A non-equilibrium species distribution model reveals unprecedented depth of time lag responses to past environmental change trajectories

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Title

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Abstract

Previous studies have demonstrated legacy effects of current species distributions to past environmental conditions, but the temporal extent of such time lag dynamics remains unknown. Here, we have developed a non-equilibrium SDM approach quantifying the temporal extent that must be taken into account to capture 95 % of the effect that a given time series of past environmental conditions has on the current distribution of a species. We applied this approach on the distribution of 92 European forest birds in response to past trajectories of change in forest cover and climate. We found that non-equilibrium SDMs outperformed traditional SDMs for 95 % of the species. Non-equilibrium SDMs suggest unprecedented long-lasting effects of past global changes (average time lag extent ranged from 9 years to 231 years). This framework can help to relax the equilibrium

hypothesis of traditional SDMs and to improve future predictions of biodiversity redistribution in response to global changes.

Keywords: Lagged dynamics – Delayed dynamics – Relaxation time – Colonization credit – Extinction debt – Climatic debt – Disequilibrium hypothesis – Biodiversity redistribution – Climate change – Land use change

Introduction

Lagging dynamics in ecology occur when biodiversity is not in equilibrium with current environmental conditions, meaning that current species distribution or community composition still depend on past environmental conditions. The concept of extinction debt was thus defined as a delayed loss in species number due to a decline in habitat suitability and connectivity (Diamond, 1972; Tilman et al., 1994). Immigration credit was then used to describe a delayed increase in species number due to a lack of colonization events towards newly suitable areas (Nagelkerke et al., 2002). For instance, by relying on empirical observations of past species distributions, recent syntheses on biodiversity redistribution have demonstrated evidence for extinction debts and immigration credits at the trailing and leading edge of species distributions, respectively (*e.g.*, Lenoir et al., 2020; Zurell et al., 2024). The question of whether or not to abandon the concept of equilibrium in ecology has been raised, due to the overwhelming body of evidence suggesting time-lagged dynamics in ecological responses to past environmental changes (Coulson, 2021). However, the concept of equilibrium is still widely used in ecology, especially so by the scientific community working with species distribution models (SDMs), for which the equilibrium between a species distribution and the current state of its environmental drivers is the main underlying assumption (Fig. 1C; Essl et al., 2024). Hence, the assessment of the consequences of environmental changes on biodiversity redistribution often rely on a questionable assumption.

The relevance of legacy effects on current and future biodiversity dynamics has been argued from a variety of approaches ranging from SDMs (*e.g.*, Dullinger et al., 2012; Rumpf et al., 2019), but also analyses of time series of community weighted means for specific functional traits (*e.g.*, Bertrand et al., 2011; Lajeunesse et al., 2022), space-for-time substitutions (Kuussaari et al., 2009), species-area relationships (*e.g.*, Chen et al., 2017; Ridding et al., 2021), and mechanistic species or community models (*e.g.*, Aguadé- Gorgorió et al., 2024). Few studies have applied these methods to map the spatial patterns of the extinction debts and the immigration credits. Some of them provided evidence of long-lasting legacy effects of anthropogenic pressures aggregated at the country or the biome levels (Devictor et al., 2012; Dullinger et al., 2013; Liao et al., 2022). Other studies have reported delayed biodiversity dynamics by paying more attention to their spatial patterns (Bertrand et al., 2016; Chen et al., 2017; Duchenne et al., 2021; Haddou et al., 2022), which suggest that extinction debts could mostly be located in areas that do not match with the current network of protected areas (Chen et al., 2017; Haddou et al., 2022). For instance, Haddou et al. (2022) mapped the distribution of birds across the conterminous United States in 2016 and compared the dependence of bird distribution on landscape composition in 2016 and 2001, demonstrating lagging dynamics to past landscape composition.

However, to estimate lagging effects, these studies chiefly relied on just two distant events in time at a given location (*i.e.*, diachronic analyses with one or two standardized or opportunistic biodiversity sampling associated with environmental conditions recorded at two dates; *e.g.*, Fig. 1C), thus missing the complex dynamic that may happen in between and that can only be captured by refined time series (Daskalova et al., 2020; Liao et al., 2022). First, the detected duration of a time lag depends on the total duration of the time series available for the environmental variable under consideration. The starting date of this time series is often defined according to data availability, and is not necessarily old enough to capture the real temporal extent of a time lag effect (Fig. 1B vs. Fig. 1A). Second, the direction and magnitude of the effect for a given environmental factor is not sufficient to understand

its importance. Indeed, the rate at which the effect decreases over time (*i.e.*, the shape of the time lagged effect) also indicates if it has a more recent or historic influence (Fig. 1A).

To solve the aforementioned knowledge gaps, we developed a non-equilibrium SDM based on multivariate and temporally-weighted generalized linear regressions to infer a time lag parameter that captures two important features (Fig. 1A): (i) the time lag extent that must be considered to capture 95 % of the effect that a given time series of past environmental conditions has on the current species distribution and (ii) the shape of the time-lagged dynamic along the time lag extent. First, to illustrate the capabilities of our non-equilibrium SDM approach, we performed a simulation exercise that captures the temporal extent of a lagging response we imposed to a given predictor variable. We then applied this framework to the current (2013-2017) distribution of 92 European forest birds using long-term time series of past forest cover (850-2017) and climate (1850-2017). Finally, we illustrated the ability of our non-equilibrium approach to map the extinction debt and immigration credit by comparing outputs from our non-equilibrium SDMs against outputs from traditional equilibrium SDMs. We expect this study to pave the way for the use of non-equilibrium SDMs to better understand the ability of species to track global changes.

Materials and methods

Biodiversity data

For the purpose of our work and to illustrate the relevance of our framework, we focused on forest bird species. Birds are suitable biological models because they have long been monitored by ornithologists and now by citizen science and they are highly sensitive to anthropogenic disturbances (Rosenberg et al., 2019; Keller et al., 2020). Our focus on forest-dwelling species stems from the large body of evidence that has accumulated in the scientific literature on the delayed effects that both changes in forest cover and climate conditions may have on forest biodiversity (Bertrand et al., 2011; Perring et al., 2018; Daskalova et al., 2020; Richard et al., 2021). Birds are fast-dynamic species,

which means that the identification of time lags for this taxonomic group is more likely to be generalized to other taxonomic groups of slower dynamics in terms of life history traits (Daskalova et al., 2020).

We used the European Breeding Bird Atlas (EBBA2) which provides a systematic survey of species presence-absence data at a spatial resolution of 50 km × 50 km between 2013 and 2017 (median year = 2015; Keller et al., 2020). Data from European atlases have the advantage of providing exhaustive and homogenized data on species distribution, which limits potential biases compared to opportunistic records from presence-only datasets (Keller et al., 2020). We considered the 92 species (Supplementary Information, Appendix S1) of the EBBA2 whose habitat is classified as either forest or woodland according to Tobias et al. (2022). The coarse resolution of the EBBA2's mesh size and the continental extent of the analysis have the advantage of limiting spatial autocorrelation signal due to dispersal processes on a landscape extent, which were not considered in our analysis.

Environmental predictors

We related species presence-absence data during 2013-2017 to long-term time series of changes in forest cover and climate conditions, which have been identified as the main determinants of bird species distributions at continental extent (Cooper et al., 2023). Long-term time series of changes in forest cover and climate conditions at a yearly resolution were extracted from the Land-Use Harmonization (LUH2; Hurtt et al., 2020) and the CHELSA Climate (Karger et al., 2017) databases, respectively. The LUH2 database provides time series of land use since 850 at a spatial resolution of 0.25° × 0.25°, *i.e.*, approximately 28 km × 28 km at the equator, and at a yearly resolution. We focused on the land use categories 'primary forest' and 'secondary forest' since they reflect different trends: an average decrease in the cover of primary forests, mainly to the benefit of secondary forests, and an average increase in the cover of secondary forests elsewhere in Europe, mostly due to a decline of agricultural land uses (Hurtt et al., 2020; Supplementary Information, Appendix S2). Forests are

defined as ‘primary’ if a land use has remained forest continuously over time since 850, independently of management practices. Forests are defined as ‘secondary’ if they have replaced another land use type at any time during the same period. Cases of current forests with multiple swinging states between forests and agricultural lands are considered ‘secondary’. We used standardized yearly averaged maximum temperature (hereafter called temperature) and annual sum of precipitation (hereafter called precipitation) since 1850 at a spatial resolution of 30 arcseconds, approximately 1 km × 1 km at the equator. Given the coarse spatial resolution and the continental extent of the atlas data, the predictors were projected in the same coordinate reference system (ETRS89-LAEA) and aggregated, using the mean, at a spatial resolution of 50 km × 50 km to match the EBBA2’s mesh size. Because the period covered by the EBBA2 is a 5-year period (2013-2017), we used a 5-year sliding window to average forest cover and climate conditions backward from 2015 (average year of the EBBA2 dataset) and at a yearly resolution until 852 AD for forest cover and until 1852 for climate conditions. 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).

Non-equilibrium species distribution models

Inspired by previous works in spatial ecology (Chandler et al., 2016; Miguet et al., 2017), we developed a multivariate and temporally-weighted generalized linear regression to model the response variable, that is here a binary variable (presence-absence of a given species), as a function of current and past conditions (Eq. 1):

$$\mu_i = \alpha + \sum_{j=1}^{N} \beta_j \sum_{\Delta t=0}^{\max(\Delta t)} X_{ij\Delta t} W_j(\Delta t) + \varepsilon_i \ (Eq. 1)$$

where μ_i refers to each observation i of the response variable in the model formula, α is the intercept parameter and β_j is the slope estimate of the predictor variable j out of the N covariates included as

predictor variables in the model formula. The residual error term ε is assumed to be randomly distributed. The slope estimate β_j depends on a temporal weighting function $W_j = e^{-0.5\,(\frac{\Delta t}{\gamma_j \cdot \max(\Delta t)})^2}$, which is used to weight the covariate value $X_{ij\Delta t}$ according to its age Δt. For the year 2015, $\Delta t = 0$ and it increases as we go back in time. The older the date *t* for the covariate X_{ij}, the larger the Δt and the lower is the weight assigned to $X_{ij\Delta t}$. For instance, if we consider the covariate of primary forest cover, the older date at which the weight is the lowest is 852 which corresponds to an age of 1,163 years. Thus, we assumed that the effect of a covariate decreases as we go back in time. To test the sensitivity of the results to the definition of the weighting function, we also considered an alternative hypothesis of a negative exponential decrease of the effects of the covariates with $W_j = e^{-\frac{\Delta t}{\gamma_j \cdot \max(\Delta t)}}$. We defined 'the shape of the time lag' as the shape of the weighting function that depends on the time lag parameter γ_j, which describes how the effect of a covariate *j* decreases, linearly or non-linearly as we go back in time. The time lag parameter corresponds to the year at which approximately one third (63.2 %) or one quarter (75.8 %) of the effect of the covariate has occurred over time, for a negative exponential and a half-Gaussian weighting function, respectively. We also used these functions to define the time-window that should be considered to account for 95 % of the effect that a given time series of past environmental condition has on the current distribution of a species, when summing all weighted values of that focal predictor before inferring its effect size (called 'the time lag extent', Fig. 1A). We applied this framework, using a binomial family with a logit link function, to relate the presence-absence data of a species to primary forest cover, secondary forest cover, temperature and precipitation altogether in one single multivariate model. All the analyses were performed using the R software and the *scalescape* R package for parameter inference (Lowe et al., 2022). The *scalescape* package was initially designed to fit spatially-weighted generalized linear regressions from 'landscape matrices' which include predictor values for different distance classes. Thus, the analysis of the bidimensional (*i.e.*, latitude and longitude) spatial context is reduced to a

196 one-dimensional problem, since cumulated landscape features are taken into account according to
197 their distance only, but not their direction, from the focal plot where the response variable is sampled.
198 Here, we replaced the 'landscape matrices' by 'temporal matrices' including the predictor values for
199 each Δt, instead of distance classes, in order to fit the temporally-weighted generalized linear
200 regressions. We used the maximum possible temporal extent of the predictors in order to maximize
201 the possibility of correctly estimating the temporal extent of each time lag. We did not interpret time
202 lag parameters leading to temporal extents that were larger than or equal to the maximum possible
203 temporal extent available for the predictors (*i.e.*, 1,163 years for primary and secondary forest
204 cover).We performed a simulation exercise to illustrate the capabilities of our non-equilibrium SDM
205 approach to capture the temporal extent of a lagging response to a given predictor variable for which
206 we imposed and thus know the magnitude of the lagging dynamic (Supplementary Information,
207 Appendix S3).
208
209 Model selection, validation and predictions
210 We compared the Akaike Information Criterion (AIC) of our non-equilibrium SDMs with an
211 alternative equilibrium model relying on traditional SDM approaches and for which the predictors
212 are basically averaged over the 5-year time-window of the EBBA2, namely 2013-2017. Models were
213 considered significantly different if the AIC difference was > 2 (Burnham & Anderson, 2002). The
214 comparison between the equilibrium SDMs and the non-equilibrium ones were not very sensitive to
215 the definition of the weighting functions. Both the Gaussian and the negative exponential weighting
216 functions of the non-equilibrium SDMs outperformed the equilibrium SDMs for the majority of the
217 studied bird species (87 and 79 out of 92 species, respectively). For further analyses, we retained only
218 the Gaussian non-equilibrium SDMs given that it leads to a better fit compared to the negative
219 exponential non-equilibrium SDMs for the vast majority of the species (for 82 out of 92 species).
220 The validity of the tested models depends on the typical assumptions underlying SDMs (Zurell et al,

2020). Obviously, the hypothesis of species-environment equilibrium is expected under traditional equilibrium SDMs, while the non-equilibrium SDM relaxes this assumption. For both equilibrium and non-equilibrium SDMs, observations are assumed to be unbiased and independent. The predictors are assumed to be free of errors and sufficient to capture the main determinants of European bird distributions given previous results (Cooper et al., 2023).

The residual errors were calculated, applying the *resid()* function from the *base* R package. For each species, model validity was assessed from the distribution of the residual errors, which was assumed to be Gaussian and centered on zero (tested from Student's *t* test). We tested for positive or negative spatial autocorrelation signals in the pooled residuals using the Moran's *I* index, calculated for uniformly distributed distance classes with 500 km increments, using the *correlog* function from the *ncf* R package (Bjornstad et al., 2001). We expected that the distribution of this index would be centered on 0 (no spatial autocorrelation) and tested this using a Student's *t* test. The distribution of the pooled residual errors, and the pooled Moran's *I*, among all the species are shown in the Supplementary Information (Appendix S4).

The predictive ability of the best model was evaluated using the Area Under the Curve (AUC), the specificity and the sensitivity indices, averaged over 20 replicates of a bootstrap cross-validation procedure (70 % and 30 % partitioning for calibration and validation, respectively; Fielding & Bell, 1997). We have not considered a clustered selection of cross-validated samples given that there is no extrapolation thanks to the use a European atlas with an exhaustive sampling grid and given the absence of future projections (Wenger & Olden, 2012). Species distribution models with an AUC < 0.7 were excluded from further analyses to prevent inaccurate predictions.For each predictor variable, we compared the estimates of the equilibrium SDMs against the estimates of the non-equilibrium SDMs to identify potential discrepancies in direction, magnitude (using Student's *t* test) and variability (using Fischer's *F* test).

We converted presence probabilities into binary presence-absence predictions using the maximum

true skill statistic (TSS) as a threshold adapted for presence-absence data (Liu et al., 2013). To map the extinction debt and the immigration credit of forest birds across Europe, we followed Haddou et al. (2022) who subtracted the effective number of species as predicted by stacking all species binary maps based on the non-equilibrium SDMs from that obtained by the equilibrium SDMs.

Results

We found that non-equilibrium SDMs had the lowest Akaike Information Criterion (AIC) for 95 % of the species (87 out of 92 species) confirming that equilibrium SDMs are less relevant than non-equilibrium ones, in most cases. Analyzing the effects of long-term yearly time series of land use and climate (Supplementary Information, Appendix S2), we found that time lag extents were extremely variable (Fig. 2) and were larger for changes in primary forests (mean = 231 years, SD = 229 years) compared to changes in secondary forests (mean = 137 years, SD = 190 years), and for changes in precipitation (mean = 20 years, SD = 29 years) compared to changes in temperature regimes (mean = 9 years, SD = 28 years). The shape of the temporal weighting function used in the model formula (*i.e.*, half-Gaussian compared to exponential negative as we go back in time) underlined a slower decrease of the weight attributed to environmental conditions towards the onset of the temporal extent covered by the lagging dynamic.

The non-equilibrium SDMs were valid, considering that species' residual errors followed a normal distribution centered on zero (Student's *t* p-value > 0.05; Supplementary Information, Appendix S4) and that the spatial autocorrelation signal of the species' residual errors in the correlogram of the Moran's *I* index was also centered on zero (Student's *t* p-value > 0.05; Supplementary Information, Appendix S4). The cross-validated Area Under the Curve (AUC) index indicated a good overall predictive accuracy (mean = 0.82, SD = 0.06) after excluding three species with low AUC values (AUC < 0.7). Overall, the non-equilibrium SDMs tended to better predict presences than absences (mean sensitivity = 0.83, SD = 0.06; mean specificity = 0.71, SD = 0.07).

We found some discrepancies between equilibrium and non-equilibrium SDMs when comparing the direction, magnitude and variance of the slope estimates for each predictor variable (Supplementary Information, Appendix S4). For 26 % of the studied species (27 out of 87 species), non-equilibrium SDMs indicated a positive effect of secondary forests while it was the opposite (*i.e.*, a negative effect of secondary forests) when relying on equilibrium SDMs. For the other predictor variables, the discrepancies on the direction of the effect between equilibrium and non-equilibrium SDMs concerned fewer species ($\leqslant$ 6%). We found a larger effect size and a larger variability in the slope estimates of primary forests when considering equilibrium SDMs, while the opposite was true for secondary forests (Student's t test ≤ 0.05; Fischer's F test ≤ 0.05; Supplementary Information, Appendix S4).

We found evidence for extinction debts to be particularly pronounced in primary boreal forests, near the Carpathians, and north of the Black Sea while evidence for immigration credits were mostly pronounced in secondary forests in the Mediterranean part of the Alps and Pyrenees, as well as in the Caucasus and in the mountainous areas north of the Caspian Sea (Fig. 3; Supplementary Information, Appendix S2).

Discussion

Overall, we found less support for traditional species distribution models (SDMs) that rely on the equilibrium hypothesis and which showed lower fit than non-equilibrium SDMs and this was true for 95 % of the 92 European forest bird species we studied. In line with former studies focusing on the fate of avian biodiversity in the context of global changes (*e.g.*, Devictor et al., 2012; Haddou et al., 2022), our result advocates for the abandonment of the equilibrium assumption in SDMs. Here, we have reported unprecedented long-lasting effects of global changes on current avian biodiversity distribution (up to 246 years for forest cover change) compared to previous studies (Figueiredo et al., 2019; Daskalova et al., 2020; Liao et al., 2022), even when considering potential sources of

296 inaccuracies (Essl et al., 2024). The shape of the time-lag response curve (*i.e.*, the shape of the
297 temporal weighting function being half-Gaussian or exponential negative) along a given predictor
298 variable also underlined the long-lasting effect of ancient environmental conditions. Because of that,
299 the use of equilibrium SDMs can lead to biased direction, magnitude and variability in the coefficient
300 estimates of the underlying predictor variables. The persistent use of models relying on the
301 equilibrium hypothesis in the SDM literature is unlikely to be explained solely by a lack of available
302 datasets, such as long-term time series of environmental conditions, because strong evidence of non-
303 equilibrium biodiversity dynamics has already been proven and generalized from the currently
304 available datasets, at different spatiotemporal scales (Figueiredo et al., 2019). We rather suggest that
305 the poor use of models relying on the non-equilibrium hypothesis is more likely due to a lack of
306 generic and ready-to-use modelling frameworks, something we now provide here, but also to an
307 underestimation of the importance and implications of the temporal extent behind time lags.
308
309 The low consideration for time lag dynamics in SDMs, despite recent literature (Essl et al. 2024),
310 might also be explained by the lack of a common definition of a time lag and how to measure it.
311 Indeed, time lags can either refer to the time elapsed since the occurrence of a causative perturbation
312 until the time it reaches a peak in population responses (Daskalova et al., 2020) or to the time elapsed
313 for a debt to be completely paid off or for a credit to be completely spent (Figueiredo et al., 2019), or
314 even to the time span elapsed between two dates in diachronic analyses (Haddou et al., 2020).
315 However, time-lagged responses of biodiversity to environmental change trajectories were initially
316 associated with the so-called ‘relaxation time’ which has a clear definition: the complete time window
317 during which a disturbance has consequences on biodiversity until it returns to a new equilibrium
318 state (Diamond, 1972; Tilman, 1995). References to the concept of relaxation time remain scarce in
319 the scientific literature (*e.g.*, Lalechère et al., 2018), compared to the use of the term time lag, perhaps
320 because a return to an equilibrium state is more theoretical in the context of continuous global changes,

and is rarely verified in the natural world (Essl et al., 2024). Finally, the concept of time lag remains ambiguous, although it is more commonly used than the concept of relaxation time, which has a clear definition but lacks empirical evidence. As a consequence, we propose to use the temporal extent of a time lag to accurately define its duration, abandoning the concepts of equilibrium and relaxation time, given the temporal non-interruption of global changes during the Anthropocene.

Our approach offers the possibility to assess the extent of a time lag associated with each individual predictor variable involved in explaining the contemporary distribution of a given species. For instance, we found that the distribution of European birds is strongly dependent on the historical extent of primary forests, whose decline takes longer to be paid off compared to the ongoing immigration credit to be spent following the historical increase in secondary forests. This result highlights that interacting land use changes threaten the resilience of communities, considering that some species preferentially present in primary forests are not adapted to colonize secondary forests that can have different compositional and structural characteristics (*e.g.*, Sabatini et al., 2018; Lalechère et al., 2024). The long-lasting effects of global changes that we have found here advocate for reconsidering the debate on their relative importance taking into account the dependance of species to past environmental conditions (Lalechère et al., 2022; Thompson et al., 2023). We found larger temporal extents of time lags for precipitation compared to temperature. Time lags related to precipitation is rarely considered in the scientific literature. As a consequence, previously estimated time-lagged consequences of climate change may have been underestimated because most studies use the community temperature index to estimate time lags, while some results also highlight the importance of precipitation in habitat suitability (Devictor et al., 2012; Tehrani et al., 2021; Lajeunesse et al., 2023).

Time lags can be artificially created by imperfect data, such as those caused by an inaccurate matching

between species observations, records in a database, environmental conditions and their averaging, especially when derived from model projections rather than from *in situ* measurements (Essl et al., 2024). Here, we used land use projections from an Earth System Model that was harmonized for long-term studies (LUH2; Hurtt et al., 2020). The inherent limitations (*e.g.*, Goldewijk & Verburg, 2013) due to the coarse spatial resolution and the coarse definition of land-use classes, defined in global earth system and climatic models, may potentially affect the inferred parameters and the predictions we made in our study. Then, some inaccuracies and uncertainties can be associated to the inferred time lag parameters (Supplementary Information, Appendix S3). However, these limitations are unlikely to bias the relative differences we found between equilibrium and non-equilibrium SDMs. The extent of the time lags we report here is disproportionated (several decades or centuries) compared to the potential biases that may be introduced by these different sources of inaccuracy, excepting for temperature with time lags that are mostly of the order of several years. In this case, time lags that are very close to the lower or the upper limit of Δt most likely indicates that the temporal extent of the temperature time series is too small for a proper inference of the lagging effect attributed to temperature changes (Arroyo-Rodríguez et al., 2022).

When compared with outputs from equilibrium SDMs, predictions from non-equilibrium SDMs allow us to assess the extinction debt and immigration credit (Haddou et al., 2022). We have shown that European bird communities are mostly affected by an extinction debt and not so much by an immigration credit. The extinction debt is particularly pronounced in boreal forests, which is consistent with the strong decline of primary forests therein. Overall, the immigration credit is mostly located in Mediterranean forests, the Caucasus and the mountainous areas north of the Caspian Sea, where secondary forests are increasing in cover. The presence of an extinction debt in some areas where secondary forests increase indicates an interaction between the progressive colonization of secondary forests and an ongoing decline of species with a low thermal tolerance due to increasing

temperature (Jiguet et al., 2010). These complex antagonistic interactions may have complicated the inference of the time lags related to temperature in areas with both delayed colonization and extinction dynamics.

Few other studies have ever attempted to map the extinction debt and the immigration credit of biodiversity distribution (but see, Bertrand et al., 2016; Chen et al., 2017; Duchenne et al., 2021; Haddou et al., 2022). For example, Chen et al. (2017) mapped the delayed extinction patterns of entire communities at the global extent, analyzing their dependance to forest areas in a diachronic analysis that compared the 2000s against the 16th century. They showed that delayed extinctions did not overlap with hotspots of species richness or high extinction-risk areas based on IUCN threatened status. Focusing on avian biodiversity, Haddou et al. (2022) have mapped changes that have yet to be realized over the conterminous United States, pointing out areas of conservation concern. However, they recognize that non-equilibrium spatial patterns could be obtained by considering multiple time points over a longer time period in order to improve projections of past, current and future biodiversity. Our conceptual and modelling framework paves the way to fill this gap and to anticipate future projections of non-equilibrium biodiversity patterns using shared socio-economic pathways and land use projections. Indeed, the inference procedure in our non-equilibrium SDM is not based on a specific year or a specific temporal baseline period, but it accounts for time-series of past environmental conditions. Note that it can be also applied to time-series of biodiversity monitoring data to account for temporal variation in species distribution parameters in order to anticipate changes in time lags and species affinity to future environmental conditions.

After establishing a proof of concept, one of the main perspectives of this study is to refine how species do or do not depend on past environmental conditions according to the model selection procedure. For example, this procedure could be fine-tuned considering alternative hypotheses about

the decrease of the effect size, in order to better model the dependance of current species to past environmental conditions. This can be especially true for temperature for which the temporal extent of time-lag effects is mostly shallow and vary little among species, while the literature indicates a strong variability according to species thermal tolerances (Jiguet et al., 2010). Model selection procedure can also be used to test if additional and potentially missing predictors could be identified to improve the balance of the predictive accuracy between presences and absences. However, the accessibility of long-term time series on environmental conditions is still very limited beyond land use and climate. Therefore, it would be necessary to adopt a mixed approach, by considering an equilibrium as well as a non-equilibrium hypothesis, depending on data accessibility of each predictor variable and not only based on the ecological significance. This can be easily done within the modelling framework we provide here by simply adding predictors that are invariant over time directly in Eq. 1.

A second perspective is to test whether it is possible or not to identify the functional characteristics of the species which have contrasted time lag extents and which do not respond in the same way to the model selection procedure (Tobias et al., 2022). For example, we can expect that species with a short life expectancy or able to disperse at long distances are less sensible to past environmental conditions (Kitzes & Harte, 2015; Lalechère et al., 2017; Lalechère et al., 2019; Daskalova et al., 2020; Couet et al., 2022). We could also expect time lags to be related to the trophic position of the species and impacted by cascading effects of cumulated time lags throughout the trophic food web, from primary producers to consumers, for example (Essl et al., 2015).

A third perspective is to improve our non-equilibrium modelling framework with the integration of species dispersal kernels, or the spatial extent of effect of each individual drivers of biodiversity, that are two ways to account for spatial processes (Barbet-Massin et al., 2012; Miguet et al., 2017). In this study, the coarse spatial resolution of the bird's atlas dataset had the advantage to limit spatial autocorrelation issues due to small-scale variation in environmental conditions. However, this coarse

spatial resolution can partly affect inference and predictions, by overlooking local microclimatic variation due to the buffering effect of vegetation, for example, which might also explain the small extent and variability of the time lags we found for temperature (Kim et al., 2022). Given that our approach is inspired by the concept of the spatial scale of effect, a logical follow-up would be to model spatiotemporal response curves to account for a decrease in the effect of a driver the further we go away, in space or time, from a given biodiversity survey. This perspective could pave the way to the inference of spatial and temporal extent of the effects, providing a common framework for multi-taxa analyses including species which do not respond to global changes at the same extents (Sandel, 2015).

To conclude, we contribute to fill the gap of a conceptual and modelling framework adapted to study non-equilibrium species distribution in the context of gradual global changes. We propose to model the temporal extent of time lags that account for the full effects (95 %) of past global changes on current biodiversity. We found that it can reach several centuries, that is much more than previously reported in the scientific literature. Our non-equilibrium SDM approach revealed the spatial patterns of the mismatch of the species-environment relationships at large biogeographical extent. This approach, which challenges the concept of equilibrium, also has the important implication of making it unnecessary to define an arbitrary baseline time period to project the future distribution of species.

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Figures

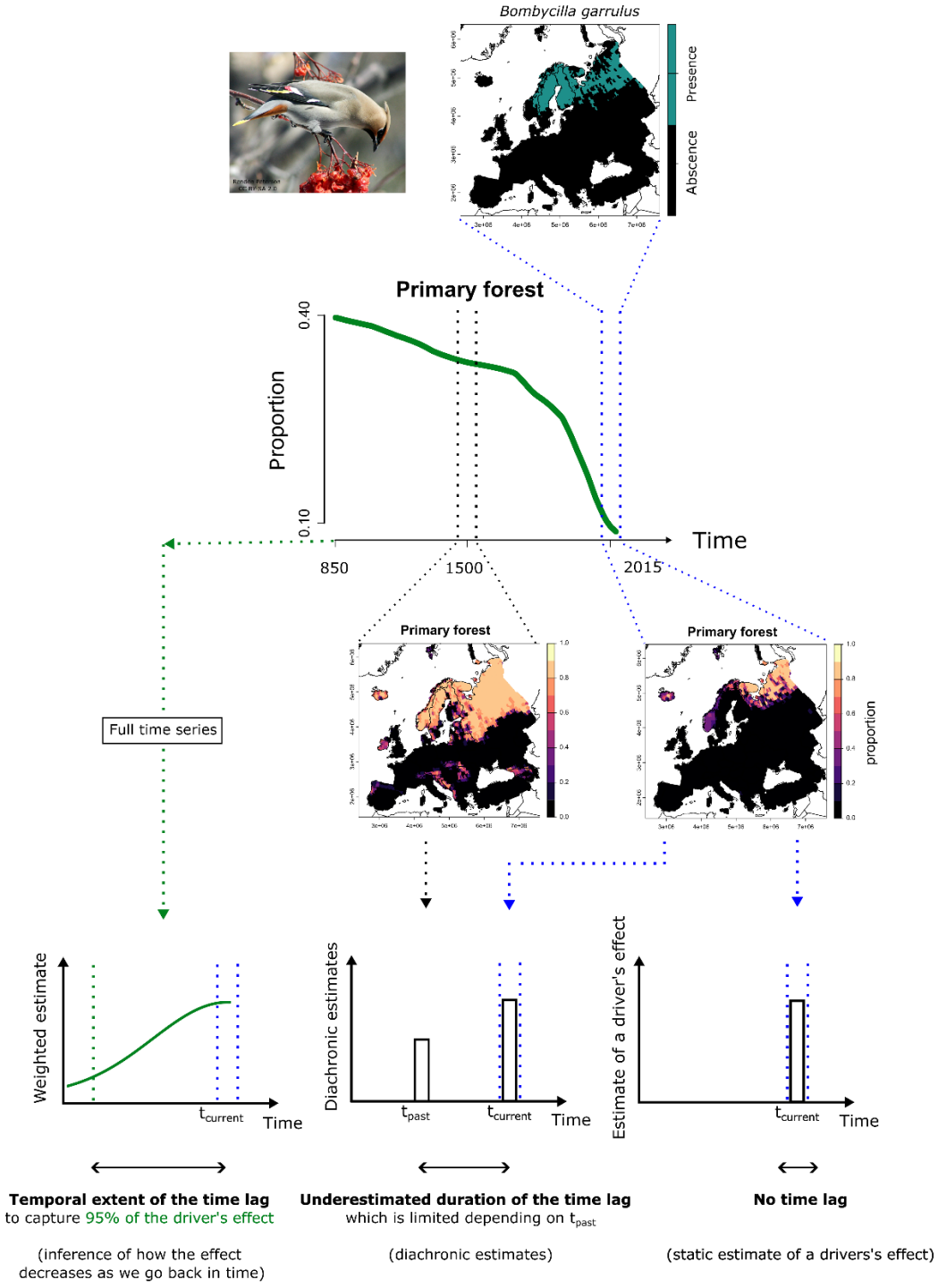


Figure 1: Example of approaches and limits to model current species distributions in the context of gradual environmental changes (B, C) and how to circumvent these limits by using weighting functions that describe how the effects of past environmental factors decrease as we go back far into the past (A).

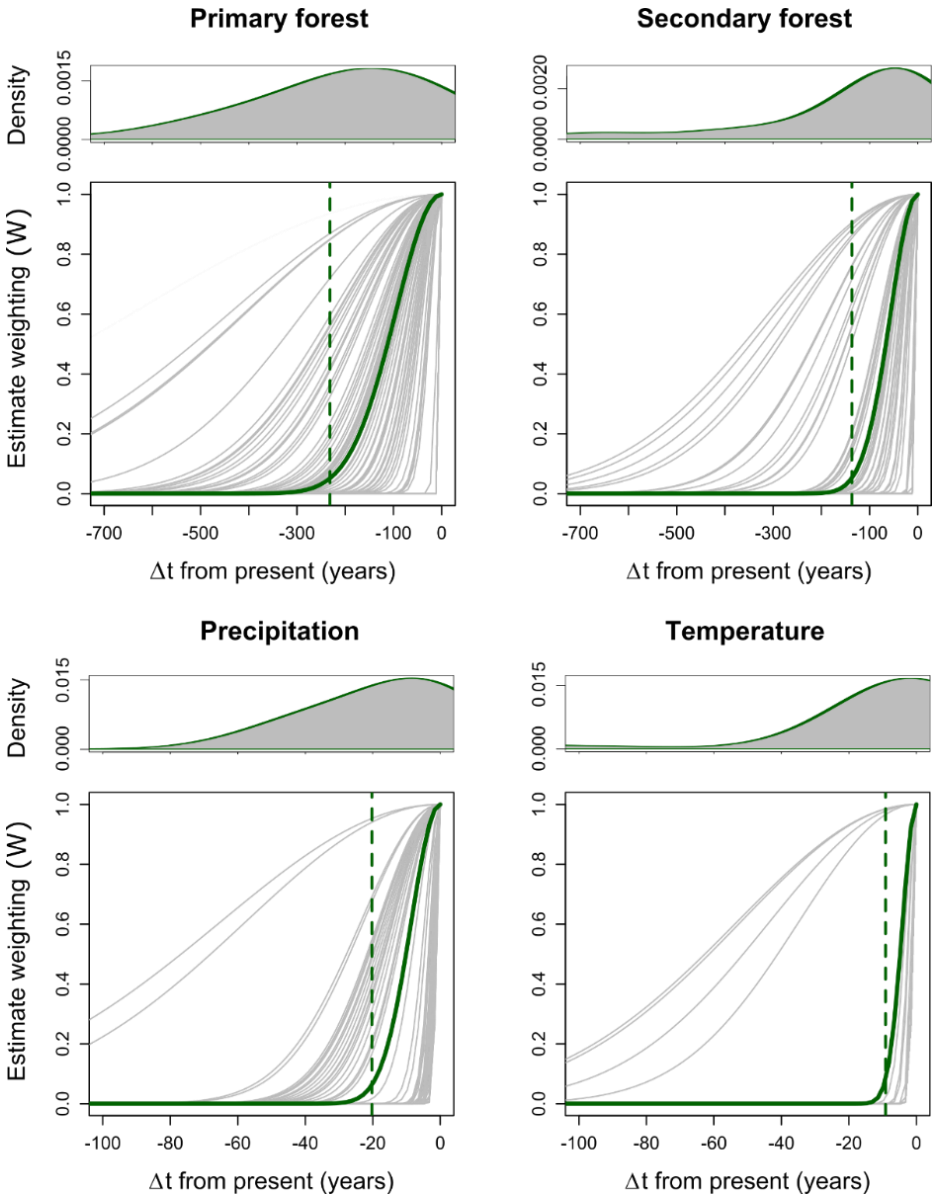
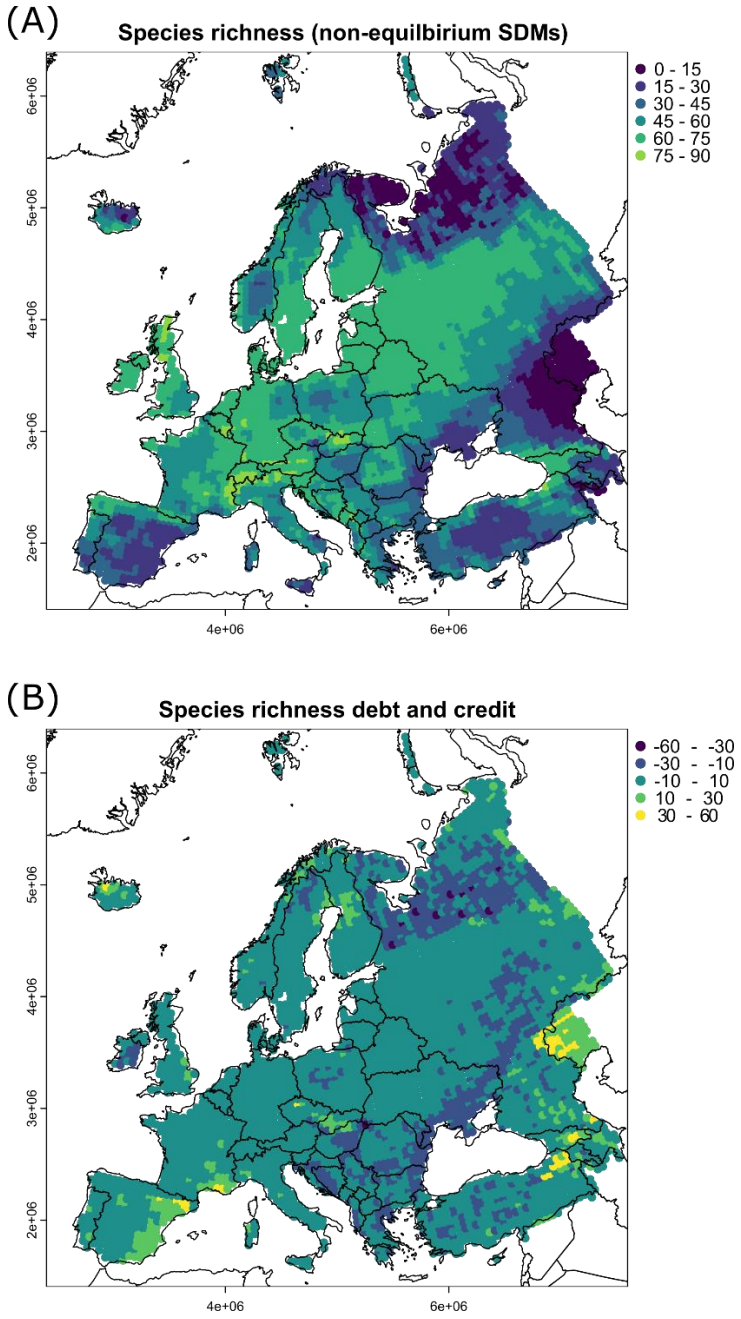


Figure 2: Decrease, as we go back in time (from the onset of 2015 for which $\Delta t = 0$), of the effects of past land use and climate predictors on current bird species distribution in Europe. The grey curves depict the half-Gaussian weighting function (W) of the estimates for each species. The mean weighting functions (solid curve) and the mean temporal extent of the time lags (vertical dashed line) are depicted in green. The temporal extent of a time lag is the date at which me must go back into the past to account for 95 % of the effect that a given time series of past environmental conditions has on the current distribution of a species. For each predictor, the number of species considered varies slightly (77 species, 69 species, 63 species and 60 species for primary forest, secondary forest, precipitation and temperature, respectively) because we did not consider time lag parameters leading

618 to temporal extents that were larger than or equal to the maximum possible temporal extent available
619 for the predictors (see Material and methods). The density plots represent the distribution of the
620 temporal extents of the time lags.
621



622

623 Figure 3: Stacked species distributions providing a richness map of current forest bird communities
624 predicted by non-equilibrium species distribution models (SDMs, A) and the associated extinction
625 debt (negative values, B) or immigration credit (positive values, B). In panel B, the colors depict the
626 difference between the species richness as predicted by stacking all species binary maps based on the
627 non-equilibrium SDM from that obtained by the equilibrium SDM. The extinction debt and the
628 immigration credit are expressed in percent of the local, within a grid cell, total number of species
629 predicted by equilibrium SDMs. The spatial resolution on the maps is 50 km.

630

631 **Supplementary Information**

632

633 Appendix S1: The bird species list.

634 Using the European Breeding Bird Atlas (EBBA2), we selected the 92 species of birds whose habitat
635 is classified as either forest or woodland according to Tobias et al. (2022). The use of a threshold of
636 a minimum number of presences was unnecessary because the proportion of occupied EBBA2's
637 meshes was sufficient for all the 92 selected species (minimum proportion > 0.10 that is at least 508
638 meshes out of 5079 for the whole study area).

639 Table S1: Species list.
640

Acanthis flammea	*Falco subbuteo*	*Phylloscopus bonelli*
Accipiter gentilis	*Ficedula albicollis*	*Phylloscopus collybita*
Accipiter nisus	*Ficedula hypoleuca*	*Phylloscopus sibilatrix*
Aegithalos caudatus	*Ficedula parva*	*Phylloscopus trochiloides*
Aegolius funereus	*Fringilla coelebs*	*Phylloscopus trochilus*
Anthus trivialis	*Fringilla montifringilla*	*Picoides tridactylus*
Asio otus	*Garrulus glandarius*	*Picus canus*
Bombycilla garrulus	*Glaucidium passerinum*	*Picus viridis*
Bonasa bonasia	*Hieraaetus pennatus*	*Poecile montanus*
Carduelis carduelis	*Hippolais icterina*	*Poecile palustris*
Certhia brachydactyla	*Hippolais polyglotta*	*Prunella modularis*
Certhia familiaris	*Jynx torquilla*	*Pyrrhula pyrrhula*
Chloris chloris	*Lanius collurio*	*Regulus ignicapilla*
Ciconia nigra	*Leiopicus medius*	*Regulus regulus*
Circaetus gallicus	*Lophophanes cristatus*	*Scolopax rusticola*
Clanga pomarina	*Loxia curvirostra*	*Serinus serinus*
Coccothraustes coccothraustes	*Loxia pytyopsittacus*	*Sitta europaea*
Columba oenas	*Lullula arborea*	*Spinus spinus*
Columba palumbus	*Luscinia megarhynchos*	*Streptopelia turtur*
Coracias garrulus	*Lyrurus tetrix*	*Strix aluco*
Corvus corax	*Merops apiaster*	*Strix uralensis*
Cuculus canorus	*Milvus migrans*	*Sylvia atricapilla*
Cyanistes caeruleus	*Muscicapa striata*	*Sylvia borin*
Dendrocopos leucotos	*Nucifraga caryocatactes*	*Tetrao urogallus*
Dendrocopos major	*Oriolus oriolus*	*Troglodytes troglodytes*
Dendrocopos syriacus	*Otus scops*	*Turdus iliacus*
Dryobates minor	*Parus major*	*Turdus merula*
Dryocopus martius	*Passer montanus*	*Turdus philomelos*
Emberiza rustica	*Periparus ater*	*Turdus pilaris*
Erithacus rubecula	*Pernis apivorus*	*Turdus viscivorus*
Falco columbarius	*Phoenicurus phoenicurus*	

Appendix S2: Spatial and temporal patterns of land uses and climate.

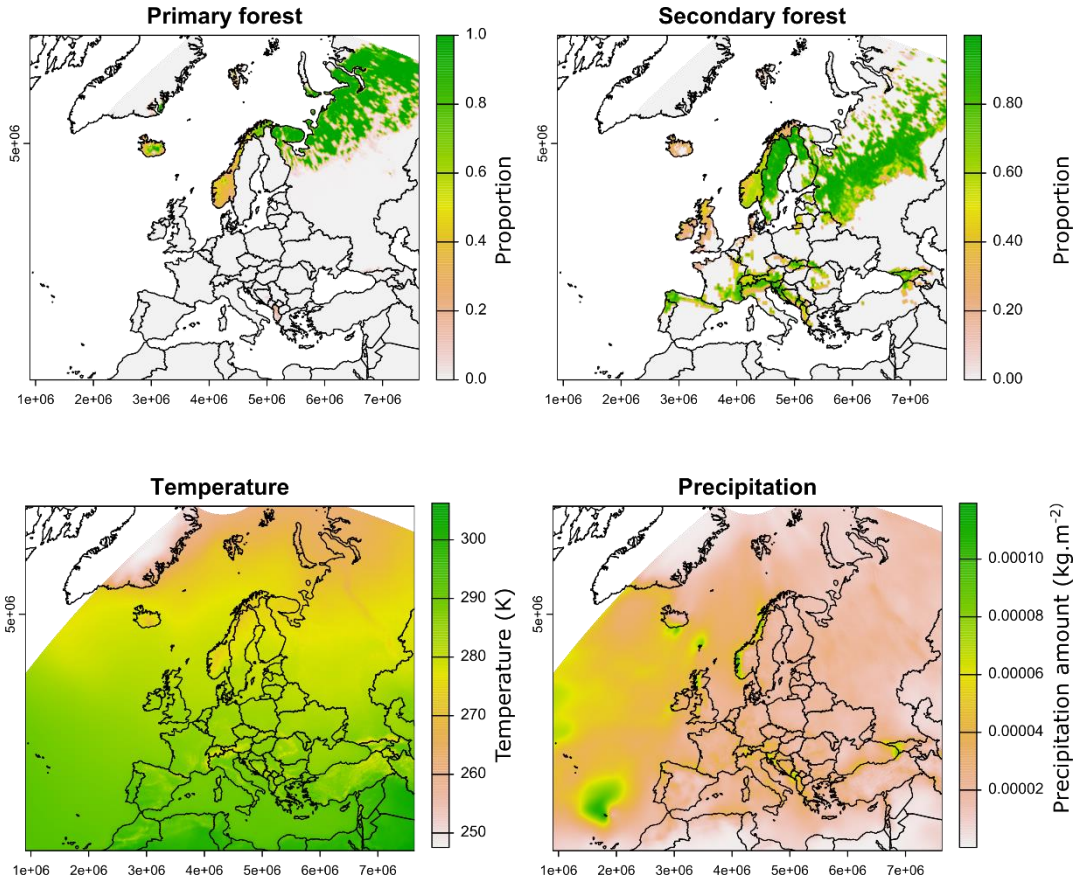


Figure S1: Spatial patterns of land uses and climate in 2015.

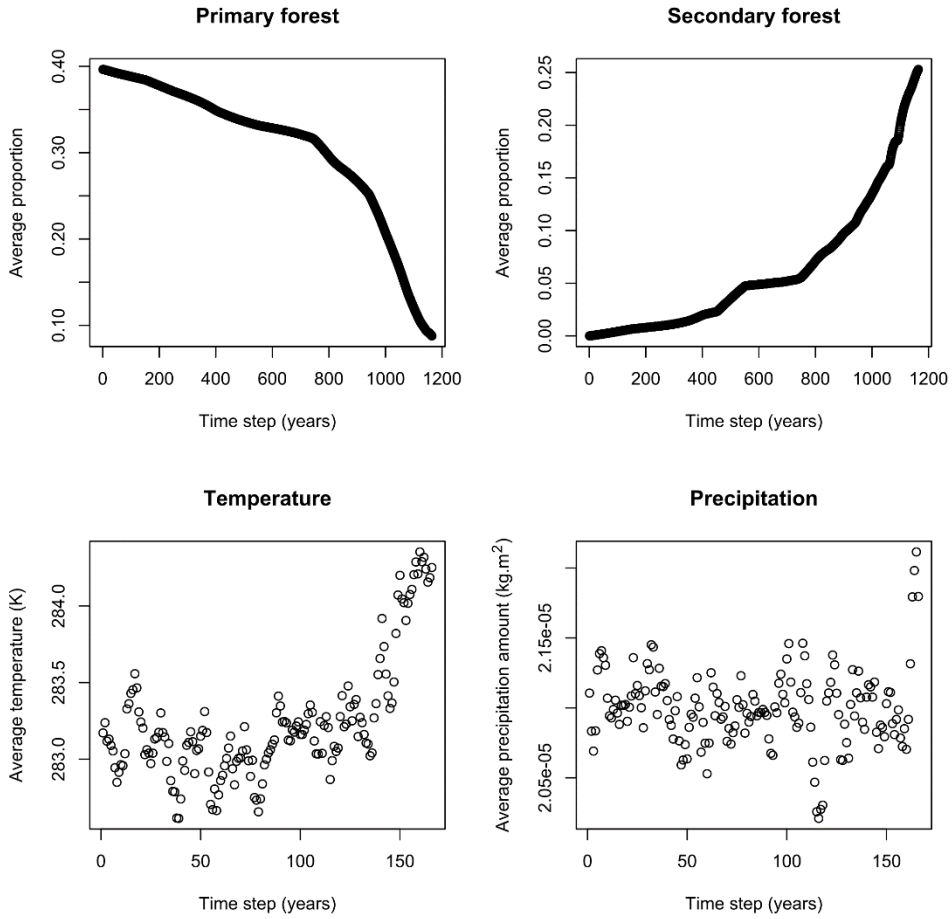


Figure S2: Temporal patterns of land uses and climate conditions until 2015. Values are averaged over the whole study area. Time series begin in 852 and in 1852 for land uses and climate conditions, respectively. The historical data time series were pooled with the projections of a business-as-usual scenario (SSP2, RCP 4.5) that begins after 2005, or after 2015, for the CHELSA and the LUH2 time series, respectively (Karger et al., 2019; Hurtt et al., 2020).

Appendix S3: Comparison between simulated and inferred time lag parameters.

To illustrate the capability of our non-equilibrium species distribution modelling (SDM) approach to capture the slope estimates (β_j) and the time lag (γ_j) parameters of a lagging response to a given predictor variable *j*, we performed a simulation exercise by focusing on multiple reference species. First, the slope and the time-lag parameters (Eq. 1) we inferred from the bird species dataset (EBBA2), using our non-equilibrium SDM approach, were considered as the reference or the target (*i.e.*, the "true parameters", Fig. S3) to rely on realistic parameter combinations. For each predictor, the number of species considered varies slightly (77 species, 69 species, 63 species and 60 species for primary forest, secondary forest, precipitation and temperature, respectively) because we did not consider time lag parameters leading to temporal extents that were larger than or equal to the maximum possible temporal extent available for the predictors (see Material and methods). Then, for the sake of comparison between our simulations and the empirical observations, we used the exact same set of environmental predictors (*i.e.*, long-term time series of changes in forest cover and climate conditions at a yearly resolution) and we focused on the exact same study area (*i.e.*, Europe) as for the bird data. For each combination of true parameters (*i.e.*, each bird reference species), we generated 30 replicates of 5079 predicted occurrences (across the entire study area), using the predicted probability of presence of each species as obtained from the non-equilibrium SDM fitted with the empirical data. From these simulated set of occurrences available for each of the reference species, we fitted 30 replicates of non-equilibrium SDMs from which we extracted the estimated slope and time-lag parameters (30 sets for each reference species). Finally, we used a linear regression to evaluate both the accuracy and the uncertainty of the estimated parameters using the median values of the 30 replicates for a given species. We found that the true slope parameters (those we used to perform the simulations), for the four predictor variables, were retrieved by our non-equilibrium inference procedure with a very large accuracy and a very small uncertainty ($R^2 \geq 0.99$, Fig. S4). This

was also true for the time-lag parameter associated with primary forests (R^2 = 0.97, Fig. S4), while the accuracy and the uncertainty associated to the time-lag parameters of the other predictor variables were smaller and larger, respectively ($R^2 \geq 0.7$, Fig. S4).

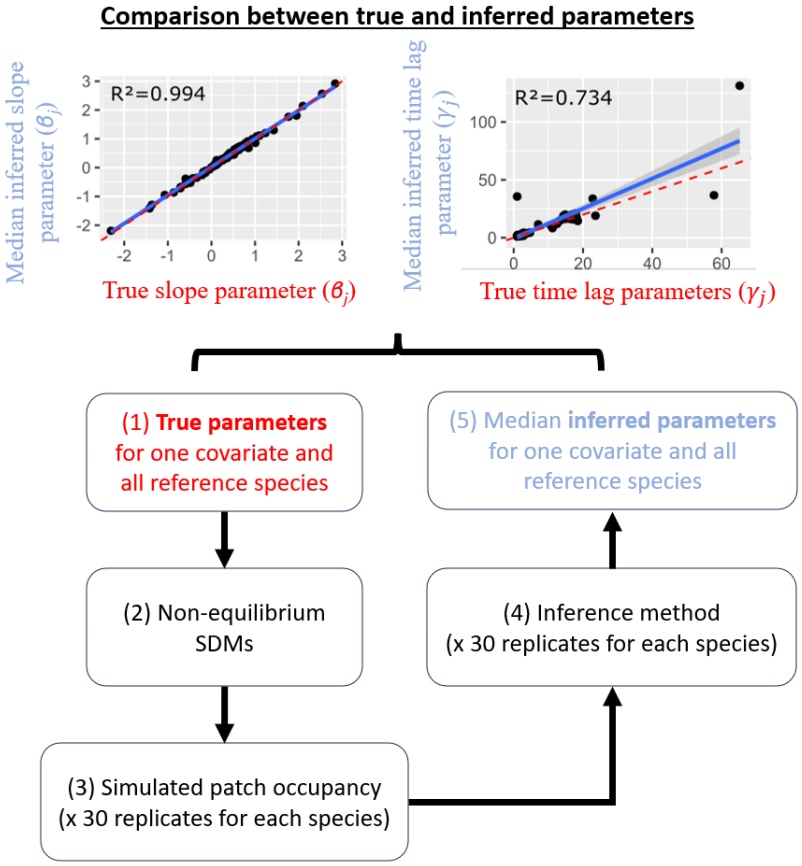
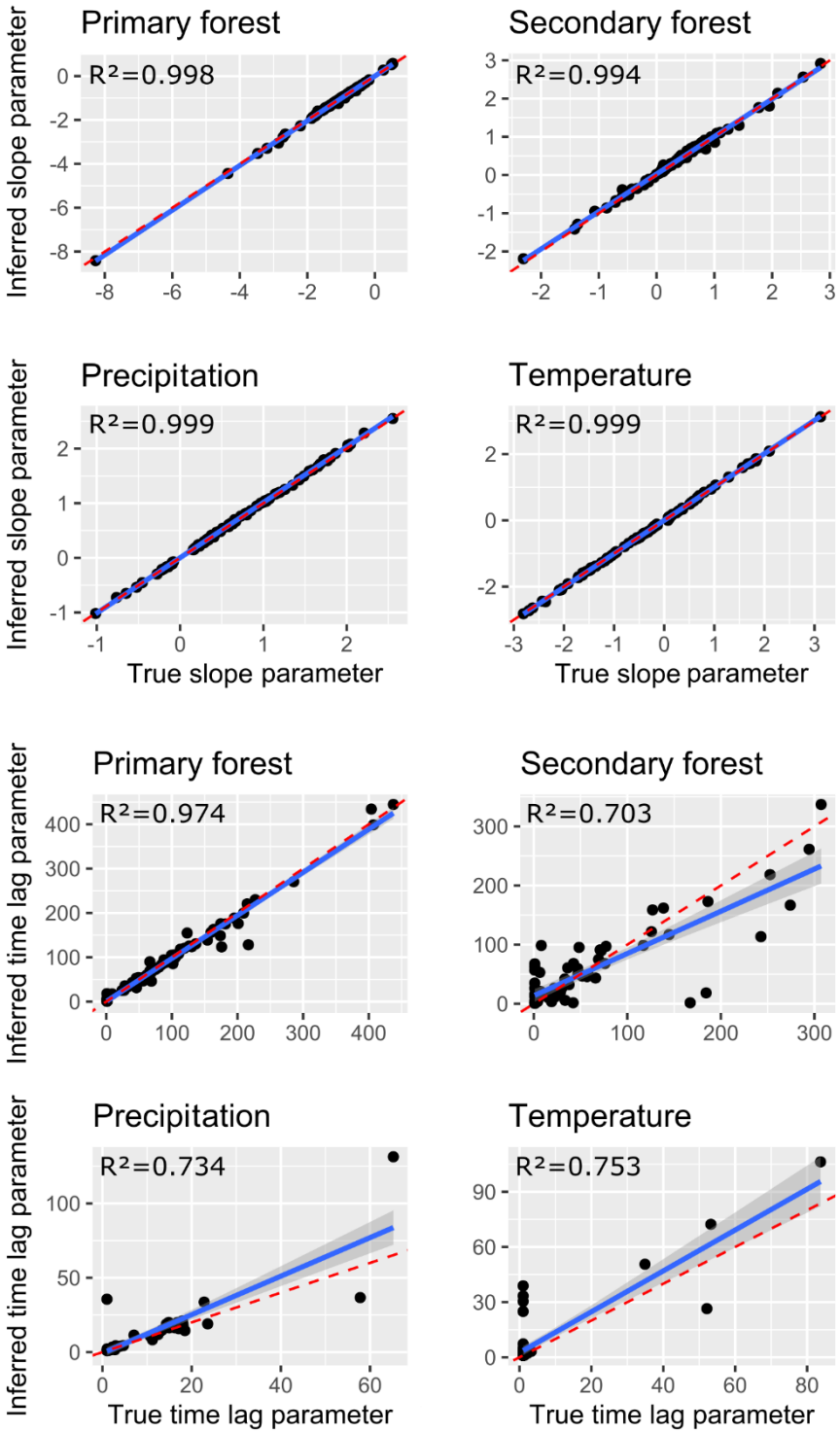


Figure S3: Summary of the procedure used to assess the capacity of the non-equilibrium modelling approach to recover the original parameter values set in the model formula (Eq. 1). The procedure is depicted for all reference species and one covariate *j*, for which we know the true values associated with the slope (β_j) and the time-lag (γ_j) parameters. The accuracy and the uncertainty of the parameters, inferred from the non-equilibrium approach, are assessed from a linear regression line (in blue), the 95 % confidence intervals (in gray), the coefficient of determination (R^2), and by comparing the regression line with the 1:1 line (in red).



690

691 Figure S4: Relationship between the true and the inferred slope (β_j) and time lag (γ_j) parameters. The

692 R^2 value is the coefficient of determination, the blue line is a regression line with confidence intervals

693 in gray, and the red line is the 1:1 line.

694

Appendix S4: Model estimates and distribution of the residual errors.

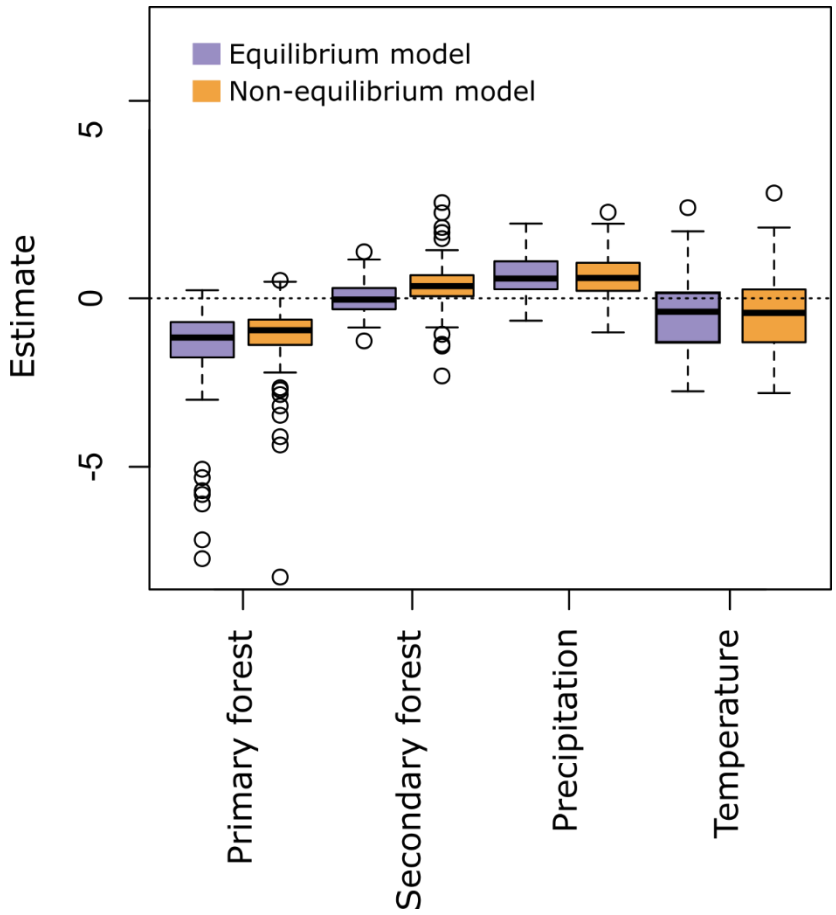
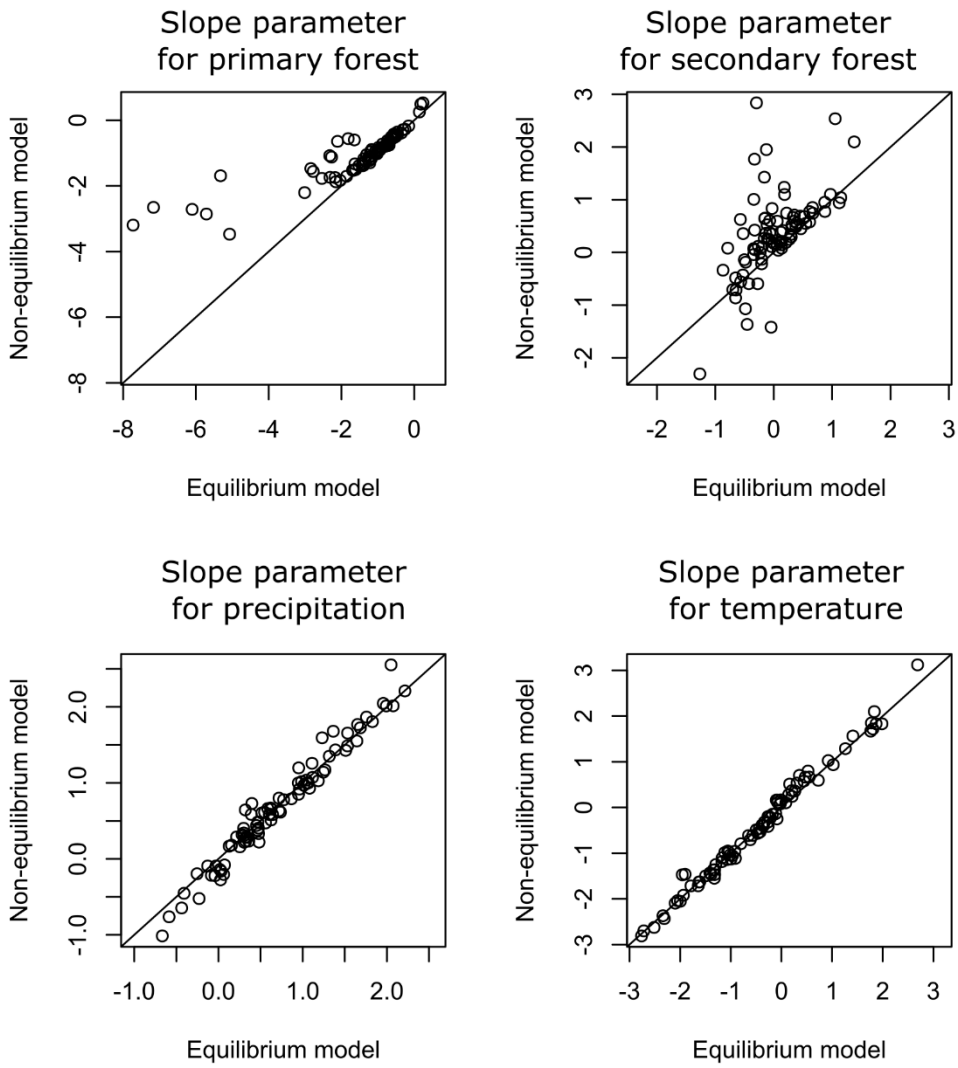


Figure S5: Distribution of the estimates of the predictors for the equilibrium and the non-equilibrium models.



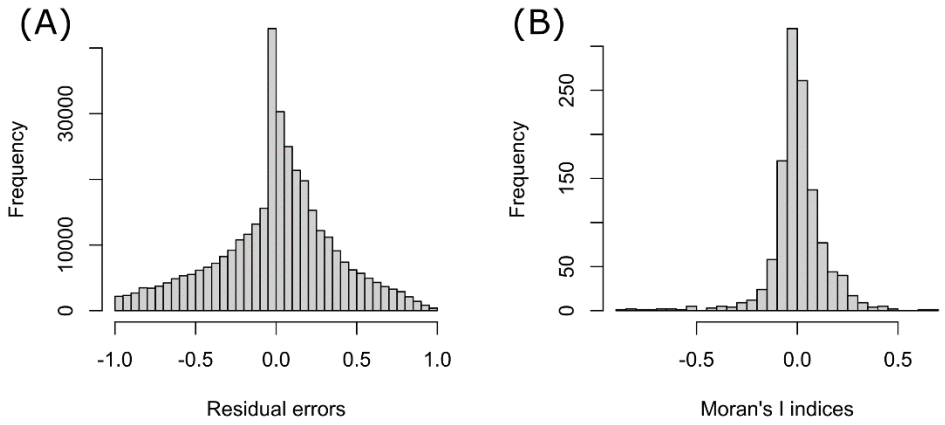
701

702 Figure S6: Comparison between the slope parameters of the predictors (β_j) for the equilibrium and

703 the non-equilibrium models. The larger the time lags and the more the discrepancies between the

704 two models.

705



706

707 Figure S7: Validity of the non-equilibrium models according to the distribution (A) and the spatial
708 autocorrelation (B) of the residual errors. The residual errors (A) were calculated with the R *resid*
709 function and pooled here among all the non-equilibrium species distribution models (SDMs), for
710 clarity purpose. The Moran's *I* indices were calculated by distance classes for each species and then
711 pooled (B). The pooled residual errors followed a normal distribution centered on zero (mean = 0.000,
712 SD = 0.365, Student's $t = 0.000$, p-value > 0.05) such as for the pooled distribution of the Moran's *I*
713 index (mean = 0.003, SD = 0.14; Student's $t = 0.893$, p-value > 0.05).