Article title

Growing disequilibria in species distributions and assemblage diversity until the end of the 21st-century

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dynamics – Time lagged or time delayed biodiversity dynamics – Temporal influence functions – Temporal extent of time lags

Aknowledgments

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Abstract

Biodiversity forecasts almost universally assume that species are in equilibrium with contemporary environmental conditions. The consequences of this assumption are rarely tested, yet it may systematically bias inference and prediction whenever past natural or anthropogenic disturbances leave legacy effects keeping biodiversity in disequilibrium. Here we test how accounting for such legacy effects alters estimated species' niches, and projected biodiversity trends, using a general framework quantifying species niche under disequilibrium dynamics.

Using a hypervolume-based approach, we quantified the realised niche of 84 European forest breeding birds and compared two niche models: one equilibrium model using only forest cover and climatic conditions that are contemporary to bird species distribution data vs. one disequilibrium model that also incorporates past trajectories of change in forest cover and climate. We then projected the future distribution of all bird species across Europe (under two coupled climate and land-use scenarios) by using stacked range maps to derive the α, β, and γ components of taxonomic, functional, and phylogenetic diversity, towards the end of the 21st century.

Accounting for past environmental trajectories to quantify 'the disequilibrium niche', we revealed a dramatically expanded realized niche space (by a factor of 8.1), indicating a substantial niche truncation by equilibrium-based models. Despite broadly consistent average temporal trends in projected bird diversity under equilibrium and disequilibrium assumptions, this apparent agreement masks pronounced and increasingly divergent regional differences which are projected to increase towards the end of the 21st century.

Our study shows how violations of the equilibrium assumption can reshape biodiversity

projections. Unveiling the hidden legacy of past forest cover and climate on the current distribution of forest breeding birds allowed us to provide the first spatially explicit projections of how future biodiversity disequilibria may increase under accelerating climate and land-use change. This calls for including disequilibrium dynamics in biodiversity forecasting.

Introduction

Projecting future biodiversity trends plays a key role in biodiversity assessments aiming to provide robust evidence on the impact of human activities on biodiversity from up-to-date ecological models (IPBES, 2019). Future projections of species distributions mostly rely on Hutchinson's conception of the realized niche, which is the environmental space within which a species can survive and reproduce (Pulliam 2000; Guisan & Thuiller, 2005). This environmental and multidimensional space can be illustrated and measured by a hypervolume that encapsulates all the environmental conditions where the focal species occurs within the geographical space (Blonder, 2018). Occurrence data also reflect dispersal limitations, habitat availability and accessibility, species interactions, as well as lagging dynamics that are intrinsically linked with environmental conditions in defining a species' realized niche (Webber et al., 2023). Recently, Chevalier et al. (2024) proposed that a substantial proportion of marine and terrestrial species might be partly pre-adapted to future climatic non-analogues, given similar climatic conditions they experienced in the past. They introduced the idea of the "ghost of past ecological niches" to suggest that current environmental conditions represent a truncated view of current species' realized niche, which is also determined by past environmental conditions (Lalechère et al. 2025a,

2025b). However, this hidden component of the niche hypervolume has yet to be revealed and incorporated into biodiversity forecasts.

Going back into the past to explore current species' realized niche truncation is also an opportunity to move beyond the traditional assumption of an equilibrium between current species distribution and their contemporary environmental drivers. This assumption (hereafter called "equilibrium assumption") implies that the impact of biodiversity drivers unfolds immediately, despite evidence of lagging dynamics in biotic responses to environmental changes (Bertrand et al., 2011). Evidence of lagging dynamics suggests that long-term effects on biodiversity accumulate over time, leading to a disequilibrium between species responses and their contemporary drivers (Bertrand et al., 2011; Coulson et al., 2020). Retrospective studies have provided evidence that non-equilibrium dynamics are widespread among different biodiversity drivers, levels of biological organizations and eco-evolutionary processes (Figueiredo et al., 2019). However, the equilibrium assumption remains the only possible assumption when projecting future species distribution from state of the art ecological niche models (Essl et al., 2023).

Here, we aim to make the legacy of past ecological niches explicit in order to reveal future disequilibrium dynamics in species redistributions and diversity. For this purpose, we build on a recently published framework that explicitly embraces the non-equilibrium assumption in species distribution models (SDMs; Lalechère et al., 2025a), using a set of paired SDMs (equilibrium vs. non-equilibrium SDMs) calibrated for 84 European forest breeding birds (Lalechère et al., 2025b). In this study, the non-equilibrium SDMs enable us: (i) to reveal the truncated part of species' realized niches by accounting for time lags in response to past trajectories of change in environmental conditions right where species currently occur, (ii) to look back at past environmental

conditions until the temporal extent of time lags is reached, and (iii) to capture the general trend of the lagging dynamics in species responses through temporal influence functions. All of these features allow us to test how violations of the equilibrium assumption reshape biodiversity forecasts highlighting disequilibrium dynamics in species redistribution. By stacking current and future projections of species distributions across Europe, we compared the outcome on the different components (α, β and γ diversity) of taxonomic, functional and phylogenetic diversity in response to different scenarios of land-use and climate changes to assess future impacts on bird assemblages. Our objectives are to better quantify the hypervolumes of species' realized niches by unveiling the imprints left by past environmental conditions, and to reveal the future disequilibrium dynamics in the spatiotemporal patterns of bird distribution and diversity within a general framework that can be extended to other taxa and environmental drivers.

Methods

Description of the study case

We focused on 84 European forest breeding birds, for which equilibrium and non-equilibrium SDMs were fitted as in Lalechère et al. (2025b). More specifically, model fitting was based on occurrence data extracted from 4099 meshes of the European Breeding Bird Atlas (EBBA2) because it provides a systematic survey of bird check lists, at a spatial resolution of 50 km × 50 km between 2013 and 2017 (Keller et al., 2020). Since bird occurrence data were averaged over 5-years, we choose to refer to this time period of 2013-2017 using the date that corresponds to the upper limit of the interval (hereafter, we used 2017). Occurrence data were related to the main determinants of forest breeding bird species distribution that were formerly identified

by Cooper et al. (2023) at a continental extent in Europe, namely: the proportion of forest cover (i.e., distinguishing between primary and secondary forests), annual precipitation, and mean annual temperature. All four predictor variables were available as time series at a yearly resolution using the LUH2 dataset for forest cover (Hurtt et al., 2020) and the CHELSA dataset for climate conditions (Karger et al., 2017), at a native spatial resolution of 0.25° × 0.25° and 1 km^2, respectively. The time series ranged from the years 854 to 2017 for forest cover and from 1854 to 2017 for annual precipitation and mean annual temperature. Forests were either defined as 'primary', if this land-use category has remained the same over time since 854, or as 'secondary' otherwise (Hurtt et al., 2020). To match the 5-year resolution of the EBBA2 occurrence data, we aggregated the four time series of the four predictor variables, computing the mean for each 5-year interval. Similarly, to match the spatial resolution of the EBBA2 occurrence data, we aggregated all four predictor variables using the 50 km × 50 km grid of the EBBA2 data, computing the mean within each grid cell. There were no multicollinearity issues between the averaged predictor variables considering that the absolute Spearman correlation coefficient was systematically < 0.7 (Dormann et al. 2013).

To fit the traditional set of equilibrium SDMs, we only used environmental conditions during the 2013-2017 period, referred to as 2017, which are contemporary to the 2017 data on bird occurrences (Lalechère et al., 2025b). To fit the non-equilibrium SDMs, we relied on temporal influence functions (see Lalechère et al., 2025a) that use the entire time series of past environmental conditions, i.e., 1164 years at 5-year interval for forest cover and 164 years at 5-year interval for climate conditions, to quantify the temporal depth of the effect of past trajectories of environmental changes on current bird species distribution. These non-equilibrium SDMs provided the best fit to observed

occurrences and outperformed equilibrium SDMs (Lalechère et al., 2025b), so we here use them as the reference models to investigate the consequences of relaxing the equilibrium assumption for biodiversity projections.

Data on future time series of forest cover and climate conditions, from 2018 to 2100, were extracted from the same datasets that were used during model fitting (i.e., the LUH2 dataset for land use and the CHELSA dataset for climate; Hurtt et al., 2020; Karger et al., 2017) and further aggregated at a 5-year interval and at 50 km × 50 km resolution. We compared two contrasting shared socioeconomic pathways (SSPs) that cover the breadth of plausible environmental changes, i.e., a mild one (SSP 245) and a severe one (SSP 585). Averaged over the study area, the latter was characterized by a larger decline of primary forest cover at the benefit of secondary forest cover (in the north of the study area), by lower annual precipitation and higher mean annual temperatures, compared to the former (Supplementary Information, Appendix S1).

Quantifying niche hypervolume

The hypervolume of a species' realized niche was defined as the product of the range (the 0.99 quantile minus the 0.01 quantile) of each of the four relevant environmental predictor variables we used in our equilibrium and non-equilibrium SDMs (Blonder 2018). The values of the environmental conditions were rescaled between 0 and 1 to give them the same importance. For the non-equilibrium SDMs, the measure of the hypervolume was based on both past and contemporary environmental conditions (from 1854 to 2017 or from 854 to 2017, depending on the driver). Past environmental conditions were only accounted for if they contributed to explain the current pattern of occurrences for the focal bird species. For that, we only considered past environmental

conditions until we reached the threshold date for which past environmental conditions had no effect on the contemporary distribution of the focal bird species. This threshold date corresponds to the temporal extent of a time lag, after which the effect of the focal predictor variable is not different from zero in the distant past (Lalechère et al., 2025a). For each species, half-Gaussian temporal influence functions (W_j) were used in order to define the weight (or the importance) assigned to each past environmental conditions *j* (Lalechère et al., 2025b):

$$W_j(\Delta t; \theta_j) = e^{-0.5(\frac{\Delta t}{\theta_j})^2} \quad \text{(eq. 1)}$$

where Δt_j is the temporal distance from 2017 (i.e., Δt increases as we go back in time from 2017). The number of time step Δt depends on the predictor variables *j* (i.e., 1164 years for forest cover variables or 164 years for climate variables). The vector θ_j is a set of parameters (already inferred in Lalechère et al., 2025b) that defines the shape of the temporal influence functions associated to each environmental condition and species.

We used eq. 1 to weight each environmental condition over time, and calculate the hypervolume of each species' realized niche, as previously defined (i.e., as the product of the range of each of the four environmental predictor variables). We then qualitatively compare the distribution of the hypervolumes estimated from the equilibrium SDM vs. the non-equilibrium SDM. The definition of the hypervolume of a given bird species is the same for the both SDMs (Blonder, 2018), but the weights of the environmental conditions decreased (from $W_j = 1$, in 2017, when $\Delta t = 0$) as we go back in time for the non-equilibrium SDM ($W_j < 1$, in the past, when $\Delta t > 0$), while all the weights were kept to a value of 1 ($W_j = 1$, in 2017) when using the equilibrium SDM of the focal species (which is equivalent to considering that there is no weighting). For

both SDMs, we also compared the range of each weighted environmental condition to understand their respective contribution to the overall variation of the hypervolumes.

Projecting future species, phylogenetic and functional diversity

We stacked all 84 projected species distributions to assess future (from 2018 to 2100) trajectories of bird assemblages. Our projections are based on the assumption of niche conservatism for both the equilibrium and the non-equilibrium SDMs. The latter has the potential to improve the projection reliability of future biodiversity trends by looking back at the past, potentially avoiding over-extrapolation. Extrapolation is defined by projections that are beyond the range of the environmental conditions that are considered during model fitting (i.e., beyond the realized data space, Velazco et al., 2024. The assessment of extrapolation is described in Supplementary Information (Appendix S2).

The α, β and γ components of taxonomic, functional and phylogenetic diversity were considered to reflect the trajectories of bird assemblages. For each of the three facets of biodiversity (taxonomic, functional and phylogenetic), γ was the regional diversity, i.e., the total number of forest breeding bird species, out of the 84 studied species, at the spatial extent of the whole study area. The α diversity metric was considered the local diversity calculated within each 50 km × 50 km grid cell of the EBBA2 mesh. Finally, the spatial β diversity metric which captures the spatial turnover in bird assemblages was calculated as as $1-(\alpha/\gamma)$, following Bennett & Gilbert (2015). Taxonomic diversity was defined as the total number of species, either per grid cell for α or across the study area for γ, while we used the total length of tree branches, either

per grid cell for α or across the study area for γ, for functional and phylogenetic diversity.

The functional tree (Supplementary Information, Appendix S3) was created through a hierarchical clustering approach based on a Euclidean dissimilarity matrix of species functional traits (using the *cluster* R package, Maechler et al., 2025). Branch lengths were defined using the Criscuolo's method (Criscuolo & Gascuel, 2008) implemented in the *ape* R package. We extracted functional characteristics from Tobias et al. (2022), selecting those that were previously related to time lags in bird responses to habitat and climate changes (see Supplementary Information, Appendix S3). The phylogenetic tree (Supplementary Information, Appendix S3) was extracted from the Open Tree of Life, using the *rotl* R package (Michonneau et al., 2016; OpenTreeOfLife, 2019). This tree includes all the bird species considered in the study area (Lalechère et al., 2025b), except *Emberiza rustica* that was removed from the Open Tree of Life (OpenTreeOfLife, 2019). Branch lengths were defined using the Grafen's method from the *ape* R package (Paradis & Schliep, 2019).

We assessed the correlation between taxonomic, functional and phylogenetic diversity, using the Spearman correlation coefficient, before comparing their average temporal trends in α diversity, and their temporal trends in β and γ diversity. The projected spatial pattern in α diversity was mapped at two time steps (2020 and 2100), from the equilibrium and the non-equilibrium SDMs. The future disequilibrium in the spatial pattern of α diversity was defined following Haddou et al. (2022), by comparing the difference between the α diversity projected through the equilibrium SDMs (EQ α diversity), and the α diversity projected through the non-equilibrium SDMs (NEQ α diversity):

$$Disequilibrium = (EQ\ \alpha\ diversity - NEQ\ \alpha\ diversity) / EQ\ \alpha\ diversity \quad \text{(eq. 2)}$$

Results

Niche hypervolumes

For the 84 European forest breeding birds studied, the mean hypervolume of species' realized niches increased by a mean factor of 8.1 (minimum = 1.0, median = 2.1, maximum = 78.0) when relying on non-equilibrium SDMs, relative to the traditional use of equilibrium SDMs (after excluding three outliers outpacing 50 times the median value). Among the four environmental conditions that are accounted for, the increase of bird species' hypervolumes (Figure 1A) were primarily driven by an increase in the range of the mean annual temperature as well as by an increase in the range of the proportion of primary forest cover (Figure 1B). The former increased by a mean factor of 1.3 (minimum = 1.2, median = 1.3, maximum = 1.4) because the niches expanded towards lower temperatures. The latter increased by a mean factor of 8.2 (minimum = 0.9, median = 1.7, maximum = 97.5) because the niches expanded towards a larger proportion of primary forest. The median range of values remained more stable for annual precipitation, and decreased by a mean factor of 0.86 (minimum = 0.49, median = 0.89, maximum = 0.98) for secondary forest, when comparing the hypervolumes of the realized niche from the equilibrium and the non-equilibrium SDMs.

Future taxonomic, phylogenetic, and functional diversity

The extrapolation rate decreased, when considering the non-equilibrium SDMs, improving the projection reliability of future biodiversity trends (Supplementary

Information, Appendix S2). Extrapolation is defined by projections that are beyond the range of the environmental conditions that are considered during model fitting (i.e., beyond the realized data space). Assessing these projections, we found large Spearman correlation coefficients (≥ 0.91) between different components of avian diversity that are taxonomic, functional and phylogenetic bird diversity. Therefore, we chose to only report in the main text findings for functional diversity as it is the most direct representation of different functions of species to depict future bird diversity trajectories in subsequent analyses (the full results are reported in Supplementary Information, Appendix S4).

We found that the average future trend in γ diversity remains constant through time, irrespective of the type of SDMs used (equilibrium vs. non-equilibrium), and the shared socioeconomic pathways (SSPs) considered (i.e.; a mild one, SSP 245; and a severe one, SSP 585). The equilibrium SDMs slightly underpredicted the α component of functional diversity, and slightly overpredicted the β component of functional diversity, compared to the non-equilibrium SDMs (Figure 2). For SSP 245, α and β diversities remained stable over time, while for SSP 585 α diversity kept decreasing and β diversity kept increasing until 2100.

When comparing the spatial projections of functional diversity from the non-equilibrium SDMs between 2020 and 2100, the shift in the spatial pattern in α diversity was less pronounced, than the shift projected with equilibrium SDMs, due to time lagged responses of birds (Figure 3, for SSP 585; Supplementary Information, Appendix S5, for SSP 245). Overall, α diversity was higher under SSP 245 compared to SSP 585. For both scenarios, the relative difference between equilibrium and non-equilibrium projections (eq. 2) was characterized by pronounced spatial patterns in both underestimating (i.e., negative values suggesting local extinction lags) and

overestimating (i.e., positive values suggesting local colonization lags) α diversity when relying on equilibrium SDMs (Figure 4, for SSP 585; Supplementary Information, Appendix S5, for SSP 245). The maximum absolute relative difference reached 80% of the α diversity predicted by the equilibrium SDMs.

Discussion

Our results show that the widely used equilibrium assumption can systematically truncate species' realized niches and obscure lagged responses to environmental change. The framework we propose allows us to explicitly account for these lags when quantifying niche hypervolumes, which unveil the truncated part of the realized niche that is totally ignored under the equilibrium assumption. Removing this niche truncation unveiled the disequilibrium dynamics between species distributions and their environmental drivers, allowing us to forecast local extinction and colonization lags in future species assemblages.

To highlight these two different aspects (niche truncation and disequilibrium dynamics), and their importance for biodiversity forecasting, we propose to introduce the term "disequilibrium niche" that is defined as the current and past multidimensional environmental gradient along which a species is present in a disequilibrium state. We argue that one should define the multidimensional temporal extent of the disequilibrium niche according to the temporal extent of the time lag associated with each environmental driver separately, thus limiting the temporal depth considered, since very old conditions could no longer be relevant to explain current and forecast future species distribution (Lalechère et al., 2025a, 2025b). Indeed, the use of too distant (e.g., palaeoecological) distribution data can overestimate ecological niche hypervolume, if the tolerance of current species to environmental conditions has

changed over time due to eco-evolutionary processes (Svenning et al., 2015; Mills et al., 2024). This temporal delimitation of the legacy effect of each driver provides a general rule to quantify the disequilibrium niche.

In support of former work (Chevalier et al., 2024), we unveiled the ghosts of past environmental niches by capturing a substantial fraction of the hypervolume to which current species occurrences are still responding today, which is impossible to capture under the equilibrium assumption. Embracing the concept of a disequilibrium niche revealed that contemporary patterns of forest breeding bird species occurrences are also explained by their affinity for higher historic cover of primary forests, and lower historic temperatures. Accounting for past environmental conditions to model species distributions also improved the reliability of the future projections we made because a larger variability of combinations of environmental conditions were accounted for during model fitting limiting over-extrapolation (Supplementary Information, Appendix S2).

To our knowledge, this is the first study to provide spatially explicit projections of future disequilibria in species distribution and assemblage patterns. Previous efforts to quantify biodiversity disequilibria have mainly compared the effects of current and past environmental conditions at a few discrete time points, limiting the possibility to identify and forecast the general temporal trends in biodiversity disequilibria (e.g.; Lenoir et al., 2020; Gaüzère et al., 2021; Haddou et al., 2022; Zurell et al., 2024). Here, we instead model disequilibrium as an explicitly dynamic process by fitting temporal influence functions to long time series of past and present environmental conditions (Lalechère et al., 2025a, 2025b). This approach estimates how strongly and how long species are impacted by past environmental conditions, and then propagates these empirically derived lags into the future. With only a few parameters (eq. 1), we can thus map where

and when disequilibria in species distributions and assemblages are expected to intensify.

Leclère et al. (2020) projected the average temporal trajectories of global biodiversity, using a space-for-time substitution approach to account for the influence of temporal lags in the response of biodiversity to different restoration scenarios. However, the assessment of time lags is indirect in this study, and Evans et al. (2025) recently illustrated why space-for-time substitution approaches must no longer be recognized as an appropriate method to assess biodiversity disequilibria. Block et al. (2022) projected transient plant community responses to 21st century climate change. They transplanted alpine species to lower elevations and used species demographic responses to parameterize community dynamics models forced by scenarios of gradual climate change. This combination of approaches was used to best reproduce the gradual effect of climate change, while the transplant experiment alone corresponds to a less realistic abrupt climate change. Projections of future non-equilibrium dynamics can be found in other fields of scientific inquiry. For example, Felton et al. (2022) projected future primary productivity in the western USA, comparing two contrasting scenarios assuming either a complete equilibrium or a maximum disequilibrium. They concluded that the uncertainty related to the assumption of climate disequilibrium was larger than uncertainties coming from different climate models and emission pathways. The findings of Felton et al. (2022) stress the importance of accounting for future disequilibria in global biodiversity assessment, given the well-studied relationship between biodiversity and ecosystem functioning (Loreau et al., 2001).

We have shown that the α, β and γ components of forest breeding bird diversity across Europe can remain quite stable over time under a mild scenario of climate and land-

use changes (SSP 245), while increasing anthropogenic forcing (SSP 585) can lead to both a decline in α diversity and an increase in β diversity over time, while keeping γ diversity to a steady state level. These findings suggest low extinction risks at the continental extent (i.e., γ diversity is steady) but higher risks of local extinctions within bird assemblages (i.e., α diversity decreases) which mechanically translates into a high spatial turnover in bird assemblages over time (i.e., spatial β diversity increases). While global biodiversity trends were characterized by no systematic loss of α diversity and increasing changes in community composition (temporal β diversity), continental Europe remains a hotspot of decline in α diversity (Blowes et al., 2019). The constant trend in γ diversity we identified is consistent with the comparison between the first and second European Breeding Bird Atlases, which indicates no overall change in γ diversity in the last 30 years, despite the identification of significant distribution changes (Keller et al., 2020). Thus the threats that bird species will face can increase in the future, as previously highlighted in other studies (Barbet-Massin et al., 2015; Pereira et al., 2021).

We found only modest differences in the projected temporal trajectories of α and β diversity when comparing projections from equilibrium SDMs against projections from non-equilibrium SDMs. These small differences in temporal trajectories across the entire study area mask strong regional disequilibrium dynamics that are already visible under present conditions (Lalechère et al., 2025b), and that will most likely increase in the future, depending on the SSP (Figure 4). Both the largest positive (i.e., local colonisation lags) and negative (i.e., local extinction lags) values of disequilibrium dynamics were detected in boreal forest in the northeastern part of the study area. Local extinction lags that are particularly pronounced across northeastern Europe could be due to the persistent influence of large forest cover values (since 854) and

historically low temperature values (since 1854) which can lead to the transient local persistence of cold-adapted forest specialists. Local colonization lags may simultaneously occur further north of those locations and towards habitats that would be newly suitable for warm-adapted species originating from southwestern locations. These results are consistent with previous findings that emphasized that climate change occurs more rapidly at higher latitudes in the Northern Hemisphere (Rantanen et al., 2022). Our results confirm that time lags are likely to be more extensive, resulting in delayed effects on population dynamics, where anthropogenic and natural drivers of biodiversity change rapidly (Gaüzère et al., 2021). We stress the importance of accounting for disequilibria in biodiversity forecasting, as it is projected to increase with the accelerating pace of climate and land-use changes at the end of the 21st century.

Accounting for past environmental conditions to model species distributions improved the reliability of the future projections we made because a larger variability of combinations of environmental conditions were accounted for during model fitting, limiting extrapolation. Temperatures that are as warm as the ones projected for the end of the 21st century were already observed in Europe a long time ago, during the Paleocene-Eocene thermal maximum (Svenning et al., 2015). Analogues of future climates are so ancient that they are not useful to project future distribution of species which did not exist at that time, given the pace of eco-evolutionary processes. From our approach, using longer climatic time series can still reveal older legacy effects of past temperatures on the contemporary patterns of bird species assemblages, and can help to further reduce extrapolation issues due to the higher temperatures that will arise in the Mediterranean region (Wang et al., 2024).

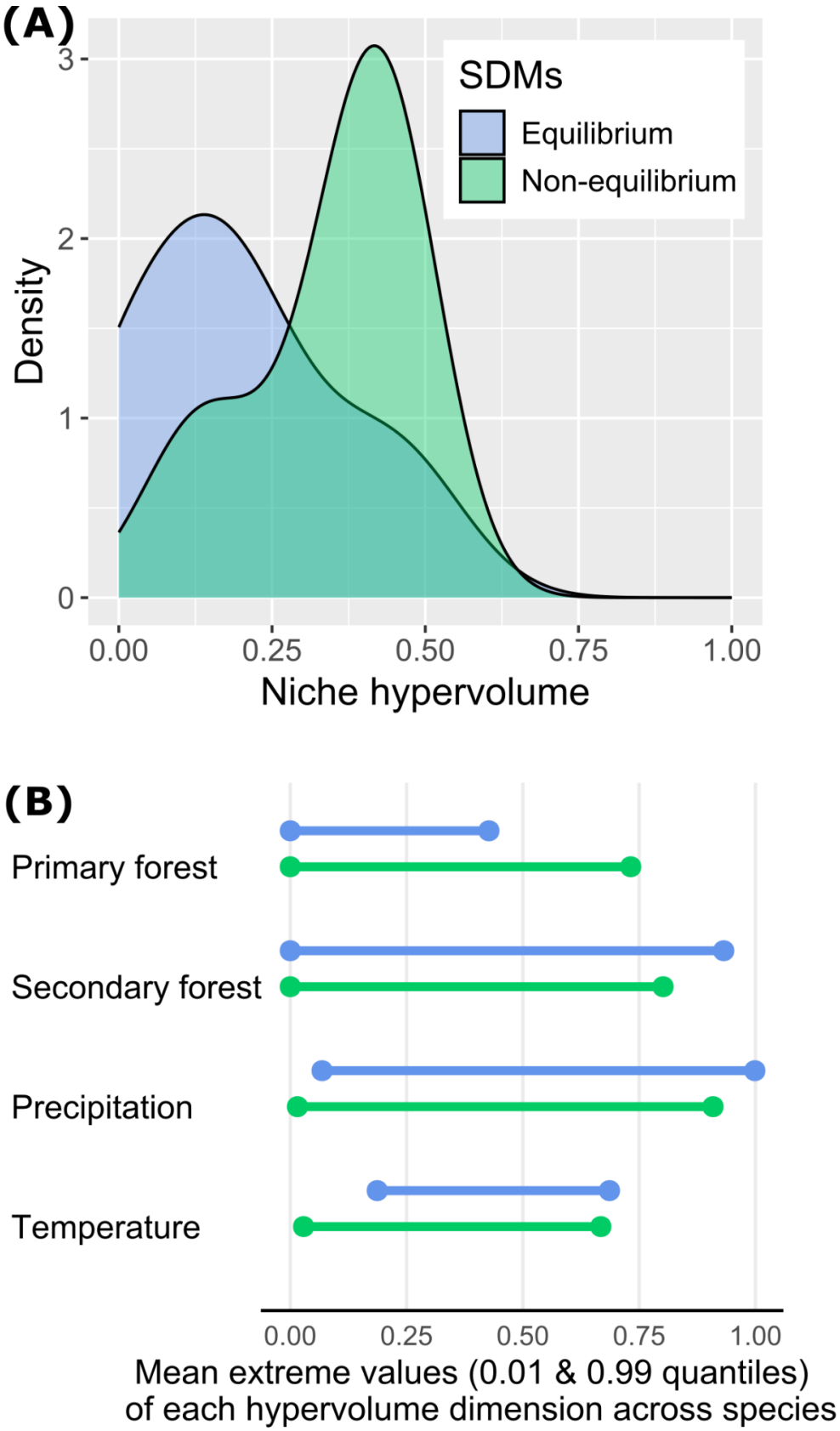
Although the α, β and γ components of diversity showed distinct trends, it was not the case for taxonomic, functional and phylogenetic diversity, which were very close due

to the large correlation we found between these metrics. Our results corroborate the general assumption of surrogacy of taxonomic, functional and phylogenetic diversity measures (Safi et al., 2011). However, this result differs from some studies that showed the complementarity of taxonomic, functional and phylogenetic diversity (Meynard et al., 2011; Monnet et al., 2014), while some other studies highlighted that their correlation depends on methodological choices, such as the number of functional traits considered (Calba et al., 2014; Voskamp et al., 2017). Distinct taxonomic, functional and phylogenetic diversity metrics were primarily obtained from abundance data allowing to calculate the effective number of equally abundant species, instead of species richness (Meynard et al., 2011; Monnet et al., 2014; Gaüzère et al., 2022).

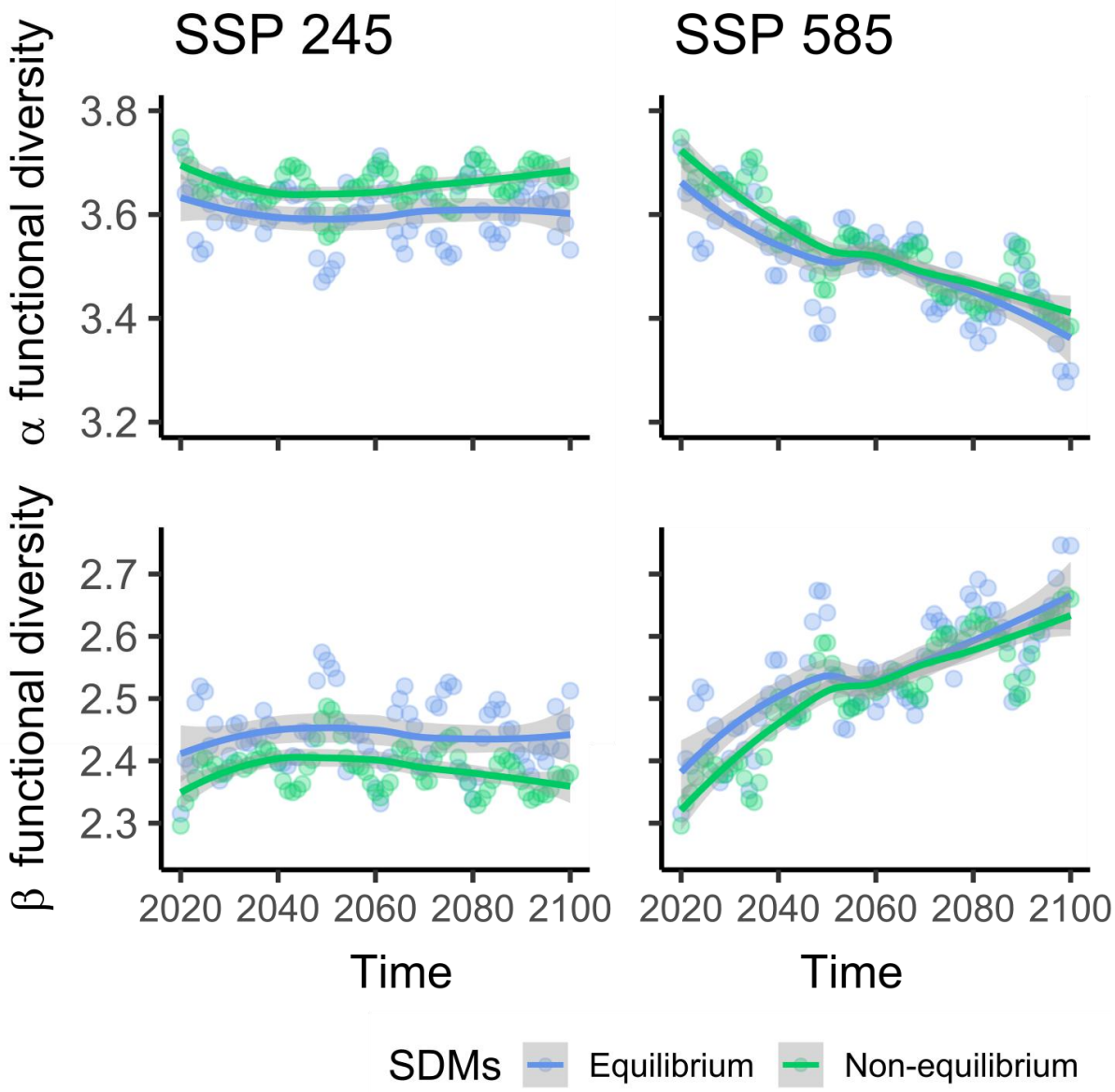
Further progress can be made in improving the way we quantify the hypervolume of species' realized niche. Here, we based our analyses on the use of the entire range of values (more precisely, the 0.01 and the 0.99 quantiles) associated with each environmental variable used as predictor in our SDMs. Blonder et al. (2018) proposed to define ecological niche hypervolume according to the density of the distribution of environmental conditions within species' ranges. The more basic definition we used may be less accurate to define the hypervolume of species' realized niche, but it is not introducing any bias to the relative comparison between equilibrium and non-equilibrium SDMs. Another key avenue for future research is to disentangle the respective contributions of environmental filtering, dispersal, and biotic interactions in shaping the lagged dynamics of species redistributions. Addressing this question is possible by extending the current modelling framework to explicitly incorporate these processes (Sanczuk et al., 2024; Sandel et al., 2025). Additional datasets must probably be considered, since the bird occurrence data used here reflects the realized niche, and therefore the indiscriminate consequences of these different processes.

In conclusion, by unveiling the ghosts of past ecological niches, our study shows that disequilibria in species distributions and diversity can increase in time periods of rapid environmental changes. More broadly, operationalising the disequilibrium niche concept through temporal influence functions offers a general framework for incorporating legacy effects and lagged responses into biodiversity forecasts.

Figures


(A)
SDMs
Equilibrium
Non-equilibrium
Density
0
1
2
3
0.00
0.25
0.50
0.75
1.00
Niche hypervolume
(B)
Primary forest
Secondary forest
Precipitation
Temperature
0.00
0.25
0.50
0.75
1.00
Mean extreme values (0.01 & 0.99 quantiles)
of each hypervolume dimension across species

458 Figure 1: Description of the hypervolumes of species' realized niches when considering the equilibrium
459 or the non-equilibrium SDMs. A hypervolume encapsulates all the environmental conditions where the
460 focal species occurs within the geographical space. The distribution of the hypervolumes of species'
461 realized niches is described by density, in panel A (using the geom_density R function, from the ggplot2
462 package). For a given species, the hypervolume is defined as the product of the extreme values (i.e.,
463 the 0.99 quantile minus the 0.01 quantile) of each of the four climate and land use predictor variables.
464 The mean extreme values across species are shown, in panel B, to highlight the contribution of each
465 environmental predictor to the hypervolumes.



466

467 Figure 2: Future trends in α and β functional diversity projected from the equilibrium and the non-
468 equilibrium SDMs, for the SSP 245 and the SSP 585 scenarios. The α diversity metric is the local diversity
469 calculated within each EBBA2 mesh. The β diversity metric captures the spatial turnover in bird
470 assemblages among EBBA2 meshes. SSP 245 represents a mild scenario of climate and land-use
471 changes, while SSP 585 considers increasing anthropogenic forcings.

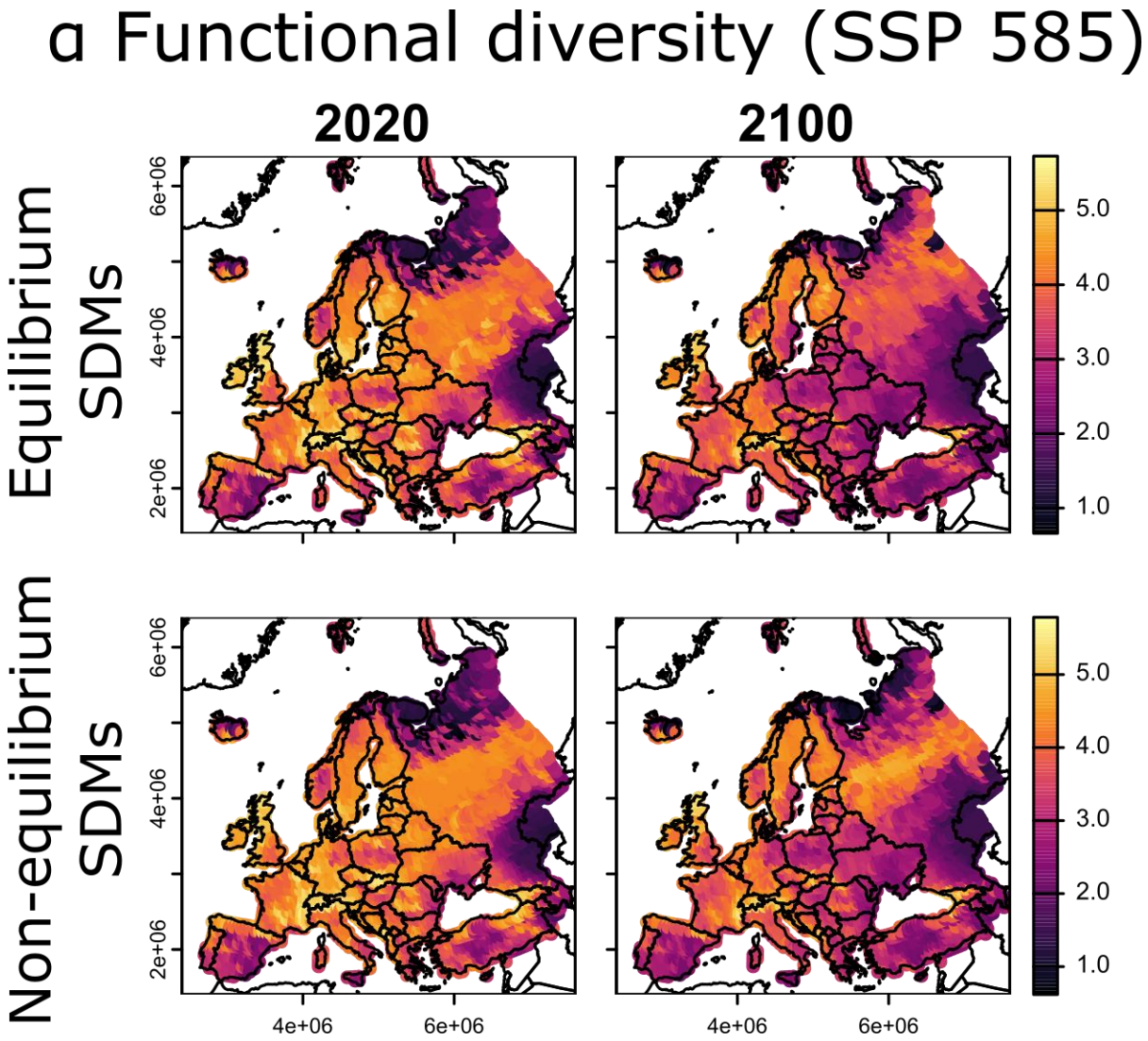
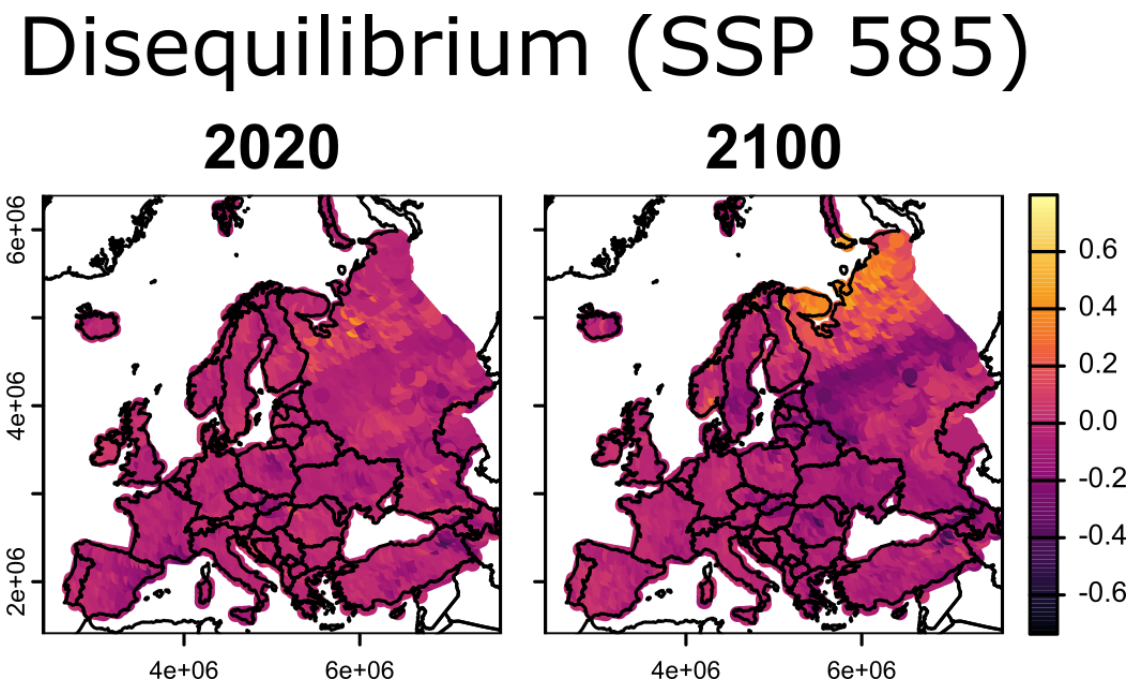


Figure 3: Future α functional diversity derived from the equilibrium and the non-equilibrium SDMs, for SSP 585. The non-equilibrium SDMs account for time lags in bird responses to habitat and climate changes, on the contrary to the equilibrium SDMs. Functional diversity is based on a tree created through a hierarchical clustering approach from 11 functional characteristics of birds (Supplementary Information, Appendix S3). The spatial pattern of α functional diversity was derived from the stacked distribution of 84 bird species. Results from SSP 245 are available in Supplementary Information, Appendix S5.



480

481 Figure 4: Future disequilibrium in α diversity based on a comparison between projections of the

482 equilibrium and the non-equilibrium SDMs, for SSP 585. The disequilibrium is calculated following eq.

483 2, by comparing the output of the equilibrium and the non-equilibrium SDMs. Results from SSP 245

484 are available in Supplementary Information, Appendix S5.

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Supplementary Information

Appendix S1: Future scenarios of changes in the environmental conditions

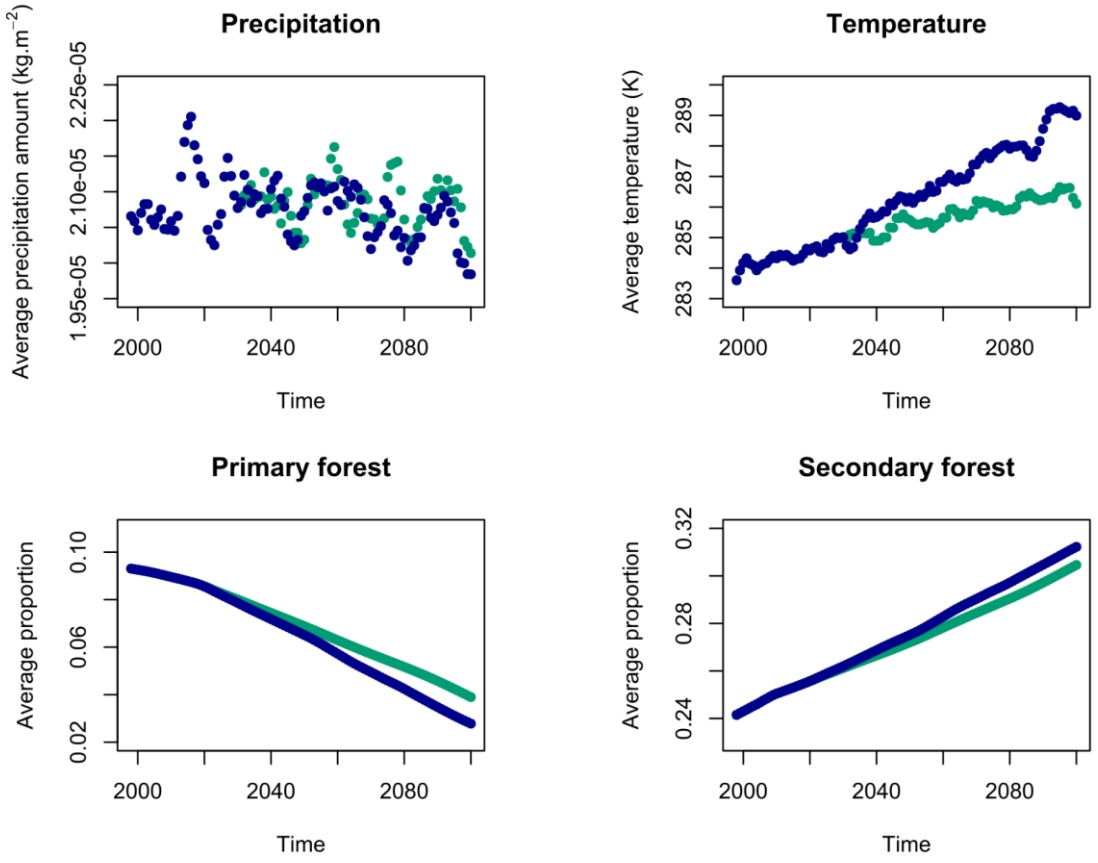


Figure S1: Mean temporal trajectories of climate (mean annual temperature, mean precipitation amount) and the extent of forests (primary and secondary forests) in grid cells 50 km × 50 km from 2000 to 2100) shown for the mild (SSP 245, green) and severe (SSP 585, blue) scenarios.

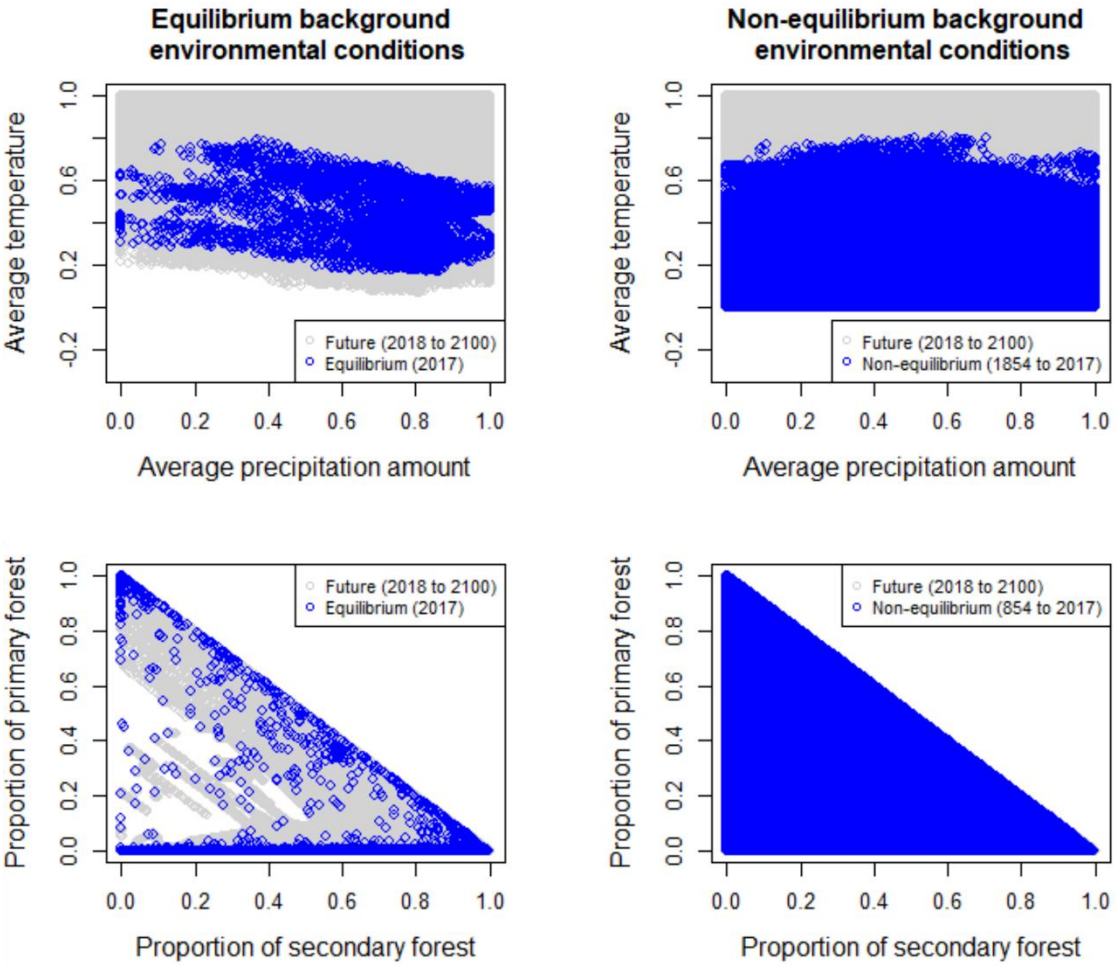
Appendix S2: Extrapolation rates

Looking back at the past has the potential to avoid over-extrapolation, and to improve the projection reliability of future biodiversity trends (Webber et al., 2023). Extrapolation is an inherent issue in predictive ecology. It can be defined as predicting beyond the range of the environmental conditions that are considered during model fitting (i.e., beyond the realized data space, Velazco et al., 2024). Fitting an ecological niche model based on the environmental conditions that are contemporary to species occurrence data increases extrapolation risks, possibly leading to biased or less reliable predictions (Sandel et al., 2024). This is more likely when projecting into a distant future, when novel combinations of environmental conditions (i.e., non-analogues), not recently experienced by the species, will arise. Here, we assessed projection validity given the potential of non-equilibrium SDMs to limit model extrapolation.

For the equilibrium and the non-equilibrium SDMs, we assessed projection reliability through extrapolation rates defined as the total number of 50 km × 50 km grid cells, in the future, for which at least one predictor variable exceeded the range of the environmental conditions observed during model fitting (Owens et al., 2013; Velazco et al., 2024). Spatial units of 50 km × 50 km were considered independently at different time steps, meaning that the total number of spatial units include all the future combinations of environmental conditions over space and time. We additionally provided a qualitative comparison of the distributions of the future environmental conditions (from 2018 to 2100), with those used to fit the equilibrium SDMs (in 2017), and the non-equilibrium SDMs (from 1854 to 2017, or from 854 to 2017, depending on the driver).

We found that the extrapolation rate decreased from 45% to 31% for SSP 245, and from 70% to 39% for SSP 585, when considering the equilibrium and the non-equilibrium SDMs, respectively. This extrapolation rate was chiefly due to future low and high temperature extremes, both low and high extremes, which have never been encountered in the past, before the temporal extent of a time lag was reached, but that will arise in the future (Figure S1). The non-equilibrium SDM approach covers a larger variability of background environmental conditions compared to the equilibrium SDM approach (Figure S1).

Projected future temperatures will exceed current and historic temperatures, while no such extrapolation was found for the other land-use changes predictors. This extrapolation issue was reduced in the non-equilibrium SDMs, because they allowed colder and, to a lesser extent, warmer temperatures to be captured from past environmental conditions. The resulting extrapolation that still persisted for high temperatures is unsurprising, given that the mid-19th century corresponds to the end of the little ice age. Analogues of future climates are so ancient that they probably don't provide useful information to understand current and future distribution of species, which did not exist at that time (Svenning et al., 2015).



691

692 Figure S2: Comparison between future (2018 - 2100), and past background environmental conditions,
693 that are accounted for during the model fitting phase when using the equilibrium or the non-
694 equilibrium SDMs. Model fitting of the equilibrium SDMs is based on the 2017 environmental
695 conditions (i.e., to match the date of the occurrence data), while model fitting of the non-equilibrium
696 SDMs is based on a time series of past environmental conditions. Times series ranged from 1854 to
697 2017 for temperature and precipitation, and from 854 to 2017 for primary and secondary forests. The
698 background environmental conditions are pooled, from SSP 245 and SSP 585, to account for all the
699 future possible environmental conditions.

700

Appendix S3: Functional and phylogenetic trees

The functional characteristics we considered described species ecological preferences, morphology, and species distribution range size and location. The functional tree was built considering non correlated functional characteristics (Spearman correlation coefficient < 0.7) including: hand wing index, mass, habitat density; minimum, centroid, and maximum latitude; centroid longitude, range size, trophic level, trophic niche, and migration status (Tobias et al., 2022). Hand wing index and species mass are associated to dispersal, which is one of the main drivers of time lags, species with low dispersal being likely to respond more slowly to environmental changes (Lalechère et al., 2019; Tobias et al., 2022; Arroyo-Rodríguez et al., 2023). The characteristics of species range (size and position) are associated with species thermal preferences, species with low and large thermal preferences being more likely to be in disequilibrium in response to climate change (Jiguet et al., 2010). Functional characteristics linked to trophic relationships (trophic level: either carnivore, herbivorous or omnivorous; and tropic niche: aquatic predator, granivore, herbivore terrestrial, invertivore, omnivore, vertivore) were also considered because time lags, at lower trophic levels, can propagate and accumulate to higher trophic levels (Essl et al., 2015). Migration status was included because migratory birds are impacted by different climate regimes. We also considered the sensitivity to habitat density which could explain variation in the responses to land use changes.

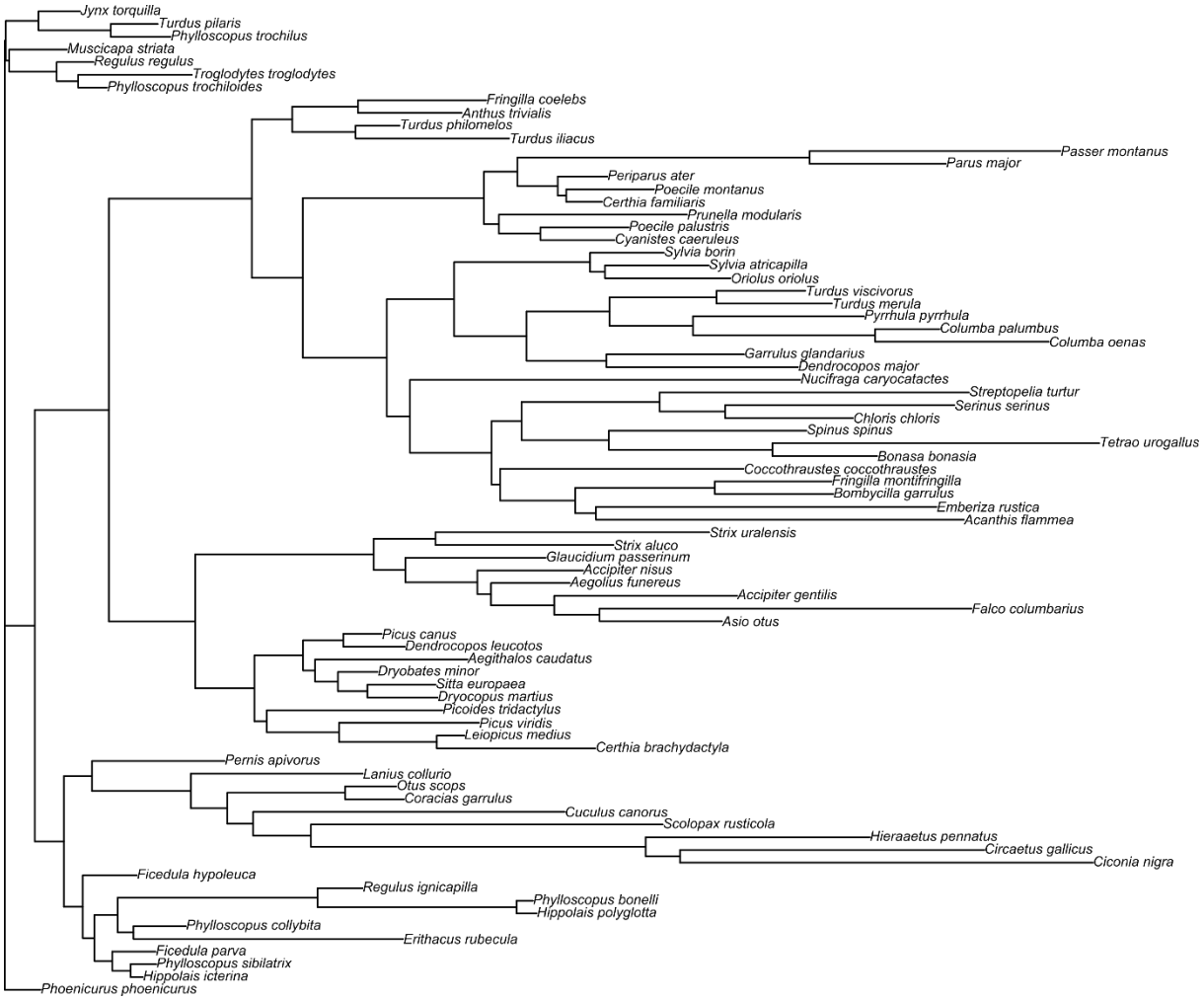


Figure S3: Functional tree of bird species.

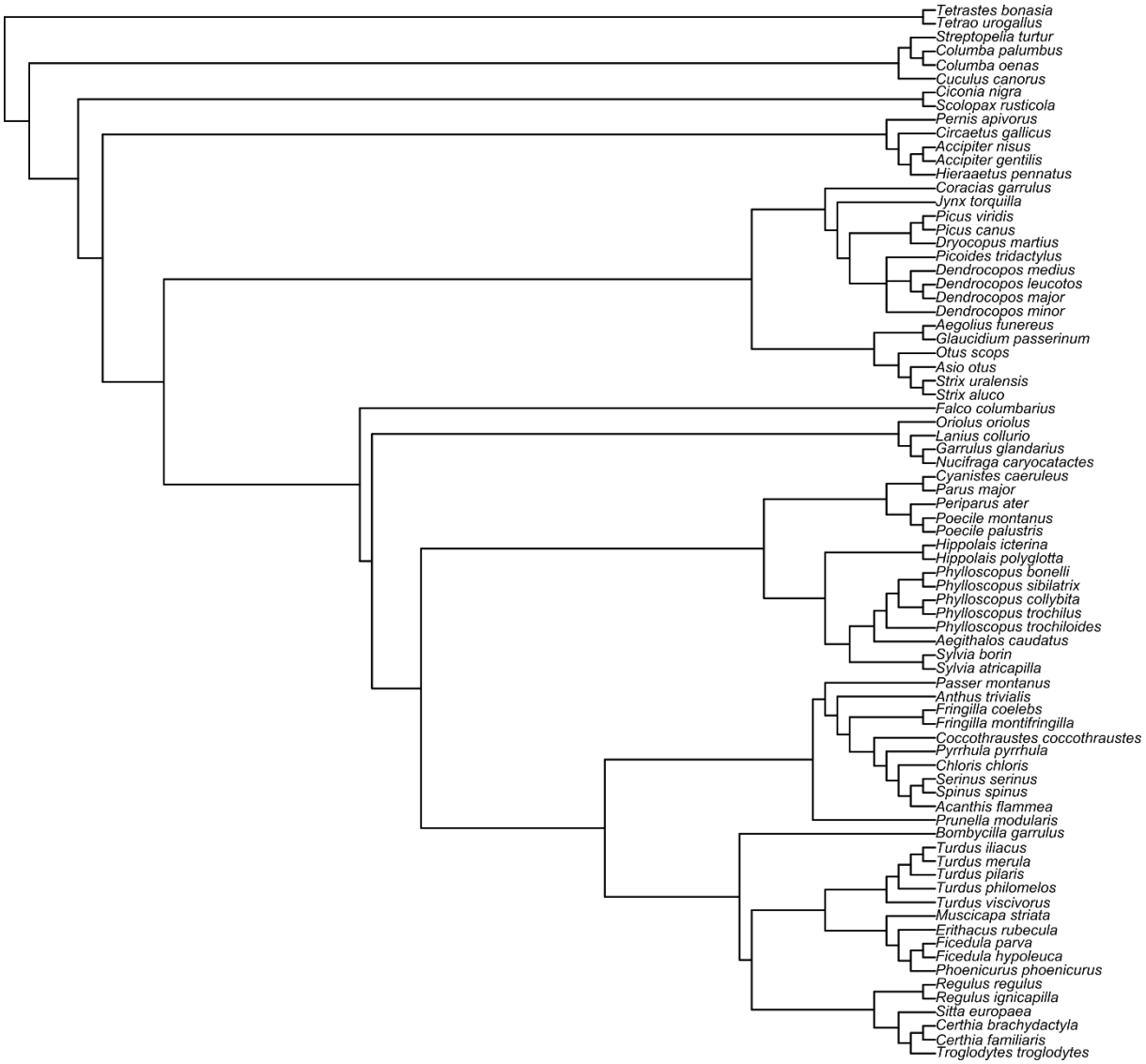


Figure S4: Phylogenetic tree of the bird species. The phylogenetic tree was extracted from the Open Tree of Life (OpenTreeOfLife, 2019). The tree includes all the bird species, except *Emberiza rustica*, which was removed from the Open Tree of Life. Branch lengths were defined using the Grafen's method from the ape R package (Paradis & Schliep, 2019).

Appendix S4: Phylogenetic and taxonomic diversity

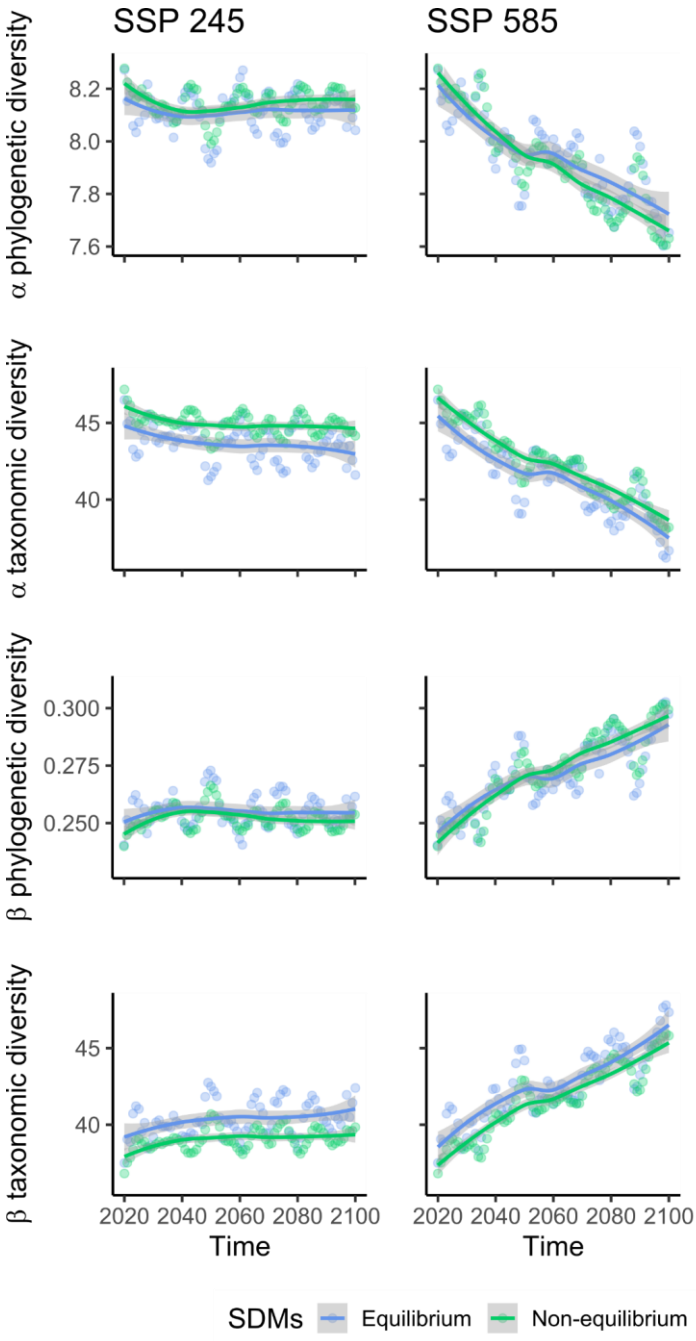
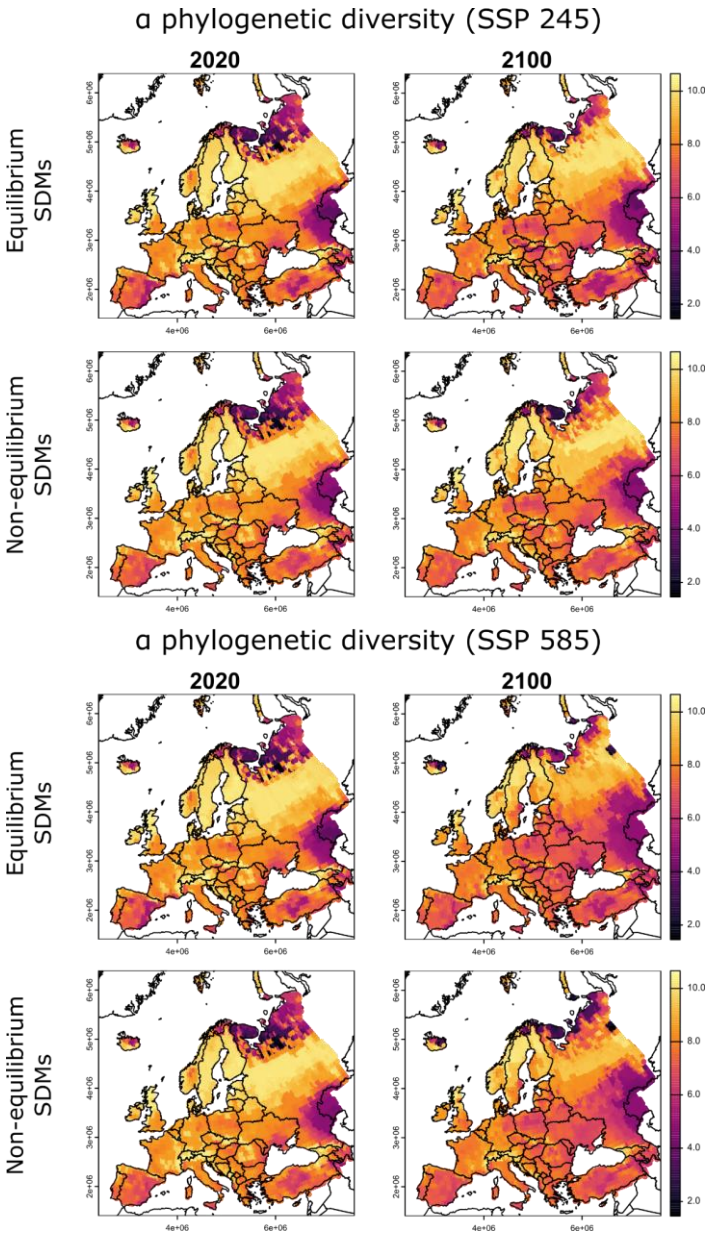


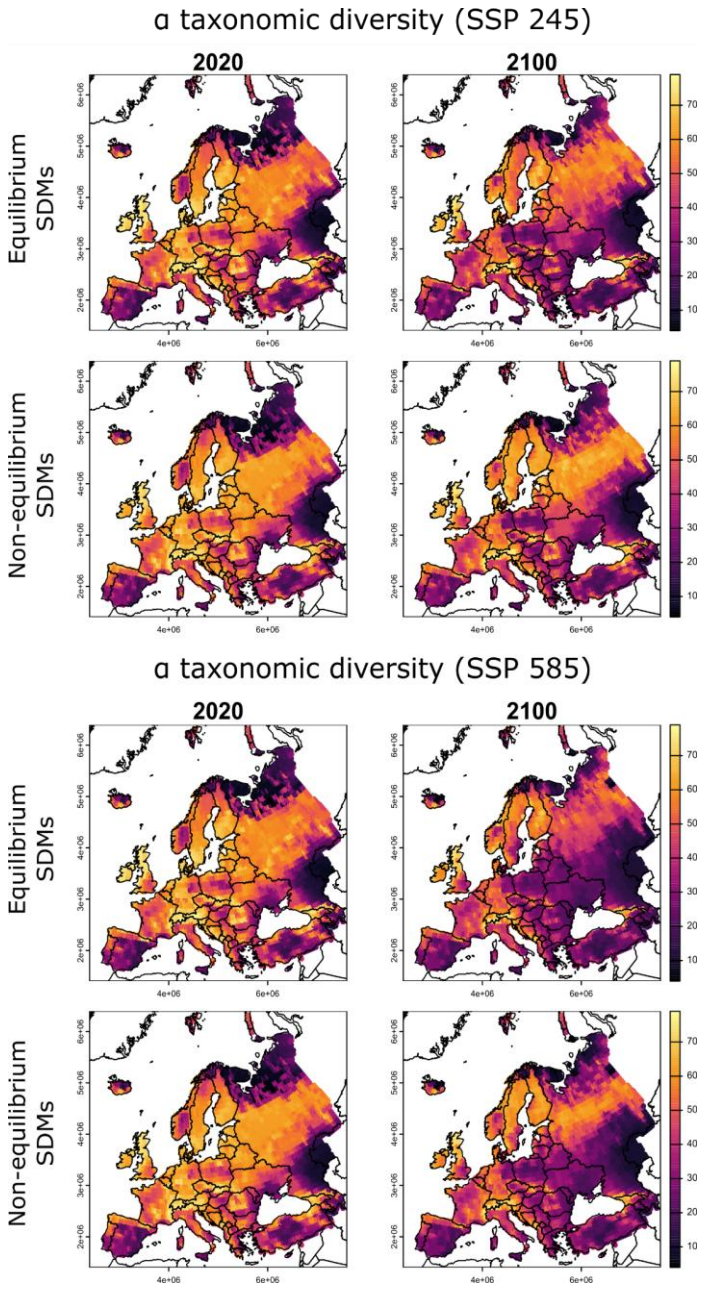
Figure S5: Future trends in α and β phylogenetic and taxonomic diversity projected from the equilibrium and the non-equilibrium SDMs, for the SSP 245 and the SSP 585 scenarios. The α diversity metric is the local diversity calculated within each EBBA2 mesh. The β diversity metric captures the spatial turnover in bird assemblages among EBBA2 meshes. SSP 245 represents a mild scenario of climate and land-use changes, while SSP 585 considers increasing anthropogenic forcings.



735

736 Figure S6: Future α phylogenetic diversity derived from the equilibrium and the non-equilibrium SDMs,
737 for SSP 245 and SSP 585. The non-equilibrium SDMs account for time lags in bird responses to habitat
738 and climate changes, on the contrary to the equilibrium SDMs. Phylogenetic diversity is based on a
739 tree created from the Open Tree of Life (OpenTreeOfLife, 2019; Supplementary Information, Appendix
740 S5). The spatial pattern of α phylogenetic diversity was derived from the stacked distribution of 84 bird
741 species.

742



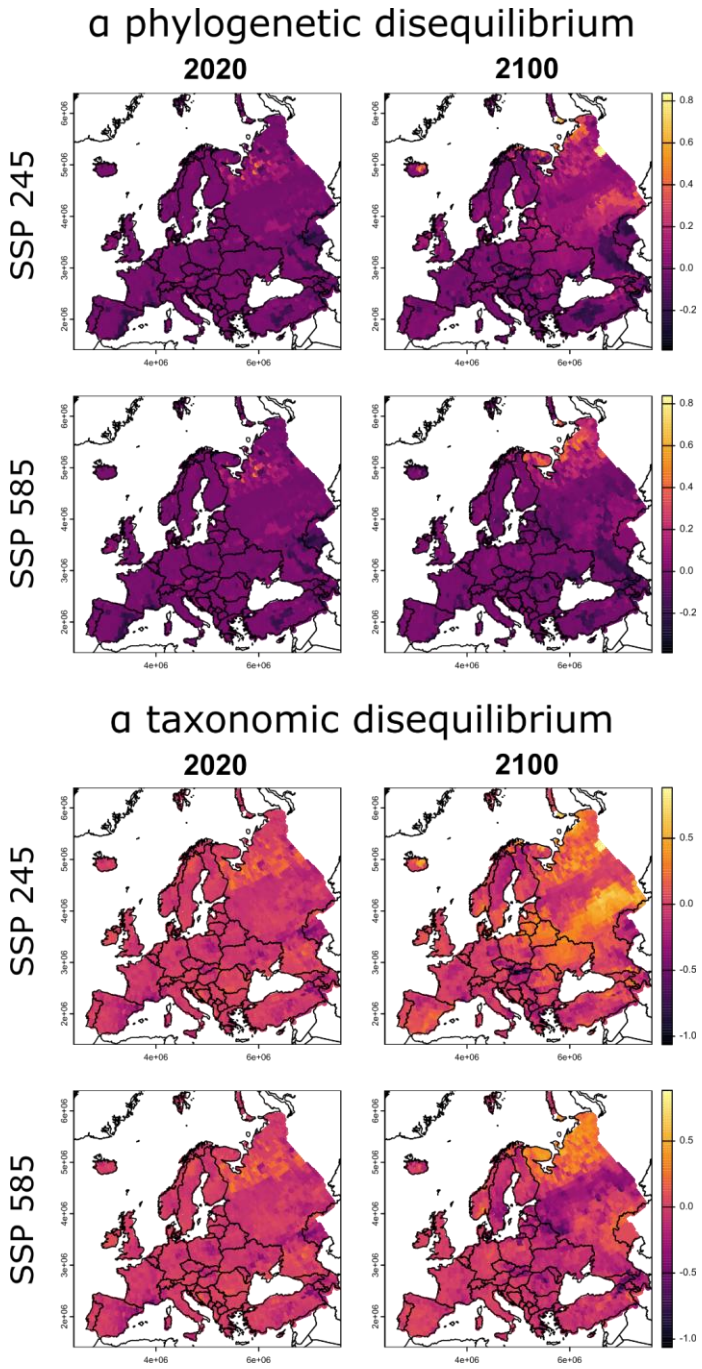
743

744 Figure S7: Future α taxonomic diversity derived from the equilibrium and the non-equilibrium SDMs,

745 for SSP 245 and SSP 585. The non-equilibrium SDMs account for time lags in bird responses to habitat

746 and climate changes, on the contrary to the equilibrium SDMs. The spatial pattern of α taxonomic

747 diversity was derived from the stacked distribution of 84 bird species.



748

749 Figure S8: Future disequilibrium in α phylogenetic and taxonomic diversity based on a comparison

750 between projections of the equilibrium and the non-equilibrium SDMs, for SSP 245 and SSP 585. The

751 disequilibrium is calculated following eq. 2, by comparing the output of the equilibrium and the non-

752 equilibrium SDMs.

Appendix S5: Functional diversity under SSP 245.

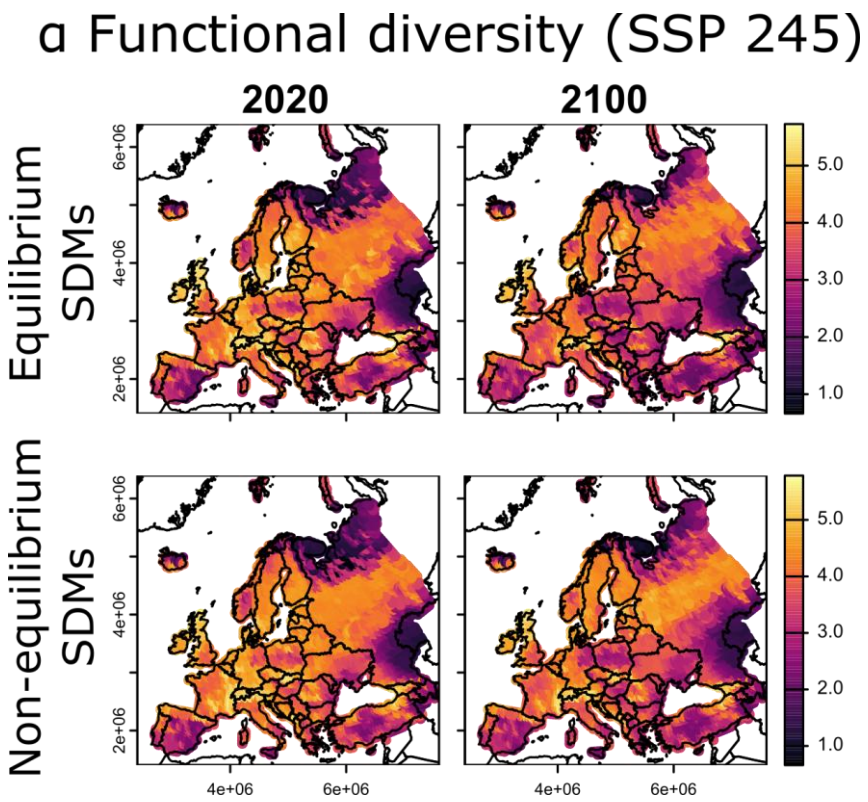
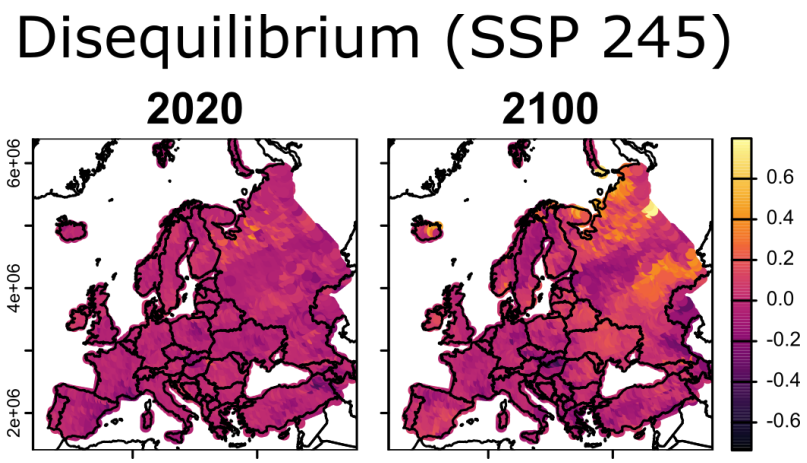


Figure S9: Future α functional diversity derived from the equilibrium and the non-equilibrium SDMs for SSP 245. The non-equilibrium SDMs account for time lags in bird responses to habitat and climate changes, on the contrary to the equilibrium SDMs. Functional diversity is based on a tree created through a hierarchical clustering approach from 11 functional characteristics of birds (Supplementary Information, Appendix S5). The spatial pattern of α functional diversity was derived from the stacked distribution of 84 bird species



762

763 Figure S10: Future disequilibrium in α diversity based on a comparison between projections of the
764 equilibrium and the non-equilibrium SDMs, for SSP 245. The disequilibrium is calculated following eq.
765 2, by comparing the output of the equilibrium and the non-equilibrium SDMs. The maximum absolute
766 disequilibrium value reaches 80% of the α diversity predicted by the equilibrium.

767

768