciduous) scenario. If these possibilities did not exist, the new composition was determined by the tree species with the highest occurrence probability, notwithstanding whether it was coniferous or deciduous. Forests unsuitable for any tree species were labelled "degraded forests" and considered unsuitable for birds. These forests, outside favourable climatic conditions may persist under the form of poorly functional ecosystems providing fewer resources for birds and with high tree mortality rates (Morin et al., 2007; Taccone et al., 2019). We also used the "degraded forests" class to the current situation to make the 2020 and 2050 maps as comparable as possible. For the 2020 map, when a mismatch existed between the national predictions and the actual composition of a polygon as defined by the BD Forêts™ v.2 map, the polygon was assumed to represent a current "degraded forest."

### 2.5 Landscape connectivity modelling for birds

For birds, we defined a habitat suitability index (HSI), at a 5-m resolution, as the mean occurrence probability from the national and the regional model predictions combined. In the landscape matrix, resistance to dispersal was derived from the HSI with a negative exponential transformation, following Keeley et al. (2016):

$$\text{Matrix resistance} = 1000 - 999 \times \frac{1 - e^{-c \cdot HSI}}{1 - e^{-c}} \quad (1)$$

The parameter $c$, that determines the shape of the curve, was fixed to four considering an intermediate strength of barrier effect of the least favourable areas between habitats. A variation of this parameter rarely results in significant differences in model outputs (Meyer et al., 2020; Zeller et al., 2018). The resistance of degraded forests was arbitrarily fixed to the 95th quantile of resistance values in forests. Landscape planar graphs were created with the Graphab v.2.5 software (Foltête et al., 2012) from the habitat map defined from an optimal threshold applied on the HSI map (Liu et al., 2013), the resistance maps derived from Equation (1), and species home-range size and maximal dispersal distances derived from several sources and allometric relationships (Sutherland et al., 2000; Bowman, 2003; Lislevand et al., 2007; see Appendix S2). The landscape graph defines connected pairs of habitat patches, according to a least-cost-path algorithm (Adriaensen et al., 2003; Foltête et al., 2012). The amount of reachable habitat was calculated for a given species $i$ and scenario $j$ based on the equivalent connectivity index (Saura et al., 2011) as follows:

$$\text{EC}_{ij} = \sqrt{\sum_{k=1}^{n} \sum_{l=1}^{n} q_{ik} q_{jl} p_{kl}^d} \quad (2)$$

where $n$ is the number of habitats, $q_{ik}$ and $q_{jl}$ are the habitat area weighted by quality (or mean HSI) of patches $k$ and $l$, and $p_{kl}^d$ is the maximum product (or dispersal) probability between the pair of habitats $k$ and $l$. The maximum product probability was calculated from all the possible paths $p_{kl} = e^{-\alpha d_{kl}}$, where $d_{kl}$ is the cost-weighted distance of the path between habitat pair $k$ and $l$, and $\alpha$ is a parameter fixed according to species dispersal distance to control the decay of dispersal probability with increasing resistance distance. If patches $k$ and $l$ are directly connected without an intermediary patch, the maximum product probability is simply the cost-weighted distance of the least-cost path ($p_{kl}^d = p_{kl}$).

We compared equivalent connectivity ($\text{EC}_{ij}$) in 2050 to the current equivalent connectivity ($\text{EC}_{i2020}$) for species $i$ as follows:

$$\Delta\text{EC}_{ij} = \left( \frac{\text{EC}_{ij}}{\text{EC}_{i2020}} \times 100 \right) - 100 \quad (3)$$

The index $\Delta\text{EC}_{ij}$ was qualitatively compared to species thermal maximum extracted from Jiguet et al. (2007) while the links between $\Delta\text{EC}_{ij}$ and changes in landscape indices (habitat area, quality and mean cost distance of the least-cost paths) were depicted in (Appendix S4).
2.6 | Isolating indirect effects of climate changes for birds through forest land use change

Finally, four scenarios were built for each bird species. These scenarios included the direct effects of climate changes (bird responses to bioclimatic variables through the direct occurrence-climate relationship) and the indirect effects (climate-induced changes in tree species composition and their cascading effects on birds). We compared the above-mentioned four scenarios including full effects (i.e., direct and indirect, hereafter called the “full model”) to 4 additional scenarios including the indirect effects of changes in climate-induced tree species composition and the climatic envelop of the bird species as an invariant (hereafter called the “land use model”). For the full model, we used the 2050 GAM projections based on landscape factors and the 2050 GAM projections based on bioclimatic variables, to average bird occurrence probabilities and intersect bird distributions. For the land use model, we used the 2050 GAM projections for landscape factors and the 2020 GAM projections for bioclimatic variables considering the bird climatic envelop stable over time (Figure 1). By convention, the direct effect of climate changes was calculated by subtracting $\Delta EC_i$ computed with the full model from $\Delta EC_i$ computed with the land use model (indirect effects; Equation 4).

$$\Delta EC_i(\text{direct}) = \Delta EC_i(\text{full}) - \Delta EC_i(\text{indirect})$$ (4)

3 | RESULTS

3.1 | Isolating the indirect effects of climate changes on birds due to changes in tree species composition

For the bird species, AUC indices ranged from 0.75 to 0.83 for the GAM accounting for climatic conditions at the national scale. At the regional scale, AUC and CBI indices ranged from 0.61 to 0.76, and from 0.57 to 0.82, respectively. AUC and CBI indices were slightly low for P. collybita and C. brachydictyla (0.63 and 0.77 and 0.61 and 0.57, respectively). For R. regulus, the $\Delta EC_i$ showed that the indirect effects of climate changes were more often preponderant, with positive or negative effects depending on the scenario (Figure 2). The direct effects were always slightly negative due to shrinkage in the climatic envelope in future projections, while the indirect and the full effects were either positive or negative depending on the scenario (Figures 2, 3). For P. collybita and S. europaea, the climatic envelope was fully favourable and stable over time, indicating that the effects of climate changes were entirely explained by the indirect effects due to changes in tree species composition (Figure 2, see Appendix S1, S10). For D. major and C. brachydictyla, direct effects were preponderant and positive: the climatic envelope expanded in future projections (Figure 2). These direct effects were especially strong for C. brachydictyla as mixed forest areas decreased (Figure 3, Table 1). $\Delta EC_i$ showed opposite direct and indirect effects of climate changes for C. brachydictyla, depending on the scenario (Figure 2). The predominance of the direct effects of climate changes were positively correlated with species thermal maximum (Figure 2).

3.2 | Projection of tree species composition in 2050

For tree species, AUC indices ranged from 0.75 to 0.88 for the GAM accounting for climatic conditions at the national scale. At the regional scale, AUC ranged from 0.78 to 0.85 for tree species (except for P. menziesii for which model validity was low: AUC = 0.57). The two management scenarios resulted in contrasted tree species composition under the RCP 2.6 climate scenario (Table 1, see Appendix S1). For the “deciduous 2.6” scenario, F. sylvestica occupied a large part of the forest area in 2050 (28%) while Quercus spp. (9%) only modestly increased in area (Table 1). However, forest areas occupied by P. menziesii also increased, meaning that deciduous tree species were excluded from these areas (Table 1). For the “coniferous 2.6” scenario, forest areas were largely dominated by P. menziesii (58%) while climatic conditions had become poorly suitable for A. alba (7%). Under the RCP 8.5 climate scenario, the two management scenarios displayed close results (Table 1, Appendix S1). Most of the forested area (58%) was occupied by “degraded forests” outside the tree species distribution envelopes, thus indicating that climatic conditions had become unsuitable for all of the considered tree species. For both management options under the RCP 8.5 climate scenario, future forests appeared suitable mainly for F. sylvestica and, to a lower extent, for Quercus spp. (17% and 11% of the forested area, respectively). See Supporting Information for details on tree species distribution and responses to climatic conditions (Appendix S5), topography and soil acidity (Appendix S6) and their combination (Appendix S7).

3.3 | Variations in equivalent connectivity among scenarios

For P. collybita and R. Regulus, EC increased slightly under the two RCP 2.6 scenarios and decreased slightly under the two RCP 8.5 scenarios, compared to the current situation (~39% ≤ $\Delta EC_i$ ≤52%, Figure 4). For C. brachydictyla, EC increased for all the scenarios, but much more for RCP 8.5 (295% ≤ $\Delta EC_i$ ≤737%, Figure 4). For D. major, EC also increased, but more so for the RCP 2.6 scenarios (138% ≤ $\Delta EC_i$ ≤ 159%, Figure 4). For S. europaea, $\Delta EC_i$ varied with management, contrary to the other species: $\Delta EC_i$ was higher in the “deciduous 2.6” scenario than in the “coniferous 2.6” scenario (Figure 4). See Supporting Information for details on tree species distribution and responses to climatic conditions (Appendix S8), landscape factors (Appendix S9) and their combination (Appendix S10).
4 | DISCUSSION

4.1 | Isolating the indirect effects of climate changes on birds due to changes in tree species composition

We provided the first study investigating the importance of climate-induced changes in forest-tree species distribution and their cascading effects on birds via landscape processes. We showed that climate changes can drive birds’ amount of reachable habitat, mostly by indirect effects due to changes in tree species composition, depending on species and scenario. For example, climate changes only indirectly impact species with an intermediate thermal maximum (P. collybita and S. europaea) because the climatic envelopes for these two species were actually stable. However, habitat area, quality and spatial configuration, and matrix resistance did change after we accounted for changes in climate-induced tree species composition. For species with a high thermal maximum (D. major and C. brachydactyla), future climatic conditions have positive direct effects. Low negative indirect effects could be offset by strongly positive direct effects, leading to an increase in the amount of reachable habitat for the full effects of climate changes (C. brachydactyla). Both direct and indirect effects can also be at play for species with a low thermal maximum (R. regulus). As a consequence, the importance of the indirect effects of climate changes must be accounted for in projection scenarios and conservation management to evaluate strategies that...
could leverage suitable land use mitigating climate changes impacts. Our results also suggested that the relative importance of the direct effects of climate changes can be mediated by species thermal preference. Despite a growing interest in integrating multiple global stressors into conservation management, the combined effects of land use and climate changes have largely been disregarded (Sirami et al., 2017). Consequently, the indirect effects of climate changes on land use and their cascading effects on species are poorly known (De Kort et al., 2020). Previous works comparing the importance of climate and land use on birds commonly used Earth system models that integrate complex feedback mechanisms between climate, land use, human population and the macro-economy (Barbet-Massin et al., 2012; Triviño et al., 2011). However, the effects of climate-induced changes on tree species composition were hidden by a more general assessment of the relative importance of climate and land use (Albert et al., 2017; Ay et al., 2014; Barbet-Massin et al., 2012; Triviño et al., 2011). For example, Ay et al. (2014) also accounted for the indirect effects of land use change on birds, but they overlooked species dispersal. In their model, land use change depended on both climate and an econometric function of land use utility. Bonnot et al. (2017) incorporated metapopulation and forest composition projections to predict the impacts of climate changes on two bird species. However, even though they mentioned complex interactions between climate change, forest succession and land management, including the occurrence of indirect effects of these drivers on metapopulation dynamics, they did not evaluate their respective parts. McRae et al. (2008) proposed a modelling framework that integrates individual-based plant models and animal population models to simulate spatial and temporal changes in the habitat and populations of two bird species. The above-mentioned modelling studies were conducted at regional scales and consistently showed the importance of land use among other drivers (Ay et al., 2014; Bonnot et al., 2017; McRae et al., 2008). On the contrary, Barbet-Massin et al. (2012), who aimed to encompass the full realized niche of bird species, concluded that a direct impact of climate changes was preponderant at the European scale. These results highlight the importance of assessing the processes governing species response to global changes at different scales (Sirami et al., 2017). At the large scale, changes in species distribution could be explained by expanding or contracting climatic envelopes at distribution range limits (Morin et al., 2007; Vissault et al., 2020). At the regional scale (within the climatic envelope), the role of changes in habitat area, quality and spatial configuration and matrix resistance must be taken into account (Riva & Nielsen, 2020). Our study demonstrates the importance of disentangling tree and forest bird responses to climate changes. We highlight a strong potential effect of changes in climate-induced tree species composition on the amount of reachable habitat for forest birds, when climatic conditions remain suitable.

4.2 | Projection of tree species composition in 2050

Forested areas with P. menziesii increased for the RCP 2.6 scenario but decreased for RCP 8.5, while forested areas with A. alba decreased in both cases. Quercus spp. and F. sylvatica responded positively to climate changes in the study area. These findings...
are concordant with the “winner” and “loser species” reported at a larger scale by Dyderski et al. (2018). In our study, land use projections showed that the influence of forest management on tree species composition will be strongly constrained by climate change, in accordance with previous findings (Dyderski et al., 2018; Hanewinkel et al., 2013). The proportion of the different tree species varied across management scenarios when climate change intensity was moderate (RCP 2.6 scenario), but this was no longer true with more severe climate changes (RCP 8.5 scenario). Degraded forest areas drastically increased with severe climate changes (RCP 8.5 scenario). This result indicates that the tree species currently found in most of the study area are likely to suffer from the consequences of global warming (Taccoen et al., 2019).

Here, we did not consider the introduction of allochtonous tree species for two reasons: first, we were aiming above all to assess the future of the current tree species and second, the role of allochtonous species in offsetting climate changes and improving biodiversity conservation is being largely debated (Bremer & Farley, 2010; Quine & Humphrey, 2010). Finally, our results suggest that the heterogeneity of the current tree species composition could drastically decrease in the future, because few tree species responded positively to climate changes.

4.3 | Variation in equivalent connectivity among scenarios

Here, we illustrated the potential of simulation studies to evaluate conservation strategies in a context of global changes. Not surprisingly, we found that climate changes would mainly drive future equivalent connectivity for birds. Conservation strategies might have limited impact because bird species did not necessarily respond to management scenarios and tree species composition was almost completely driven by climate change when it was strong. Albeit, promoting *Quercus* spp. and *F. sylvatica* at the expense of *P. menziesii* could be an efficient conservation strategy to maximize landscape connectivity if climate change intensity remains limited. The coniferous management scenarios were characterized by a high proportion of Douglas-fir, an introduced species poorly suitable for several taxa (Schmid et al., 2014). Birds with a strong affinity for deciduous trees responded positively to climate changes because *Quercus* spp. and *F. sylvatica* increased, mostly independently of forest management trajectories. Future amounts of reachable habitat could slightly decrease for species preferring coniferous trees because of their conversion into degraded forest. The decrease in equivalent connectivity for *P. collybita* was explained by its affinity for *A. alba*. The strong increase
in equivalent connectivity for *C. brachydactyla* can be explained by a low proportion of favourable habitats under current climatic conditions coupled with a strong positive effect of climate changes.

### 4.4 Study limitations

Our study does have several limitations. First, though our predictions were generally accurate, model validity was rather low in some cases, especially when relating *P. menziesii* to topography and soil acidity. This is not surprising given that the species was introduced to France in the middle of the 19th century and has only been intensively planted since the end of World War II. Indeed, the difficulty to species distribution model for provenance among European populations. However, we felt that a species distribution model for *P. menziesii would still be useful since it would provide more information than a random model, and most importantly, because the high accuracy of the climate model would lead to France in the middle of the 19th century and has only been intensively planted since the end of World War II. Indeed, the difficulty to assess the response of forest birds in general. Focal species are carefully selected, for example to cover a range of habitat requirements and species traits (Lalechère & Bergès, 2021; Meurant et al., 2018). In our study, we considered a wide range of maximal dispersal distances (from 5.0 km for *R. regulus* to 28.0 km for *D. major*). We included the species most sensitive to climate warming (*R. regulus*) according to Jiguet et al. (2007) and covered a wide range of thermal preferences (72% of the range of values defined by the authors for a large set of species). Here, we acknowledged the importance of species thermal maximum, previously highlighted for bird communities (Jiguet et al., 2007, 2010), thanks to the wide range of species thermal maximum considered.

Third, climatic conditions could also be related to metabolic, physiological and behavioural adaptive responses triggered to maintain thermoregulation (Møller et al., 2010). For example, fitness is affected when individuals stop regular activities for the benefit of survival and at the expense of reproduction (Wingfield et al., 2017). Accounting for these drivers could be a promising approach to better understand the consequences of climate change.

Fourth, we did not account for forest succession while dynamic process-based models offer the opportunity to simulate tree growth and competition and to dissociate forest structure and composition (Bonnot et al., 2017; McRae et al., 2008). However, a large amount of knowledge, dependent on the study area, must be accumulated to calibrate such models. We are unaware of any study coupling dynamic process-based models with landscape connectivity models but this could be a promising way to better account for species interactions in mixed stands.

Fifth, the equivalent connectivity index compared two static independent landscape graphs (in 2020 and 2050) to provide information about the actual and future need for conservation actions, but did not evaluate metapopulation dynamics over time. We point out that the equivalent connectivity index can be incorporated into discrete time metapopulation models to evaluate species dynamics and the speed of colonization and extinction processes over time (Lalechère et al., 2018).

### 5 Conclusion

Finally, species distribution modelling has improved our knowledge of the relationships between climate and land use changes, while integrating climate changes into landscape connectivity models is still in its infancy (Costanza & Terando, 2019; De Kort et al., 2020; Keeley et al., 2018; Littlefield et al., 2017). We believe that the innovative framework we have provided here, linking species distribution and landscape connectivity models to climate and land use changes, is a promising approach to finely evaluate the interactive effects of global changes. In this study, we assessed the importance of climate-induced tree species composition change in habitat connectivity for common forest bird species with different thermal maximum. We highlighted the risk of a decrease in landscape heterogeneity and an increase in forest degradation. Our simulations underlined that the decision by forest managers to promote deciduous trees could maximize landscape connectivity for several forest birds. Further investigations are required to refine the complex interactive effects of climate and land use changes on forest species at regional scale, in particular in less heterogeneous forest landscapes or in agricultural or urbanized landscapes.

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### Conflict of interest

The authors declare that they have not known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability statement

The data that support the findings of this study are openly available in dryad at https://doi.org/10.5061/dryad.6hdr7sr23.

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**BIOSKETCH**

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Author contributions: E.L. and L.B. designed the study, E.L. conducted the analyses, E.L. drafted the first version of the manuscript, E.L. and L.B. contributed to the writing.

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