MASTER

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The influence of climate variability on the productivity of common songbirds

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SUMMARY

INTRODUCTION

Human-induced climate change leads to an increased frequency and intensity of climate and weather extremes, including hot extremes and drought, which impact ecosystems and people to an extent even larger than estimated in the past (IPCC, 2022). For instance, France experienced in 2022 the warmest year ever recorded (Figure 1a), characterized by both a high mean temperature and a succession of heat waves, with 33 extremely hot days (Meteo France, 2022). Heat waves often – though not always – accompany droughts (Albright et al., 2010) and 2022 was also the 3rd longest dry period France has ever seen. These extreme climatic events (ECEs) due to climate change lead to a widespread deterioration of ecosystem structure and function, resilience and natural adaptive capacity associated with phenomenon such as desertification (IPCC, 2022). Yet, consequences of the diverse aspects of climate change may vary between locations and groups of organisms. To be able to predict population dynamics and changes in ecosystem functioning, we need to understand through what biological processes these changes of climatic conditions alter living beings and their interactions within ecosystems.

Indeed, in addition to the global climate change, we are currently facing the 6th mass extinction (Ceballos et al., 2015) with a million species at risk of extinction and a decrease by at least 20% of the average abundance of native species in major land-based habitats (IPBES, 2019). Birds are largely impacted by anthropogenic pressures (Rigal et al., 2023) and are one of the best documented taxonomic class of organisms, allowing the most complete and complex assessment of the impacts of global environmental changes on living beings. (Lees et al., 2022). Thus, birds are an ideal group to study the ecological effects of climate variability as they are easily observed, well documented, and responsive to environmental changes (Cady et al., 2019). Global warming induces range shifts towards the poles: warmer temperatures at Northern latitudes enable species previously constrained by cold temperatures to breed, while warmer and dryer climatic conditions in the Southern range edge become unfavorable (Bateman et al., 2015). These range shifts lead to a redistribution of species and abundance shifts (Albright et al., 2009; Gorzo et al., 2016), often associated with reduced species richness (Albright et al., 2009). Extreme climatic events such as heat waves and drought also affects population dynamics by reducing breeding success (Colón et al., 2017; Skagen & Adams, 2012). Species present over a large range tend to be less negatively affected by variations in temperature, as they are more tolerant to a wide range of temperature. Jiguet et al. (2006) found that species showing the sharpest decrease in population growth rate during the 2003 heat waves had small thermal ranges, indicating that the geographically deduced thermal range is a reliable predictor of species' resilience to extreme temperatures.

A crucial period for birds is the breeding season, and climate variability can have important impacts on bird reproduction. Following the earlier onset of spring with global warming, some bird species show an advancement of laying dates (Brown & Brown, 2014; Marrot et al., 2017). Yet, if warm temperatures and an early breeding tend to benefit bird reproduction (Hoover & Schelsky, 2020; Meller et al., 2018) by improving breeding success and extend the duration of the breeding season, consequences of climate change on offspring production are unequivocal and vary among species and populations. Some studies have found offspring production to be unchanged (Dyrcz & Czyż, 2018) or reduced because of trophic mismatch (Visser & Gienapp, 2019) and heat stress caused by more frequent weather extremes (Sergio et al., 2018). Responses of bird productivity to climate variability depends on their traits and species whose offspring production tend to be reduced are usually large and long-distance migrants (Halupka et al., 2023). Indeed, phenology shifts occurring during warmer springs differ among trophic levels with lower trophic levels shifting faster (Thackeray et al., 2010). Birds at higher trophic levels shift slower and suffer from a time lag between the peak of food supply and food demand of nestlings. The impact of this trophic mismatch is stronger in long-distance migrants, whose migration date is mainly determined by photoperiod (Dawson et al., 2001). The date of arrival at their breeding ground is therefore not very flexible, and they tend to arrive after the peak of food supply during warm springs: this is called the trophic mismatch hypothesis (Ross et al., 2017). The direction and magnitude of species responses to drought are also habitat-dependent (Roberts et al., 2021), with grassland species and avian communities from dry and semi-arid habitat being more strongly affected (Albright et al., 2009; Cady et al., 2019). An intense drought might also be deleterious to aquatic species in case lakes completely dry up during summer.

Therefore, the effects of climatic variability is expected to differ between species. If focusing on a precise endangered species might help target specific conservation actions, studying multiple species may help identify a global pattern in the response of species, which is often necessary to better understand this global phenomenon, affecting many aspects of birds' life cycle and highly dependent on species characteristics.

Thus, characterizing the consequences of climate change on bird reproduction requires to account for many factors, both at the species (life-history traits) and environmental level (variables reflecting climatic variation). Climate change is indeed a phenomenon with multiple components acting at various temporal and spatial scales (Garcia et al., 2014), which may be involved in complex interactions and have potentially opposite consequences on organisms.

Therefore, it is important to identify predictors that accurately represent both meteorological and biological processes involved in the response of organisms to climate change, to try disentangling the complex confounding effects of its components. The first critical issue is to choose appropriate environmental predictors and appropriate shapes for the reaction norm of reproduction success to these predictors. For instance, temperature can have contradictory effects whether we consider mean values or extreme events. Indeed, if an increase in mean temperatures can benefit productivity (Meller et al., 2018), there may be a threshold above which individuals cannot cope with extreme heat anymore (Gardner et al., 2017). These extreme events exceeding ecological or physiological tolerances of some species may have a greater influence on population trends than changes in mean conditions (Jentsch et al., 2007), and focusing on these extreme events might allow a better understanding of the effects of temperature anomalies overall. Positive effects of an increased temperature on productivity can also be counterbalanced by a co-occurrence of drought. It is therefore necessary to and consider potential confounding effects due to the collinearity between meteorological events. If disentangling the effects of heat waves and drought can be challenging, it is nonetheless important to gain a more appropriate understanding of how organisms are affected by past environmental variability, and therefore improve our ability to forecast population trajectories under different scenario of climate change (Albright et al., 2010).

The notion of drought itself, if it is easy to understand, is not easy to characterize and is often insufficiently defined in ecological studies (Slette et al., 2019). Drought is generally defined as "a deficit of water availability relative to normal condition" (Sheffield & Wood, 2011). A definition for ecological – or environmental – drought has been proposed to emphasize the negative effects of a water deficit on ecosystem functioning: an ecological drought is defined as"an episodic deficit in water availability that drives ecosystems beyond thresholds of vulnerability, impacts ecosystem services, and triggers feedback in natural and/or human systems" (Crausbay et al., 2017). Not all ecosystem services are affected to the same extent by water deficiency, but this definition emphasizes the multifactorial aspect of drought, whose effects depend on both abiotic and biotic components of ecosystems. This deficit of water is usually attributed to a lack of precipitation, but the importance of evaporation and transpiration in the reduction of available ground water should not be neglected. Vicente-Serrano et al. (2010) developed on purpose the Standardized Precipitation Evapotranspiration Index (SPEI), a metric that simultaneously accounts for precipitation and potential evapotranspiration (PET). The SPEI is now considered one of the best indices, among the numerous (>100) that have been proposed, for capturing the impacts of drought on agricultural, hydrological and ecological variables (Tian et al., 2018) as it is better able to reflect the temporal variability of river discharge and reservoir storage (Lorenzo-Lacruz et al., 2010). Furthermore, drought does not depend only on meteorological parameters and not all ecosystems react similarly to a lack of precipitation: the effects of drought may be buffered by ecosystem-level compensation between species and soil properties influence the quantity of water actually available for organisms. Therefore, climate indices may not capture accurately the actual stress experienced by plants and consumer organisms (Zang et al., 2020). Moreover, vegetation stress is not only influenced by moisture conditions and can be affected by soil type and events such as floods, wildfires, diseases or insect infestations (Zargar et al., 2011). Using a more integrative index of the biological effects of drought (at least on plant anabolism) might better document the potential impact of drought on ecosystem functions, such a biomass productivity and trophic interactions. The Normalized Difference Vegetation Index (NDVI) has been developed with this purpose, providing a standardized measure of plant productivity derived from the remote sensing of vegetation greenness (Kriegler et al., 1969; Rouse et al., 1974; Tucker, 1979). NDVI proves to be a relevant integrated measure of plant productivity in ecology (Yildirim et al., 2022), explaining for instance the spatial progression of migratory species returning to their breeding grounds (Thorup et al., 2017; Youngflesh et al., 2021) or between-year variation in productivity of common birds (Dubos et al., 2018).

Not all species breed at the same time. They are therefore not exposed to drought simultaneously and may not be most sensitive to drought at similar periods. Thus, it is important to consider the stage that is critical in determining the breeding success to be able to detect potential effects of climate variability (Bailey & Van De Pol, 2016). Drought can be quantified at various temporal grains to capture different characteristics of water resources and hydrological systems. Drought quantified over a year represents groundwater availability and reservoir storage, while shorter drought periods (e.g. at week scale) mainly affect soil moisture (Cady et al., 2019). The SPEI and NDVI also capture drought at different time scales, as drought reduces vegetation vigor over the long term and may restructure plant communities. These vegetation changes affect food availability for frugivores, granivores and especially insectivorous species feeding on caterpillars and larvae highly dependent on primary productivity, while soil moisture affects invertebrate abundance (Carroll et al., 2011).

Most research on the incidence of out of norm events has been carried out on individual-based monitoring of reproductive events (Marcelino et al., 2020), using for instance nest boxes (Marrot et al., 2017). But this approach limits the geographical and taxonomical scope and generality of the acquired knowledge. Broader scales are required to consider that the results obtained are general, applying to most common species, in most places over vast study areas.

In the present study, we used mist-net capture data from common passerine bird species, collected over more than 30 years at multiple sites across France. First, we aimed at understanding how bird productivity if affected by climate variability, particularly disentangling the influences of temperature, drought and primary production. We expected productivity to be positively influenced by higher temperatures (Meller et al., 2018), enabling an earlier onset of the breeding season, resulting in a higher breeding success, and more breeding attempts (Townsend et al., 2013). Empirical data seems to be concordant with this prediction as the evolution of observed productivity (Figure 1b) follows a similar pattern than temperature anomalies (Figure 1a), with cold years associated with the lowest productivity estimates. Yet, we expect extremely high temperatures to affect negatively productivity, because of heat stress reducing the nestling and fledging survival (Ross et al., 2017). Productivity is also expected to be reduced by drought (Figure 1b-c), impairing food supply, leading to smaller clutch size (Conrey et al., 2016; Glądalski et al., 2022; Skagen & Adams, 2012), lower fledgling rates (Carleton et al., 2019; Glądalski et al., 2022; Marrot et al., 2017) and decreased nestling survival (Conrey et al., 2016; Gardner et al., 2017; Marcelino et al., 2020; Skagen & Adams, 2012). We used two distinct drought indices, the SPEI and NDVI, based on meteorological conditions and vegetation greenness respectively, to disentangle a direct effect of weather from indirect effects mediated by primary productivity. Productivity might be more tightly related to the NDVI, as primary productivity is the main predictor of food supply for most species. Then, we analyzed how the sensitivity of productivity to climate variability depends on the life-history traits of species. We predicted that species with a different migration status to react differently to climate variabilities (Telenský et al., 2020). Indeed, while an earlier spring onset favors productivity in resident species, long-distance migrants are less flexible and are at a higher risk of trophic mismatch.

Table 1: Table summarizing the main predictions for our research questions

Research question	Environmental variable	Hypothesis
To what extent is productivity affected by climate variability?	Temperature anomalies	• Positive relationship with productivity (Meller et al., 2018) under a temperature threshold • Deleterious effects for out of norm conditions (extreme heat)
	SPEI	• Negative effect of drought on primary productivity → lower food supply → lower bird productivity (Glądalski et al., 2014; Skagen & Adams, 2012) • NDVI more tightly related to productivity than SPEI
	NDVI	
How does the response vary between life-history traits?	Migration status	Long-distance migrants more strongly affected because of higher risk of trophic mismatch (Ross et al., 2017) and competition with resident species
	Number of broods	Multi-brooded species benefit more from prolonged breeding seasons in warmer springs than single-brooded species (Halupka & Halupka, 2017)
	Habitat	Species living in open habitats and species that rely heavily on water (aquatic species) more strongly affected by drought
	Thermal range (STI; Moussus et al., 2011)	Species with a wider thermal range less impacted because more resilient to temperatures variations (Jiguet et al., 2006)

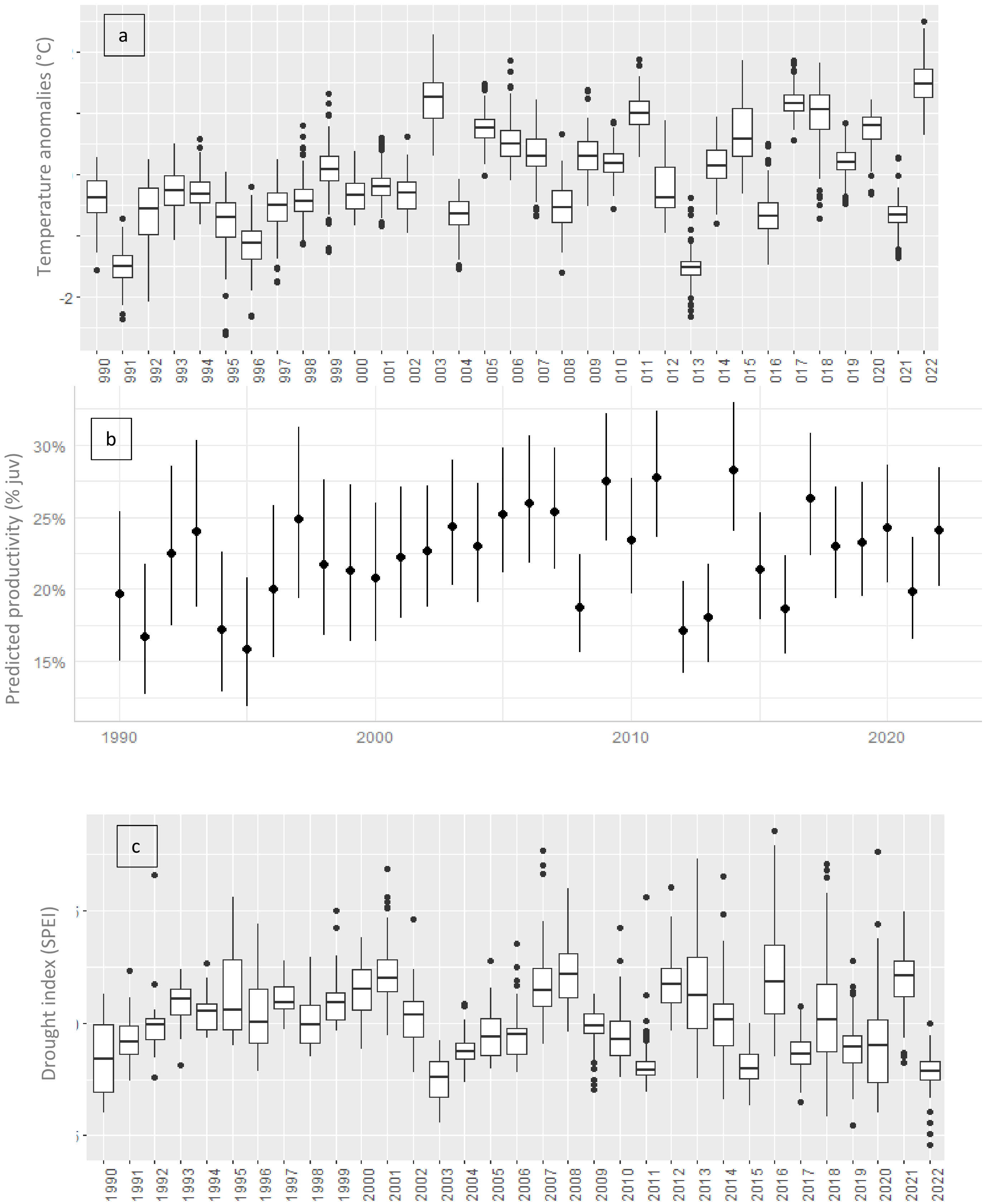


Figure 1: Evolution of drought (a) and temperature anomalies (c; difference with local average temperature) in capture sites, and productivity (b; ± sd) predicted from the data using *glmmTMB* and *ggpredict*

MATERIAL AND METHODS

Bird ringing data

We used data collected by the French Constant bird ringing Effort Sites (CES) scheme, between 1989 and 2022. The monitoring design consists in 3 to 5 capture sessions with 3m-high mist-nets, conducted by skilled volunteers, during the breeding season, between beginning of May and mid-July. For a given CES site, the monitoring design is mainly fixed: same mist-net locations (mean ± sd: 12 ± 6), similar dates, same number and duration of capture sessions. The number of monitored sites range from 6 in 1989 to 154 in 2021 (Figure 2). Capture sites are scattered throughout France (Figure 3) in various habitats. Yet as capture sites are chosen by volunteer bird ringers, there is a selection bias in favor of wetlands (16% of sites) and areas with dense shrub layer (Crbpo, 2020; Dubos et al., 2018; Eglington et al., 2015) of protected areas, where bird abundance and productivity tend to be higher. Thus, capture sites are not representative of the diversity of habitats in France, but this bias reduces the inter-sites variability of productivity and still allows us to investigate the variability associated to climate variability.. Each captured bird is individually ringed and its age and species are recorded.

A total of 162 bird species have been captured, among which 48 have been consistently encountered in more than 10 sites with more than 30 individuals captured per year (Appendix 2). Only these 48 species have been used in the species-specific part of the analyses.

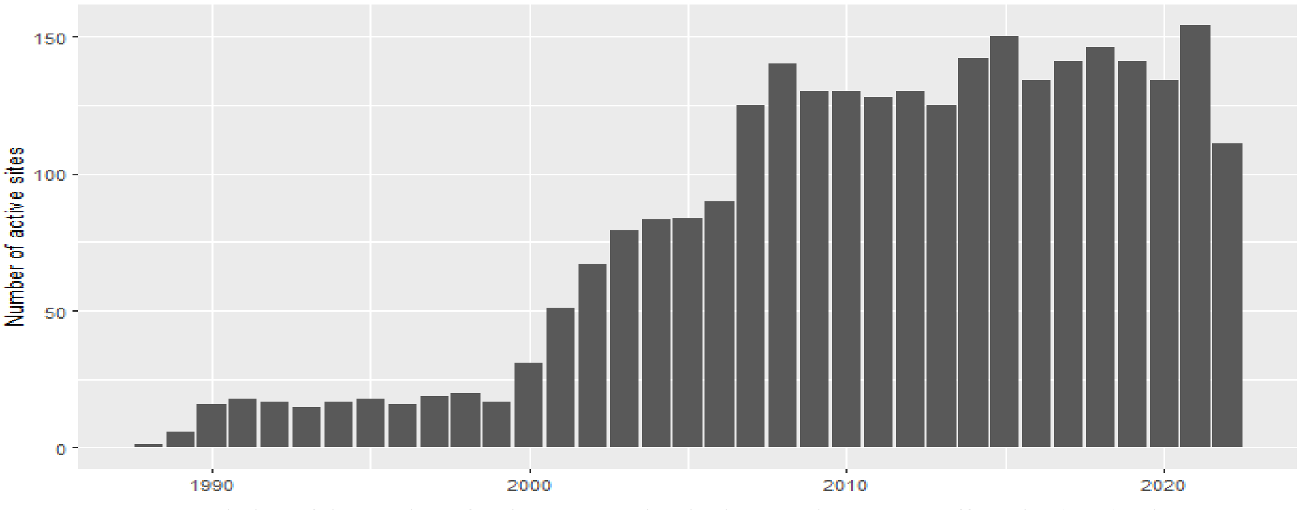


Figure 2: Evolution of the number of active capture sites in the French Constant Effort Site (CES) scheme

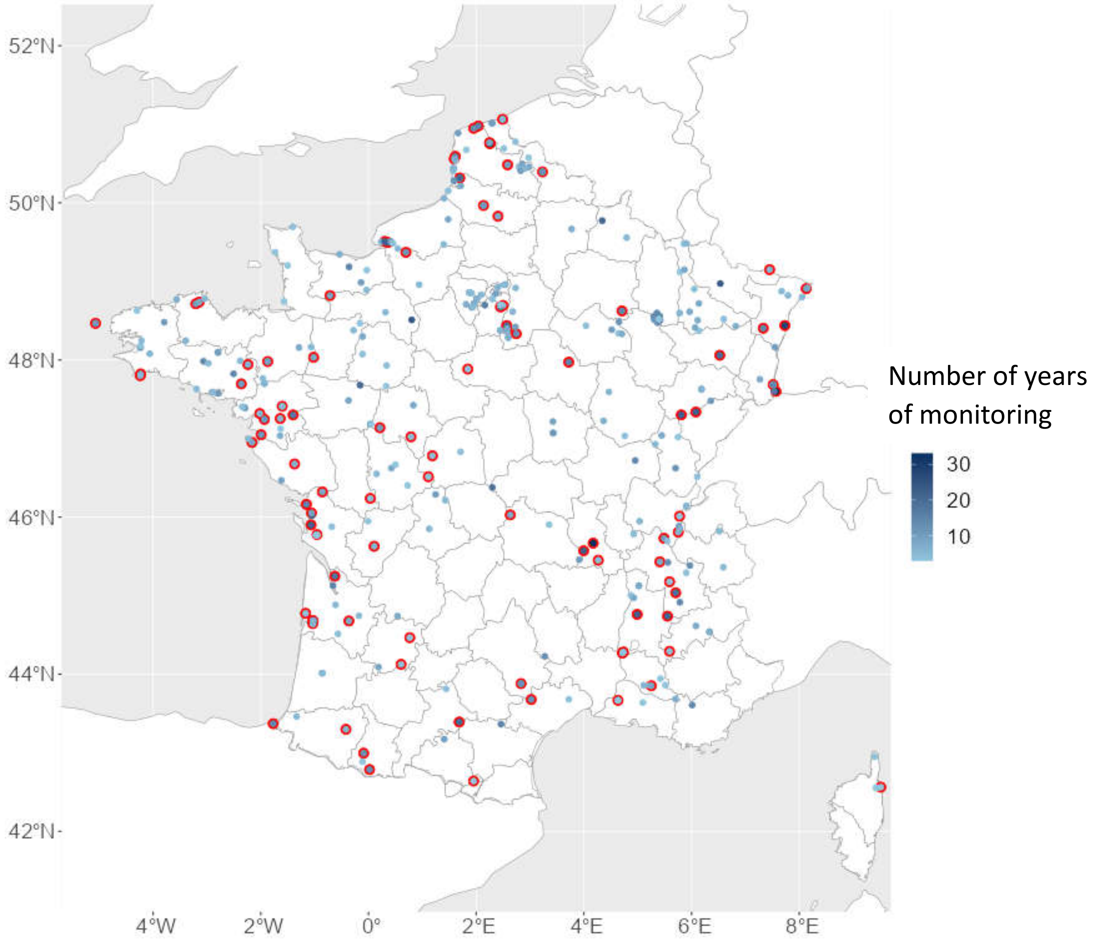


Figure 3: Location of sites monitored between 1989 and 2022. Sites that were active in 2022 are represented in red, and the shade of blue represents the number of years of monitoring

Definition of explanatory environmental variables

Meteorological data:

We used temperature data from the forecast model SAFRAN (Durand et al., 1993), provided by the French agency of meteorology (Meteo France). This model, based on an optimal interpolation method from climatologically homogeneous zones, provides daily values for meteorological variables such as temperature, precipitation and evapotranspiration.

We considered both local average temperature, to take into account between-site variability in temperature, and temperature anomalies (aT) as a measure of the interannual variation in temperature around the local average temperature (Van De Pol & Wright, 2009). A preliminary analysis revealed a non-linear dependence of productivity on local average temperature, with a rapid drop of productivity for sites hotter than 13°C (Appendix 4). To account for this major difference in productivity between sites, we classified sites in two categories: cool (≤ 13°C) and warm (>13°C) sites.

Temperature anomalies were first computed for each day as the difference between the temperature at a given day and the average temperature for this day over the 1989-2022 period. Daily temperature anomalies were then averaged either over the whole breeding period or shorter time windows covering the early and late breeding period.

To characterize drought, we used the Standardized Precipitation Evapotranspiration Index (SPEI ; Vicente-Serrano et al., 2010). The SPEI measures the difference between the water supply (i.e. precipitation) and demand (i.e. evapotranspiration). It is therefore a more physically realistic drought index than those only taking precipitation into account, and is easily comparable among sites and time scales (Beguería et al., 2014). We used the SPEI package (Beguería et al., 2014) to compute the SPEI for each site from precipitation and potential evapotranspiration data obtained from the SAFRAN model. As this index quantifies deviations from climatic water balance at each site over a defined period, *de facto* SPEI values are temporal drought anomalies. Dry conditions are characterized by negative values of SPEI, while positive values indicate relatively wet conditions. Values ranging from -1 to 1 are considered within the normal range of variation (Table 2) and a drought is considered extreme when SPEI < -2.

Table 2: Moisture categories associated with SPEI values (Potopova et al., 2015)

Moisture categories	**SPEI**
Extremely wet	≥ 2.00
Severely wet	1.50-1.99
Moderately wet	1.49-1.00
Normal	0.99 to -0.99
Moderate drought	-1.00 to -1.49
Severe drought	-1.50 to -1.99
Extreme drought	≤ -2.00

Average moisture per site was characterized by the water balance (BAL ; Vicente-Serrano et al., 2010), defined as the difference between average precipitations (P) and average potential evapotranspiration (PET):

$$BAL = P - PET$$

As for mean temperatures, mean spring water balance was computed for each site over the 1990-2022 period.

Extreme weather events:

As a biological response is often hard to measure, ECEs are often defined using relative threshold, the most commonly used being a 10% frequency of occurrence over some historical period (Van De Pol et al., 2017). Based on the distribution of our variables (Appendix 8), we decided to use a 5% threshold to define out of norm events: we considered a day as extremely warm when the daily temperature anomaly was within the 5% highest values of all sites within the 1990-2022 period, and an extremely dry day was defined by a SPEI within the 5% lowest values. It corresponds to a SPEI < -1.5, i.e. a severe to extreme drought (Table 1). We then summed the number of extreme days over the breeding season (whole period or divided into early and late breeding period).

Vegetation index:

The Normalized Difference Vegetation Index (NDVI) is a reliable indicator of net primary productivity (Kerr & Ostrovsky, 2003; Su et al., 2017) and allows to detect drought-driven deficiency in of primary production. It is the most common vegetation greenness index (Pettorelli et al., 2005; Yildirim et al., 2022) and is extensively used to characterize drought in ecology (Kchouk et al., 2022).

Based on remote sensing, the NDVI measures spectral reflectance to quantify vegetation greenness:

$$NDVI = \frac{NIR - VIS}{NIR + VIS}$$

where VIS is the spectral reflectance measurement acquired in the visible (red) and NIR the spectral reflectance acquired in the near-infrared region of the spectrum. As green leaves absorb visible light and reflect near-infrared light, the more green leaves a plant has, the higher the NDVI (Su et al., 2017).

We extracted NDVI values for each CES site using 16-day composite 1km spatial resolution MODIS (Moderate Resolution Imaging Spectroradiometer), downloaded from *Aρρ*EEARS (https://appeears.earthdatacloud.nasa.gov/). Low quality values were excluded based on the "usefulness" information of the quality assurance (QA) provided, as in Kern et al. (2016) . Most of the time, low quality values are due to clouds, as the NDVI is a remote sensing index based on satellite images. Therefore, the low quality data excluded were mainly in the Northwestern part of France, which may have led to a spatially biased data selection. After this first data selection, 15% of NDVI values had been excluded. To maximize the number of NDVI values for sites and years, we decided to replace missing values with the following criteria: when only 1 or 2 values were missing for spring at a site, we replaced missing values by the mean of the previous and following values. However, when more than 2 consecutive values, or when more than 40% of the values were missing for a spring at a site, we considered that the NDVI value was unreliable, and the corresponding site-year were excluded from analyses requiring NDVI values.

Time window:

To investigate the effects of meteorological variation on songbirds productivity, most studies have considered the whole breeding season (Dubos et al., 2018; Eglington et al., 2015; Gorzo et al., 2016; Marcelino et al., 2020; Meller et al., 2018; Saracco et al., 2022). Yet, the breeding period is divided in distinct stages: nest building, laying, rearing etc. The sensitivity of the reproduction process to meteorological conditions likely differ between these different stages. To identify the most sensitive stages, we tried to use the *Climwin* R package (Bailey & Van De Pol, 2016), using a sliding window to test various time windows. However, with our large dataset, computation time was too long to be able to test all combinations, and the first results were not biologically relevant. We therefore chose a simpler approach, based on the common consideration that the reproduction process can be divided in two main stages: reproduction initiation, egg-laying and incubation, which are relatively inexpensive in terms of energy expenditure; and the chick rearing stage, which is the most critical as it is the most energy demanding for both chicks and parents, and largely determines breeding success (and the strength of natural selection of breeding phenology). Hence, following Albright et al. (2010), we divided the breeding season in 2 distinct stages:

- the early breeding season, from the beginning of spring (mid-March) to hatching, corresponding to prelaying, laying and incubation,
- and the late breeding period, which corresponds to the period when the juveniles rely on their parents to feed them. We set the end of the late breeding season to mid-July, when the last capture sessions take place, as we do not have productivity data after this date.

The hatching date was first determined for each species from the fledging date, estimated as the peak of new juveniles captured, to which we subtracted the average rearing period (Storchová & Hořák, 2018) for each species. As the interspecific variation between hatching dates was small (sd = 5.3 days), we eventually decided to use the same date for all species to be able to include a greater number of species, as the fledging date could not be determined in case few individuals of a species are captured . The median hatching date, distinguishing the two breeding stages was May 14th. Across all species, the interannual variation of hatching date was also very limited (sd = 1.6 days) so we consistently used the same periods for each year, to standardize measures and facilitate the computation of environmental variables.

Relationship between variables:

We expect environmental variables to be correlated as droughts are often associated with heat waves and both precipitation and temperatures influence primary productivity. We did not detect strong collinearity preventing us from including them in a single model (Pearson pairwise correlation coefficients <0.6). Yet, to better understand the association between drought and temperature components, we performed a principal components analysis (PCA) on the 15 centered-reduced environmental variables derived from the SPEI, temperature and NDVI anomalies calculated over various time windows. We used the mean site conditions (BAL, mean NDVI and mean temperature) as supplementary variables.

Low (negative) SPEI values are associated with high temperature anomalies (Figure 4), meaning that drought events are often associated with eat waves. This is what happened in 2003 and 2022, two exceptionally warm and dry years (Julliard et al., 2004; Figure 1) as we can see on the Figure 4. B), while 2021 had a colder and wetter spring. However, if a high primary productivity described by positive NDVI anomalies is slightly associated with wetter conditions (positive SPEI values), it does not appear to be influenced by temperature. Thus, the NDVI does reflect broader processes than just weather variables.

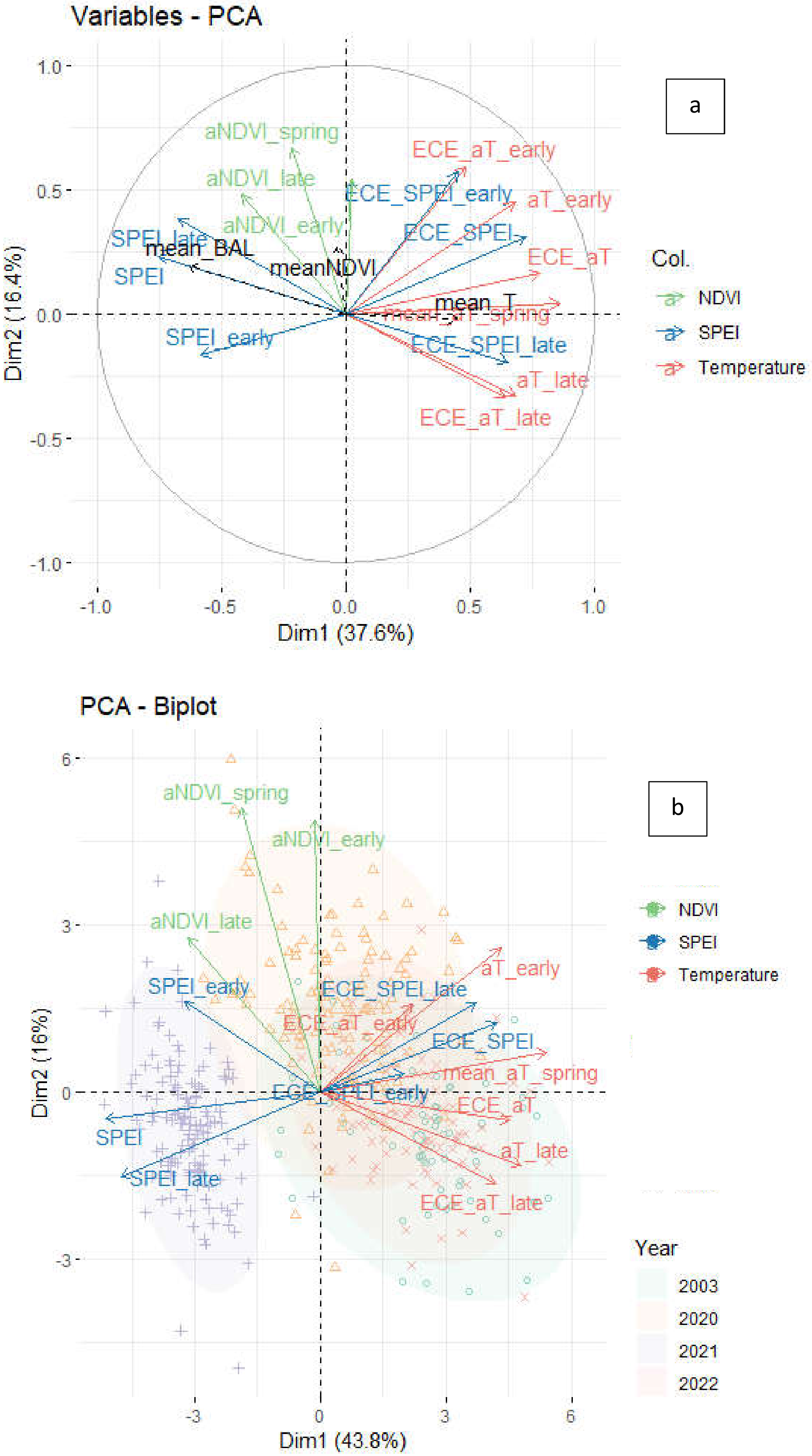


Figure 4: PCA plots with environmental variables. Variables derived from the NDVI are shown in green, from the SPEI in blue and from temperature in red. A) Variables represented in black represent the local average site conditions and were used as supplementary variables in the PCA

B) Observations for the years 2003, 2020, 2021 and 2022 are represented by the ellipses. These years were chosen to be representative of particularly warm and dry (2003, 2020 and 2022) or cold and wet (2021)

Species traits

Phenology:

Breeding phenology was estimated from the peak of juveniles fledging. The progressive emergence of juveniles throughout the breeding season, from no juveniles in early spring to a maximal number of juveniles captured in early summer, follows a sigmoid shape (Appendix 5). It was modeled in a Bayesian hierarchical random effects framework using Markov Chain Monte Carlo simulation (Cuchot et al., in preparation). Breeding phenology was estimated for species whose number of captured individuals was sufficient to ensure the convergence of the model (48 species). To evaluate the robustness of this method, we compared it to a method developed by Moussus et al. (2011), fitting GAMM to capture data to estimate species' phenological adjustment to temperature. For each species, we estimated the annual deviation from the species' reference breeding phenology and analyzed the correlation between the results of both methods. Pearson'scorrelation coefficients varied between species (Appendix 6); mean ± sd: 0.57 ± 0.27), and no method performed significantly better than the other across species. As the breeding phenology estimated with Cuchot's method seemed biologically relevant, we decided to use this one.

Life-history traits:

Species' response to meteorological variability between reproductive seasons may depend on their life history traits. Indeed, some groups of species may respond more to meteorological variability (either because they are more exposed or more sensitive to it). For instance, long-distance migrants are exposed to different climatic factors during their annual cycle, and they have been shown to be more strongly affected by climate variability than residents or short-distance migrants (Telenský et al., 2020). Diet could also be a factor influencing species' response to climate change, as strict insectivorous species (Visser & Gienapp, 2019) are more susceptible to suffer from trophic mismatch. These two traits are highly correlated, most long-distance migrants being strict insectivorous (Figure 5). Thus, to prevent collinearity we only included the migration status in our analyses. Indeed, it is a more comprehensive trait, accounting for a difference in diet but also in phenology, as migration is an adaptation to seasonality and environmental phenology. .. Previous studies have found that grassland species and avian communities from dry and semi-arid habitat tended to be more strongly affected (Albright et al., 2010; Cady et al., 2019). Therefore, we also included in our models the habitat, independent from diet and migration status (Figure 4), to compare species living in terrestrial habitat to aquatic species.

Species' sensitivity to temperature may also influence their responsiveness to climate variability (Addo-Bediako et al., 2000). It can be estimated from the thermal niche width, measured as a thermal specialization index (TSI), which corresponds to the difference between the thermal maximum and thermal minimum (Jiguet et al., 2006; Moussus et al., 2011). We also tested the effect of this variable on the response to climate variability, to see to what extent thermal tolerance plays a role in the effects of temperature and drought on productivity. The number of broods (Storchová & Hořák, 2018), associated with phenology and the length of the breeding season (Halupka & Halupka, 2017), may also affect productivity.

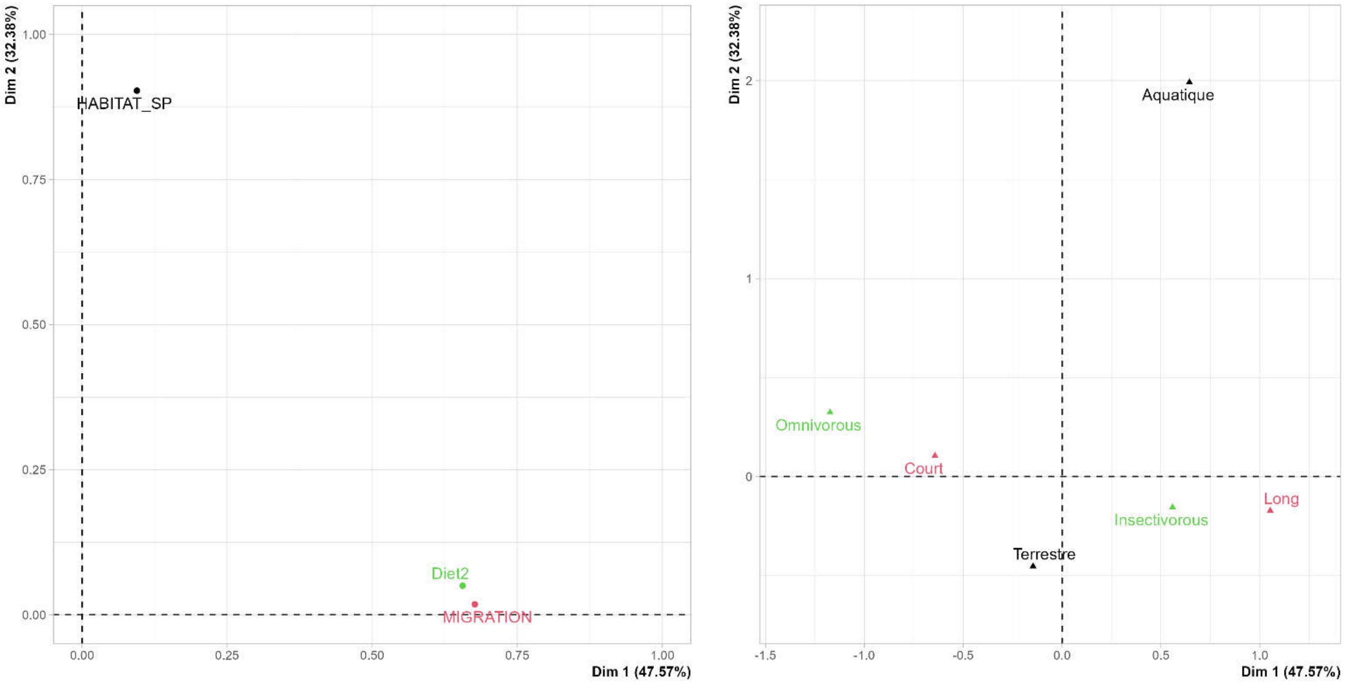


Figure 5: MCA plots with categorical life-history trait variables. Variables are presented in A) and categories within these variables are detailed in B)

I. Cross-species models

We used generalized linear mixed models (GLMM; glmmTMB package; Brooks et al., 2017) to assess the effects of yearly anomalies of temperature, SPEI and NDVI on productivity, and their interaction with local average conditions. Productivity, the response variable, was included as the total number of juveniles and adults captured at a given site and year, representing the proportion of juveniles and following a binomial distribution. We also included density to account for the major influence of negative density-dependence on productivity: following Telensky et al. (2020), we included density as a yearly anomaly of the total number of adults per species and per site.

We also added random effects to account for the random component of between-site variation and residual between-year variations. In this first step, we did not focus on interspecific differences but investigated how climate variability affected an average songbird. Therefore, we accounted for between-species variations by including species as a random effect.

Non-linear relationships between productivity and environmental variables are expected when optimal intermediate environmental conditions favor a high productivity. We used univariate generalized additive mixed models (GAMM ; mgcv package; (Wood, 2011) to explore non-linearities. In case non-linear relationships were found, we added quadratic terms to the GLMM..

- *Model selection procedure*

The influence of explanatory variables on productivity was inferred using a multi-model selection approach, based on Akaike's information critera corrected for small sample size: AICc = AIC + (2K (K + 1))/(n - K - 1), where n is the sample size, and K the number of parameters estimated in model (Burnham & Anderson, 2004) with the MuMIn R package (Bartoń, 2023). AIC (and AICc) takes into account how well the model fits the data, while favouring models with fewer parmeters (Symonds & Moussalli, 2011). The AIC weight (wm) quantifies the statistical support for a model relative to all other models considered, which can be interpreted as the probability that a given model is the best approximating model. We estimated the relative importance of an explanatory variable by summing the wm of models containing this variable. This predictor weight (w_i) corresponds to the probability that the predictor is a component of the best model (Symonds & Moussalli, 2011). We used the MuMIn function *dredge()* to build all possible models given a set of candidate explanatory variables. A quadratic effect was allowed for all environmental variables to allow for hump-shaped relationships, assuming optimality of intermediate environmental conditions (i.e. optimal for average, local conditions since all environmental variables were centered for the mean site value). The generated models were then compared by calculating the difference between their associated AICc (i.e. ΔAICc). The best fitting model was the one with the lowest AIC. In case the ΔAICc between the two best models was < 2, there was uncertainty about whether or not adding a parameter improved the fit of the model. In this case, we kept the most parsimonious model among the ones with ΔAICc < 2.

Ideally, we would have defined all possibly relevant environmental / meteorological conditions assumed to influence productivity, discarded collinear variables (by retaining the variable with the strongest a priori biological relevance), and would have constructed all possible models, so that any combination of explanatory variables would have been represented by one model in the selection procedure. Unfortunately, this full model selection has been impeded by too long computation time, which increases exponentially with the number of variables in the model. To test all possible combinations among environmental, several weeks would be needed.

To limit the number of potential models in competition, and keep computation time reasonable, we used a hierarchical approach on increasing modelling complexity, based on five sequential multi-model selections detailed below. We started with the analysis of the statistical support of the simplest and most trivial effects, such as the effects of average local climate (null model M0), and simple annual anomalies of meteorological conditions per site. Then, we progressively refined the modelling of retained explanatory variables by considering more complex effects, such as potential quadratic relationships, dependence on the stage of the reproductive season, interactions with average local conditions and differential effect of extreme conditions (assuming out-of-norm effects on productivity).

1. **Null model**: considers the effects of average local climates: mean NDVI, mean temperature (as categories), and mean BAL, and corrects for density dependence.

$$Productivity \sim \alpha + \beta_1.meanNDVI + \beta_2.meanT + \beta_3.BAL + \beta_4 density + \varepsilon_s + \varepsilon_y + \varepsilon_{sp} + \varepsilon_r \quad \text{(M0)}$$

where α is the average productivity, β_1 is the slope for the effect of local average NDVI *meanNDVI*, β_2 is the slope for the effect of local average temperature *meanT*, β_3 is the slope for the effect of local average water balance *BAL*, β_4 is the slope for the effect of local density anomaly, and ε_s, ε_y and ε_{sp} hold respectively for the random terms for site, year and species effects; ε_r is the residual variation.

To determine which meteorological variables among our set of candidate predictors best explains variations in productivity, we performed a model selection on models containing either:

2. a) **Meteorological variables for the whole breeding season**: SPEI and averaged temperature anomalies computed over the whole breeding season

2. b) **Meteorological variables for early/late breeding season**: SPEI and averaged temperature anomalies computed over the early and/or late breeding season

3. **Extreme climatic events (ECE)**: number of extremely dry or warm days during either a) the whole breeding season or b) the early and/or late breeding season

This model selection allows on the one hand determining at each step whether temperature and SPEI is a better predictor of variations in productivity, or if both variables explain part of the variation. This information is provided by the predictor weights (Table 2). On the other hand, the model selection gives us indications on the period during which meteorological variability most influences productivity and whether extreme events are more influential than the overall variation. Predictors included in the model with the lowest AICc enabled a better fit of the data and therefore better explained the variation in productivity.

After we have determined the relative importance of temperature and SPEI as indicators of heat waves and drought, we assessed whether accounting for variations of vegetation greenness by including NDVI anomalies improved the fit of the model and could replace the SPEI as a drought index. Similarly to the previous steps, we evaluated statistical support for NDVI anomalies computed over the different periods:

4. **NDVI**: NDVI anomalies computed over
    a) The whole breeding period
    b) The early/late breeding period

At the end of the selection process, we obtained a best model containing the most relevant environmental variables. This best model (BM) was used as a reference for the next steps of the analyses.

5. **Habitat**:

Species may react differently to drought depending on the habitat they live in. Indeed, terrestrial and aquatic habitats have different structures, which make them more or less likely to cope with drought and climate variability. Therefore, primary productivity may be affected differently in terrestrial and aquatic habitats, which can influence songbirds' productivity.

To test the effect of habitat on the average productivity, we added to the best model (BM) a variable describing the habitat of each site (terrestrial or aquatic) as a fixed effect. We also included interactions between habitat and the environmental variables to assess if the effects of these predictors on productivity diverged between terrestrial and aquatic habitats.

6. **Phenology**:

Phenological change in organisms is one of the most observed consequences of climate change. Phenological plasticity is linked to breeding success and species that are able to breed earlier in warmer, more precocious spring tend to have a higher productivity than less flexible species (Halupka et al., 2023; Moussus et al., 2011).

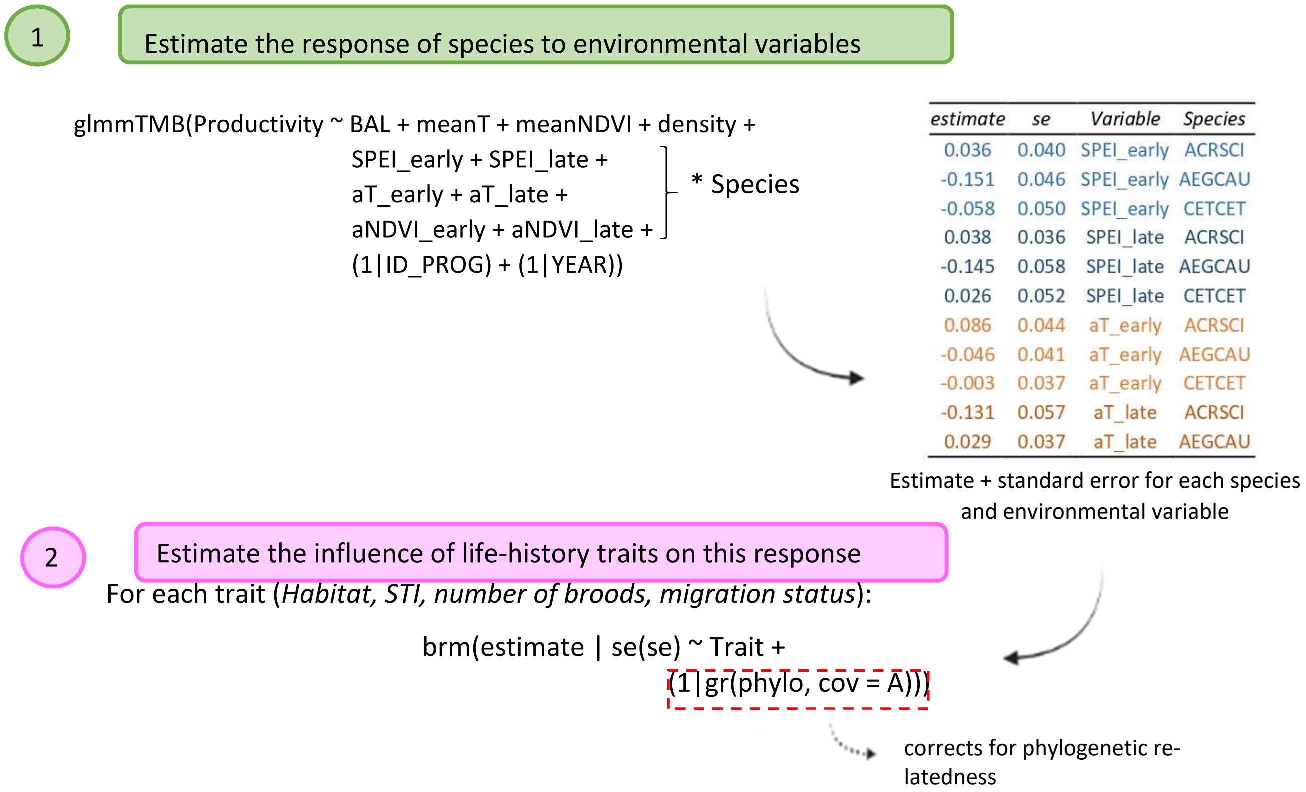
Our main objective in this study is to investigate the effects of climate variability on productivity, whether this effect is due to a shift in phenology or other co-occurring environmental anomalies. This is why we did not include phenology in the previous steps to determine which environmental variables influence productivity. Yet, temperature anomalies are one of the main drivers of phenological change (Moussus et al., 2011). Therefore, part of the effects of temperature anomalies on productivity evaluated in our previous models might be due to phenological flexibility. To evaluate the role of phenology in productivity's response to temperature and the residual influence of temperature when accounting for phenology, we added phenology as a fixed effect to the best model. This variable corresponds to the annual deviation for each species from its mean breeding phenology (across all sites, at national level): negative when breeding earlier than usual and positive in case of late breeding.

II. Role of life-history traits in the response to meteorological anomalies

Once we identified which environmental variables have an effect on the productivity of the average common songbird species, we tested for potential differences between species in their response to the main environmental variables.

To do so, we added a species fixed effect in interaction with the environmental variables of the best model (BM) identified at the end of the sequential multi-model inferences (Figure 5, step 1.). Thus, we could extract an estimate and standard error of the response of each species to the environmental variables.

These estimates per species were then used as a response variable in a second model using the *brms* R package (Bürkner, 2017) to estimate the influence of life-history traits on specific response to environmental variables (Figure 5, step 2.). Standard errors were included to account for the precision of the estimation for each species. Species that are more closely related might tend to show more similar responses to climate variability. Therefore, we corrected for phylogenetic relatedness by including a phylogenetic variance-covariance matrix obtained from a 50% consensus tree built with *phytools* (Revell, 2012) from a set of 1000 generated phylogenetic trees from Jetz et al. (2014).



```
glmmTMB(Productivity ~ BAL + meanT + meanNDVI + density +
                        SPEI_early + SPEI_late +         ⎤
                        aT_early + aT_late +              ⎬ * Species
                        aNDVI_early + aNDVI_late +        ⎦
                        (1|ID_PROG) + (1|YEAR))
```

estimate	se	Variable	Species
0.036	0.040	SPEI_early	ACRSCI
-0.151	0.046	SPEI_early	AEGCAU
-0.058	0.050	SPEI_early	CETCET
0.038	0.036	SPEI_late	ACRSCI
-0.145	0.058	SPEI_late	AEGCAU
0.026	0.052	SPEI_late	CETCET
0.086	0.044	aT_early	ACRSCI
-0.046	0.041	aT_early	AEGCAU
-0.003	0.037	aT_early	CETCET
-0.131	0.057	aT_late	ACRSCI
0.029	0.037	aT_late	AEGCAU

```
brm(estimate | se(se) ~ Trait +
                        (1|gr(phylo, cov = A)))
```

Figure 5: Steps of the meta-analysis performed to estimate the influence of life-history traits on the response of environmental variables. For visualization purposes, quadratic and interaction terms included in the GLMM are not shown here

RESULTS

Effects of environmental variability on productivity

Results of the selection model process are presented in Table 3. We decided to report results per environmental variable rather than per selection step to make the main results easier to stand out, as the selection process was just a way to get to the final best model while maintaining a reasonable computation time.

Effects of temperature

On average, across all species, temperature was the main environmental factor driving productivity. The effect of temperature anomalies was statistically supported in almost all steps of the selection process, with most covariates having an AIC weight of 1.00 (Table 3), meaning that they were in all best models.

Temperature anomalies have an overall positive effect on productivity.

Dividing the breeding season into an early and late breeding season significantly improves the model (Table 3, ΔAICc(M4 – M1) = 192.7). Temperature anomalies seem to have contrasting effects during these two periods. Warmer temperatures during the early breeding period are beneficial for productivity, and this is even more the case in cold sites in which temperature is a limiting factor (Figure 6a). Yet, this effect is not linear and the significant quadratic term indicates that a temperature optimum is reached: during the early breeding season, in cold sites, the beneficial effect of temperature stagnates for temperature anomalies higher than +2°C. In warm sites, the optimum is reached for temperature anomalies of +1°C (Figure 6a). In contrast, this positive effect of temperature is not found during the late breeding period. The influence of temperature variability is less pronounced than during the early breeding period with no apparent effect in warm sites and a slight decrease in productivity associated with increasing temperature anomalies in cold sites (Figure 6b).

Extreme events:

Using the number of ECEs rather than temperature anomalies or the SPEI did not improve the model, as the best model including the number of ECEs had a significantly lower AICc (Table 3, ΔAICc(M7 – M4) = 58.5). The effect of number of ECEs was similar (same direction and strength) to the effect of temperature anomalies. Hence, we did not detect a peculiar effect of out-of-norm high temperatures (exceptional heat waves effect) or extreme drought.

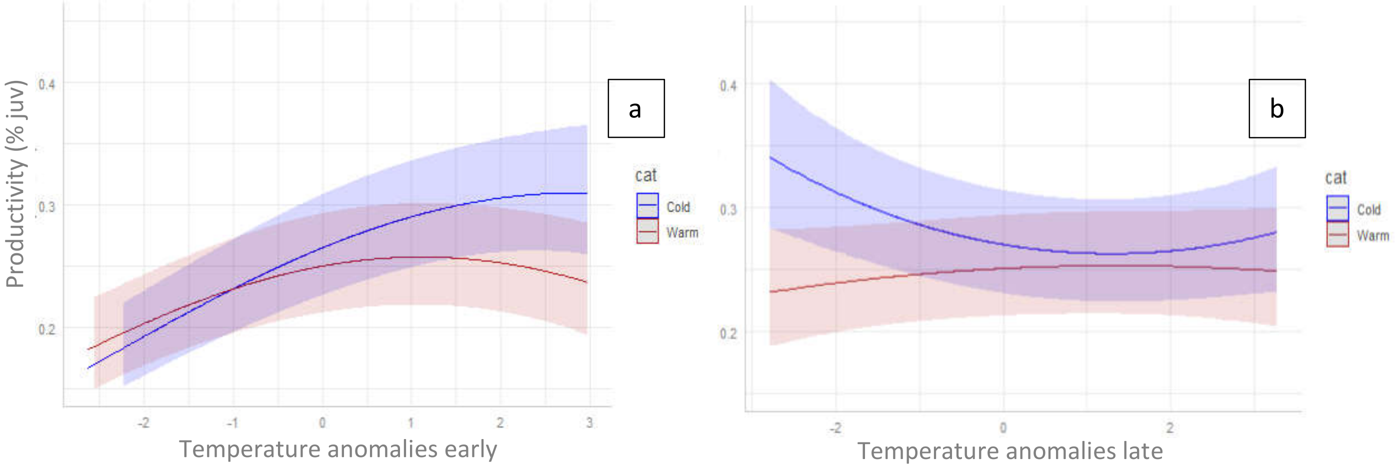


Figure 6: Effects of temperature anomalies on productivity during a) the early breeding season and b) the late breeding season, in interaction with the site temperature category.

These graphs – and the next ones – were obtained using the *ggpredict* function (*ggeffects* package), which computes predicted values based on the best model (MB) for levels of specified predictors. Colour ribbons represent 95% confidence intervals

Effects of drought

Contrary to temperature, we did not find support for a simple, linear effect of SPEI on productivity. The effect of early SPEI appeared to be rather non-linear as we found statistical support for quadratic terms (Table 3). As for temperature, we found a stronger effect of the SPEI during the early breeding season than during the late breeding season. Productivity was maximal for SPEI values within the normal range of variation (-1<SPEI<1), whereas productivity decreased for out-of-norm (both negative and positive) SPEI values associated to very dry or wet conditions for the local climate. However, we found opposite and counter-intuitive results for the late breeding period, with the highest productivity being observed at extremely dry or wet conditions. The SPEI seems to be involved in complex interactions with water balance (BAL), as we observe diverging responses to the SPEI in dry (BAL<0) and wet (BAL>0) sites (Figure 7), and with the mean site temperature (Figure 7), which makes results difficult to interpret.

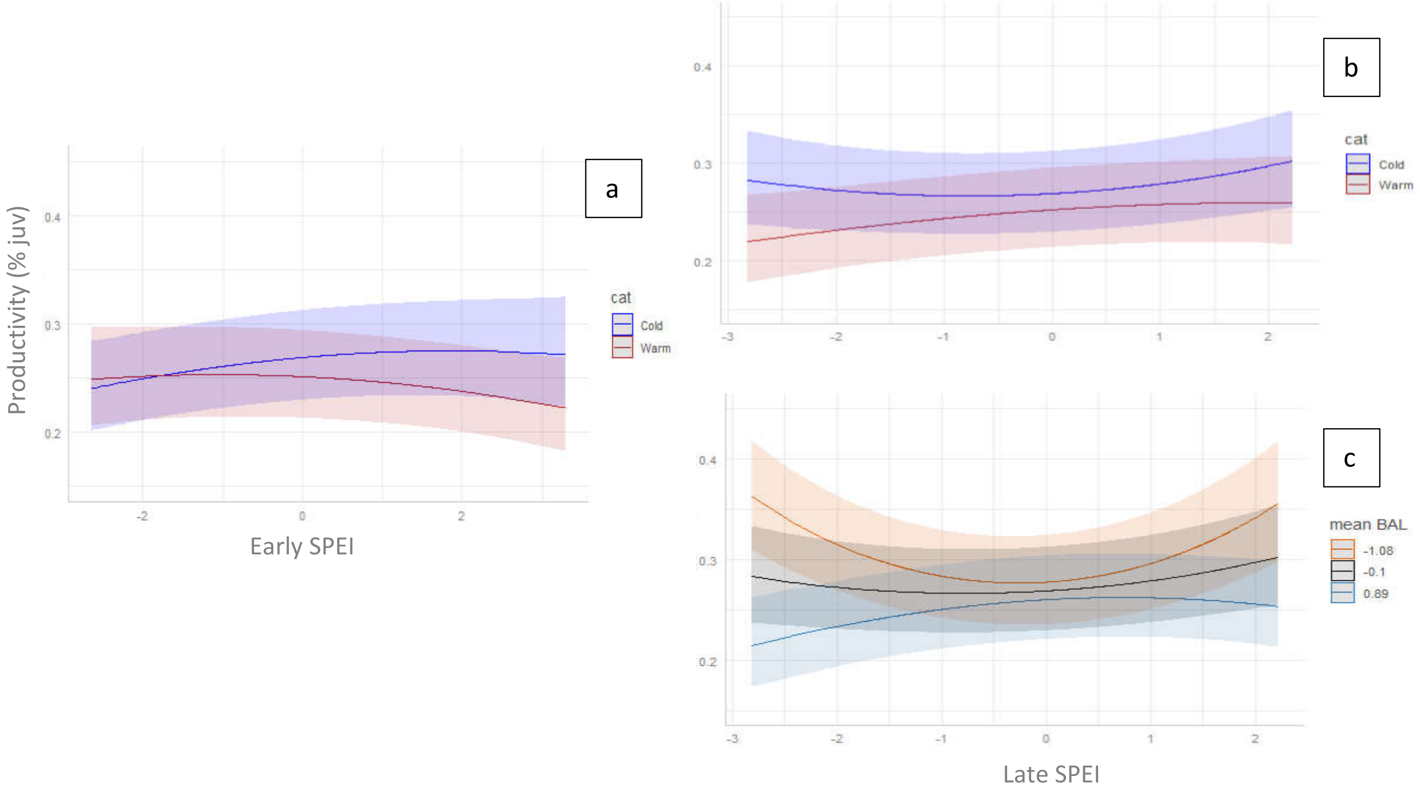


Figure 7: Effects of drought on productivity during a) the early breeding season and b-c) the late breeding season, in interaction with the site temperature category (a-b) and average site water balance (c).

Effects of primary productivity

Including the NDVI in the best model improves the fit of the model (Table 3, ΔAICc(MB – M4) = 36.6), meaning that primary productivity has an effect on productivity. The intensity of the effect is similar to SPEI (based on z-score values). We also found contrasting results during the early and the late breeding season. As expected, the higher the local primary productivity (NVDI anomaly), the higher bird productivity. In poorly productive sites (low mean NDVI values), an increase of the primary productivity (positive NDVI anomalies values) leads to a greater bird productivity. Whereas in sites that are already very productive on average, an increase in primary productivity has no effect on bird productivity (Figure 8).

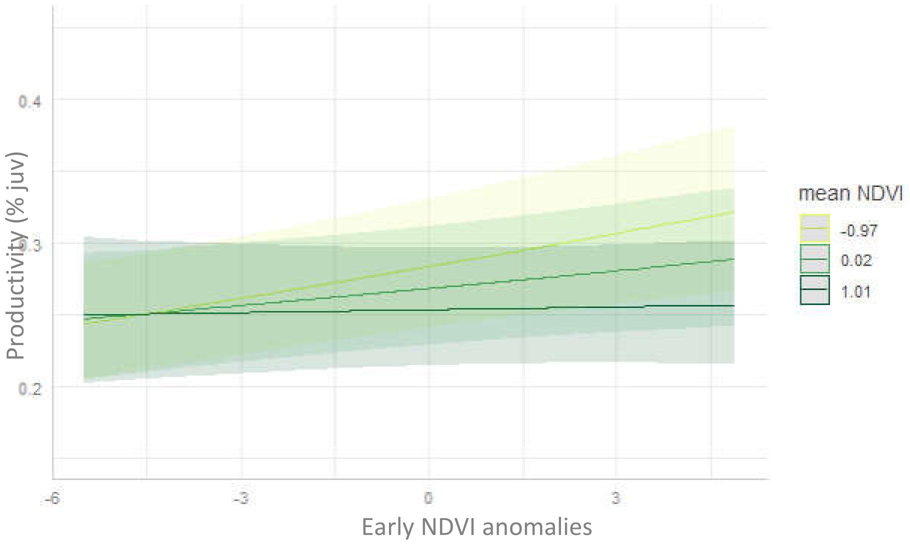


Figure 8: Effects of NDVI anomalies on productivity during the early breeding season in interaction with the average site NDVI

Critical approach of the best model

The best model among all tested combinations (Table 3) contained most predictors, with complex quadratic effects and interactions. These terms improved the fit of the model, as the deletion of one term of the model would lead to a significant decrease in AICc (> 2). Yet, results obtained for the late breeding season do not seem to have a biological meaning, with U-shaped responses to environmental variables (Figure 7c) meaning that productivity is the lowest for average environmental conditions. These results made us questionning the relevance of these terms we have approximated using quadratic effects. Predictions for some ranges of values were extrapolated to fit a quadratic effect to our data, and if it was better suited than a linear effect, it may not be sufficient to accurately estimate the whole range of variation.

Influence of habitat

Productivity also varied between habitats, and including an additive habitat effect to the best model improved the fit (ΔAICc = 15.5). The effect of some environmental on productivity also differs between terrestrial and aquatic habitats (Figure 9): while mean water balance (BAL) had no effect on productivity in terrestrial habitats, in aquatic shrubs an increase in water availability (BAL >0) significantly improves productivity (Figure 10).

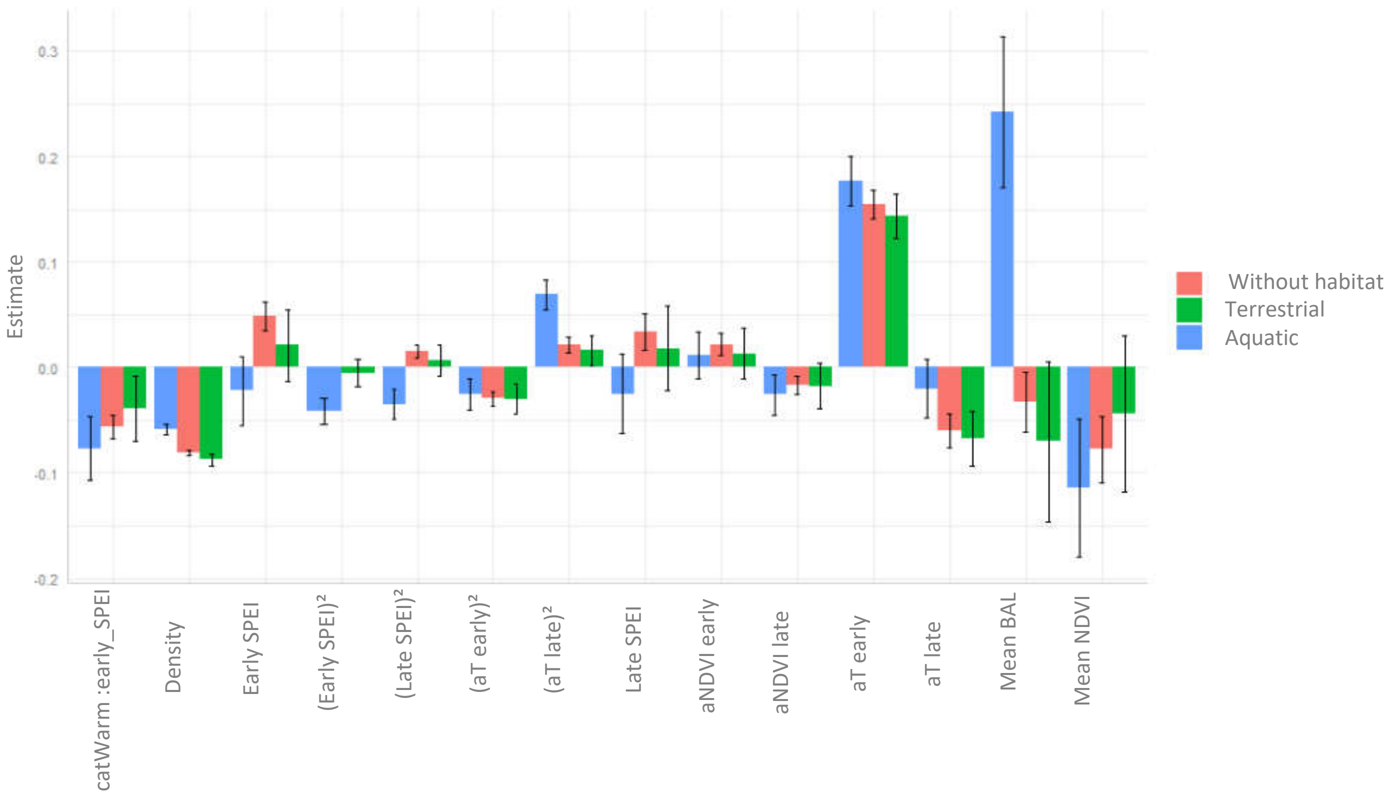


Figure 9: Estimates (± se) of the response of productivity to environmental predictors (x axis), without accounting for habitat (pink bars), in terrestrial habitats (Green bars) and aquatic habitats (Blue bars).

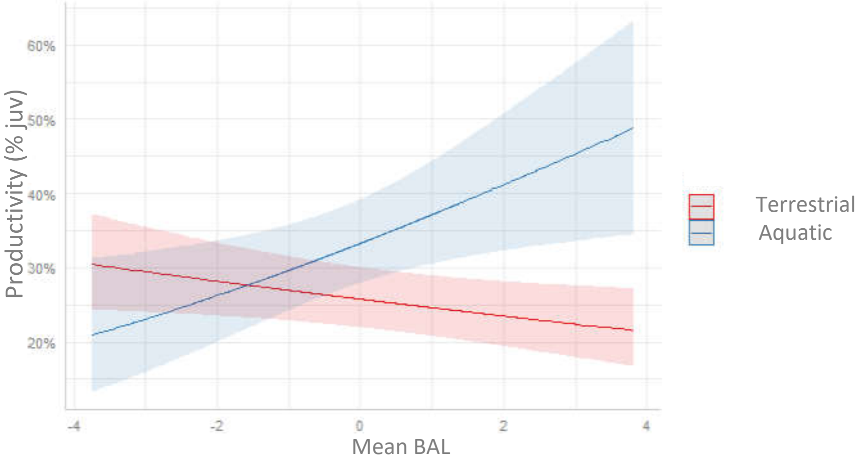


Figure 10: Effects of average site water balance on productivity in terrestrial and aquatic habitats

Influence of phenology

As expected, the earlier the reproduction (negative phenological anomaly in Fig. 10), the higher the productivity. The intensity of the phenological effect is similar to temperature anomalies during the early breeding season (similar z values) and adding phenology to the model greatly improved the fit to the data compared to without accounting for phenology (ΔAICc = 150).

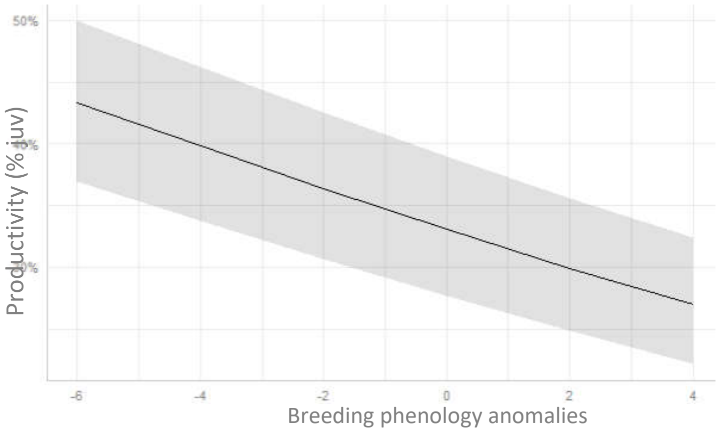


Figure 11: Effects of phenological change on productivity

Differences between groups of species

Our meta-analysis revealed that long-distance migrants showed a stronger response to climatic events during the early breeding season than resident species. They were more affected by drought: the slope of their response to SPEI was more pronounced, which means that negative values of SPEI (dry conditions) were associated to lower productivity (Figures 12c-13b). The response to temperature variations did not significantly differ between migration statuses, but long-distance migrants tended to be slightly more negatively affected by warmer temperatures during the early breeding period. As their breeding phenology is less flexible than in resident species, they suffer more from trophic mismatch and might not be able to avoid the negative effects of drought on their trophic resource by reproducing earlier. However, we did not observe differences between migration statuses during the late breeding period as long-distance migrants have already arrived at their breeding sites and experience the same weather conditions as resident species.

In contrast, differences between terrestrial and aquatic species were more pronounced during the late breeding period, when aquatic habitats may dry up because of a lack of precipitation associated with high temperatures. We therefore observe a negative response to drought for aquatic species during the late breeding period, whereas terrestrial species are less strongly affected. However, our meta-analysis revealed that aquatic species benefited more from high temperatures than terrestrial species.

Furthermore, the response to early NDVI anomalies varied according to number of broods species are able to produce (Figure 12e). The productivity of multi-brooded species increased when the environment was more productive (positive NDVI anomalies), whereas single-brooded species did not respond to varying primary productivity (Figure 13d). In favorable environmental conditions, multi-brooded species are more susceptible to successfully raise two broods, which improves productivity. In contrast, when primary productivity is low, they might attempt to breed only once as conditions are more difficult and there is less food supply for their offspring.

However, the STI did not influence species' responses to meteorological variations.

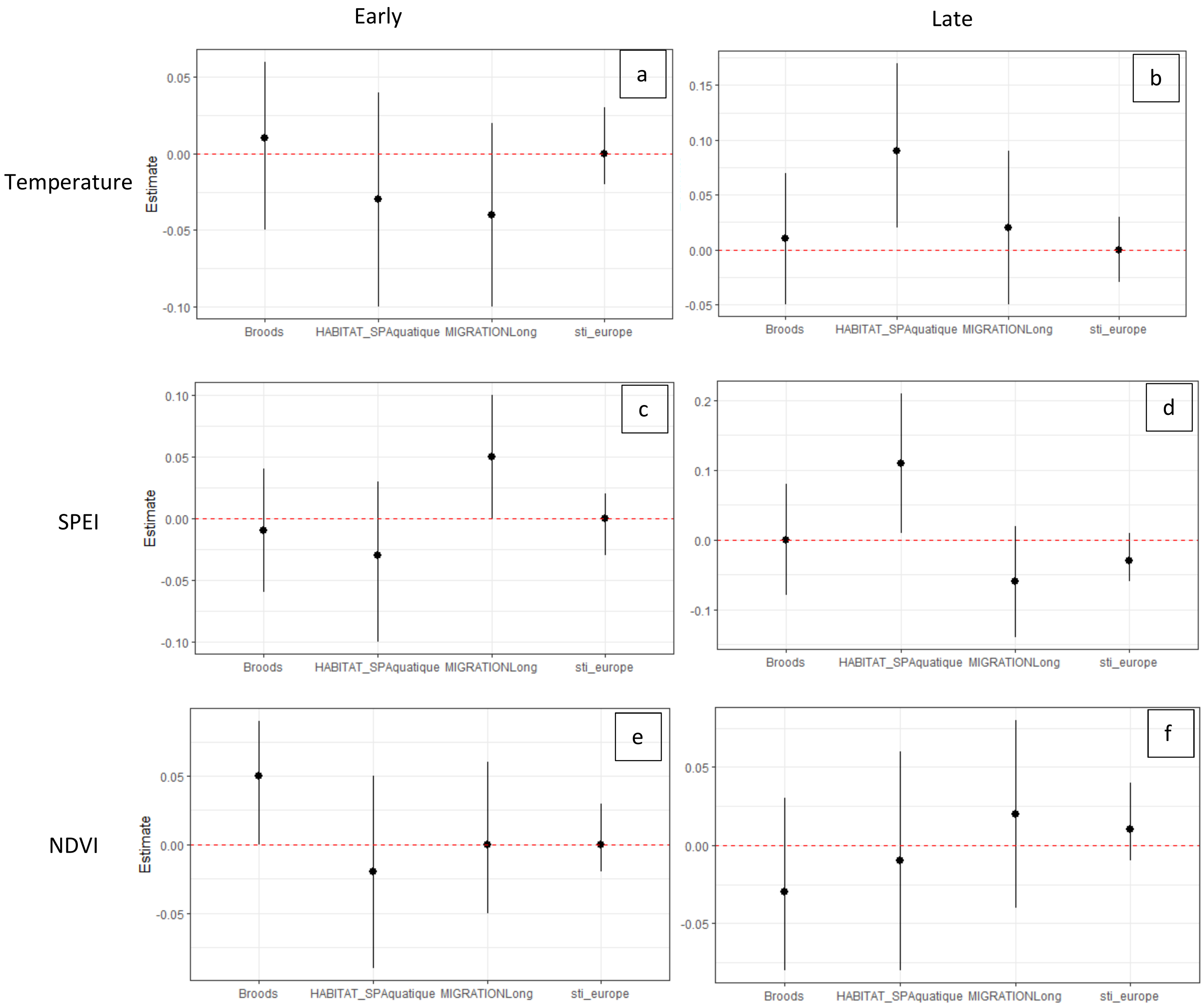


Figure 12: Differential responses of life-history traits to climate variability.
These graphs represent the estimates (±se) obtained for each environmental variable in the meta-analysis using the

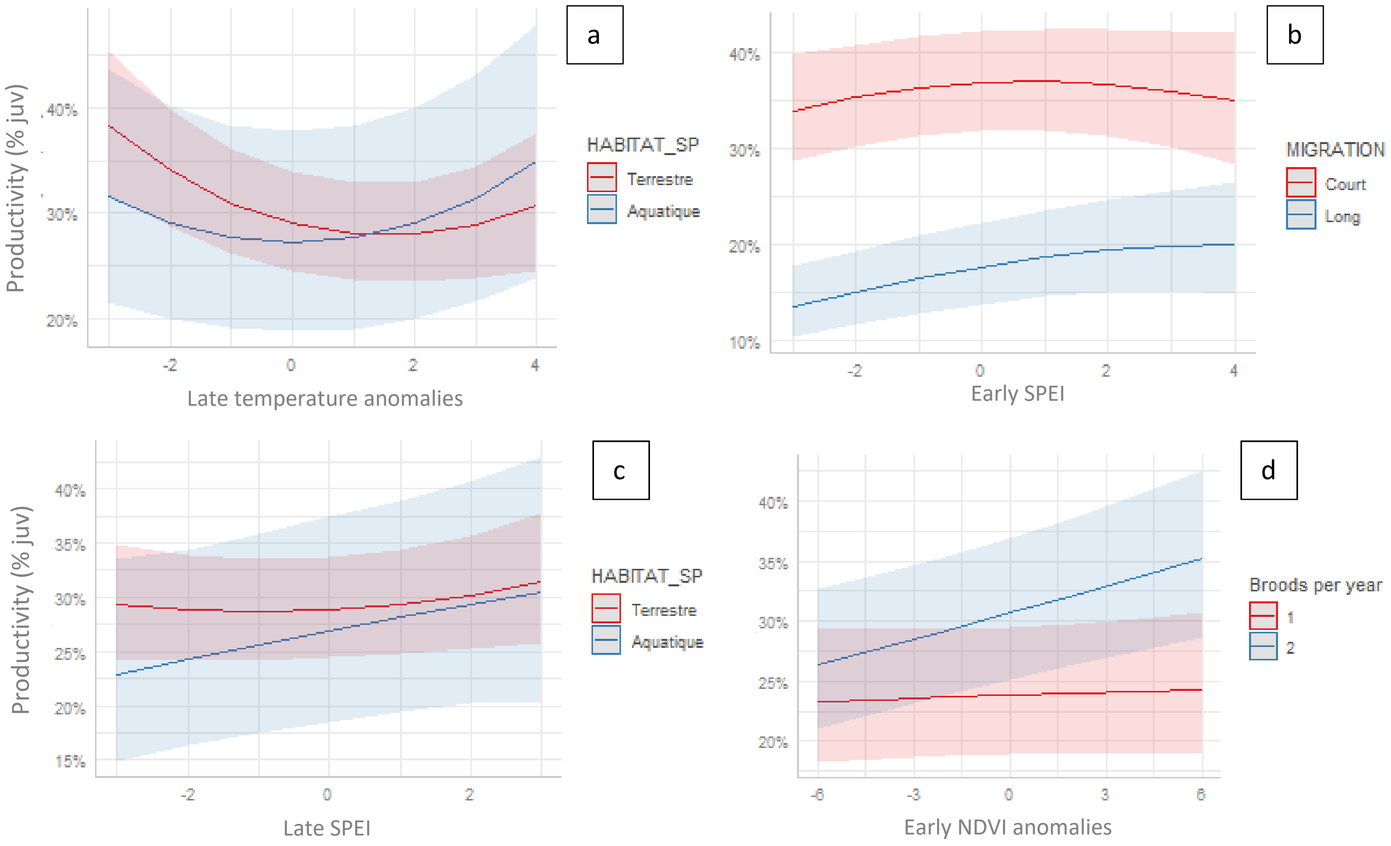


Figure 13: Effects of environmental variables on productivity for the different life-history traits that differed significantly in their response

Table 3: Summary of the best models selected at each step. Covariates' cumulative AICc weights are indicated in brackets and variables whose w(AICc) = 1 appear in bold. ΔAICc corresponds to the difference with the AICc of the best model (BM), and ΔAICc step corresponds to the difference with the best model identified within the selection step. Variables included in the null model are not represented here as they were common to all models

ID	Model	Temperature	SPEI	NDVI	AICc	ΔAICc	ΔAICc step
M0	**Null**				109050.5	282.2	
M1	**Meteo spring interactions + quadratic**	**aT** + aT^2 + cat:aT (1.00) + (0.97) + (0.80)	**SPEI + SPEI^2 + BAL:SPEI** (1.00) + (1.00) + (1.00)		108997.6	229.3	0
M2	**Meteo spring**	**aT** (1.00)			109020.8	252.5	23.2
M3	**Meteo spring interactions**	**aT** (1.00)			109024.5	256.2	26.9
M4	**Early/late + interactions + quadratic terms**	**aT early** + **(aT early)^2** + **aT late** + (aT late)^2 + **cat:aT early** + **cat:aT late** + cat:(aT late)^2 (1.00) + (1.00) + (1.00) + (0.96) + (1.00) + (1.00) + (0.94)	**(early SPEI)^2** + **(late SPEI)^2** + **BAL:(early SPEI)^2** + **BAL:(late SPEI)^2** (1.00) + (1.00) + (1.00) + (1.00)		108804.9	36.6	0
M5	**Early/late**	**aT early** + (aT late)^2 (1.00) + (0.73)	early SPEI (0.75)		108978.9	210.6	174
M6	**Early/late + interactions**	**aT early** + **cat:aT early** + **aT late** + **cat:aT late** (1.00) + (1.00) + (1.00) + (1.00)	early SPEI (0.90)		109010.1	241.8	205.2
M7	**ECE SPEI + best aT**	mean_aT_late + (mean_aT_early)^2 + (mean_aT_late)^2 + cat:mean_aT_early + cat:mean_aT_late + cat:(mean_aT_early)^2 + cat:(mean_aT_late)^2 fixed	early_nb_ECE_SPEI + **late_nb_ECE_SPEI** + BAL:early_nb_ECE_SPEI + BAL:late_nb_ECE_SPEI + cat:early_nb_ECE_SPEI + **cat:late_nb_ECE_SPEI** (0.99) + (1.00) + (0.79) + (0.69) + (0.77) + (1.00)		108863.4	95.1	0
M8	**ECE aT + best SPEI**	**early_nb_ECE_aTemp** + **late_nb_ECE_aTemp** + **(early_nb_ECE_aTemp)^2** + **cat:early_nb_ECE_aTemp** + **cat:late_nb_ECE_aTemp** (1.00) + (1.00) + (1.00) + (1.00) + (1.00)	early_SPEI + late_SPEI + (early_SPEI)^2 + (late_SPEI)^2 fixed		108977.4	209.1	114
M9	**Early/late ECE + interactions**	**early_nb_ECE_aT** + **late_nb_ECE_aT** + **cat:early_nb_ECE_aT** + **cat:late_nb_ECE_aT** (1.00) + (1.00) + (1.00) + (1.00)	late_nb_ECE_SPEI (0.89)		109010.1	241.8	146.7
M10	**Early/late ECE**		late_nb_ECE_SPEI (0.97)		109044.4	276.1	181
M11	**ECE**				109050.5	282.2	187.1
MB	**Early/late + interactions + quadratic terms with NDVI**	aT early + (aT early)^2 + aT late + (aT late)^2 + cat:aT early + cat:aT late + cat:(aT late)^2 fixed	(early SPEI)^2 + late SPEI + (late SPEI)^2 + BAL:(early SPEI)^2 + BAL:(late SPEI)^2 + cat:early SPEI	aNDVI_early + aNDVI_late + meanNDVI:aNDVI_early	108768.3	0	0
M12	**Early/late + interactions NDVI**	early aT + cat:aT early + late aT + cat:aT late + (late aT)^2 fixed	early SPEI (0.75)	aNDVI early (0.99)	108905.1	136.8	136.8
M13	**Early/late NDVI**	early aT + late aT + (late aT)^2 fixed	early SPEI (0.66)	**aNDVI early** (1.00)	108954.8	186.5	186.5
M14	**Meteo spring NDVI**	aT fixed		aNDVI (0.79)	109018.2	249.9	249.9
M15	**Meteo spring interactions NDVI**	aT fixed		aNDVI + meanNDVI:aNDVI (0.90) + (0.72)	109020.5	252.2	252.2

Table 4: Effects of environmental predictors on productivity. These estimates were obtained from the best model (BM)

	Parameter	*Estimate*	*Std. Error*	*z value*	*p-value*		*Estimate*	*Std. Error*	*z value*	*p-value*
Fixed effects										
Null model	mean_BAL	-0.0489	0.0317	-1.54	0.1230					
	catWarm	-0.1244	0.0644	-1.93	0.0532					
	meanNDVI	-0.0777	0.0315	-2.47	0.0137 *					
	density	-0.0811	0.0024	-33.38	< 2.00e-16 ***					
	Early					**Late**				
SPEI	early_SPEI	0.0331	0.0155	2.14	0.0321 *	late_SPEI	0.0308	0.0181	1.7	0.0887
	$(\text{early\_SPEI})^2$	-0.0069	0.0066	-1.06	0.2895	$(\text{late\_SPEI})^2$	0.0051	0.0074	0.69	0.4889
	catWarm : early_SPEI	-0.0511	0.0127	-4.01	5.98e-05 ***					
	BAL:early_SPEI	-0.0014	0.0077	-0.19	8.46e-01	BAL : late_SPEI	0.0003	0.0082	0.04	0.9664
	BAL:$(\text{early\_SPEI})^2$	0.0169	0.0040	4.22	2.40e-05 ***	BAL : $(\text{late\_SPEI})^2$	-0.0380	0.0046	-8.23	< 2e-16 ***
Temperature	aT_early	0.1512	0.01336	11.32	< 2e-16 ***	aT_late	-0.0580	0.0160	-3.62	0.0003 ***
	$(\text{aT\_early})^2$	-0.0265	0.0076	-3.48	0.0005 ***	$(\text{aT\_late})^2$	0.0207	0.0077	2.69	0.0071 **
	catWarm : aT_early	-0.0802	0.0115	-7	2.60e-12 ***	catWarm : aT_late	0.0742	0.0141	5.28	1.32e-07 ***
	catWarm : $(\text{aT\_early})^2$	-0.0061	0.0083	-0.74	4.57e-01	catWarm : $(\text{aT\_late})^2$	-0.0293	0.0080	-3.65	0.0003 ***
NDVI	aNDVI_early	0.0209	0.0104	2.01	0.0440 *	aNDVI_late	-0.0174	0.0085	-2.04	0.041 *
	meanNDVI : aNDVI_early	-0.0175	0.0041	-4.23	2.35e-05 ***					
Random effects										
		Variance	Std.Dev.							
ID_PROG	(Intercept)	0.27783	0.5271							
YEAR	(Intercept)	0.01783	0.1335							
ESPECE	(Intercept)	0.99631	0.9982							

DISCUSSION

This study assessed the effects of climate variability on productivity. The most salient effect of meteorological conditions on productivity was the dominating positive influence of temperature: the warmer springs, the higher the offspring production. This is congruent with previous studies such as Meller et al. (2018) who found a positive relationship between spring temperature and productivity in 20 songbird species living at Northern latitudes, and Hoover & Schelsky (2020) who showed that warmer temperatures in early spring enhanced productivity by favouring an earlier breeding. McLean et al. (2022) also identified temperature as the most important contributor to breeding productivity, with 48% of temporal changes in offspring number was attributed to temperature. Yet, the timing of warming is key to determine the effect on productivity: during the early breeding season (before egg hatching), warmer temperatures improve productivity, probably because an earlier spring allows earlier breeding and a greater number of breeding attempts. However, unlike Meller et al. (2018), we did not find a linear relationship between temperature and productivity. Our models rather suggested that productivity reached a plateau, for temperature anomalies greater than +2°C in cold sites (Figure 6a). At warm sites, the positive effect of temperature is weaker, with a plateau reached for temperature anomalies of +0.5°C. This difference between warm and cold sites might explain that Meller et al. did not find a quadratic relationship, as the sites studied were located at higher latitudes, where temperatures are colder: the productivity plateau may not be reached, even during warm events. Overall, there was no major effect of temperature during late spring, only a slight declining trend of productivity with increasing temperature anomalies in cold sites. Other studies found more pronounced negative effects of warmer temperatures during the late breeding period: Albright et al. (2010) found consistent negative responses of productivity to extreme weather occurring in the late breeding period. Temperatures in the late breeding season are indeed higher, and the heat stress caused by extremely high temperature may affect nestlings survival, leading to a lower breeding productivity (Sergio et al., 2018).

The tighter relationship of breeding productivity with early spring temperature, also found by Telensky et al. (2020), may be explained by the importance of phenological flexibility. When spring arise earlier (i.e. earlier warming), most species achieve to breed earlier, and benefit from this earlier breeding, either because warmer conditions reduce the cost of reproduction, or because earlier breeding allows a better match between the peak of energetical demand for chick rearing and the seasonal peak of invertebrate prey production. Indeed, productivity was strongly influenced by breeding phenology (cf. phenology effect), what supports the hypothesis that part of the gain in productivity in warmer years is attributable to beneficial earlier breeding (Hoover & Schelsky, 2020), rather than to a reduced cost of breeding throughout the breeding season. Whereas high temperatures occurring after nestlings have hatched will not influence breeding phenology and might not favor primary productivity as in early spring. Aquatic species were less negatively affected by heat during the late breeding season than terrestrial species (Figure 13a). Terrestrial species might be more sensitive to heat stress, or more exposed in case of species living in open and agricultural landscapes. Yet, these results may be influenced by the high number of terrestrial species included in our dataset compared to aquatic species (Appendix 3). Analyzing terrestrial habitats in more details would allow to distinguish species living in forest and therefore less exposed to extreme heats, from species living in more open areas.

However, we did not detect significant influence of the STI, the number of broods and migratory status on species' response to temperature, contrary to what was expected (Halupka & Halupka, 2017; Ross et al., 2017). It may be because of a lack of statistical power, and including more species – as in Halupka & Halupka (2017) – might allow us to detect differences. Otherwise, as France is located at intermediate latitudes, warmer temperatures might not allow a longer breeding period as much as at higher latitudes: warm temperatures in the early spring may allow an earlier onset of breeding, but the increased occurrence of heat waves and droughts in the late spring could constrain the end of the breeding season. Thus, the breeding season would shift earlier, but not be longer.

Beside the effect of temperature, precipitations also generated interannual variation in productivity. Indeed, the two considered drought indices (SPEI and NDVI) explained some variation in productivity, even in models adjusted for the effect of temperature. During the early breeding period, we found that productivity was maximal for SPEI conditions slightly wetter than on average. Hence, as well as excessively humid years, drought had a negative impact on breeding productivity, as expected (Carleton et al., 2019; Conrey et al., 2016; Gardner et al., 2017; Glądalski et al., 2014; Marcelino et al., 2020; Marrot et al., 2017; Skagen & Adams, 2012). This effect was stronger for long-distance migrants. It had already been shown that these species are negatively affected by climate variability to a greater extent that resident species (Albright et al., 2009; Telenský et al., 2020), due to their limited flexibility of breeding phenology (constrained by their fixed, photoperiodic timing of initiation of the return trip to breeding grounds (Dawson et al., 2001). As they arrive later to their breeding ground, an early drought may have already affected vegetation, reducing the available food supply. Thus, even if a different response to temperature would be expected between migration statuses because of phenology mismatch (Jones & Cresswell, 2010), we only detected a different response to SPEI reflecting the influence of an early drought on long-distance migrants.

with grassland species and avian communities from dry and semi-arid habitat being more strongly affected (Albright et al., 2010; Cady et al., 2019).

The NDVI gave similar results for the average songbird, with vegetation greenness anomalies being positively correlated with productivity in low productive sites: droughts affecting vegetation greenness are associated with a lower breeding productivity. Even if disentangling the effects of heat waves and drought is not easy, drought seems to either affect productivity by counterbalancing positive effects of warm springs, or accentuate the negative effects of heat waves. Therefore, Albright et al. (2010) showed that while co-occuring droughts and heat waves strongly affect bird communities, droughts with relatively cool temperature or heat waves with relatively abundant precipitation have a weaker influence on avian abundance.

However, unexpectedly, we dit not find an impact of drought during the late breeding period – i.e. the most critical stage of reproduction, when chick rearing requires maximal quality and quantity of food. Results were indeed biologically unexpected, and are to be considered cautiously. This may be due to complex interactions that we are not able to properly account for (e.g. more complex that two-way interactions or quadratic relationships). A drought occurring during the late breeding period may also not be as influential as temperature, as there is a lag in the response of primary productivity to drought and a drought occurring during chick rearing might have a greater influence afterwards. Albright et al. (2010) emphasizes the importance of July and August temperatures, which are generally the hottest of the year, on avian abundance. As the late breeding period we considered stops mid-July, we might miss an important period for population dynamics. Therefore, temperature and drought occurring after hatching might have a greater influence on the survival of fledging during summer than on breeding productivity.

Choosing the right time scale is indeed a key issue in analyzing biological responses to climate variability. In this study, we focused on spring weather as we expect spring temperature and precipitation to influence plant anabolism, and therefore food availability for songbirds (Smith et al., 2011), which is very likely to affect breeding success (Eglington et al., 2015). Winter precipitations may also influence primary productivity via groundwater storage, but we considered it to be negligible compared to soil moisture in the soil top layer (Entin et al., 2000), which also predicts invertebrates abundance (Carroll et al., 2011). Even though most studies considered weather conditions averaged over the whole breeding season(Dubos et al., 2018; Eglington et al., 2015; Gorzo et al., 2016; Marcelino et al., 2020; Meller et al., 2018; Saracco et al., 2022), we wanted to examine finer time windows to determine when passerine birds are most sensitive to heat and drought. This is why we divided the breeding season in two distinct periods based on a priori assumptions (Albright et al., 2010; Telenský et al., 2020), during which birds may have different needs. Weather signals during the early breeding season will influence laying dates (Bailey et al., 2022), while food (e.g. insect larvae) abundance after hatching will be a key parameter for nestlings survival. Accounting for environmental variables during the early and late breeding period separately rather than during the whole breeding period significantly improved the fit of the model (Table 3, ΔAIC(M14 – M13) = 63.4), showing that productivity is affected differently by the weather during these time periods. Considering multiple time windows allows to identify the 'best' possible window as well as potential co-occuring effects of short- and long-time weather signals acting on a trait (Bailey & Van De Pol, 2016). As the effect of weather signals can be complex and there is not much a priori knowledge about the period of highest sensitivity for passerine birds – which is species-specific (Cady et al., 2019) – we also wanted to use a systematic approach to identify the temporal windows of maximal sensitivity of productivity to each meteorological variable and for each species. We used the *climwin* R package (Bailey & Van De Pol, 2016), which uses a sliding window approach to vary the start and end time of the climate window used in the models, and then compare the models with an information criterion approach. However, due to our large dataset, computation time to test multiple time windows was too long, and results obtained for the first species were not biologically relevant. *Climwin* identified very short time windows (a few days), which is usually a sign of false positives: the package will always identify a climate window as "the best one", even if there is no climate signal in the dataset. *Climwin* offers an interesting approach and it would have been great to be able to apply this approach to more species, to identify the most appropriate time window to consider, allowing more precision in the prediction of responses to environment variability than with the larger time windows we considered. Applying *climwin* to groups of species rather than on single species might improve the statistical power, as this approach requires large datasets. Yet, in case of large interspecific variation in the responses to climate variability, we might not be able to detect a shared time-window of sensitivity.

The SPEI, contrary to other drought indices such as the Palmer's Drought Severity Index (PDSI (Kchouk et al., 2022; Yildirim et al., 2022); Palmer, 1965), offers a great flexibility in terms of definition of temporal grain (i.e., duration of the period over which it is computed) and temporal window (i.e., timing of drought with respect to calendar date). These characteristics made it the ideal candidate for our study as we wanted to consider various time windows. Our results reaffirmed the choice of the SPEI and the NDVI, that are also among the most widely used drought indices (Kchouk et al., 2022; Yildirim et al., 2022). Combining the SPEI with the NDVI allowed us to determine whether the water deficit affected birds directly, or only via a change in primary production. As correlation between the two variables was low and both were retained in the best model, we can conclude that they convey different information and one cannot be used instead of the other. Indeed, the NDVI may reflect longer-term processes and is not only influenced by the current precipitations and temperatures, but also by winter precipitations affecting groundwater availability and reservoir storage, especially in forests where deeper root systems can mitigate the effects of short water shortages on vegetation. Since the correlation between the SPEI and NDVI varies between habitats (Li et al., 2015), we could expect the relative importance of these two aspects of drought to vary between species: species living in forests could be less affected by short droughts than species living in open areas, while species feeding on ground invertebrates (e.g. blackbirds, thrushes) may be more sensitive to short-term SPEI affecting ground moisture. Performing a path-analysis may help discern the multiple causal pathways through which the SPEI and NDVI act on productivity and could be considered in further analyses to disentangle direct and indirect effects of drought.

All environmental variables used in this study appear to influence productivity to a certain extent, but climate variability was not the main factor driving variations of breeding productivity. Indeed, climate variability affects the habitat and food resource of passerine birds, but this interannual variation remains smaller than differences observed between sites (Morrison et al., 2022). We used random effects to consider this variation, but did not incorporate spatial structure into our models as sites are spread across France (Figure 3) and computing time would increase due to a greater complexity. Adding a distance matrix might help better represent spatial variability and improve the models. Abundance and productivity indicators are produced yearly for each site, so that volunteer bird ringers can follow variations of population dynamics at their capture site, and compare it to other stations (Appendix 7). They were produced at the national scaled and recently adapted to a regional scale, grouping stations within a biogeographical region.

As productivity determines fluctuations in abundance (Albright et al., 2009), abundance influences productivity via a density-dependent effect. Indeed, we controlled for variations in density in our models and it appeared to be the major driver of productivity among the variables we considered (z-score 3 times higher for density than for early temperatures). This density-dependence could lead to carry-over effects, i.e. processes (like meteorological effects) occurring in one season that carry over to the next (Walker et al., 2015). A highly productive season would lead to a high number of juveniles, which could negatively affect productivity the next year. This would cause temporal correlation, but we did not consider indirect carry-over effects in the models to focus on direct effects. Indeed, passerine birds have a short life span and only 20% of juveniles (55% of adults) survive until the following year. Moreover, the increasing frequency and intensity of summer droughts and heat waves observed with climate change also negatively affects survival (McLean et al., 2022), and especially post-fledging survival as they are more fragile than adults at this stage of development. Yet, young adults (1 year old) represent about 45% of breeding birds. Therefore, population trends are highly dependent on productivity (Morrison et al., 2022) and post-fledging survival (Halupka et al., 2023). Further studies on post-breeding data would be required to investigate the effects of climate variability on survival and have a more complete understanding of the implications of climate change on population dynamics. However, our dataset only covers the breeding period and does not record survival during the rest of the year. A way to estimate juveniles' survival is to assess the proportion of individuals born the previous year. But we might have to cross our dataset with data from other monitoring programs to be able to disentangle effects of heat waves and drought in the late summer from the effects of winter conditions on survival.

CONCLUSION

In conclusion, breeding productivity is affected by climate variability, but the density-dependence effect explained the greatest part of variation in productivity. Among the environmental variables considered, temperature variation was the main factor driving changes in productivity, with warmer temperatures during the early breeding season leading to an increased productivity mediated by a change in phenology. A warmer early spring allows passerine birds to reproduce earlier, which favors offspring production. However, heat during the late breeding season rather tends to have a negative effect on productivity, with terrestrial species being more impacted. Drought also affects negatively productivity, but to a lesser extent. Long-distance migrants, which are less flexible, suffer more from droughts in the early breeding season than resident species. Investigating juvenile survival might emphasize an importance of climate variability during summer, when heat waves and drought are the most intense. Moreover, it would allow a better understanding of the influence of climate variability on long-term population trends, with species abundances driven by previous productivity and survival via a density-dependence effect.

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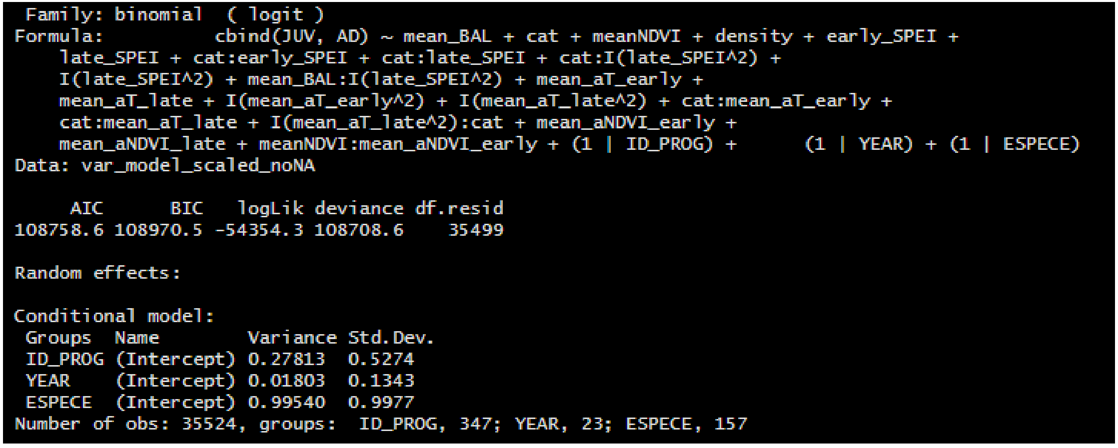
ANNEXES

Appendix 1 – Statistical analyses: Annotated script of statistical analyses

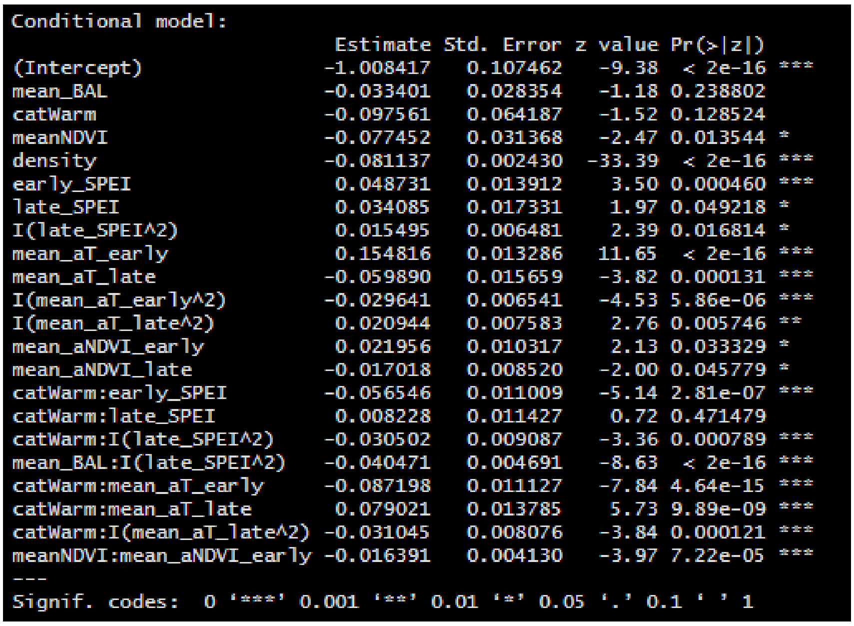
Here are presented only parts of the scripts used for the main analyses. The rest of the script I used during my internship is available on my github

I. Annotated script showing the model selection procedure to identify the effects of climatic variability on productivity

```
library(dplyr)
library(data.table)
library(glmmTMB)
library(MuMIn)

cat(" ------------------   Import data   ---------------------")

var_model_scaled <- fread("/scratchbeta/adenotn/data/var_model_final_allsp_scaled.csv")

options(na.action = "na.fail") # Required for dredge to run

# delete all years-site-species with NA for NDVI or SPEI
var_model_scaled_noNA <- var_model_scaled %>%
  filter(!is.na(meanNDVI)) %>%
  filter(!is.na(early_SPEI)) %>% filter(!is.na(early_nb_ECE_SPEI))

cat(" ------------------   Run model   -----------------------")

mod <- glmmTMB(cbind(JUV, AD) ~ mean_BAL + cat + meanNDVI + density +
          early_SPEI + late_SPEI + cat:early_SPEI + cat:late_SPEI + I(early_SPEI^2) + I(late_SPEI^2) +
          mean_BAL:I(early_SPEI^2) + mean_BAL:I(late_SPEI^2) +          mean_aT_early +
          mean_aT_late + I(mean_aT_early^2) + I(mean_aT_late^2) + cat:mean_aT_early + cat:mean_aT_late
          + I(mean_aT_early^2):cat + I(mean_aT_late^2):cat +          mean_aNDVI_early +
          mean_aNDVI_late + meanNDVI:mean_aNDVI_early +
   (1|ID_PROG) + (1|YEAR) + (1|ESPECE),
   family=binomial, data=var_model_scaled_noNA)

summary(mod)
```



```
 Family: binomial  ( logit )
Formula:          cbind(JUV, AD) ~ mean_BAL + cat + meanNDVI + density + early_SPEI +
    late_SPEI + cat:early_SPEI + cat:late_SPEI + cat:I(late_SPEI^2) +
    I(late_SPEI^2) + mean_BAL:I(late_SPEI^2) + mean_aT_early +
    mean_aT_late + I(mean_aT_early^2) + I(mean_aT_late^2) + cat:mean_aT_early +
    cat:mean_aT_late + I(mean_aT_late^2):cat + mean_aNDVI_early +
    mean_aNDVI_late + meanNDVI:mean_aNDVI_early + (1 | ID_PROG) +      (1 | YEAR) + (1 | ESPECE)
Data: var_model_scaled_noNA

     AIC      BIC   logLik deviance df.resid
108758.6 108970.5 -54354.3 108708.6    35499

Random effects:

Conditional model:
 Groups  Name        Variance Std.Dev.
 ID_PROG (Intercept) 0.27813  0.5274
 YEAR    (Intercept) 0.01803  0.1343
 ESPECE  (Intercept) 0.99540  0.9977
Number of obs: 35524, groups:  ID_PROG, 347; YEAR, 23; ESPECE, 157
```

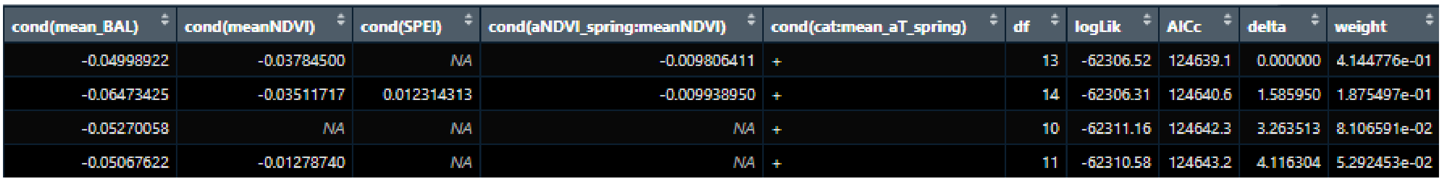


```
Conditional model:
                        Estimate Std. Error z value Pr(>|z|)    
(Intercept)            -1.008417   0.107462   -9.38  < 2e-16 ***
mean_BAL               -0.033401   0.028354   -1.18 0.238802    
catWarm                -0.097561   0.064187   -1.52 0.128524    
meanNDVI               -0.077452   0.031368   -2.47 0.013544 *  
density                -0.081137   0.002430  -33.39  < 2e-16 ***
early_SPEI              0.048731   0.013912    3.50 0.000460 ***
late_SPEI               0.034085   0.017331    1.97 0.049218 *  
I(late_SPEI^2)          0.015495   0.006481    2.39 0.016814 *  
mean_aT_early           0.154816   0.013286   11.65  < 2e-16 ***
mean_aT_late           -0.059890   0.015659   -3.82 0.000131 ***
I(mean_aT_early^2)     -0.029641   0.006541   -4.53 5.86e-06 ***
I(mean_aT_late^2)       0.020944   0.007583    2.76 0.005746 ** 
mean_aNDVI_early        0.021956   0.010317    2.13 0.033329 *  
mean_aNDVI_late        -0.017018   0.008520   -2.00 0.045779 *  
catWarm:early_SPEI     -0.056546   0.011009   -5.14 2.81e-07 ***
catWarm:late_SPEI       0.008228   0.011427    0.72 0.471479    
catWarm:I(late_SPEI^2) -0.030502   0.009087   -3.36 0.000789 ***
mean_BAL:I(late_SPEI^2) -0.040471  0.004691   -8.63  < 2e-16 ***
catWarm:mean_aT_early  -0.087198   0.011127   -7.84 4.64e-15 ***
catWarm:mean_aT_late    0.079021   0.013785    5.73 9.89e-09 ***
catWarm:I(mean_aT_late^2) -0.031045 0.008076  -3.84 0.000121 ***
meanNDVI:mean_aNDVI_early -0.016391 0.004130  -3.97 7.22e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
cat(" ----------------    Model selection MuMIn    --------------------")
```

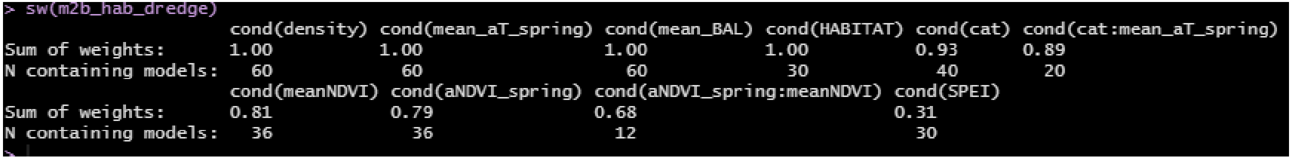
```
# Generate a model selection table of models with combinations (subsets) of fixed effect terms in mod
mod_dredge <- dredge(mod, trace = 2) # trace = 2 to see the advancement
```

```
head(mod_dredge)
```



cond(aNDVI_spring)	cond(cat)	cond(density)	cond(HABITAT)	cond(mean_aT_spring)	cond(mean_BAL)	cond(meanNDVI)	cond(SPEI)	cond(aNDVI_spring:meanNDVI)	cond(cat:mean_aT_spring)	df	logLik	AICc	delta	weight
3.344037e-03	+	0.02450928	+	0.08608725	-0.04998922	-0.03784500	NA	-0.009806411	+	13	-62306.52	124639.1	0.000000	4.144776e-01
2.358158e-03	+	0.02450833	+	0.08613514	-0.06473425	-0.03511717	0.012314313	-0.009938950	+	14	-62306.31	124640.6	1.585950	1.875497e-01
NA	+	0.02445732	+	0.08538160	-0.05270058	NA	NA	NA	+	10	-62311.16	124642.3	3.263513	8.106591e-02
NA	+	0.02447126	+	0.08589132	-0.05067622	-0.01278740	NA	NA	+	11	-62310.58	124643.2	4.116304	5.292453e-02

```
# print sum of weights
sw(mod_dredge)
```



```
> sw(m2b_hab_dredge)
                      cond(density) cond(mean_aT_spring) cond(mean_BAL) cond(HABITAT) cond(cat) cond(cat:mean_aT_spring)
Sum of weights:       1.00          1.00                 1.00           1.00          0.93      0.89
N containing models:    60            60                   60             30            40        20
                      cond(meanNDVI) cond(aNDVI_spring) cond(aNDVI_spring:meanNDVI) cond(SPEI)
Sum of weights:       0.81           0.79               0.68                        0.31
N containing models:    36             36                 12                          30
> 
```

```
options(na.action = "na.omit") # set back to default
```

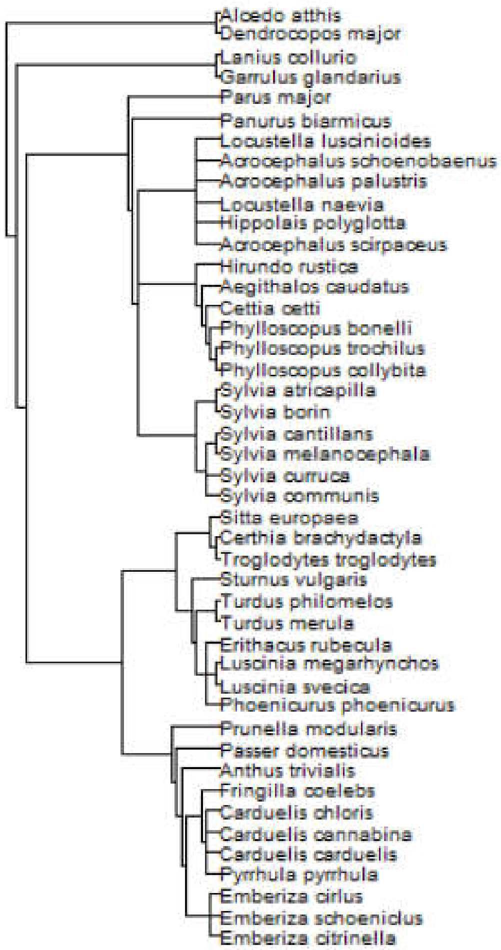
II. Annotated script showing the meta-analysis performed to test the effects of life-history traits on the response to climatic variability

```
require(tidyverse)
require(data.table)
require(ggplot2)
require(glmmTMB)
require(brms)
require(phytools)


cat(" ------------------   Import data    -----------------------")

var_model_scaled <- fread("/scratchbeta/adenotn/data/var_model_final_allsp_scaled.csv")

## there are 162 species captured, we keep only 48 for which we have enough data

sp_capt <- fread("/scratchbeta/adenotn/data/sp_capt.csv") # Table with the number of captured individuals per species
sp_capt <- sp_capt %>% mutate(phylo = gsub(" ", "_", nom_sc)) %>%
  mutate(phylo = gsub("Cyanistes", "Parus", phylo)) # in the tree, Cyanistes caeruleus is Parus caeruleus

species <- sp_capt$ESPECE

# keep the 50 most captured species, without PANBIA and SYLALA that are captured in only a few sites
var_model_scaled50 <- var_model_scaled %>% filter(ESPECE %in% species[1:50]) %>%
  filter(!(ESPECE %in% c("PANBIA","SYLALA")))


cat(" ------------------  RUN glmm   -----------------------")

mod <- glmmTMB(cbind(JUV, AD) ~ mean_BAL + cat + meanNDVI + density +
                early_SPEI + late_SPEI +
                I(early_SPEI^2) + I(late_SPEI^2) +
                                mean_aT_early + mean_aT_late + I(mean_aT_early^2) +           I(mean_aT_late^2) +
                                early_SPEI:ESPECE + late_SPEI:ESPECE + cat:early_SPEI + cat:late_SPEI +
                mean_aNDVI_early + mean_aNDVI_late + mean_aNDVI_early:meanNDVI+
                I(early_SPEI^2):ESPECE + I(late_SPEI^2):ESPECE +
                mean_BAL:I(early_SPEI^2) + mean_BAL:I(late_SPEI^2) +
                mean_aT_early:ESPECE + mean_aT_late:ESPECE + I(mean_aT_early^2):ESPECE +
I(mean_aT_late^2):ESPECE +
                cat:mean_aT_early + cat:mean_aT_late + I(mean_aT_early^2):cat + I(mean_aT_late^2):cat +
                mean_aNDVI_early:ESPECE + mean_aNDVI_late:ESPECE +
                ESPECE + (1|ID_PROG) + (1|YEAR),
              family=binomial, data=var_model_scaled50)


## Save estimates and standard errors in a dataframe
s <- summary(mod)
coef <- as.data.frame(s[["coefficients"]][["cond"]])
coef$var <- row.names(coef)
# extract species name
coef_sp <- coef %>% filter(grepl("ESPECE", var) & nchar(var)>12) %>%
  mutate(Species = substr(var,nchar(var)-6+1, nchar(var)))
# extract environmental variable name
coef_sp <- coef_sp %>%
  mutate(var_name = substr(var,1, nchar(var)-13))
```

Var	Trait	Estimate	Est.Error	l-95%_CI	u-95%_CI
early_SPEI	HABITAT_SPAquatique	-0.01	0.04	-0.1	0.06
early_SPEI	MIGRATIONLong	0.05	0.03	-0.01	0.12

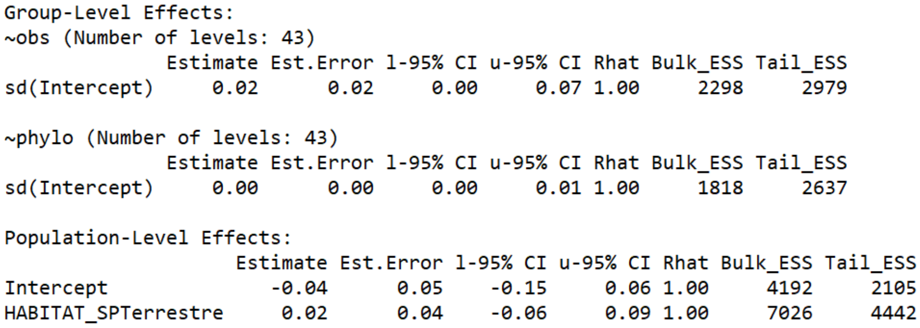
early_SPEI	Broods	0	0.03	-0.06	0.06
early_SPEI	sti_europe	0	0.01	-0.03	0.03
late_SPEI	HABITAT_SPAquatique	0.11	0.05	0.01	0.21
late_SPEI	MIGRATIONLong	-0.04	0.04	-0.13	0.05
late_SPEI	Broods	0	0.04	-0.09	0.07
late_SPEI	sti_europe	-0.03	0.02	-0.07	0.01
I(early_SPEI^2)	HABITAT_SPAquatique	-0.06	0.03	-0.11	0
I(early_SPEI^2)	MIGRATIONLong	-0.01	0.03	-0.06	0.04
I(early_SPEI^2)	Broods	0.02	0.02	-0.02	0.06
I(early_SPEI^2)	sti_europe	0	0.01	-0.02	0.02
I(late_SPEI^2)	HABITAT_SPAquatique	-0.01	0.04	-0.08	0.06

```
cat(" ------------------   Save file   -----------------------")

write.csv(coef_sp, file = "/scratchbeta/adenotn/output/coef_sp_meta2.csv", row.names = FALSE)



cat(" ------------------    Prepare data brms    -----------------------")

cat(" ------------------    Import tree    -----------------------")
phylo <- ape::read.nexus("/scratchbeta/adenotn/data/AllBirdsEricson1.nex")


cat(" ------------------    Build consensus tree    -----------------------")
## The nexus file phylo is composed of 100 trees
## We build a 50% consensus tree to use in the analyses

list_trees <- vector("list",100)
# select species from our data for each tree
for(i in 1:100){
  tree <- phylo[[i]]
  phylo_sp <- ape::drop.tip(tree, setdiff(tree$tip.label,sp_capt$phylo))
  list_trees[[i]] <- phylo_sp
}
# save trees with only our species in a new nexus file
ape::write.nexus(list_trees, file = "/scratchbeta/adenotn/data/test_subset_100.nex", translate = TRUE)

phylo_sub <- ape::read.nexus("/scratchbeta/adenotn/data/test_subset_100.nex")


# Compute consensus tree
t1<- phytools::consensus.edges(phylo_sub)
```



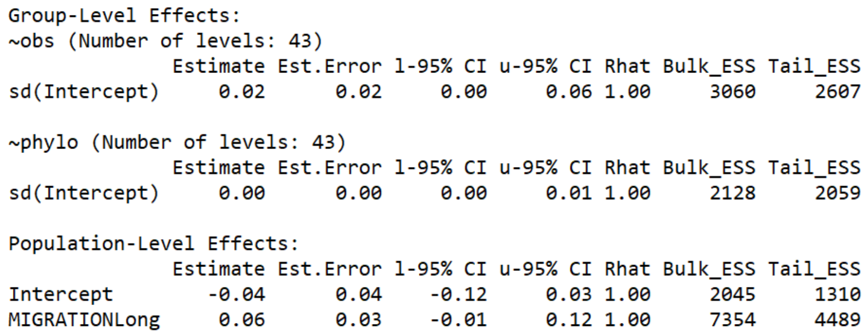
```
cat(" -----------    Phylogenetic variance-covariance matrix    ------------")
A <- ape::vcv.phylo(t1)

# import file with latin species name to match names from the tree to our data
nom_especes <- fread("/scratchbeta/adenotn/data/nom_especes.csv", encoding = "Latin-1")


cat(" -----------    Import THV    ------------")

# Import life-history traits
THV <- fread("/scratchbeta/adenotn/data/THV_all_sp.csv", encoding = "Latin-1")

# transform species name
coef_sp_brms <- coef_sp %>%
  left_join(nom_especes, by = c("Species" = "SP")) %>%
  dplyr::select(Estimate, `Std. Error`, var, var_name, Species, nom_sc) %>%
  mutate(nom_sc = gsub(" ", "_", nom_sc)) %>%
  left_join(THV, by = c("Species" = "ESPECE")) %>% #add THV
  rename(Broods = `Broods per year`) %>%
  mutate(nom_sc = gsub("Cyanistes", "Parus", nom_sc)) # in the tree, Cyanistes caeruleus is Parus caeruleus

colnames(coef_sp_brms)[1:7] <- c("est", "se", "var", "var_name", "ESPECE", "phylo", "nom_sc")

# check that all species are in the phylogeny
diff <- setdiff(unique(coef_sp_brms$phylo), colnames(A))

# delete species that are not in the tree from the dataframe
coef_sp_brms <- coef_sp_brms %>% filter(!(phylo %in% diff))
```

```
# relevel factor to have terrestrial species as a reference
coef_sp_brms <- coef_sp_brms %>%
  mutate(HABITAT_SP = as.factor(HABITAT_SP)) %>%
  mutate(MIGRATION = as.factor(MIGRATION))

coef_sp_brms$HABITAT_SP <- relevel(coef_sp_brms$HABITAT_SP, ref = "Terrestre")


cat(" --------------    Loop on environmental variables     ------------------")
# We run the brms model on each environmental variable to examine if life-history traits influence the response

for(x in unique(coef_sp_brms$var_name)){
  cat(paste0("brms on ", x, "\n"))
  df <- subset(coef_sp_brms, var_name == x)
  df$obs <- 1:nrow(df)


  cat(paste0("MODEL HABITAT_SP \n"))

  model_meta_hab <- brm(est | se(se) ~ HABITAT_SP +
                          (1|gr(phylo, cov = A)) + (1|obs),
                        data = df, family = gaussian(),
                        data2 = list(A = A),
                        prior = c(prior(normal(0, 10), "Intercept"),
                                  prior(student_t(3, 0, 10), "sd")),
                        control = list(adapt_delta = 0.95),
                        chains = 2, cores = 2, iter = 4000, warmup = 1000)

  print(summary(model_meta_hab))
```



```
Group-Level Effects:
~obs (Number of levels: 43)
              Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(Intercept)     0.02      0.02     0.00     0.07 1.00     2298     2979

~phylo (Number of levels: 43)
              Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(Intercept)     0.00      0.00     0.00     0.01 1.00     1818     2637

Population-Level Effects:
                    Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
Intercept              -0.04      0.05    -0.15     0.06 1.00     4192     2105
HABITAT_SPTerrestre     0.02      0.04    -0.06     0.09 1.00     7026     4442
```

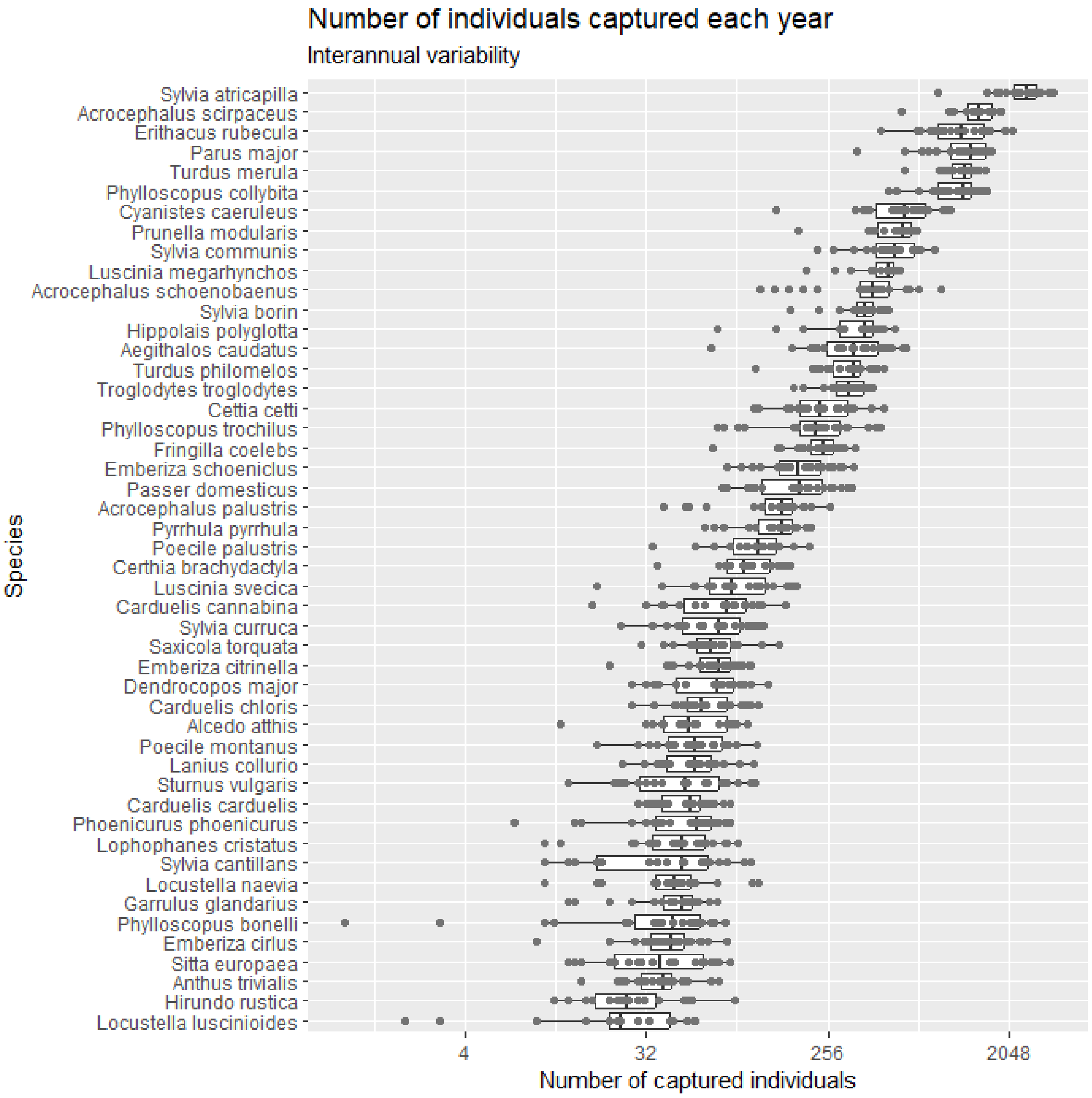
```
 # plot estimates
  png(paste0("/scratchbeta/adenotn/output/plot_model_meta_hab", x, ".png"))
  plot(model_meta_hab)
  dev.off()


  cat(paste0("MODEL MIGRATION \n"))

  model_meta_migr <- brm(est | se(se) ~ MIGRATION +
                           (1|gr(phylo, cov = A)) + (1|obs), # control for phylogenetic relatedness
                         data = df, family = gaussian(),
                         data2 = list(A = A),
                         prior = c(prior(normal(0, 10), "Intercept"),
                                   prior(student_t(3, 0, 10), "sd")),
                         control = list(adapt_delta = 0.95),
                         chains = 2, cores = 2, iter = 4000, warmup = 1000)

  print(summary(model_meta_migr))
```



```
Group-Level Effects:
~obs (Number of levels: 43)
              Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(Intercept)     0.02      0.02     0.00     0.06 1.00     3060     2607

~phylo (Number of levels: 43)
              Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(Intercept)     0.00      0.00     0.00     0.01 1.00     2128     2059

Population-Level Effects:
              Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
Intercept        -0.04      0.04    -0.12     0.03 1.00     2045     1310
MIGRATIONLong     0.06      0.03    -0.01     0.12 1.00     7354     4489
```

```
 # plot estimates
 png(paste0("/scratchbeta/adenotn/output/plot_model_meta_migr", x, ".png"))
 plot(model_meta_migr)
 dev.off()

 cat(paste0("MODEL NB BROODS \n"))

 model_meta_broods <- brm(est | se(se) ~ Broods +
                           (1|gr(phylo, cov = A)) + (1|obs),
                          data = df, family = gaussian(),
                          data2 = list(A = A),
                          prior = c(prior(normal(0, 10), "Intercept"),
                                    prior(student_t(3, 0, 10), "sd")),
                          control = list(adapt_delta = 0.95),
                          chains = 2, cores = 2, iter = 4000, warmup = 1000)

 print(summary(model_meta_broods))

 # plot estimates
 png(paste0("/scratchbeta/adenotn/output/plot_model_meta_broods", x, ".png"))
 plot(model_meta_broods)
 dev.off()


 cat(paste0("MODEL WITH STI \n"))

 model_meta_sti <- brm(est | se(se) ~ sti_europe +
                        (1|gr(phylo, cov = A)) + (1|obs),
                       data = df, family = gaussian(),
                       data2 = list(A = A),
                       prior = c(prior(normal(0, 10), "Intercept"),
                                 prior(student_t(3, 0, 10), "sd")),
                       control = list(adapt_delta = 0.95),
                       chains = 2, cores = 2, iter = 4000, warmup = 1000)

 print(summary(model_meta_sti))

 round(t(apply(post[, 11:14], 2, quantile, c(.5, .025, .975))), digits = 2)

 # plot estimates
 png(paste0("/scratchbeta/adenotn/output/plot_model_meta_sti_", x, ".png"))
 plot(model_meta_sti)
 dev.off()
 cat("DONE \n \n")
}
```

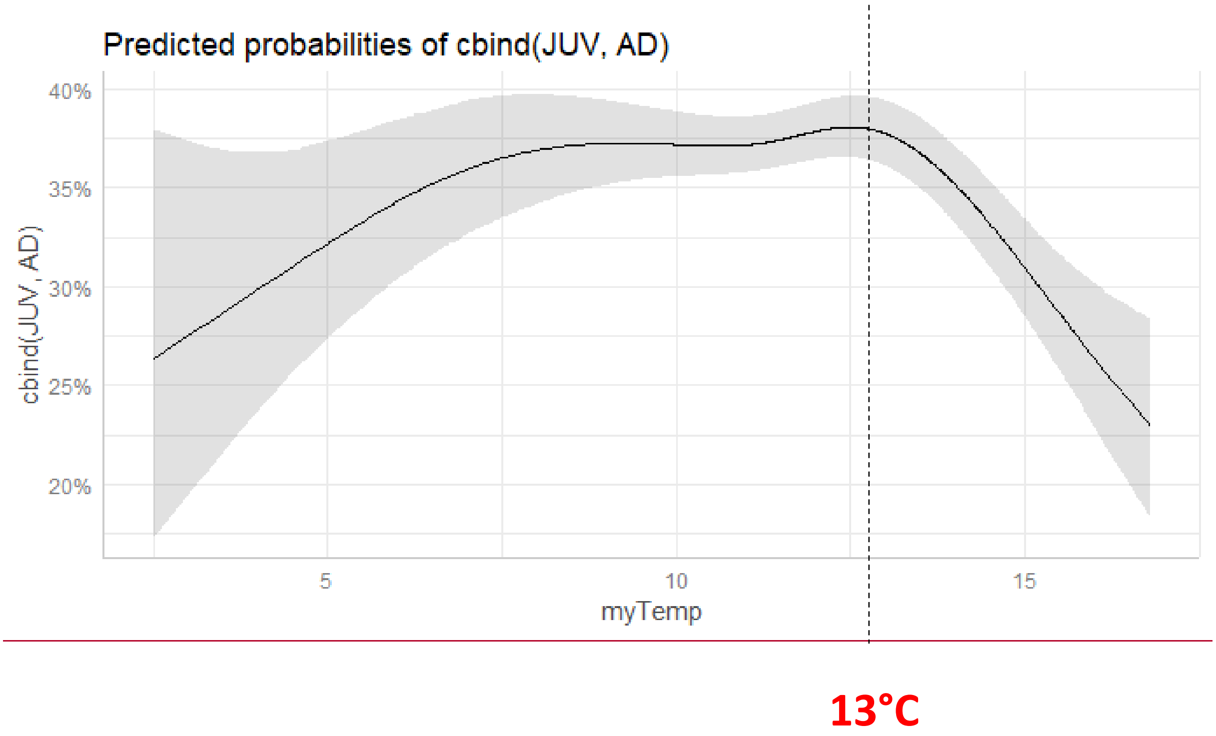
Appendix 2 – Number of individuals captured each year for the 50 most captured species



Appendix 3 – List of species used in the 2nd part of the analyses and their associated life-history traits

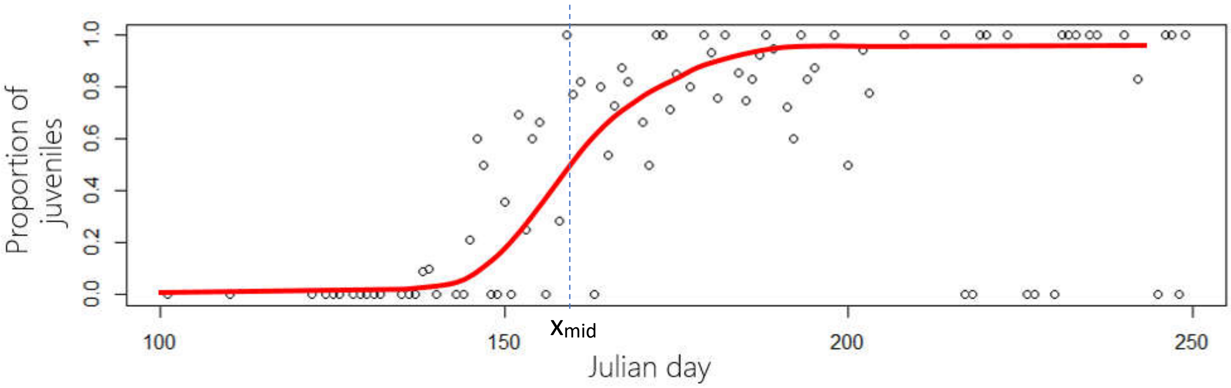
Species	code	HABITAT	MIGRATION	Broods per year	TSI
Sylvia atricapilla	SYLATR	Terrestrial	Short	1	12.62
Acrocephalus scirpaceus	ACRSCI	Aquatic	Long	1	NA
Erithacus rubecula	ERIRUB	Terrestrial	Short	2	12.00
Parus major	PARMAJ	Terrestrial	Short	1.5	12.34
Turdus merula	TURMER	Terrestrial	Short	2.5	12.58
Phylloscopus collybita	PHYCOL	Terrestrial	Short	2	11.95
Sylvia communis	SYLCOM	Terrestrial	Long	1	12.65
Prunella modularis	PRUMOD	Terrestrial	Short	2	10.91
Cyanistes caeruleus	PARCAE	Terrestrial	Short	1	12.74
Luscinia megarhynchos	LUSMEG	Terrestrial	Long	1.5	14.49
Acrocephalus schoenobaenus	ACRSCH	Aquatic	Long	1	NA
Sylvia borin	SYLBOR	Terrestrial	Long	1	11.32
Hippolais polyglotta	HIPPOL	Terrestrial	Long	1	14.84
Aegithalos caudatus	AEGCAU	Terrestrial	Short	1	12.66
Troglodytes troglodytes	TROTRO	Terrestrial	Short	2	12.24
Turdus philomelos	TURPHI	Terrestrial	Short	2.5	11.40
Cettia cetti	CETCET	Aquatic	Short	2	15.95
Phylloscopus trochilus	PHYLUS	Terrestrial	Long	1	NA
Fringilla coelebs	FRICOE	Terrestrial	Short	1	12.30
Passer domesticus	PASDOM	Terrestrial	Short	3	12.26
Emberiza schoeniclus	EMBSCH	Aquatic	Short	1.5	NA
Acrocephalus palustris	ACRRIS	Aquatic	Long	1	NA
Pyrrhula pyrrhula	PYRULA	Terrestrial	Short	2	NA
Poecile palustris	PAPALU	Terrestrial	Short	1	NA
Certhia brachydactyla	CERYLA	Terrestrial	Short	2	NA
Luscinia svecica	LUSSVE	Aquatic	Long	NA	NA
Sylvia curruca	SYLCUR	Terrestrial	Long	1	11.64
Poecile montanus	PARNUS	Terrestrial	Short	1	NA
Carduelis cannabina	CARINA	Terrestrial	Short	NA	NA
Emberiza citrinella	EMBCIT	Terrestrial	Short	2	11.55
Saxicola torquata	SAXTOR	Terrestrial	Short	NA	13.99
Carduelis chloris	CARCHL	Terrestrial	Short	NA	12.60
Dendrocopos major	DENMAJ	Terrestrial	Short	1	12.12
Alcedo atthis	ALCATT	Aquatic	Short	1.5	NA
Lanius collurio	LANRIO	Terrestrial	Long	1	NA
Sturnus vulgaris	STUVUL	Terrestrial	Short	1.5	11.80
Lophophanes cristatus	PARCRI	Terrestrial	Short	1	11.71
Phoenicurus phoenicurus	PHOPHO	Terrestrial	Long	2	11.31
Carduelis carduelis	CARLIS	Terrestrial	Short	2	NA
Locustella naevia	LOCNAE	Aquatic	Long	2	NA
Anthus trivialis	ANTTRI	Terrestrial	Long	1.5	11.24
Garrulus glandarius	GARGLA	Terrestrial	Short	1	12.47
Phylloscopus bonelli	PHYBON	Terrestrial	Long	1	13.86
Sitta europaea	SITEUR	Terrestrial	Short	1	12.79
Sylvia cantillans	SYLCAN	Terrestrial	Long	2	16.42
Emberiza cirlus	EMBCIR	Terrestrial	Short	2	15.05
Locustella luscinioides	LOCLUS	Aquatic	Long	1.5	NA
Hirundo rustica	HIRRUS	Terrestrial	Long	2.5	12.43

Appendix 4 – Graphical representation of the GAMM investigating the effects of mean temperature on productivity

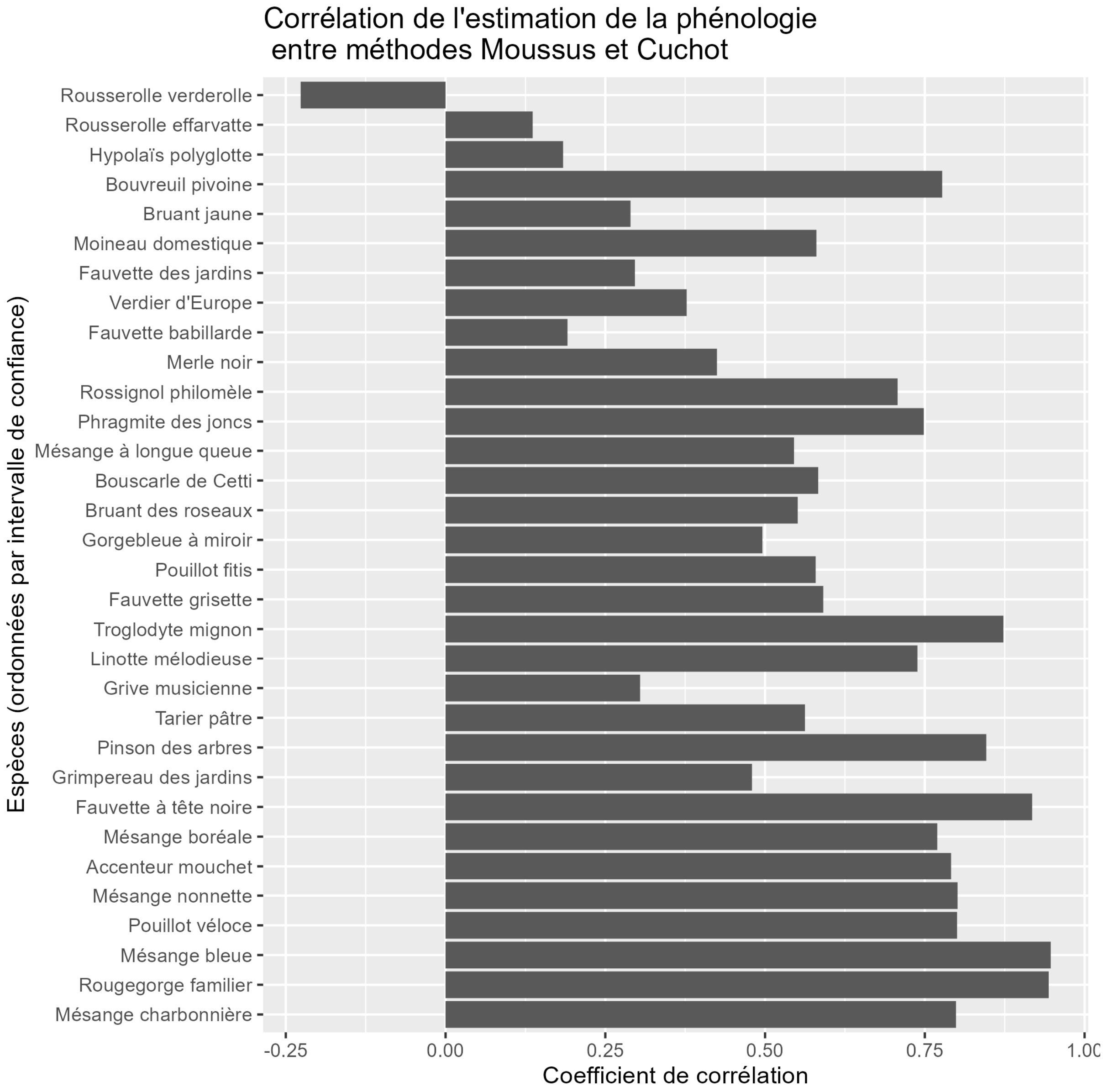


Appendix 5 – Evolution of the proportion of juveniles captured.

The inflexion point Xmid corresponds to the fledging peak, the proxy we used for breeding phenology (Cuchot et al., in prep.)



Appendix 6 – Pearson's correlation coefficients between estimations of phenological change obtained with Cuchot's and Moussus's methods



Appendix 7 – Extract of the reports produced for volunteer bird ringers (her for the site n°204)

Indice de survie locale : le taux de retour entre années

Le taux de retour des individus correspond à la proportion des individus capturés l'année t qui sont recapturés l'année $t+1$. Il est la résultante de la survie annuelle et de la fidélité des individus au site de reproduction (pour les adultes) ou au site de naissance (pour les juvéniles).

Pour le calcul de cet indicateur, il faut au moins 2 ans de suivi consécutifs.

L'indice du taux de retour est calculé et représenté pour la communauté d'espèces, par classe d'âge et type de migration (figure **42**).

Pour les 5 espèces (table **3**) assez abondantes (nombre médian d'individus capturés supérieur ou égal à 10), les variations du taux de retour sont présentées dans les figures **43-47**.

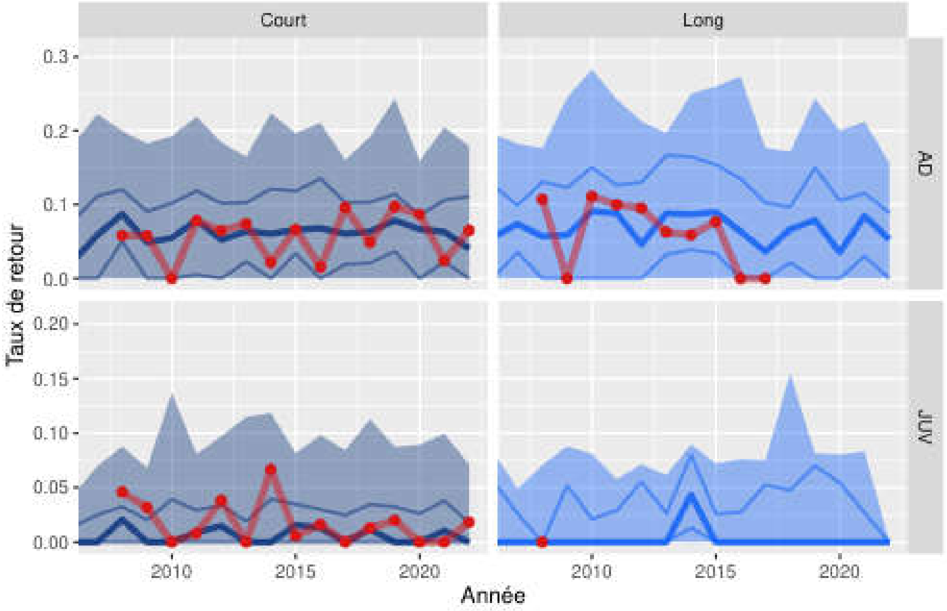


Figure 42: Variation du taux de retour sur l'ensemble des espèces pour la station 204. Le taux de retour de l'année t est la proportion des individus qui sont revus à l'année $t+1$. En bleu, la variation des quantiles de l'indicateur de référence (médiane, 50% et 95%) des stations de type Terrestre de la region ' atlantique ', en rouge et orange la variation pour la station 204.

L'indice de productivité

L'indice de productivité correspond au nombre de jeunes produits par adulte. Il reflète les effets des conditions environnementales sur la reproduction et la survie jusqu'à l'envol (à nombre d'adultes égaux, donc indépendamment des fluctuations de taille de population reproductrice). Il renseigne ainsi sur la variation de la qualité de l'habitat pour la reproduction des passereaux communs.

Cet indice de productivité est défini comme le nombre de jeunes divisé par le nombre d'adultes (capturés sur les 3 sessions) tel que :

$$\frac{N_{juv}}{N_{Ad}} \tag{1}$$

Enfin cet indice est tout d'abord calculé de façon globale pour la communauté en regroupant les espèces selon le type de migration qu'elles réalisent ("*Court*" pour à courte distance, "*Long*" pour à longue distance, voir la figure **26**). En effet, la productivité documentée étant très différente entre les migrateurs à longue distance (transsahariens) et les autres espèces, l'indice de productivité est calculé séparément pour ces deux groupes d'espèces.

Pour les 9 espèces (table **3**) assez abondantes (nombre médian d'individus capturés supérieur ou égal à 5) les variations des productivité sont présentées dans les figures **27-35**.

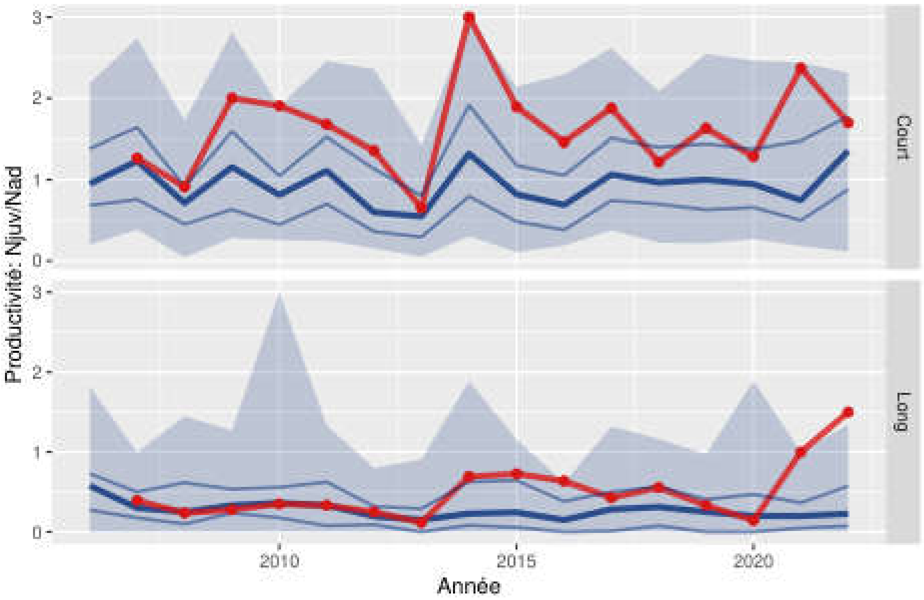
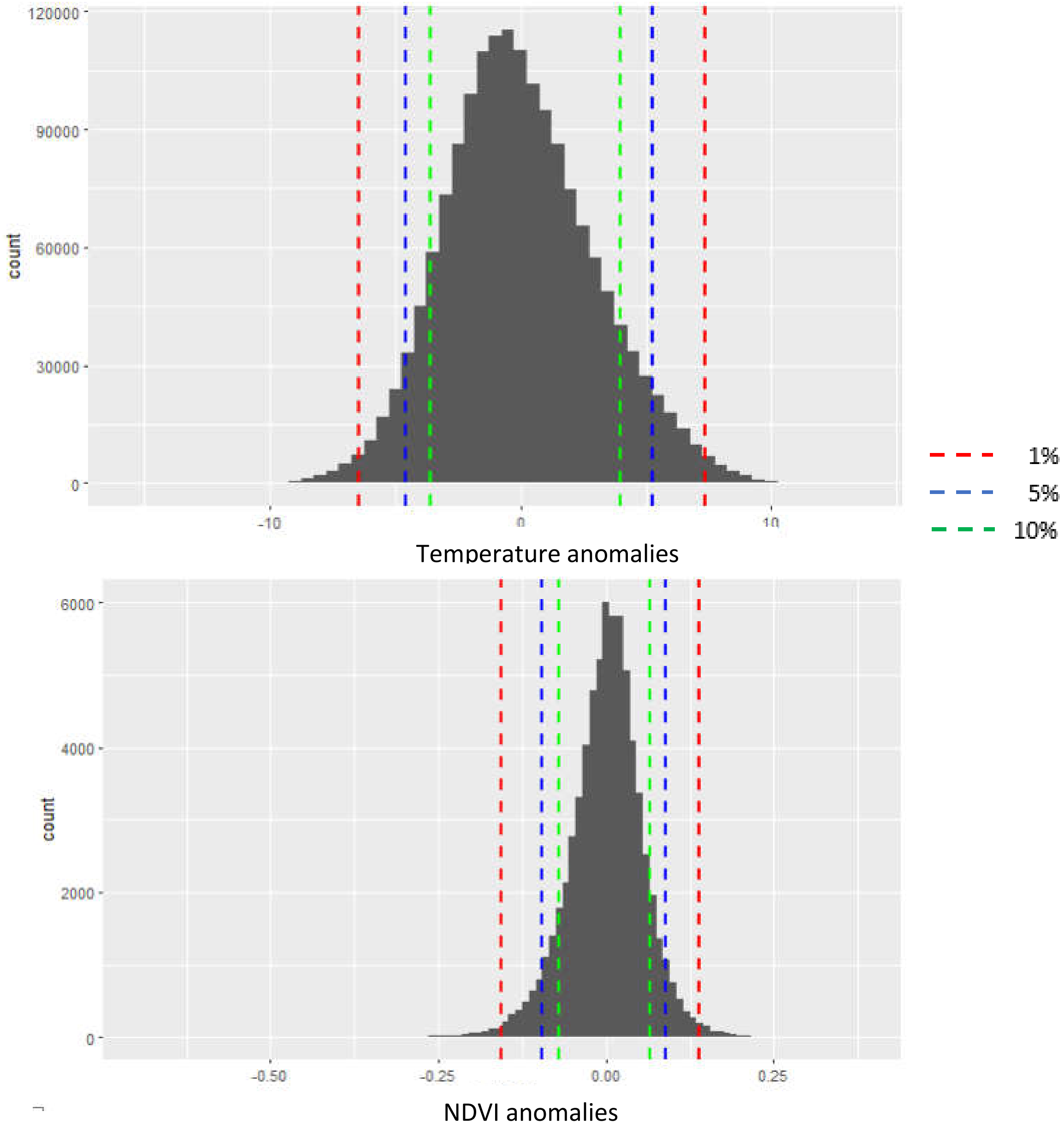


Figure 26: Variation de la productivité globale pour la station 204. En bleu, la variation régionale des quantiles de l'indicateur (médiane, 50% et 95%) pour les station de type Terrestre de la region ' atlantique ', en rouge la variation pour la station 204.

Appendix 8 – Distribution of temperature and NDVI anomalies



INFLUENCE DE LA VARIABILITE CLIMATIQUE SUR LA PRODUCTIVITE DES PASSEREAUX COMMUNS

Le changement climatique affecte la dynamique des populations par le biais d'un réchauffement global et d'une augmentation de la fréquence et de l'intensité des événements climatiques extrêmes. De nombreuses études se sont concentrées sur l'influence de la température sur la reproduction des oiseaux, mais les effets de la variabilité climatique sur la productivité restent mal compris. Nous avons utilisé des données collectées sur 23 ans provenant du programme français de baguage STOC Capture (Suivi Temporel des Oiseaux Communs par capture) pour étudier l'impact global de la sécheresse et des vagues de chaleur sur la productivité des passereaux et pour déterminer si les caractéristiques des espèces, telles que le statut migratoire ou l'habitat, influençaient les réponses à la variabilité climatique. La température a été le principal facteur environnemental expliquant des variations interannuelles de la productivité, par le biais d'un changement dans la phénologie de la reproduction. Des températures plus chaudes au début de la période de reproduction ont eu un effet positif sur la production de jeunes, tandis que la sécheresse a eu un effet négatif sur la productivité. Ces réactions à la variabilité climatique étaient plus prononcées dans les sites où la température moyenne locale était plus basse et chez les espèces vivant dans un habitat terrestre. Les migrateurs de longue distance ont été plus fortement touchés par une sécheresse précoce, en raison de la flexibilité limitée de leur phénologie de reproduction. En fin de période de reproduction, après l'éclosion des œufs, la variabilité météorologique a eu un effet plus faible sur la productivité et nous n'avons pas trouvé de tendances clairs. Néanmoins, les variations de productivité associées à la variabilité météorologique sont faibles par rapport aux variations induites par la densité-dépendance. Par conséquent, d'autres processus doivent être pris en compte pour expliquer les changements de dynamiques de population.

MOTS-CLES - *changement climatique – sécheresse – productivité – passereaux*

THE INFLUENCE OF CLIMATE VARIABILITY ON THE PRODUCTIVITY OF SONGBIRDS

Climate change affects population dynamics through a global warming and increase of extreme climatic events in both frequency and intensity. Many studies have focused on the influence of temperature on bird reproduction, but the effects of climate variability on productivity remains poorly understood. We used a 23-year long dataset from the French constant effort site ringing scheme to investigate the overall impact of drought and heat waves on the productivity of songbirds and whether species' traits such as migration status or habitat influenced responses to climate variability. Temperature was the main environmental driver of interannual variations in productivity, mediated by a change in breeding phenology. Warmer temperatures during the early breeding period had a positive effect on offspring production, while drought negatively affected productivity. These responses to climatic variability were more pronounced in sites with a lower local average temperature and species living in a terrestrial habitat. Long-distance migrants were more strongly impacted by an early drought because of their limited flexibility of breeding phenology. Later in the breeding period, after eggs have hatched, meteorological variability had a weaker effect on productivity and we did not find clear patterns. Nevertheless, variations in productivity associated with meteorological variability are small compared to variations driven by density-dependence. Therefore, more processes have to be considered to explain changes in population dynamics.

KEY WORDS - *climate change – drought – offspring productivity - songbirds*