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Long-term effects of combined land-use and climate changes on local bird communities in mosaic agricultural landscapes

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ABSTRACT

Rural landscapes of western Europe have considerably changed in the last decades under the combined pressure of climate and land use changes, leading to a dramatic decline of farmland biodiversity, including common farmland birds. The respective roles of climate and land use and cover changes in driving bird population trends are primarily assessed at national or continental levels. Yet, it is often challenging to integrate their intertwined effects at such large scales due to the lack of data on fine-scale land cover changes. Here, we used a long-term bird monitoring scheme, combined with a land cover survey, conducted during 30 years (1981–2011) across 780 sites in a 20,000 ha study area in south-western France, dominated by low-intensity farming systems. We tested the direct effect of temporal changes in climate and land use on the dynamics of two community-level metrics: the bird Community Thermal Index (CTI) and bird Community Generalization Index (CGI). We used a novel method to assess the contribution of species-specific dynamics to CTI and CGI trends. We observed a significant increase in CTI and a significant decrease in CGI between 1981 and 2011, i.e., bird communities now have higher thermal preferences and are more specialized than 30 years ago. Bird CTI and CGI changes were both related to local climate- and land use-related drivers, especially mean temperature increase and hedgerow loss. Trends in CTI and CGI were primarily driven by the loss of cold-dwelling and generalist species, and secondly by a gain in hot-dwelling specialists. Our long-term study brings new empirical evidence that the effects of climate and land cover changes on bird communities are intrinsically intertwined, and need to be considered together to monitor and predict the future of farmland biodiversity. It also suggests that low-input, diversified agriculture combined with the maintenance of semi-natural habitat cover can contribute to the conservation of both specialist and generalist bird communities in agricultural landscapes experiencing rapid climate change.

1. Introduction

Human pressure on biodiversity includes habitat fragmentation, conversion and degradation as well as climate change and pollution (Newbold et al., 2015). Land use and climate changes are considered among the main drivers of biodiversity dynamics at different spatial and temporal scales (Sala et al., 2000; Thomas et al., 2004; Parmesan, 2006; Turner, 2010; Díaz et al., 2019). Their interactions might result in a 'deadly anthropogenic cocktail' (Travis, 2003) able to trigger strong changes in the composition and structure of ecological communities across all biomes and ecosystems (Newbold et al., 2015). However, only a few studies have explicitly integrated both climate and land use

changes, along with their interaction, as drivers of community changes (Eglington and Pegarce-Higgins 2012, Sirami et al., 2017; Titeux et al., 2016; Reino et al., 2018). This lack of climate - land use change integration is likely to have led to an underestimation of their respective and combined effects on biodiversity (but see (Clavero et al., 2011; Princé and Zuckerberg, 2015; Titeux et al., 2016).

Land cover change primarily drives bird community and species dynamics through ecological processes occurring at both local and landscape scales (Vickery and Arlettaz, 2014). Consequently, while large-scale responses of biodiversity to global change have been largely documented, the interplay between climate and land use changes as a key environmental driver remains poorly understood (but see Eglington

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and Pearce-Higgins, 2012; Betts et al., 2019). Moreover, taking into account long-term historical changes in land cover appears critical (Andrieu et al., 2011), because birds often display delayed responses to both land use and cover change and 'catastrophic-type' climatic events such as very cold winters or severe droughts (Jiguet et al., 2011; Lehikoinen et al., 2016).

Farmland birds are particularly sensitive to the combined effects of land use and climate changes (Eglington and Pegarce-Higgins, 2012), mostly through changes in food resources and intensification of agricultural practices, especially in western Europe (Chamberlain and Siriwardena, 2000; Donald et al., 2006; Bas et al., 2009; Heldbjerg et al., 2018; Reino et al., 2018). While the underlying mechanisms have been extensively studied in Europe and North America (Jerrentrup et al., 2017; Stanton et al., 2018), agricultural policies (e.g., UE CAP; see (Pe'er et al., 2014) have been unable to slow down farmland bird declines. In Europe, bird populations have declined by more than 50 % since 1980 (see https://pecbms.info/european-wild-bird-indicators-2017-update).

One of the main reasons for the limited understanding of the combined effects of climate and land use changes on bird communities is the lack of reliable data on long-term land cover changes over large geographical zones. However, recent works suggest that these global effects of land cover changes on biodiversity are not only quantifiable, but likely huge (Newbold et al., 2015; Song et al., 2018). The second reason for the limited understanding of these combined effects is that studies exploring the effect of climate-land use changes on biodiversity generally focus on either species-level trends or community-scale approaches (Newbold et al., 2015), but rarely combine both approaches. On one hand, species' specific responses to land use and climate changes provide limited taxonomic inference because they depend on their respective life history traits (Jiguet et al., 2007). On the other hand, trait-based community indicators are useful integrative tools to unravel the relative importance of these two main drivers of biodiversity changes (Vandewalle et al., 2010; Vollstädt et al., 2017; Kampichler et al., 2012). While these approaches are valuable tools to investigate large spatial and long temporal scales responses of biodiversity to global changes, they often provide limited understanding of underlying dynamics.

One of these trait-based approaches relies on the spatial and temporal monitoring of community-weighted mean of traits (CWM; (Ricotta and Moretti, 2011). Community-weighted mean trait values are based on the relative species abundances sharing a particular trait within the community (Lepš et al., 2011) reflecting species' sensitivity to a given environmental feature (e.g., local temperature or forest cover). Community weighted mean based indicators have been successfully used to track changes in community composition induced by climate (e.g., the Community Temperature Index, hereafter CTI : (Lepš et al., 2011; Devictor et al., 2008a, 2008b; Lindström et al., 2013), land use and cover change (Community Specialization/Generalization Index, hereafter CSI/CGI : (Kampichler et al., 2012; Godet et al., 2015), or both (Barnagaud et al., 2013; Gaüzère et al., 2015). However, they also have important methodological limitations (Clavero et al., 2011). Several authors have highlighted that temporal changes in CTI can also be affected by land use change not directly determined by climate, or driven by interactions between climate and land use changes (Barnagaud et al., 2012; Reino et al., 2018; Devictor et al., 2008a, 2008b; Barnagaud et al., 2012; Reino et al., 2018). The validity of the CSI, based on species' habitat specialization, has also been questioned because the range and extent of land cover gradients used to estimate specialization can differ widely across geographical regions (Julliard et al., 2006; Clavero et al., 2011; Le Viol et al., 2012). Moreover, previous studies on breeding birds in both Europe and North America have shown that climate-induced community changes could trigger an increase in CGI (Gaüzère et al., 2015), or that landscape composition and configuration could affect bird CTI response to temperature (Jarzyna et al., 2015). We therefore suggest that there is a critical need to

integrate both climate and land use predictors in the analyses of changes in community-aggregated indices such as CTI and CSI.

However, a change in community indices does not indicate which species or trait values were lost or gained, and whether the change is driven by large changes in a few species, or by small, but widespread changes across the entire species pool. This limitation has prevented a clear interpretation of community dynamics and of the mutual effects of both climate and land use changes on each indicator. The absence of linkage between community and species dynamics has also impaired a widespread use of community-aggregated indices in biodiversity conservation, which often focuses on the species and population scales (Davey et al., 2013). It is only recently that novel approaches have successfully provided a framework to link species and community-level dynamics (Princé and Zuckerberg, 2015; Tayleur et al., 2016; Gaget et al., 2018; Gaüzère et al., 2019). Bridging the gap between community and species level dynamics provides summarized information over large taxonomic inference, and allows a fine interpretation of changes through the quantification of species contribution to overall trends. This novel approach overcomes most of the limits of species-centered and community-centered approaches, and thus provides a valuable framework to understand the combined effects of climate and land use changes on biodiversity.

Here, we studied the combined effects of climate and land use changes on bird communities in agricultural landscapes of south-western France. We used data from a standardized monitoring scheme of bird communities and land cover changes collected in 780 sampling sites distributed over a c. 20000 ha area between 1981 and 2011 (Balent and Courtiade, 1992). Combined with climatic data, such a high-definition, long-term dataset on both bird communities and land cover is particularly relevant to test hypotheses on the combined effects of climate and land use changes. We used two community-level metrics to measure the respective responses of bird to climate and land use changes: the bird Community Thermal Index (CTI) and Community Generalization Index (CGI). We predicted a temporal increase in bird CTI in line with the rise of mean regional temperatures (Gaüzère et al., 2015). We also expected CGI to increase following the landscape simplification and agricultural intensification described at national scale (Le Viol et al., 2012).

Importantly, as we expected combined effects of land use and climate changes on bird community dynamics, we aimed at assessing whether independent, antagonistic, and/or additive effects between climate and land use changes were driving specific aspects of community dynamics (namely CTI and CGI). In order to provide a deeper understanding of community-scale dynamics, we calculated the relative species-specific contributions to changes in community indices (Gaüzère et al., 2019), and investigated how the link between species and community dynamics were related to their thermal and habitat preferences.

2. Methods

2.1. Study area

The study area is the Aurignac district, covering 190 km^2 located between the Garonne and Gers rivers in south western France (43″1602800 N, 0″5101100E, WGS 1984). Since 2017, the area is labelled by French CNRS as a LTSER (Long-Term Socio-Ecological Research), the 'Zone Atelier Pyrénées Garonne' (http://www.za-inee. org/fr/reseau). Elevation within the study area ranges from 200 m to 400 m, with an atlantic sub-climate subject to mediterranean influences. A multidisciplinary research work started back in 1981 in the district of Aurignac, to study changes in agricultural systems and their consequences on biodiversity and landscape dynamics. Main land uses of the study area include crops (mainly cereals, sunflower, rapeseed, alfalfa and field bean), mesohygrophilous meadows, grazed and mown grasslands, dry calcareous grass-scrubland mosaics, woodlands and

hedgerows. Woodlands are generally fragmented and dominated by *Quercus robur* and *Q. pubescens,* but some large forest patches still remains. Hedgerows are composed of various shrubs and mature trees, mainly *Quercus* spp.

2.2. Data

2.2.1. Bird monitoring

A systematic 500 m grid-based survey of breeding bird communities was conducted in 1981, 1991, 2001 and 2011 across the entire Aurignac district (N = 780 square cells of 0.25 km^2 in each year). Twenty-minute long point counts were established in the center of each square and conducted by six qualified ornithologists working simultaneously, between sunrise and 11am during the breeding period (end of April and May). Observers recorded all individual birds heard or seen on a high-resolution aerial photograph of each grid square to avoid double counting the same birds between two adjacent squares.

2.2.2. Land cover monitoring

Within each 0.25 km^2 grid, land cover was described using a sub-grid of 100 pixels of 0.0025 km^2. We associated each pixel to a land cover category, as follows: (i) woodland = pixel located within a forest patch; (ii) hedgerow = pixel located within a linear tree structure, generally along an agricultural stand border; (iii) farmland = pixel located within an agricultural stand, including crops, alfalfa and temporary grasslands, and (iv) permanent grassland = pixel located in semi-natural meadow or grazed grassland based on visual validation by the same observer from aerial photographs. We used black and white (1981), then color (1991, 2001, 2011) aerial photographs from the French National Geographical Institute (IGN), shot at comparable scale (around 1/30000) and georeferenced in ArcGIS 10.3. This land cover classification was cross-validated with field observations realized during point-bird counts. Furthermore, changes in land cover was quantified as the % change within each grid square compared to the baseline of 1981, at the start of the survey. The conversion from grassland to farmland represented the main land cover change during the study period. To take into account the collinearity between % farmland change and % grassland change, we only included %Farmland change in further analyses.

2.2.3. Temperature data

Temperature data were extracted from the SAFRAN meteorological model (Quintana-Seguí, 2008). SAFRAN provides monthly means of 2 m air temperature on an 8 × 8 km grid over France. For each monitored grid square, we extracted the monthly mean temperature from the closest SAFRAN cell centroid. For each square and each year (1981, 1991, 2001, 2011) we then calculated the mean breeding season temperature (March to August, in °C), as an estimate of the thermal conditions experienced by birds during the entire breeding season.

2.2.4. Species indices

The Species Thermal Index (STI, expressed in °C; (Devictor et al., 2008a, 2008b)) is an integrative species attribute representing the thermal centroid of its distribution range. STI was calculated as the average temperature experienced by a species across its geographical range during the breeding season. STI values were computed from ~1 km^2 resolution temperature grids (April–July averages for the period 1950–2000; Worldclim database) coupled with western Palearctic distributions of species at a 1 km^2 resolution from the EBCC atlas of European breeding birds (Hagemeijer and Blair, 1997). STI values are higher for species breeding in ranges with a higher temperature (e.g., southern distribution), and have proven useful to predict the sensitivity of hot vs. cold dwellers to climate change (Jiguet et al., 2006; Lindström et al., 2013; Gaüzère et al., 2016).

The Species Generalization Index (SGI) (Godet et al., 2015) represents the ecological niche breadth of a given species. SGI is

computed as the coefficient of variation of the species density across 18 land cover classes at national scale (Devictor et al., 2008a, 2008b) and corresponds to the inverse value of the Species Specialization Index (SSI, (Julliard et al., 2006). It reflects how narrowly or widely species are distributed across land cover classes (i.e., the habitat niche width of a given species). SGI and SSI have been successfully used to characterize habitat specialization in birds at various geographical scales (Clavero and Brotons, 2010; Devictor et al., 2010; Guetté et al., 2017). Note that SGI and STI values were not correlated when considering the species pool present in our dataset (linear model coefficient = 0.0161 ± 0.237, p–v alue = 0.946, Adj. R-squared: −0.014).

In order to describe how the local bird populations are responding to habitat composition in the study area, we inferred realized species habitat niche at the local scale, independently from the national scale estimation of habitat specialization (i.e. SGI). To do so, we used the outlying mean index analysis ((Karasiewicz et al., 2017), a multivariate niche analysis method quantifying species' habitat niches along orthogonal axes summarizing the main environmental gradients. The outlying mean index analysis uses site-habitat and site-species matrices to compute principal components as a combination of collinear predictors, as in Principal Component Analysis. We selected the first axis (explaining 57.2 % of the projected inertia) as the main habitat niche axis. It was negatively correlated with the proportion of open land cover (farmland and grassland covers) and positively correlated with the proportion of woodland cover within the landscape. Note that such a description of the habitat niche does not take into account the variability associated to habitat niche position, (i.e. the habitat niche breadth), which is quantified at species scale by the SGI.

2.3. Analyses

2.3.1. Calculating community indices

We measured community scale response to climate and land use changes by calculating indices based on the average value of a given species trait in the community, weighted by the relative abundance of each species. In order to measure community scale responses to climate of land use and cover change, we used community weighted mean of trait values, which calculate the average trait value of species composing the community, weighted by their relative abundance. A given community weighted mean trait value (CWM) is thus given by:

$$ \mathrm{CWH} = \sum_{i=1}^{n} \frac{a_i X_i}{A} $$

Where, a_i and X_i designates the abundance and the specific trait value of the ith species in this community, respectively, while A is the total abundance of all individuals in the community. Several dimensions of changes in community composition can then be assessed by applying this formula to different traits X_i (Kampichler et al., 2012; Godet et al., 2015). The Community Temperature Index (CTI$_{ij}$, as the community weighted mean of trait X_i = STI) and the Community Generalisation Index (CGI$_{ij}$, as the community weighted mean of trait X_i = SGI) were calculated for each point-count and year using the R function cwi {s3cR}.

2.3.2. Estimating temporal changes in community indices

To estimate temporal changes in CTI and CGI, we used linear mixed models (LMM) were CTI and CGI were considered as the dependent variable, regressed over year considered as a categorical fixed effect, and sampling site considered as a random effect on intercept, to account for non-independence of sampling sites and the potential influence of spatial gradients (Grueber et al., 2011). This model does not make the assumption that indices have linear temporal trends but summarizes the effect of each year individually. Plots resulting from this model reflect year-to-year changes in CTI and CGI with associated uncertainty. The integration of random intercept effect was efficient enough to take into

account the low spatial autocorrelation observed in the data set. As we did not find support for temporal autocorrelation in the residuals, we ignored this potential source of non-independence. Linear trends over the whole study period were also estimated (for community indices and environment descriptors) using the same LMM model structure, but considering year as a continuous fixed effect rather than a categorical fixed effect.

2.3.3. Testing the effects of climate and land use and cover change on community indices

To test whether temporal changes in CTI and CGI were driven by concomitant changes in climate and land use, we first calculated the magnitude of changes in CTI (ΔCTI) and CGI (ΔCGI), breeding temperature (climate) and landscape composition (land use and cover change) as the difference between the observed value at a given time and the baseline, set as the 1981 value (first year of the study). We then used linear mixed models (LMM) in which ΔCTI or ΔCGI was considered as the dependent variable, regressed over four environmental changes variables measured at the grid square scale, namely temperature change [ºC], % of farmland cover change, % of hedgerow cover change, % of woodland cover change (see Fig. 2). Model predictors were scaled to zero mean and unit standard deviation to facilitate comparisons of estimated effects. We considered sampling site as a random effect on intercept to account for non-independence of bird sampling locations. We controlled for temporal autocorrelation in response variables among successive years with a first-order autoregressive structure, selected over more complex structures (ARMA and higher lags) on the basis of AIC and graphical checks (Zuur et al., 2010). To further test for potential interaction between land use and cover change and climate effects on CTI and CGI temporal changes, we ran the same models while adding first order interactions between temperature change [ºC] and % of farmland cover change or % of hedgerow cover change (depending on model). Detailed analysis on interaction terms between climate and land use and cover change is presented in supplementary material S1.

2.3.4. Calculating species contributions to temporal changes in community indices

To assess which species and/or trait values are declining or increasing with time, and how these trends drive the observed changes in community indices, we quantified the extent to which a species contributed to trends observed at the community level. To do so, we used the s3cR package implementing the methodological framework presented in (Gaüzère et al., 2019). The contribution of a species is defined as the difference between linear change in CTI/CGI estimated on the whole dataset and the linear change in slope value estimated on the whole dataset after excluding the focal species (Princé and Zuckerberg, 2015). Species contribution can be either positive or negative. A species contributing positively to the trend intensifies the observed change in community mean trait value (stronger change -but same sign- induced by the dynamic of that species), while a species contributing negatively to the trend decreases the observed change in community mean trait value (weaker change induced by the dynamic of that species). Species-specific contributions thus result from both the combination of the originality of their traits (i.e., the absolute difference between species trait value and average trait value of the community) and the change in their relative abundance in the community. As a result, the higher the difference between the species trait value and the average trait value in the community, the higher is its relative abundance trend and its absolute contribution to CTI/CGI trends. Positive contributors to CTI/CGI trends are species for which the relative abundance trend and the trait originality have the same direction, and reversely for negative contributors (see Gaüzère et al., 2019 for full detailed mathematical background and code).

2.3.5. Investigating predictors of species contributions

In order to facilitate the investigation and the interpretation of

species-specific contributions, we defined four discrete species groups per index. As pecies contributions result from the combination of both their trait values and changes in their relative abundance, we built these predictive groups based on the interplay between the local change in species relative abundance and the species relative trait value. Because they aimed at summarizing the information contained in contribution values, these predictive groups do not incorporate the variability associated with the change in relative abundance, which were assessed by the raw contribution values. For STI, we first defined "cold" and "hot" species based on the species thermal index (see Section 2.3.5). Cold-dwelling species were species with thermal index below the average values of all the species recorded in the study (i.e STI < 13.5 °C), and conversely hot-dwelling species were defined as species with thermal index above this average value. Thus, the four thermal groups defined by the interplay of the species thermal index and the population trends were increasing-cold (n = 16 species), decreasing-cold (n = 22), increasing-hot (n = 18), and decreasing-hot (n = 15), respectively. For SGI, we defined specialist and generalist groups based on the species generalization index (see Section 2.3.5). Specialist species are species with generalization index below the average values of all the species recorded in the study (i.e SGI < 1.8), and conversely generalist species were defined as species with generalization index above the average value. Thus, the four specialization groups defined by the interplay of the species generalization index and the population trends were increasing-specialist (n = 16 species), decreasing-specialist (n = 13), increasing-generalist (n = 18) and decreasing-generalist (n = 24), respectively.

We then tested how the relationship between species contributions to CTI and CGI varied among *thermal groups* by running a linear model in which species contribution to CTI was considered as the dependent variable, regressed over the species contribution to CGI in interaction with *thermal group*. We then plotted the linear slope between CTI contribution and CGI contribution for each *thermal group*.

Finally, we tested how local habitat niche was linked to species' contributions to CGI, accounting for their habitat niche width. We ran a linear model in which species contribution to CGI was considered as the dependent variable, regressed over the habitat specialization level (i.e., specialist or generalist) in interaction with the local habitat niche position estimated from OMI analysis (see Species indices section). We then plotted the linear slope between CGI contribution and local habitat niche separately for generalist and specialist species. Note that these species-scale tests did not account for the phylogenetic relatedness potentially affecting the independence of values in the models, as the phylogenetic signal present in the species' contributions in our set of 71 species is probably negligible enough to be ignored among the model predictors. We however kept being conservative when interpreting p–values and only considered significant results at α = 1 % (p–value = 0.01).

All statistical analyses were performed in R 3.3.0 (R Core Team, 2017). LMMs were run with the R function lme{nlme} (Pinheiro et al., 2014). The s3cR package used to compute community weighted mean trait values and species contributions can be freely downloaded at https://github.com/pgauzere/s3cR (Gaüzère et al., 2019).

3. Results

3.1. Temporal changes in bird community indices

Temporal changes in CTI increased significantly during the study period (LMM coefficient 0.0074 ± 0.0005 °C.year^{-1} [estimate ± SE], N = 3120 observations, df = 2339, p–value < 0.0001, Fig. 1a). More specifically, CTI displayed a substantial increase between 1981 and 2001 and a slight decrease between 2001 and 2011 (Fig. 1a). Meanwhile, temporal changes in CGI decreased significantly during the study period (LMM coefficient -0.000686 ± 0.0001 [estimate ± SE], df = 2339, p–value < 0.001, Fig. 1b). CGI showed a substantial
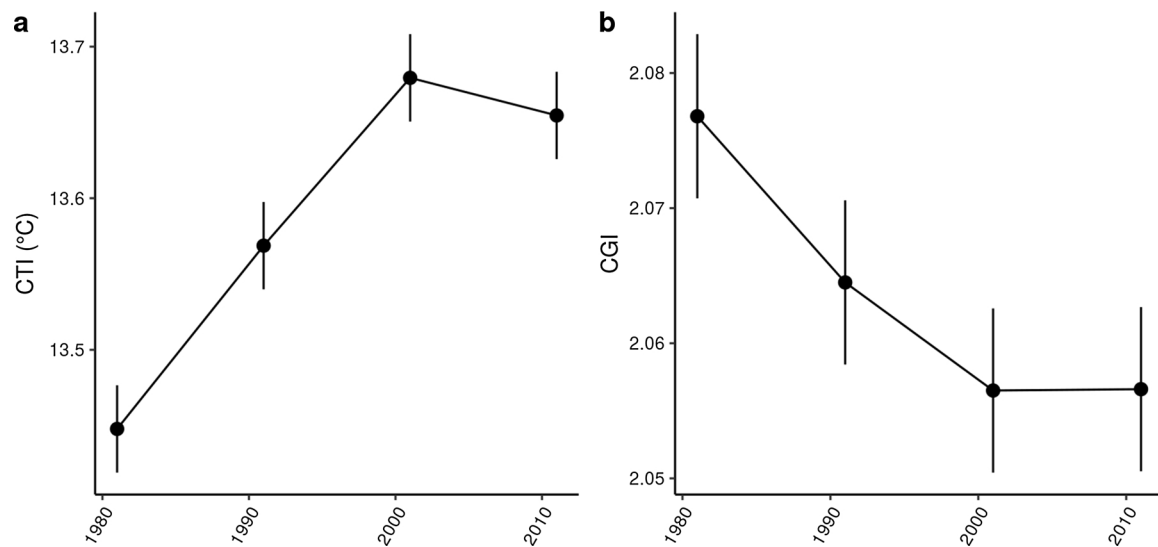
a

b

Fig. 1. Temporal changes in modelled values (LMM estimates ± CI95%, y-axis) of CTI (a) and CGI (b) during the study period (x-axis). Real survey dates were 1981, 1991, 2001 and 2011.

decrease between 1981 and 2001 but no change between 2001 and 2011. Overall, temporal changes in bird communities showed a relative increase in both hot-dwelling and specialist species at the expense of cold-dwelling and generalist species between 1981 and 2011, with most changes occurring between 1981 and 2001.

3.2. Spatial distribution of temporal changes in climate and land cover

Over the 30 years of survey, the mean temperature increased by 0.047 ± 0.00044 °C.year^{-1} (LMM estimate ± standard error, N = 3120, df = 2339, p–value < 0.001, Fig. 2a) while farmland cover increased by 0.340 ± 0.0187 %.year^{-1} (LMM estimate ± standard error, N = 3120, df = 2339, p–value < 0.001, Fig. 2b). The increase in farmland cover was strongly correlated with a decrease in grassland cover (Pearson's correlation coefficient: −0.917, 95% CI inf = −0.9227, 95% CI inf = − 0.9115, N = 3120, p–value < 0.0001). In other words, the increase in agricultural crop fields (i.e., farmland cover) mainly occurred at the expense of former natural grasslands and meadows, especially in the northern and central parts of the study area (Fig. 2b, c). In addition, the % cover of hedgerows decreased by -0.0997 ± 0.0065%.year^{-1} (LMM estimate ± SE, N = 3120, df = 2339, p–value < 0.0001, Fig. 2c), while the % cover of woodland did not change significantly (−0.0058 ± 0.0067 %.year^{-1} [LMM estimate ± SE], N = 3120, df = 2339, p–value = 0.394, Fig. 2d), except in the south-western and northern parts of the study area, where important changes occurred (Fig. 2d).

3.3. Effects of climate and land cover changes on temporal trends in bird community indices

Temporal changes in CTI were positively related to changes in breeding temperature and farmland cover, and negatively related to changes in the amount of hedgerows (see Fig. 3a. and Table 1 for detailed coefficients). In other words, the relative increase in hot-dwelling species observed between 1981 and 2011 (i.e., increase in CTI, Fig. 1a) was driven by the combined effects of climate and land use and cover change, and more precisely by the parallel increases in local temperature during the breeding season and farmland cover, and by the loss in the amount of hedgerows (Fig. 2 and Table 1). The effect of changes in breeding temperature on CTI had the largest magnitude among the set of predictors (Table 1) (Fig. 3).

Temporal changes in CGI were negatively related to changes in breeding temperature and positively related to changes in the amount

of hedgerows (see Fig. 3b and Table 1 for details on coefficients). In other words, the relative increase in specialist bird species observed between 1981 and 2011 (i.e., a decrease in CGI, Fig. 1b) was linked to both climate and land use and cover change, in particular the increase in breeding temperature and the decrease in the amount of hedgerows (Fig. 2 and Table 1). Loss of hedgerows displayed the highest magnitude on CGI trend compared to temperature (Table 1).

Supplementary analyses testing the interaction between temperature change and farmland cover and/or the amount of hedgerows on CTI and CGI changes did not show any significant interaction between climate- and land use and cover change-related predictors (Table S1a–c).

3.4. Species contributions to temporal changes in community indices

The analysis of species contributions to temporal changes in community indices showed that the increase in CTI was positively driven by both the increase in abundance of hot-dwelling species and the decrease in abundance of cold-dwelling species (Fig. 4a). More than ten species exhibited negative contributions (i.e., mitigating the increase in CTI). They include in particular, one hot-dwelling species with decreasing abundance, the cirl bunting *Emberiza cirlus,* and five cold-dwelling species with increasing abundances: common chiffchaff *Phylloscopus collybita*, Eurasian blackcap *Sylvia atricapilla,* common woodpigeon *Columba palumbus,* common chaffinch *Fringilla coelebs* and great spotted woodpecker *Dendrocopos major.*

The negative CGI trend was mainly driven by the decrease in abundance of generalist species and, to a lesser extent, by the increase in abundance of specialist species. Many species (~20) had negligible contributions (i.e ~0) to this negative trend in CGI, and a few increasing generalists exhibited negative contributions to the CGI decrease: Eurasian blackcap, common chaffinch, common woodpigeon, common chiffchaff and common nightingale *Luscinia megarhynchos*. These five species are among the six most increasing species in terms of relative abundance across the study period (see Fig. S2).

Testing the interaction between species contributions to CGI and *thermal groups* showed that a set of 12 increasing-cold species had a significantly negative contributions to the linear decrease in CGI (interaction term estimate ± SE = -2.266 ± 0.69, N = 71 species, df = 66, p–value = 0.0018**, see Fig. 5 bottom left panel), while other thermal groups did not have a significant contribution to CGI decrease. Testing the interaction between species contributions and *specialization groups* showed that -for generalists- habitat preference along the open-
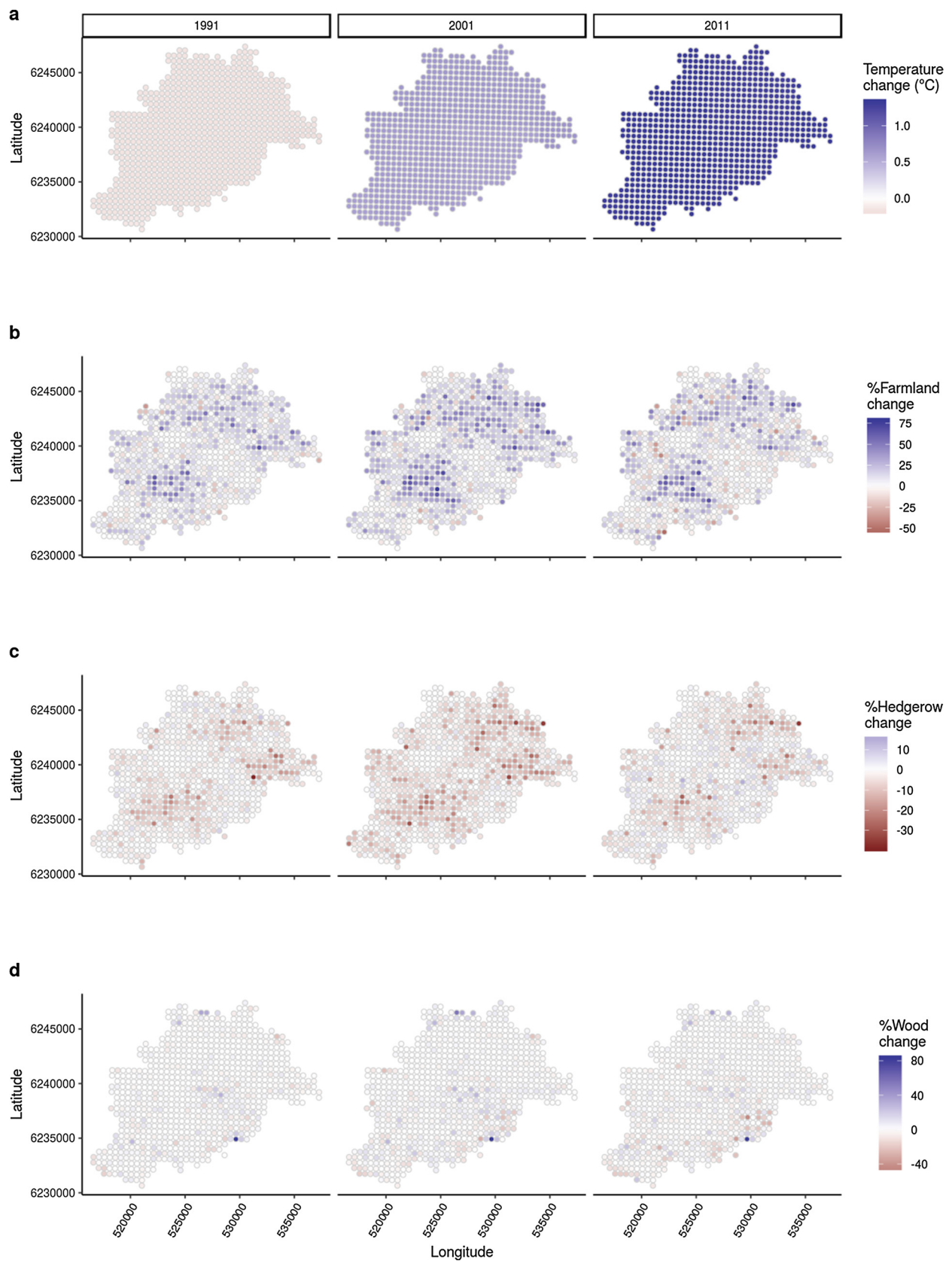
Fig. 2. Spatial distribution of temporal changes (relative to the 1981 baseline value) in climate (breeding temperature) and land covers (%Farmland, %Hedgerow, % Woodland).

Table 1
Coefficients from Linear Mixed Models relating CTI and CGI changes to climate and land cover changes. Significant results are indicated in bold.

Predictor	Effects on CTI trend					Effects on CGI trend				
	Coeff.	Std.Error	DF	t-value	p-value	Coeff.	Std.Error	DF	t-value	p-value
Temperature Change	**.0.037**	**0.006**	**1556**	**5.67**	**0**	**−0.004**	**0.001**	**1556**	**−2.68**	**0.007**
% Farmland Change	**0.027**	**0.011**	**1556**	**2.48**	**0.013**	−0.003	0.002	1556	−1.57	0.116
% Woodland Change	0.001	0.010	1556	0.13	0.895	0.003	0.002	1556	1.47	0.140
% Hedgerow Change	**−0.027**	**0.011**	**1556**	**−2.47**	**0.013**	**0.008**	**0.002**	**1556**	**3.76**	**< 0.001**

woodland habitat gradient was positively correlated with their contributions to the decrease in CGI (interaction term estimate ± SE = $2.875.10^{-4} \pm 1.035.10^{-4}$, N = 71, df = 66, p–value = 0.0071 **; see Fig. 6 left panel).

4. Discussion

In the present work based on a long-term survey of bird communities in mosaic agricultural landscapes, we observed a significant increase in bird CTI in line with the increasing mean breeding temperature experienced by birds within the study area during the survey period, as widely expected by predictions (Pearce-Higgins et al., 2015). We also found an unexpected increase in bird mean specialization with a significant CGI decrease, in contrast with predictions from the effects of land use and cover changes on birds at national and continental scale (Le Viol et al., 2012). We provide evidence for long-term changes in bird communities of this temperate rural area of south-western France

being driven by the combined effects of climate and land cover changes, in line with results from 18 farmland bird species in the UK (Eglington and Pearce-Higgins, 2012). Temporal changes in trait-based indicators monitoring bird community responses in terms of thermal niche and habitat niche breadth were both related to the increase in temperature, the increase in farmland cover and the decrease of hedgerows and permanent grasslands during the study period. Note that the biogeographical history of bird-habitat relationships and the large-scale covariation between climate and land cover along latitudinal gradients can generate intrinsic correlation between STI and SSI/SGI, which could in turn lead to misleading interpretations of community temporal dynamics. Here, we checked for the absence of intra-set correlations between species-scale indices (STI, SGI), ruling out the possibility that CTI and CGI trends numerically resulted from the scaling up of species-scale correlations.

Our study thus brings novel empirical evidence that land cover and climate changes are not driving bird community dynamics
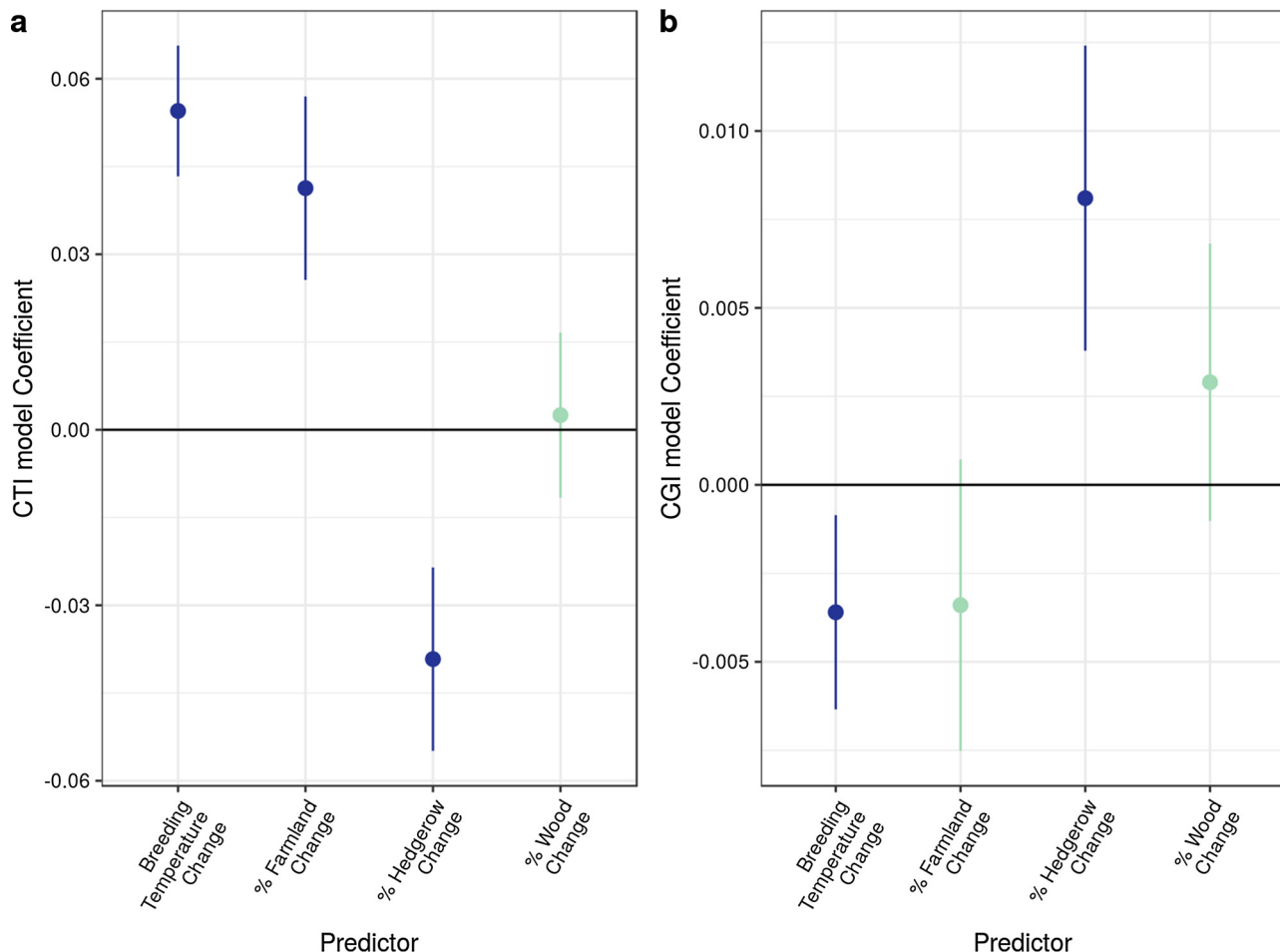

Fig. 3. Effects (Linear Mixed Models Coefficient ± 95%CI, y-axis) of climate and land cover changes (x-axis) on CTI (a) and CGI changes (b). Predictor effects are considered significant when coefficient ± 95%CI ≠ 0 (dark blue points and bars), otherwise non-significant (light green points and bars).
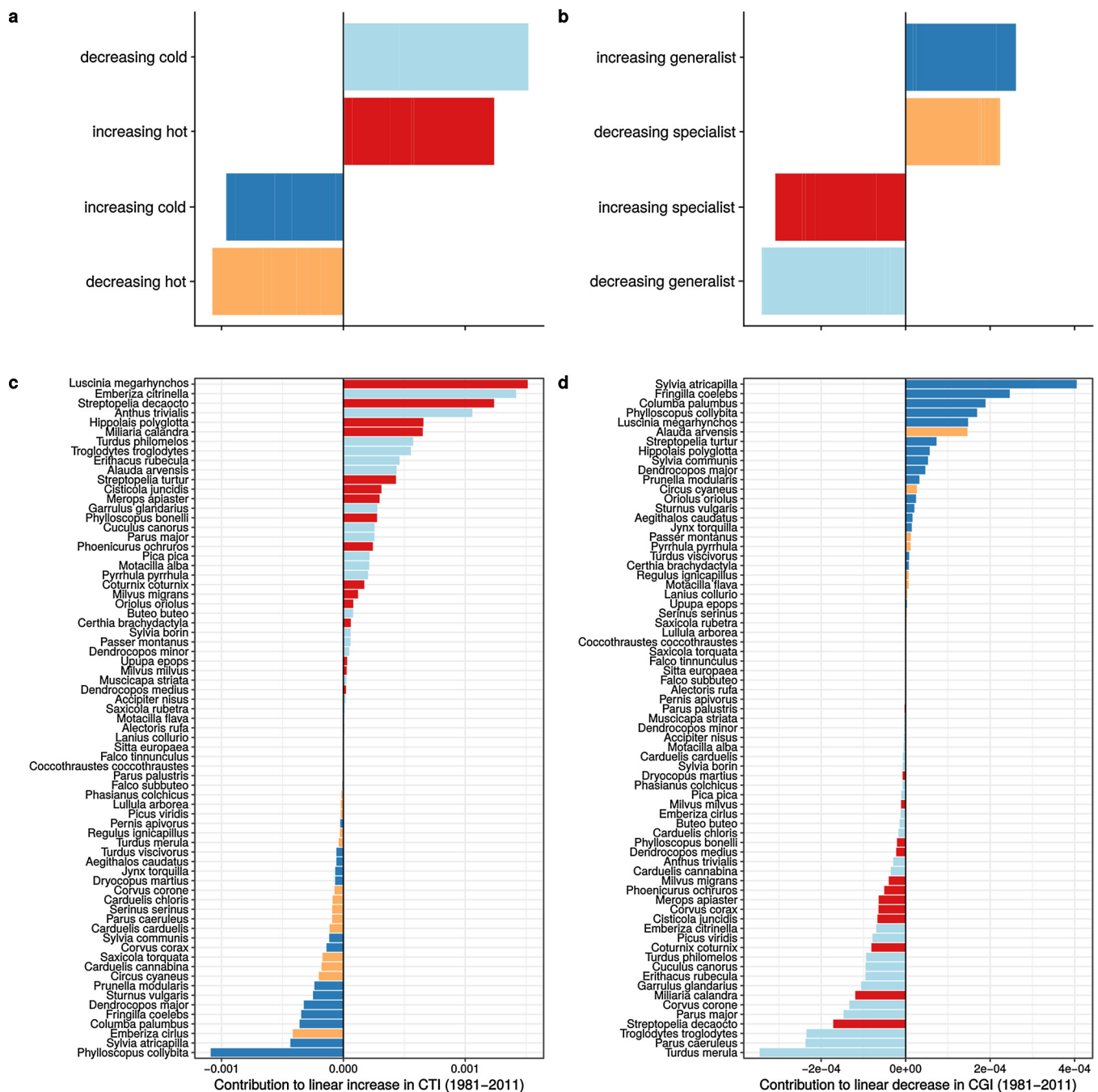
Fig. 4. Species contributions to linear increase in CTI (a,c) and linear decrease in CGI (b,d). Contributions are displayed per thermal and specialization groups defined by the interplay between species trait value and relative change in species abundance (a, b) and per each individual species (c,d). Color bars corresponds to predictive groups. For thermal groups: increasing hot = dark red, increasing cold = dark blue, decreasing hot = orange, decreasing cold = light blue. For specialization groups: increasing specialist = dark red, increasing generalist = dark blue, decreasing specialist = orange, decreasing generalist = light blue.

independently. While these two facets of global change were not interacting *per se* during the study (i.e., we did not demonstrate direct mitigating or synergistic effects of climate and land use changes on bird communities), we pointed out their combined effects in community-level responses of the local avifauna. These results are in line with recent work emphasizing synergistic effects of climate and land use changes on bird community dynamics (Betts et al., 2019; Northrup et al., 2019), and their critical importance for the prediction of species declines. Based on this empirical evidence, we argue that both drivers should be considered simultaneously to improve our understanding of farmland biodiversity response to global changes, and to develop accurate predictive models (Chiron et al., 2013; Gaüzère et al., 2017;

Reino et al., 2018; Betts et al., 2019). Directly considering the interactions between different global change dimensions will provide more robust and targeted information for the conservation of biodiversity (Northrup et al., 2019).

Our findings are further consistent with forest habitats sheltering relatively colder-dwelling bird communities compared to open habitats, likely because of evolutionary and biogeographical history rather than microclimate buffering in shady forest habitats (Clavero et al., 2011; Barnagaud et al., 2013; Pearce-Higgins et al., 2015). Our results suggest that beyond the width of their ecological niche (i.e., habitat specialist to habitat generalist), bird species habitat preference (i.e., agricultural, wooded or urban) might be a major driver of community responses to
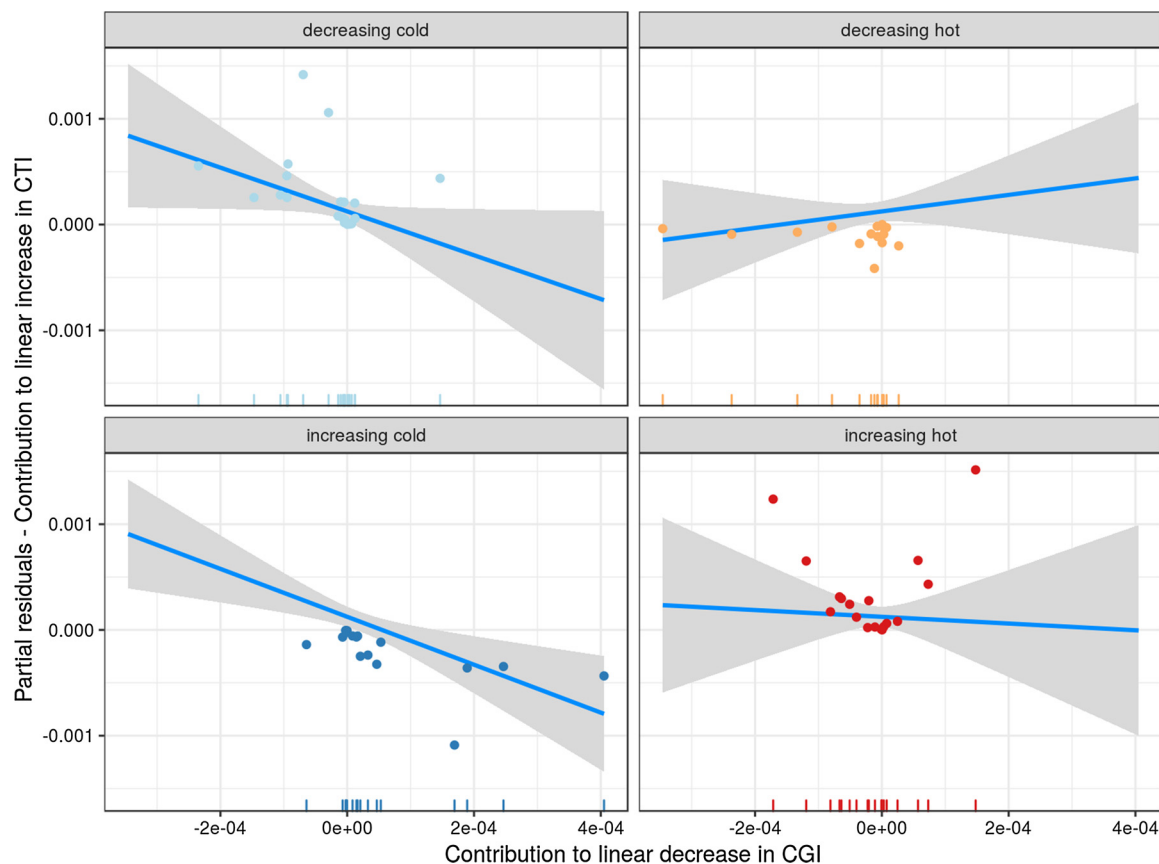
Fig. 5. Biplots of partial residuals for the relationships between species contributions to CGI decrease and contributions to CTI increase per thermal groups. Straight lines represent the linear coefficient of each interaction term.
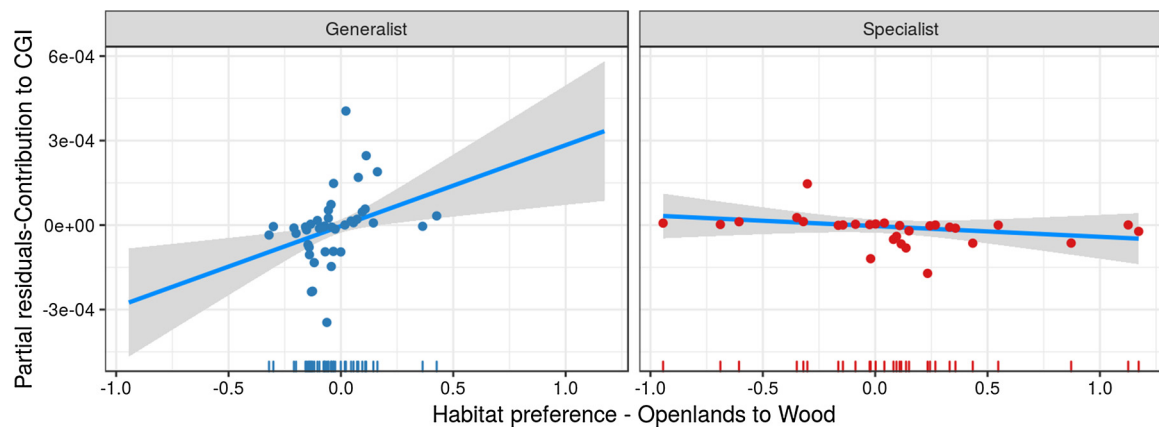

Fig. 6. Biplots of partial residuals for the relationships between species contributions to CGI decrease and local habitat niche position, estimated from OMI analysis, for generalist and specialist species (based on SGI values). Straight line represents the linear coefficient of each interaction term.

interactive effects of climate and land use changes (Sullivan et al., 2015). Reaching a deeper empirical understanding of observed community trends is therefore challenging, and our study provides a good example of how quantifying species contribution to overall trends in community-weighted indices such as CTI and CGI can help address this challenge (Gaüzère et al., 2019).

Interestingly, we found that temporal changes in community indices were due to both decreasing cold-dwellers and increasing hot-dwellers (positive CTI trend) and to both decreasing generalists and increasing specialists (negative CGI trend). Among the cold-dwelling species declining during the study period, yellowhammer *Emberiza citrinella* and tree pipit *Anthus trivialis* showed the most important declines, while among hot dwellers, the most important increases were found in

common nightingale and collared dove *Streptopelia decaocto*. It is however noticeable that some cold dwellers (e.g., chiffchaff) also increased, involving opposite trends to those expected from predictions based on climate change, while some hot dwellers (e.g., cirl bunting) have also declined significantly since 1981. Pushing further our analyses on the species-scale interactions between climate and land use changes (Fig. 5) revealed that species responses unexpected from the niche hypothesis (e.g., cold-adapted species with increasing populations) could be explained by the interaction with their responses to land use change. When comparing these species-specific trends with the ones observed for the same species at national or European levels (European Bird Census Council, BirdLife International, 2019), it appears that trends observed in our study area are consistent with the larger-scale

trends, except for the common nightingale, which is decreasing in northern Europe but rather stable in southern Europe (Holt et al., 2010). Contrarily to most western European agricultural landscapes that have been affected by dramatic land cover changes during the study period (Vickery and Arlettaz, 2014; Fahrig et al., 2011; Stanton et al., 2018), mosaic agricultural landscapes occurring within our study area seem to have been only moderately affected since the beginning of the survey in the early 80 s (Balent and Courtiade, 1992). The maintenance of mixed low-intensity farming in the study area compared to the widespread farmland intensification observed in Europe during the same period (Doxa et al., 2012; Korner et al., 2018) is likely to be the main factor explaining this pattern. Compared to other rural regions of western Europe, our study area experienced an overall maintenance of woodlands and a partial maintenance of the hedgerow network (see Fig. 2c), mainly for socio-ecological reasons (Andrieu et al., 2011; Sourdril et al., 2012; Blanco et al., 2019). These local particularities in land cover change (or maintenance) probably explain the decrease in CGI observed over the study area, while large-scale studies have reported opposite trends in France and in Europe (Donald et al., 2006; Le Viol et al., 2012; Heldbjerg et al., 2018). Similar increases of specialists have also been reported in the United Kingdom, although they did not significantly affect mean bird specialization which kept increasing due to the increase in the density of generalist species (Sullivan et al., 2015). In the present study, decreasing generalists such as blackbird *Turdus merula* or blue tit *Cyanistes caeruleus* almost had the same weight than increasing specialists such as collared dove *Streptopelia decaocto* or corn bunting *Emberiza calandra* in determining community-level changes.

Generalist birds (i.e., with SGI value greater than average) associated with woodland were negatively affected by the loss of hedgerows and are now more restricted to woodland-dominated landscapes than in 1981 (Balent and Courtiade, 1992). The decline in CGI implies an increase in mean specialization at the community level, with species being either farmland specialists or hot climate-dwelling species, or both, significantly increasing in the study area. This result thus strengthens the hypothesis that low-intensity agricultural systems providing the maintenance of semi-natural components in these rural landscapes may have been the key factor allowing the conservation of specialized farmland bird communities in our study area (Blanco et al., 2019), while they are otherwise declining elsewhere in Europe (Jeliazkov et al., 2016; Henckel et al., 2019; Doxa et al., 2012). However, we also observed a strong decline of common and generalist birds associated with woodland, which can be explained by a loss of linear landscape features, such as hedgerows, that formerly allowed their maintenance in mosaic agricultural landscapes (Korner et al., 2018; Sullivan et al., 2017; Juliet A. Vickery et al., 2014).

By exploring long-term trends in our bird community data, we found evidence that, in our study area, the 80′s and 90′s decades were the most affected by changes in bird community structure (CTI increase and CGI decrease) and the largest declines in bird abundance (see Fig. S2). These two decades matched the peak of agricultural intensification and landscape simplification at both local and macro-scales (Jerrentrup et al., 2017; Stanton et al., 2018). In our study area, generalist birds have declined more steeply overall than habitat specialists. This unexpected finding may be due to the fact that most species classified as generalist species may actually be multi-habitat species, strongly dependent on landscape complementation processes (Fahrig et al., 2011; Vickery and Arlettaz, 2014). In the present study, we made the assumption that bird communities would exhibit a short-term linear responses to climate and land cover changes. However, non-linearity, delays, thresholds, and memory effects are likely to influence the response of bird communities to climate and land cover changes (Gaüzère et al., 2015; Princé and Zuckerberg, 2015; Gaüzère et al., 2018). Like elsewhere in Europe, we also found that woodland specialists have increased during the study period, including cold-dwelling specialist species depending on old-growth oak forests such as middle spotted

woodpecker *Dendrocoptes medius* (Lehikoinen and Virkkala, 2018). This trend is opposite to the one expected based on predictions of combined effects of climate and land use changes, and highlights the need to take local habitat quality and fine-scale management practices into account to understand long-term species trends. Similarly, rodent prey availability may have increased habitat quality through enhanced foraging opportunities for many raptors that tend to increase in the study area, such as the black-winged kite *Elanus caeruleus (*Balbontin et al., 2008; Ławicki and Perlman, 2017).

5. Conclusions

High-definition, long-term coupled monitoring of biodiversity and land cover in agricultural landscapes provide an opportunity to investigate the intertwined effects of the different facets of global change on bird communities. As such, the analysis of bird species trends over 30 years in our study area suggests that multi-species dynamics were driven by the combined effects of changes in temperature and land cover, especially during the first 20 years of the survey period. The relative maintenance of semi-natural components in this rural region of south-western France has prevented the erosion of specialist farmland and woodland birds in a context where the decrease in specialist species has been identified as the most important consequence of global change for European breeding birds (Le Viol et al., 2012; Gaüzère et al., 2016). While current EU policies aiming at bird conservation at large scale might have contributed to slowing down the steep decline in farmland birds, they have clearly not been able to reverse them efficiently (Pe'er et al., 2014; Gamero et al., 2017; Vickery and Tayleur, 2018). As climate will inexorably be warmer in the next decade, it is likely that its combined effect with large-scale land cover and land use changes will become an even more important threat for farmland biodiversity in the near future (Pereira et al., 2010; Northrup et al., 2019). Limiting their combined detrimental effects on biodiversity must therefore engage all available leverages, including optimizing local agricultural practices and landscape-scale farmland management in order to mitigate the widespread and long-term negative consequences of global changes on biodiversity.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2019.106722.

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