Phenological Plasticity and Its Thermal Determinants in Common Songbirds across Europe

Paul Cuchot[1†], Timothée Bonnet[2], Rob Robinson[3,4], Juan Arizaga[5], Wolfgang Fiedler[6], Olaf Geiter[7], Ian Henshaw[8], Christof Herrmann[9], Henk van der Jeugd[10], Zsolt Karcza[11], Arantza Leal[12], Petteri Lehikoinen[13], Jan A.C. von Rönn[14], Kasper Thorup[15], Céline Teplitsky[1*], Pierre-Yves Henry[16,17*]

[1]CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France

[2]Centre d'Etudes Biologiques de Chizé UMR 7372 Université de la Rochelle-CNRS, Villiers-en-Bois, France.

[3]British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU

[4]Euring, The Nunnery, Thetford, IP24 2PU

[5]Aranzadi Sciences Society, Donostia/San Sebastián, Spain

[6]Max Planck Institute of Animal Behavior, Radolfzell, Germany

[7]Institute of Avian Research "Vogelwarte Helgoland", D 26386 Wilhelmshaven, Germany

[8]Swedish Bird Ringing Centre, Department for Nature and Environmental Monitoring, The Swedish Museum of Natural History, Stockholm, Sweden

[9]Hiddensee Bird Ringing Scheme, Goldberger Str. 12b, DE-18273 Güstrow, Germany

[10]Netherlands Institute for Ecology NIOO-KNAW, Netherlands

[11]BirdLife, Hungary

[12]SEO/BirdLife, Spain

[13]The Finnish Museum of Natural History, University of Helsinki, Finland

[14]Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland

[15]Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark

[16]Centre de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO), Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR 7204), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, Paris, France

[17]Mécanismes adaptatifs et évolution (MECADEV UMR 7179), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Brunoy, France

† Corresponding author: paul.cuchot@gmail.com

* These authors contributed equally.

Abstract

Phenological plasticity—the ability of organisms to adjust breeding timing in response to environmental variability —is the primary mechanism for seasonal organisms as it enables to synchronize their life cycles with seasonal resource availability. Theory predicts that phenological plasticity should vary among populations because of environmental heterogeneity, and among species because of life-history and phylogenetic constraints. However, comprehensive, multi-species, and cross-population analyses of phenological plasticity remain scarce. Here, we address this gap by using a unique, four-decade dataset from Europe-wide monitoring of common songbirds. Our approach reveals how variation in phenological plasticity is structured according to site thermal properties, both within and across species. We found that long-distance migrants generally exhibit lower plasticity than residents or short-distance migrants, highlighting a fundamental constraint tied to migration strategy. Within species, populations inhabiting thermally highly predictable sites showed slightly stronger plastic responses, particularly among single-brooded species and those adapted to warmer breeding conditions. Notably, populations from the fastest-warming regions demonstrated marginally greater plasticity, regardless of other ecological traits, suggesting a global tendency for increased responsiveness in rapidly changing climates. These findings confirm and extend patterns previously observed at smaller scales, offering a more nuanced understanding of how local thermal conditions drive phenological plasticity. By demonstrating that the interplay between local environmental conditions and life-history traits underpins variation in breeding phenological responses, our study refines the current framework for predicting adaptive potential across populations and species under climate change.

Introduction

Many seasonal vertebrates respond to climate change by shifting their phenology (Parmesan, 2006; Thackeray et al., 2016), that is the timing of critical life-history events. Phenotypic plasticity—the ability of a single genotype to produce different phenotypes depending on environmental conditions—is now recognized as being one of the main mechanisms responsible for these phenological shifts (Biquet et al., 2022; Merilä & Hendry, 2014; Pigliucci, 2001; Thackeray et al., 2016). Through this adaptive mechanism, organisms adjust their phenotype to local conditions, thereby maximizing their fitness across varying environments (Bradshaw, 1965; Levins, 1963; Reed et al., 2010).

Variation in breeding phenology in response to spring temperature in seasonal organisms has emerged as a "model system" for research on phenotypic plasticity (Chmura et al., 2019; Thackeray et al., 2010, 2016). Changes in seasonal timing directly affect the match between the needs of individuals and their resources (Visser & Both, 2005; Visser & Gienapp, 2019), the ability of organisms to track optimal environmental conditions over time through phenological plasticity therefore determines their reproductive success (Chevin et al., 2013; Chevin et al., 2010; Phillimore et al., 2016; Reed et al., 2010; Taff & Shipley, 2023; Vedder et al., 2013). However, as resources are shifting their phenology at a faster rate than consumers in response to temperature, spring warming under climate change can lead to an increased trophic mismatch (Gienapp et al., 2014; Kerby et al., 2012; Thackeray et al., 2010). Understanding the factors that drive plasticity across species is therefore important to predict how species will respond to current and future environmental and climatic changes.

Empirical and theoretical work emphasize how environmental characteristics can shape variation in plasticity. First, plasticity is predicted to be steeper (i.e. closer to the changes in resources) if organisms can accurately anticipate environmental variations that affect their fitness (Canale & Henry, 2010; Lande, 2009, 2014; Levins, 1963; Moran, 1992; Tufto, 2000). This requires environmental conditions to be predictable. For instance, in temperate regions, many organisms rely on indirect cues, such as early spring temperature, to best anticipate the timing of the peak of food availability, and fine-tune their breeding time (Visser & Both, 2005; Visser & Gienapp, 2019). Such impact of environmental predictability has been evidenced experimentally, in an algae, in response to salinity under different regimes of salinity variation (Leung et al., 2020). Second, recent studies suggest that shorter favorable seasons constrain the ability of organisms to adjust their phenology by limiting the time available for adjusting critical life events, such as breeding (Chmura et al., 2019; Gutiérrez & Wilson, 2021). In high-latitude/altitude regions, where the breeding season is brief, organisms thus face tight time constraints, reducing their capacity to shift the timing of life-history events in response to changing spring phenology. This narrow window for adaptation often results in lower phenological plasticity for populations, and species, that live at high latitudes. Third, under ongoing climate change phenological plasticity may reach its limits, potentially leading to less plasticity. This is in line with recent empirical studies, such as Bailey et al. (2022), having shown that tit populations exposed to the greatest spring warming rates exhibited reduced plasticity in laying date, potentially limiting their capacity to adapt to further changes (Iler et al., 2013)

Species-specific life history traits are also expected to explain variation in phenological plasticity across species (Dunn & Møller, 2014; Moussus et al., 2011). In birds, the life-history trait the most tightly linked to environmental seasonality is the migratory strategy: long-distance migrants exhibit weaker phenological responses to variation in spring temperature than short-distance migrants. Indeed, long-distance migrants rely on cues present in their wintering grounds which can be poorly linked to the conditions experienced on their breeding grounds (Jonzén et al., 2006a; Knudsen et al., 2011; Rubolini et al., 2007; Samplonius et al., 2018), when resident species experience local fluctuations and can therefore adjust more precisely to environmental variation. Species with less flexible reproductive strategies, such as those producing only one brood per year, are often better able to adjust their breeding timing to take advantage of favorable conditions, as they likely depend more on the temporal fine-tuning of the timing of their unique breeding event (Crick et al., 1993; Dunn & Møller, 2014).

Species inhabiting warmer environmental conditions are also expected to have a more plasticity breeding schedule plasticity. Finally, species diet is likely critical: species that rely exclusively on a single, thermally dependent resource, like aerial insectivores or caterpillar-specialists, are expected to exhibit greater plasticity in response to temperature cues compared to more diverse diets (Dunn & Møller, 2014).

In the present study, we analyzed within and between-species variation in phenological plasticity in response to spring temperature for 50 passerine bird species across Europe. We tested whether the thermal dimensions of the local environment, potentially in interaction with species-specific traits, influenced their breeding phenological plasticity. To achieve this, we first investigated the relationship between phenological plasticity on site-level and mean temperature, thermal predictability and warming rate. Using a meta-analysis, we then investigated how variation in fledging time plasticity across these thermal characteristics differed between species and tested whether such variation was explained by differences in life history / ecological traits (migration distance, number of broods per year, breeding range thermal maximum, diet).

Materials and methods

Capture data

Capture data were collected by volunteer bird ringers following national Constant ringing Effort Site protocols in Europe (Robinson et al., 2009; Figure 1). At each site, licensed ringers deploy each year a series of mist-nets at the same location, for the same length of time, during morning and/or evening visits, typically between April–May and July-August (the season starts and ends later at higher latitudes). The number of capture sessions and locations of mist-nets varies between countries and sites (Table S1) but are held constant within each site among sessions and years. Captured birds are identified to the species level, ringed with a unique numbered metal ring (or recorded as recapture if already ringed), sexed and aged based on plumage (juvenile for birds born during the ongoing breeding season, or adult if born in previous years; Svensson, 1992). For temperature extraction and data truncation (Appendix 1), we grouped capture sites into six regions based on protocol and biogeographical similarities (Table S1): continental Europe (German, Hungarian, Swiss and Czech sites), France (French sites only), UK (British and Irish sites); Spain (Spanish sites only); Netherlands (Dutch sites only) and Scandinavia (Finnish, Swedish and Danish sites).

Site filtering

We selected sites where data were collected during at least three consecutive years with at least 3 sessions per spring for French sites, and five for other countries where capture sessions are more frequent (Table S1). To ensure parameter estimability at site-level, for each species we only kept sites where at least three birds were captured on average per year. Only one record per individual per day was used. After data selection according to these criteria, the final data set represented a total of 2.700.299 individuals from 50 species for 1543 sites over a period of 40 years (1983 – 2023).

Temperature data

We obtained mean daily temperature data (°C) from the E-OBS Gridded Dataset v26 with a resolution of 0.25 degrees. The gridded dataset uses blended weather time series from the European wide weather station network of the European Climate Assessment & Dataset project. Blended time series utilize information from adjacent weather and synoptic stations to expand and complete missing sections within established weather station time series. Full documentation explaining blending and quality control methods can be found on the ECA&D website (https://www.ecad.eu/).

Temperature cue

For each year, species and site, we calculated the yearly temperature cue as the average daily mean temperature over a 2-month window before laying date. This window duration was chosen according to recent studies that defined the most important temperature window during which tits cue on temperature to time their reproduction as the two months before the egg-laying date (Bailey et al., 2022; Hanzelka et al., 2024). We do not have access to actual egg-laying dates for the 50 studied species, so we initially determined a 'mean fledging peak' for each species and region by identifying the inflection point of the curve representing the proportion of juveniles over time within a year (See "Estimating phenological plasticity per species" section and Cuchot et al., 2024), based on data compiled from all years and sites within each region (using mgcv; Figure S3). On average, we considered egg-laying date to occur around 50 days before the fledging peak (Storchová & Hořák, 2018). Windows were defined for each species and region, and were assumed to be constant across years.

Sites thermal characteristics

Mean site temperature had been calculated over the previously described window for each species and over the 1950-2022 period. Thermal predictability corresponds to a measure of average spring temperature variance over the 1950-2022 period (see Appendix 4 for calculation details) and therefore corresponds, in the models, to a measure of unpredictability. Warming rates for each site were extracted from the climate change atlas provided by the Copernicus network (https://atlas.climate.copernicus.eu/atlas), and expressed in degrees Celsius per decade over the 1950-2022 period. The spatial distribution of these three thermal characteristics of sites is plotted in Appendix 8 (Figure S13).

Estimating phenological plasticity per species

Following Cuchot et al. (2024), we modeled the probability for a captured individual to be a juvenile, for each species separately, in a Bayesian hierarchical framework using Markov Chain Monte Carlo sampling using the program JAGS (Plummer, 2003) via the R package *R2jags* (Su & Yajima, 2021).

The number of juveniles on day *t*, year *j* and site *k,* follows a binomial distribution (eq.2) which is characterized by two parameters: the probability that a captured individual is a juvenile $p_{t,j,k}$ and the number of captured individuals $N_{t,j,k}$.

$$Njuv_{t,j,k} \sim Bin(p_{t,j,k}, N_{t,j,k}) \tag{2}$$

Cuchot et al. (2024) assumed that during the breeding period (April to July), $p_{t,j,k}$ follows a sigmoid curve (Figure S2). We thus modeled *p* separately for each species with a 3-parameter function (eq.3).

$$p_{t,j,k} = \frac{asymptote_{j,k}}{1+e^{\frac{xmid_{j,k}-t}{scale_{j,k}}}} \tag{3}$$

The first parameter *asymptote* corresponds to the upper asymptote of the curve and describes the proportion of juveniles in the population at the end of the breeding period. The second parameter *xmid* is the inflection point of the curve, what corresponds to the peak of juvenile fledging. The date for this inflection point results from the timing of consecutive reproductive stages: egg laying (i.e., breeding phenology), eggs incubation, chick rearing, chick mortality in the nest and just after fledging (the few days when recently fledged juveniles remain in the close vicinity of their nest), and occurrence of replacement or repeat broods. If the duration of egg incubation and chick rearing is largely canalized (limited variability between sites or years), *xmid* can be considered as a proxy for egg-laying phenology.

The last parameter, *scale,* corresponds to a shape parameter and is the slope of the curve at the inflection point. *Scale* can be interpreted as a measure of the synchrony of fledging (Cuchot et al., 2024). These three parameters were assumed to vary independently, following normal distributions. All priors were set to be weakly informative. We ran this Bayesian hierarchical model with three chains of 6000 iterations each and a burn-in of 1000, and no thinning. The Gelman-Rubin convergence diagnostics (Brooks & Gelman, 1998) were satisfied (i.e., < 1.1) for all parameter estimates used for inference in the Results section. We relied on posterior distributions, their medians as point estimates and the associated 95% credible intervals (extracted from the highest posterior density) to infer the statistical support for our predictions (i.e., departure of parameter estimates from 0).

We modeled the $xmid$ parameter, i.e., fledging phenology, as a linear function of spring temperature anomaly (spring temperature deviation from mean site temperature; van de Pol & Wright, 2009). This reaction norm is usually considered as the measure of breeding phenological plasticity to temperature (Charmantier et al., 2008; Nussey et al., 2005) and can vary across sites depending on three principal thermal properties; mean site temperature (calculated over the 1950-2022 period), thermal predictability and warming rate (eq.4). We introduced two-way interaction terms between spring temperature anomaly and respectively mean site temperature $\boldsymbol{\gamma}_1$, thermal predictability $\boldsymbol{\gamma}_2$ and warming rate $\boldsymbol{\gamma}_3$.

$$fledge\ date_{k,j} = \boldsymbol{\alpha} + \mu_{0,j} + \mu_{0,k} + (\boldsymbol{\beta} + \mu_{1,k}) * T°C_{k,j} + \boldsymbol{\delta} * \overline{T°}C_k + \boldsymbol{\varphi} * pred_k + \boldsymbol{\theta} * warming_k + \boldsymbol{\gamma}_1 * T°C_{k,j} * \overline{T°}C_k + \boldsymbol{\gamma}_2 * pred_k * T°C_{k,j} + \boldsymbol{\gamma}_3 * warming_k * T°C_{k,j} + \varepsilon_{k,j} \quad (4)$$

with α corresponding to the species intercept (average phenology across sites), u_{0k} to the random site intercept, u_{0j} to the random year intercept, β to the mean slope across sites, u_{1k} to the random site slope, β_2 to the linear effect of mean site temperature, δ to the additive effect of mean site temperature, φ to the additive effect of thermal predictability, γ_1 to the interaction between mean site temperature and temperature anomaly, γ_2 to the interaction between thermal predictability, temperature anomaly, γ_3 to the interaction between warming rate and temperature anomaly and $\varepsilon_{k,j}$ to the residual error term. Site random slope $\mu_{1,k}$ and intercept $\mu_{0,k}$ were defined with a multinormal distribution, allowing us to explore the covariance between these parameters.

To discard phenological patterns from the influence of post-breeding and post-natal dispersal that could affect the juvenile/adult ratio in some species, we removed capture sessions late in the season. For more details about session filtering, see Appendix 1.

Ecological and Life history variables

Species traits data were gathered from the literature. Migration distances were extracted from Dufour et al. (2020), calculated as average distances between breeding and non-breeding ranges. If the species was considered completely resident, then the migration distance was zero. The number of broods were available in Storchová & Hořák, (2018). Trophic niche was compiled from the AVONET database (Tobias et al., 2022) and relates to the diet of the species: Granivore (n = 9), Invertivore (n = 33) and Omnivore (n = 8). As we consider a large latitudinal range, we recognize that these traits can vary within species—such as a lower number of second or third broods and increased migration distance at higher latitudes—but we lack standardized data to account for these latitudinal/elevational variations.

As the mean site temperature was centered within species, we introduced the thermal maximum to control for the fact that some species naturally inhabit warmer areas due to their ecological preferences. Thermal maximum was extracted from Jiguet et al. (2007) and defined as the mean of local spring and summer average monthly temperatures in the hottest part of the species breeding range.

Statistical (meta)analysis

We employed a meta-analytic approach to examine how species traits and phylogeny influence variability in fledging response to spring temperature anomalies, thermal predictability, warming rates, and mean site temperatures, both between and within species. First, for each of the regression parameters (eq. 4, α, β, δ, φ, θ, γ_1, γ_2 and γ_3), we estimated the cross-species mean value. In a second step, we built separate models that aimed at explaining between-species variation respectively in: average plasticity (β), mean site temperature effect on plasticity (γ_1), thermal predictability effect on plasticity (γ_2) and warming rate effect on plasticity (γ_3) according to the four life history traits described in the previous section. For each step of the analysis, we used linear mixed models accounting for variation in precision (standard deviation of the posterior distribution) of the parameter and for the non-independence among species due to shared evolutionary history (inclusion of phylogeny as a random effect). Linear mixed models were built using *brms* package (Bürkner, 2017; R Core Team, 2022). To ensure our study aligns with the latest global avian phylogeny, we combined two phylogenies by integrating the phylogeny established by Prum et al. (2015) with the maximum clade credibility (MCC) tree from Jetz et al., 2012, employing the approach outlined in Cooney et al. (2017).

Results

Most studied species (42 out of 50) fledge their chicks earlier in warmer years (β meta-analytic mean with [95% CI]: -2.18 day. °C^{-1} [-2.82, -1.56]; Figure 2; Table 1). However, the strength of plasticity (that is the relationship between fledging time and temperature anomaly, β_1) differed across species. *Locustella luscinioides* (-0.42 day. °C^{-1}) was the least plastic, and *Linaria cannabina* (-5.28 day. °C^{-1}) was the most plastic species (Table S2; Figure S7). Across species, only long-distance migrant exhibited a reduced plasticity relative to resident species (Figure 3; Table 2). All three other life-history traits did not explain variation in fledging plasticity. Finally, we found that phylogenetic inertia accounted for only 1.2% of the variation in fledging plasticity (Figure S6), suggesting that the observed variation is primarily driven by unidentified ecological factors.

For most species, bird populations from warmer sites fledged their juveniles earlier (δ meta-analytic mean with [95% CI]: -1.73 day.°C^{-1} [-2.59, -0.76]; Table 1; significant at species-level for 29 species). *Carduelis carduelis* fledging phenology was the most sensitive to mean site temperature (-5.42 day. °C^{-1}) but surprisingly, we found the opposite response in one species: *Luscinia svecica*'s fledgling phenology was positively affected by mean site temperature (2.59 day. °C^{-1}), meaning that population located at warmer sites breed later (Table S2). The effect of mean site temperature (spatial variability: -1.73 [-2.59; -0.76]; Table 1) was of the same order of magnitude as the effect of temperature anomaly (temporal variability: -2.18 [-2.82; -1.56]), but these two thermal dependencies were not correlated: the species responsiveness to yearly fluctuations in temperature is independent of its sensitivity to site mean temperature (Figure S16).

Phenological plasticity varied across populations, along the three gradients of site thermal properties. First, on average across species, phenological plasticity depended negatively on mean site temperature (γ_1 meta-analytic mean with 95CI: -0.13 [-0.24; -0.02]; Table 1; Figure S10): populations inhabiting warmer sites were more plastic. The intensity of this dependence decreases with migration distance until it becomes null in long-distance migrants (Table 2, Figure S14). Second, plasticity depended on the level of day-to-day predictability of temperature: populations located in more predictable sites exhibited higher fledging plasticity (γ_2 meta-analytic with 95% CI: 0.03 [0.01; 0.06]; Table 1; Figure S11). It means that the smoother the increase in temperature throughout spring (i.e., the higher the predictability from day to day of the spring warm-up), the higher the plasticity (Figure 2B). In general, species with a higher thermal maximum and those producing fewer clutches per year displayed steeper plasticity in response to thermal predictability at a site (Table 2; Figures S14, S15). On the contrary, there was no effect of thermal predictability in species with low thermal maximum and multi-brooded species. We found a negative effect of predictability on plasticity for two species: *Serinus serinus* (-0.44 [-0.84; -0.05]) and *Coccothraustes coccothraustes* (-0.74 [-1.43; -0.13]). Third, populations located in sites that warmed up the fastest were slightly more plastic (γ_3 meta-analytic mean with 95% CI: -1.70 [-3.27; -0.01]; Table 1; Figure S12), and this did not depend on any of the tested life history traits (Table 2). Although non-significant, we found that multi-brooded species tended to exhibit the opposite pattern, i.e., less phenological plasticity in sites that warmed up the fastest (Table 2).

Discussion

We confirmed that common songbirds fledge earlier in warmer springs and at warmer sites (Figure 2; Table 1), and that fledging plasticity is lower in long distance migrants (Figure 3; Table 2). More importantly, we revealed that populations from warmer sites, with higher thermal predictability or higher warming rates exhibit greater fledging plasticity (Figure 2A, B; Table 1). In birds, earlier breeding in warmer (earlier) springs is already well established in some model species (Bailey et al., 2022; Bonamour et al., 2019; Bourret et al., 2015; Charmantier et al., 2008; Cuchot et al., 2024; Dunn & Møller, 2014; McLean et al., 2022; Phillimore et al., 2016). However, most studies were led on either one or a small group of species, often focusing on commonly monitored species like cavity-nesting birds, which are easier to study, or on declining groups, such as long-distance migrants, leaving a significant gap in the coverage of common bird diversity, and therefore limiting the generalization of existing knowledge on phenological plasticity.

Our study also highlights that in general, there is little phylogenetic inertia in phenological plasticity so that environmental and species characteristics are the primary drivers shaping plasticity. Overall, we show that the more predictable the forthcoming breeding conditions, the stronger the phenological plasticity, at both interpopulation (thermal predictability) and interspecific (migrant vs resident) levels.

Between species differences in average fledging plasticity

Our analysis revealed little support for phylogenetic inertia in fledging plasticity across species, with only 1.2% of the variation attributable to shared evolutionary history (Figure S6). This low level of similarity of species along the phylogenetic tree suggests that the observed plastic responses are largely driven by ecological factors. This finding aligns with previous studies on the advancement of migration phenology (Rubolini et al., 2007; Végvári et al., 2010), in which differences in spring arrival dates between species were largely explained by species-specific traits, regardless of their phylogenetic relationships.

Species that migrate farther from their breeding ground exhibited lower fledging plasticity (Figure 3; Table 2). This may be because long-distance migrants rely on environmental cues from distant areas that do not accurately reflect the conditions that they will find when arriving at their breeding grounds, limiting their ability to adjust their breeding dates to local temperature conditions (Both & Visser, 2001; Briedis et al., 2024; Youngflesh et al., 2021). Indeed, short-distance migrants advance their migration period more than long-distance migrants over time (Jonzén et al., 2006b; Lehikoinen et al., 2019; Végvári et al., 2010). Our study confirms that this is likely due to differences in phenological plasticity. As a consequence, migratory species should in general be less able to synchronize their life cycle to changing environmental conditions than resident species (Visser & Gienapp, 2019).

We did not find statistical support for an effect of the other life history trait on phenological plasticity. In particular, contrary to our prediction, we did not find shallower plasticity in omnivorous species while we expected stronger plasticity in species relying on fewer resources. Since the observed phenological plasticity emerges from consumer-resource interactions, its magnitude should depend on the degree to which resource availability directly correlates with thermal conditions (Both et al., 2009). In particular, the position of the resource in the food chain, with consumers that depend on lower trophic levels often exhibiting greater responsiveness to temperature changes (Thackeray et al., 2010, 2016), which led us to expect stronger plasticity in granivorous than insectivorous species. However, we are lacking information on chick diet for most of the species, with probably insectivorous diet during nestling stages. Future comparative studies need to integrate more precise data on diet and the degree of diet specialization at nestling stage.

Between-site variation in phenological plasticity

Fledging plasticity increased with mean site temperature: populations from warmer sites were more plastic (Figure 2A; Table 1). Part of the variation in mean temperature across sites is structured along latitudinal/altitudinal gradients. In tree swallows *Tachycineta bicolor*, Dunn & Winkler (1999) showed that populations at higher latitudes (i.e. colder environments) exhibited lower laying date plasticity in response to spring temperature. This may be due to a physiological constraint, as gonadal development is slower at high latitude (Silverin et al., 2008; Wingfield et al., 1997, 2003). This could also be due to constraints on the ability to keep in pace with the phenology of their preys. For instance, a recent study on the flying date of butterflies showed that species and populations that emerge earlier display stronger plasticity of flying date in response to between-year temperature variation (Gutiérrez & Wilson, 2021). If butterflies are representative of other insect species, this could mean that in the earlier, warmer sites, the phenology of preys is more plastic, consequently selecting for stronger plasticity in birds. We found that this effect of mean site temperature on fledging plasticity (steeper plasticity in warmer sites) diminished with increasing migration distance. This is in line with limited plasticity in long-distance migratory species and can contribute to explain the fact that migratory species are the most vulnerable to climate change, declining faster than other groups (e.g., Morrison et al., 2013).

In agreement with theoretical predictions, we found that populations in environments with more predictable temperature patterns displayed stronger plasticity. Although recurrently hypothesized, the influence of environmental predictability on plasticity level has rarely been evidenced empirically (morphological trait in unicellular algae: Leung et al., 2020b; physiological and morphological traits in *drosophila*: Manenti et al., 2015; parturition date in lizards: Rutschmann et al., 2016). Our study is thus the first to show the effect of environmental predictability (here temperature) on the plasticity of a reproductive trait for a large phylogenetic group (common songbirds) at a continental level (Europe). Our results suggest that the steeper plasticity of birds in more predictable environments likely allow them to adjust their breeding phenology closer to the optimal phenology (Lande, 2009). Higher variance in temperature predicted under climate change scenarios may decrease environmental predictability. Under these new conditions, expressed plasticity may not allow to track as well the optimal breeding phenology, likely increasing the probability of phenological mismatch.

Populations from sites with the strongest spring warming rates were slightly more plastic. This pattern characterized over 50 species, contradicts the results Bailey et al. (2022), found for blue and great tit populations where the populations most exposed to temperature warming were less sensitive to temperature variations (i.e., less plastic). Here, we found that blue and great tits displayed steeper plasticity in sites warming faster (Figure S12) in line with the average cross-species response, evidencing their reliability as model species of resident common songbirds. We hypothesize that this discrepancy may be explained by the fact that, in Bailey et al.'s study, the correlation between warming rate and latitude were not accounted for. Since mean site temperature has a similar effect to that observed by Bailey et al., we might think that their observed pattern is due primarily to differences in mean site temperature. Because mean site temperature is calculated over the 1950-2022 period, average temperature in sites with faster warming rates may be underestimated during the years of our study. If this is the case, seasonal constraints may be lifted in these sites allowing a longer breeding season (Inouye et al., 2000). Alternatively, theoretical work predicts that environmental shifts may temporarily increase plasticity (Lande, 2009) or that extreme environments may affect the expression of plasticity (Chevin & Hoffman). Further work is needed to understand the origin and implications for breeding success of this increased plasticity.

Conclusion

Our study highlights the importance of thermal conditions and species specificities in shaping phenological plasticity in common songbirds, with minimal influence from phylogenetic inertia. Populations from more thermally predictable environments exhibited greater fledging plasticity, while long-distance migrants showed reduced plasticity, likely due to reliance on distal environmental cues that poorly reflect local breeding conditions. These findings align with theoretical predictions and emphasize the importance of environmental predictability in enhancing plastic responses.

Model species, such as blue and great tits, displayed patterns consistent with broader trends, validating their representativeness for comparative studies. However, variability in plasticity among populations and species suggests that some species could be more vulnerable than others, as it is the case for species migrating to distant wintering grounds, which exhibit limited adaptability to changes in prey phenology. Interestingly, populations in rapidly warming sites exhibited higher plasticity, suggesting a potential adaptive response, though the underlying mechanisms remain uncertain. This variability in plasticity across species and environments could widen the gap between optimal and realized phenology as temperatures rise, posing significant challenges for long-term reproductive success. Future work should now focus on the population and species consequences of such variation in phenological plasticity.

References

Bailey, L. D., van de Pol, M., Adriaensen, F., Arct, A., Barba, E., Bellamy, P. E., Bonamour, S., Bouvier, J.-C., Burgess, M. D., Charmantier, A., Cusimano, C., Doligez, B., Drobniak, S. M., Dubiec, A., Eens, M., Eeva, T., Ferns, P. N., Goodenough, A. E., Hartley, I. R., … Visser, M. E. (2022). Bird populations most exposed to climate change are less sensitive to climatic variation. *Nature Communications*, *13*(1), 2112. https://doi.org/10.1038/s41467-022-29635-4

Biquet, J., Bonamour, S., Villemereuil, P., Franceschi, C., & Teplitsky, C. (2022). Phenotypic plasticity drives phenological changes in a Mediterranean blue tit population. *Journal of Evolutionary Biology*, *35*(2), 347–359. https://doi.org/10.1111/jeb.13950

Bonamour, S., Chevin, L.-M., Charmantier, A., & Teplitsky, C. (2019). Phenotypic plasticity in response to climate change: The importance of cue variation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1768), 20180178. https://doi.org/10.1098/rstb.2018.0178

Both, C., Van Asch, M., Bijlsma, R. G., Van Den Burg, A. B., & Visser, M. E. (2009). Climate change and unequal phenological changes across four trophic levels: Constraints or adaptations? *Journal of Animal Ecology*, *78*(1), 73–83. https://doi.org/10.1111/j.1365-2656.2008.01458.x

Both, C., & Visser, M. E. (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, *411*(6835), 296–298. https://doi.org/10.1038/35077063

Bourret, A., Bélisle, M., Pelletier, F., & Garant, D. (2015). Multidimensional environmental influences on timing of breeding in a tree swallow population facing climate change. *Evolutionary Applications*, *8*(10), 933–944. https://doi.org/10.1111/eva.12315

Bradshaw, A. D. (1965). Evolutionary Significance of Phenotypic Plasticity in Plants. In E. W. Caspari & J. M. Thoday (Eds.), *Advances in Genetics* (Vol. 13, pp. 115–155). Academic Press. https://doi.org/10.1016/S0065-2660(08)60048-6

Briedis, M., Hahn, S., & Bauer, S. (2024). Duration and variability of spring green-up mediate population consequences of climate change. *Ecology Letters*, *27*(2), e14380. https://doi.org/10.1111/ele.14380

Brooks, S. P., & Gelman, A. (1998). General Methods for Monitoring Convergence of Iterative Simulations. *Journal of Computational and Graphical Statistics*, *7*(4), 434–455. https://doi.org/10.1080/10618600.1998.10474787

Bürkner, P.-C. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software*, *80*, 1–28. https://doi.org/10.18637/jss.v080.i01

Canale, C., & Henry, P. (2010). Adaptive phenotypic plasticity and resilience of vertebrates to increasing climatic unpredictability. *Climate Research*, *43*(1), 135–147. https://doi.org/10.3354/cr00897

Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B., & Sheldon, B. C. (2008). Adaptive Phenotypic Plasticity in Response to Climate Change in a Wild Bird Population. *Science*, *320*(5877), 800–803. https://doi.org/10.1126/science.1157174

Chevin, L., Collins, S., & Lefèvre, F. (2013). Phenotypic plasticity and evolutionary demographic responses to climate change: Taking theory out to the field. *Functional Ecology*, *27*(4), 967–979. https://doi.org/10.1111/j.1365-2435.2012.02043.x

Chevin, L.-M., Lande, R., & Mace, G. M. (2010). Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory. *PLOS Biology*, *8*(4), e1000357. https://doi.org/10.1371/journal.pbio.1000357

Chmura, H. E., Kharouba, H. M., Ashander, J., Ehlman, S. M., Rivest, E. B., & Yang, L. H. (2019). The mechanisms of phenology: The patterns and processes of phenological shifts. *Ecological Monographs*, *89*(1), e01337. https://doi.org/10.1002/ecm.1337

Cooney, C. R., Bright, J. A., Capp, E. J. R., Chira, A. M., Hughes, E. C., Moody, C. J. A., Nouri, L. O., Varley, Z. K., & Thomas, G. H. (2017). Mega-evolutionary dynamics of the adaptive radiation of birds. *Nature*, *542*(7641), 344–347. https://doi.org/10.1038/nature21074

Crick, H. Q. P., Gibbons, D. W., & Magrath, R. D. (1993). Seasonal Changes in Clutch Size in British Birds. *Journal of Animal Ecology*, *62*(2), 263–273. https://doi.org/10.2307/5357

Cuchot, P., Bonnet, T., Dehorter, O., Henry, P.-Y., & Teplitsky, C. (2024). How interacting anthropogenic pressures alter the plasticity of breeding time in two common songbirds. *Journal of Animal Ecology*, *93*(7), 918–931. https://doi.org/10.1111/1365-2656.14113

Dufour, P., Descamps, S., Chantepie, S., Renaud, J., Guéguen, M., Schiffers, K., Thuiller, W., & Lavergne, S. (2020). Reconstructing the geographic and climatic origins of long-distance bird migrations. *Journal of Biogeography*, *47*(1), 155–166. https://doi.org/10.1111/jbi.13700

Dunn, P. O., & Møller, A. P. (2014). Changes in breeding phenology and population size of birds. *Journal of Animal Ecology*, *83*(3), 729–739. https://doi.org/10.1111/1365-2656.12162

Dunn, P. O., & Winkler, D. W. (1999). Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*(1437), 2487–2490. https://doi.org/10.1098/rspb.1999.0950

Gienapp, P., Reed, T. E., & Visser, M. E. (2014). Why climate change will invariably alter selection pressures on phenology. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1793), 20141611. https://doi.org/10.1098/rspb.2014.1611

Gutiérrez, D., & Wilson, R. J. (2021). Intra- and interspecific variation in the responses of insect phenology to climate. *Journal of Animal Ecology*, *90*(1), 248–259. https://doi.org/10.1111/1365-2656.13348

Hanzelka, J., Telenský, T., Koleček, J., Procházka, P., Robinson, R. A., Baltà, O., Cepák, J., Gargallo, G., Henry, P.-Y., Henshaw, I., van der Jeugd, H., Karcza, Z., Lehikoinen, P., Meister, B., Nebot, A. L., Piha, M., Thorup, K., Tøttrup, A. P., & Reif, J. (n.d.). Climatic Predictors of Long-Distance Migratory Birds Breeding Productivity Across Europe. *Global Ecology and Biogeography*, *n/a*(n/a), e13901. https://doi.org/10.1111/geb.13901

Iler, A. M., Høye, T. T., Inouye, D. W., & Schmidt, N. M. (2013). Nonlinear flowering responses to climate: Are species approaching their limits of phenological change? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1624), 20120489. https://doi.org/10.1098/rstb.2012.0489

Inouye, D. W., Barr, B., Armitage, K. B., & Inouye, B. D. (2000). Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Sciences*, *97*(4), 1630–1633. https://doi.org/10.1073/pnas.97.4.1630

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, *491*(7424), 444–448. https://doi.org/10.1038/nature11631

Jiguet, F., Gadot, A.-S., Julliard, R., Newson, S. E., & Couvet, D. (2007). Climate envelope, life history traits and the resilience of birds facing global change. *Global Change Biology*, *13*(8), 1672–1684. https://doi.org/10.1111/j.1365-2486.2007.01386.x

Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J. O., Rubolini, D., Piacentini, D., Brinch, C., Spina, F., Karlsson, L., Stervander, M., Andersson, A., Waldenström, J., Lehikoinen, A., Edvardsen, E., Solvang, R., & Stenseth, N. Chr. (2006a). Rapid Advance of Spring Arrival Dates in Long-Distance Migratory Birds. *Science*, *312*(5782), 1959–1961. https://doi.org/10.1126/science.1126119

Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J. O., Rubolini, D., Piacentini, D., Brinch, C., Spina, F., Karlsson, L., Stervander, M., Andersson, A., Waldenström, J., Lehikoinen, A., Edvardsen, E., Solvang, R., & Stenseth, N. Chr. (2006b). Rapid Advance of Spring Arrival Dates in Long-Distance Migratory Birds. *Science*, *312*(5782), 1959–1961. https://doi.org/10.1126/science.1126119

Kerby, J. T., Wilmers, C. C., & Post, E. (2012). Climate change, phenology and the nature of consumer–resource interactions: Advancing the match/mismatch hypothesis. In T. Ohgushi, O. Schmitz, & R. D. Holt (Eds.), *Trait-Mediated Indirect Interactions* (1st ed., pp. 508–525). Cambridge University Press. https://doi.org/10.1017/CBO9780511736551.032

Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W. J., Bach, L. A., Coppack, T., Ergon, T., Gienapp, P., Gill, J. A., Gordo, O., Hedenström, A., Lehikoinen, E., Marra, P. P., Møller, A. P., Nilsson, A. L. K., Péron, G., … Stenseth, N. Chr. (2011). Challenging claims in the study of migratory birds and climate change. *Biological Reviews*, *86*(4), 928–946. https://doi.org/10.1111/j.1469-185X.2011.00179.x

Lande, R. (2009). Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *Journal of Evolutionary Biology*, *22*(7), 1435–1446. https://doi.org/10.1111/j.1420-9101.2009.01754.x

Lande, R. (2014). Evolution of phenotypic plasticity and environmental tolerance of a labile quantitative character in a fluctuating environment. *Journal of Evolutionary Biology*, *27*(5), 866–875. https://doi.org/10.1111/jeb.12360

Lehikoinen, A., Lindén, A., Karlsson, M., Andersson, A., Crewe, T. L., Dunn, E. H., Gregory, G., Karlsson, L., Kristiansen, V., Mackenzie, S., Newman, S., Røer, J. E., Sharpe, C., Sokolov, L. V., Steinholtz, Å., Stervander, M., Tirri, I.-S., & Tjørnløv, R. S. (2019). Phenology of the avian spring migratory passage in Europe and North America: Asymmetric advancement in time and increase in duration. *Ecological Indicators*, *101*, 985–991. https://doi.org/10.1016/j.ecolind.2019.01.083

Leung, C., Rescan, M., Grulois, D., & Chevin, L.-M. (2020). Reduced phenotypic plasticity evolves in less predictable environments. *Ecology Letters*, *23*(11), 1664–1672. https://doi.org/10.1111/ele.13598

Levins, R. (1963). Theory of Fitness in a Heterogeneous Environment. II. Developmental Flexibility and Niche Selection. *The American Naturalist*, *97*(893), 75–90. https://doi.org/10.1086/282258

Manenti, T., Loeschcke, V., Moghadam, N. N., & Sørensen, J. G. (2015). Phenotypic plasticity is not affected by experimental evolution in constant, predictable or unpredictable fluctuating thermal environments. *Journal of Evolutionary Biology*, *28*(11), 2078–2087. https://doi.org/10.1111/jeb.12735

McLean, N., Kruuk, L. E. B., Van Der Jeugd, H. P., Leech, D., Van Turnhout, C. A. M., & Van De Pol, M. (2022). Warming temperatures drive at least half of the magnitude of long-term trait changes in European birds. *Proceedings of the National Academy of Sciences*, *119*(10), e2105416119. https://doi.org/10.1073/pnas.2105416119

Merilä, J., & Hendry, A. P. (2014). Climate change, adaptation, and phenotypic plasticity: The problem and the evidence. *Evolutionary Applications*, *7*(1), 1–14. https://doi.org/10.1111/eva.12137

Moran, N. A. (1992). The Evolutionary Maintenance of Alternative Phenotypes. *The American Naturalist*, *139*(5), 971–989. https://doi.org/10.1086/285369

Morrison, C. A., Robinson, R. A., Clark, J. A., Risely, K., & Gill, J. A. (2013). Recent population declines in Afro-Palaearctic migratory birds: The influence of breeding and non-breeding seasons. *Diversity and Distributions*, *19*(8), 1051–1058. https://doi.org/10.1111/ddi.12084

Moussus, J.-P., Clavel, J., Jiguet, F., & Julliard, R. (2011). Which are the phenologically flexible species? A case study with common passerine birds. *Oikos*, *120*(7), 991–998. https://doi.org/10.1111/j.1600-0706.2010.18955.x

Nussey, D. H., Postma, E., Gienapp, P., & Visser, M. E. (2005). Selection on Heritable Phenotypic Plasticity in a Wild Bird Population. *Science*, *310*(5746), 304–306.

Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Phillimore, A. B., Leech, D. I., Pearce-Higgins, J. W., & Hadfield, J. D. (2016). Passerines may be sufficiently plastic to track temperature-mediated shifts in optimum lay date. *Global Change Biology*, *22*(10), 3259–3272. https://doi.org/10.1111/gcb.13302

Pigliucci, M. (2001). *Phenotypic plasticity: Beyond nature and nurture*. Johns Hopkins University Press.

Plummer, M. (2003). *JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling*. https://www.scinapse.io/papers/68436435

Prum, R. O., Berv, J. S., Dornburg, A., Field, D. J., Townsend, J. P., Lemmon, E. M., & Lemmon, A. R. (2015). A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature*, *526*(7574), 569–573. https://doi.org/10.1038/nature15697

R Core Team. (2022). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Reed, T. E., Waples, R. S., Schindler, D. E., Hard, J. J., & Kinnison, M. T. (2010). Phenotypic plasticity and population viability: The importance of environmental predictability. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1699), 3391–3400. https://doi.org/10.1098/rspb.2010.0771

Robinson, R. A., Julliard, R., & Saracco, J. F. (2009). Constant effort: Studying avian population processes using standardised ringing. *Ringing & Migration*, *24*(3), 199–204. https://doi.org/10.1080/03078698.2009.9674392

Rubolini, D., Møller, A., Rainio, K., & Lehikoinen, E. (2007). Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. *Climate Research*, *35*, 135–146. https://doi.org/10.3354/cr00720

Rutschmann, A., Miles, D. B., Le Galliard, J.-F., Richard, M., Moulherat, S., Sinervo, B., & Clobert, J. (2016). Climate and habitat interact to shape the thermal reaction norms of breeding phenology across lizard populations. *Journal of Animal Ecology*, *85*(2), 457–466. https://doi.org/10.1111/1365-2656.12473

Samplonius, J. M., Bartošová, L., Burgess, M. D., Bushuev, A. V., Eeva, T., Ivankina, E. V., Kerimov, A. B., Krams, I., Laaksonen, T., Mägi, M., Mänd, R., Potti, J., Török, J., Trnka, M., Visser, M. E., Zang, H., & Both, C. (2018). Phenological sensitivity to climate change is higher in resident than in migrant bird populations among European cavity breeders. *Global Change Biology*, *24*(8), 3780–3790. https://doi.org/10.1111/gcb.14160

Silverin, B., Wingfield, J., Stokkan, K.-A., Massa, R., Järvinen, A., Andersson, N.-Å., Lambrechts, M., Sorace, A., & Blomqvist, D. (2008). Ambient temperature effects on photo induced gonadal cycles and hormonal secretion patterns in Great Tits from three different breeding latitudes. *Hormones and Behavior*, *54*(1), 60–68. https://doi.org/10.1016/j.yhbeh.2008.01.015

Storchová, L., & Hořák, D. (2018). Life-history characteristics of European birds. *Global Ecology and Biogeography*, *27*(4), 400–406. https://doi.org/10.1111/geb.12709

Su, Y., & Yajima, M. (2021). R2jags: Using R to Run “JAGS.” *R Package Version 0.7-1, <https://CRAN.R-Project.Org/package=R2jags>.*

Taff, C. C., & Shipley, J. R. (2023). Inconsistent shifts in warming and temperature variability are linked to reduced avian fitness. *Nature Communications*, *14*(1), Article 1. https://doi.org/10.1038/s41467-023-43071-y

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., … Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, *535*(7611), Article 7611. https://doi.org/10.1038/nature18608

Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., Botham, M. S., Brereton, T. M., Bright, P. W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, J. M., Harrington, R., Johns, D., Jones, I. D., Jones, J. T., Leech, D. I., … Wanless, S. (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments: PHENOLOGICAL CHANGE ACROSS MAJOR ENVIRONMENTS. *Global Change Biology*, *16*(12), 3304–3313. https://doi.org/10.1111/j.1365-2486.2010.02165.x

Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J. M., Yang, J., Sayol, F., Neate-Clegg, M. H. C., Alioravainen, N., Weeks, T. L., Barber, R. A., Walkden, P. A., MacGregor, H. E. A., Jones, S. E. I., Vincent, C., Phillips, A. G., Marples, N. M., Montaño-Centellas, F. A., Leandro-Silva, V., Claramunt, S., … Schleuning, M. (2022). AVONET: Morphological, ecological and geographical data for all birds. *Ecology Letters*, *25*(3), 581–597. https://doi.org/10.1111/ele.13898

Tufto, J. (2000). The Evolution of Plasticity and Nonplastic Spatial and Temporal Adaptations in the Presence of Imperfect Environmental Cues. *The American Naturalist*, *156*(2), 121–130. https://doi.org/10.1086/303381 van de Pol, M., & Wright, J. (2009). A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour*, *77*(3), 753–758. https://doi.org/10.1016/j.anbehav.2008.11.006

Vedder, O., Bouwhuis, S., & Sheldon, B. C. (2013). Quantitative Assessment of the Importance of Phenotypic Plasticity in Adaptation to Climate Change in Wild Bird Populations. *PLoS Biology*, *11*(7), e1001605. https://doi.org/10.1371/journal.pbio.1001605

Végvári, Z., Bókony, V., Barta, Z., & Kovács, G. (2010). Life history predicts advancement of avian spring migration in response to climate change. *Global Change Biology*, *16*(1), 1–11. https://doi.org/10.1111/j.1365-2486.2009.01876.x

Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1581), 2561–2569. https://doi.org/10.1098/rspb.2005.3356

Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution*, *3*(6), Article 6. https://doi.org/10.1038/s41559-019-0880-8

Wingfield, J. C., Hahn, T. P., Maney, D. L., Schoech, S. J., Wada, M., & Morton, M. L. (2003). Effects of temperature on photoperiodically induced reproductive development, circulating plasma luteinizing hormone and thyroid hormones, body mass, fat deposition and molt in mountain white-crowned sparrows, Zonotrichia leucophrys oriantha. *General and Comparative Endocrinology*, *131*(2), 143–158. https://doi.org/10.1016/S0016-6480(02)00648-2

Wingfield, J. C., Hahn, T. P., Wada, M., & Schoech, S. J. (1997). Effects of Day Length and Temperature on Gonadal Development, Body Mass, and Fat Depots in White-Crowned Sparrows,Zonotrichia leucophrys pugetensis. *General and Comparative Endocrinology*, *107*(1), 44–62. https://doi.org/10.1006/gcen.1997.6894

Youngflesh, C., Socolar, J., Amaral, B. R., Arab, A., Guralnick, R. P., Hurlbert, A. H., LaFrance, R., Mayor, S. J., Miller, D. A. W., & Tingley, M. W. (2021). Migratory strategy drives species-level variation in bird sensitivity to vegetation green-up. *Nature Ecology & Evolution*, *5*(7), Article 7. https://doi.org/10.1038/s41559-021-01442-y

Figures

Figure 1: Map EuroCES

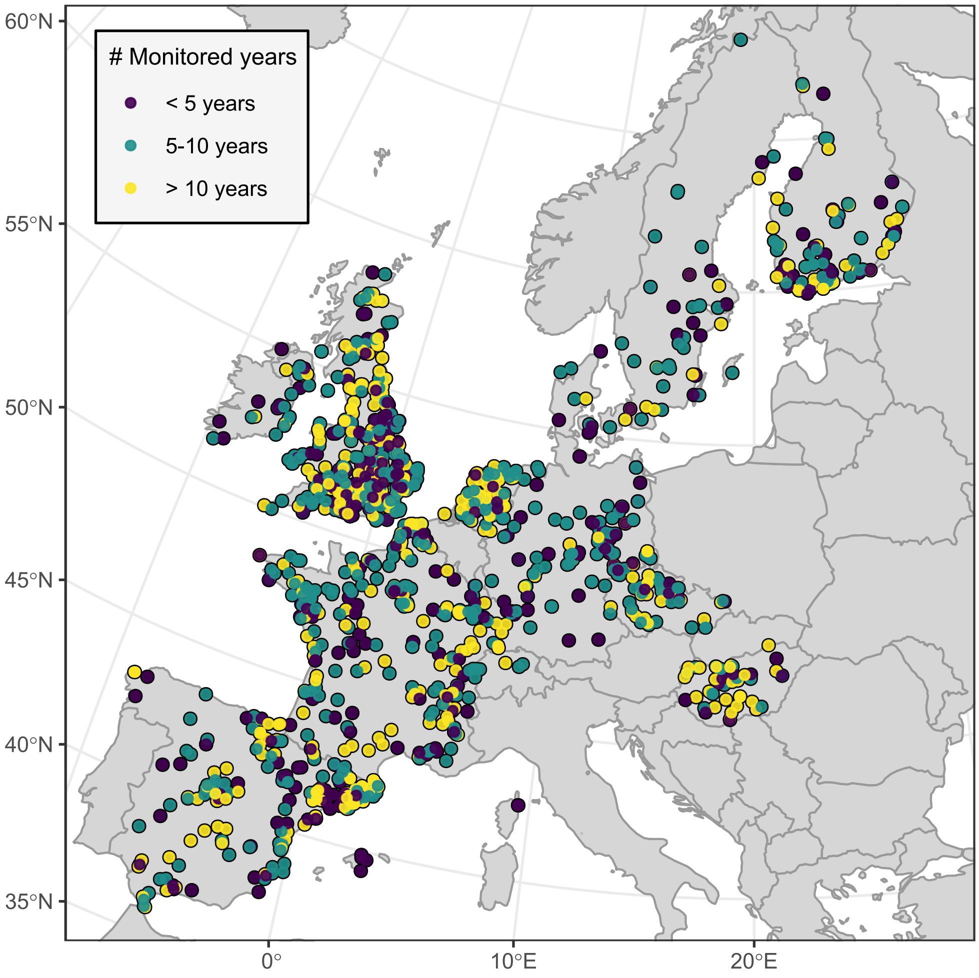
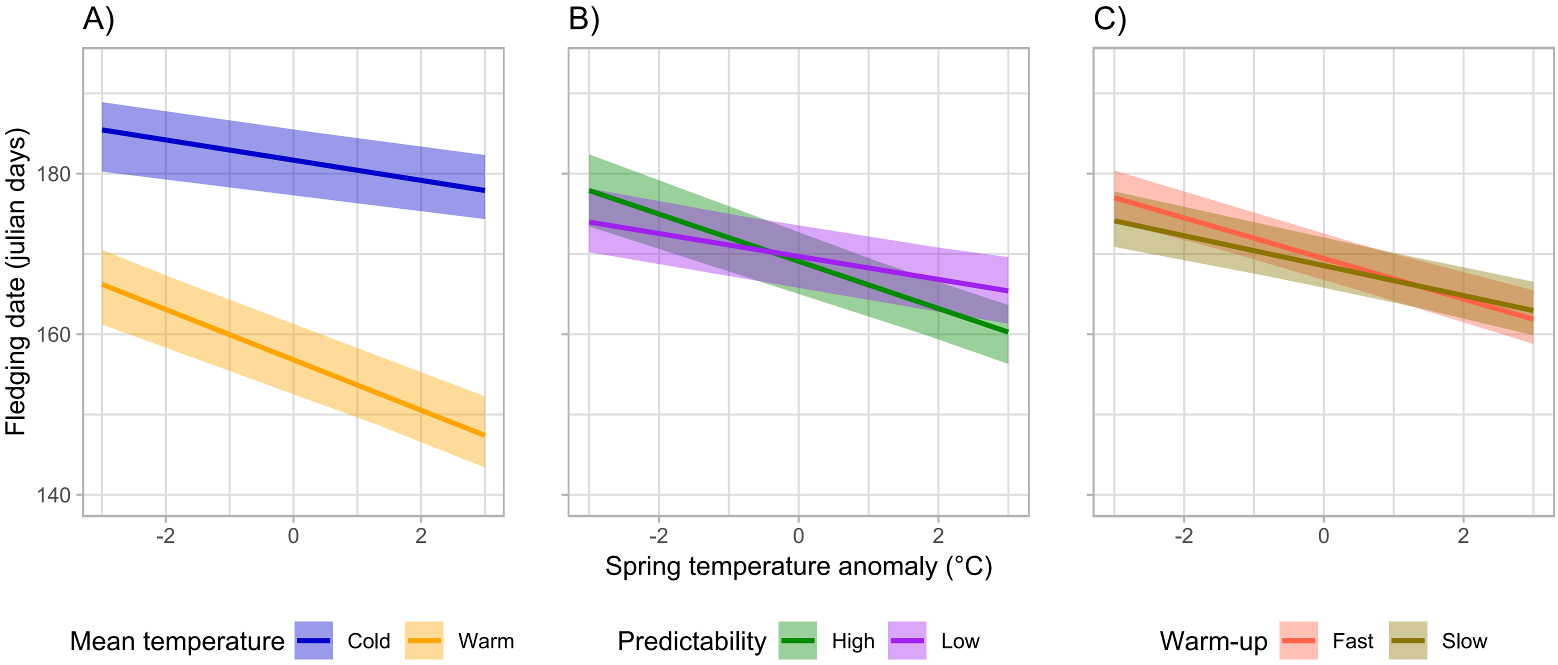


Figure 1: Locations of Constant capture Effort Sites (CES). Colors represent the number of years of monitoring per site.

621 **Figure 2: Average within-species variation**



622

Figure 2: Within-species variation in fledging plasticity in response to spring temperature anomaly and A) mean site temperature, B) thermal predictability and C) warm-up. Predictions were calculated 100 times per category and for 100 values of spring temperature anomaly, by picking in the posterior distributions of the estimates of the intercept models for each parameter (Table 1). The lower and upper bounds of the predictions correspond to respectively the minimum and maximum of the 100 predicted values. Categories (i.e., cold/warm for mean temperature, high/low for predictability, fast/slow for warm-up) had been chosen according to the 0.1 and 0.9 quantiles in their distribution among captures sites.

Figure 3: Mean plasticity ~ migration distance

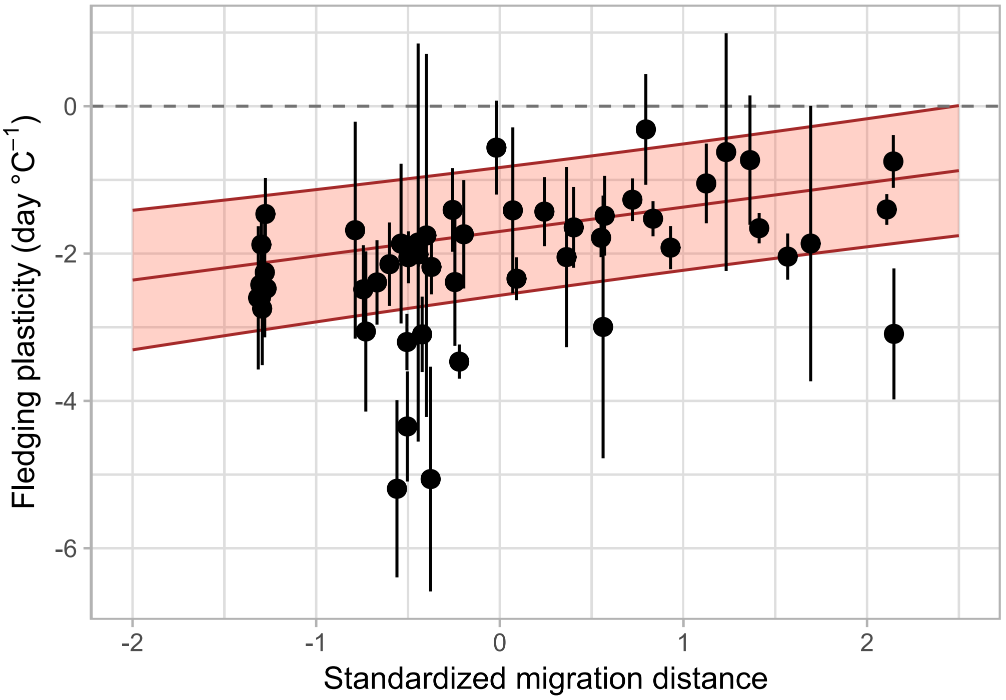


Figure 3: Mean fledging plasticity in response to local temperature anomaly according to standardized species migration distance. Points represent the mean of the posterior distribution and the associated range corresponds to the 95% of the distribution.

Tables

Table 1: Mean effects

Table 1: Meta-analytic mean (i.e., cross-species) effects of temperature anomaly, mean site temperature, thermal predictability, and warming rate on fledging date. Interactions between temperature anomaly and mean site temperature, thermal predictability or warming-rate characterize the effects site thermal traits on fledging plasticity. These mean effects Were estimated in separate intercept only models that estimate independently the mean parameter across the 50 species, after adjusting for phylogenetic distance between species. Bold term terms correspond to estimates for which their 95% posterior distribution do not cross 0.

Parameters	Variables	Median [95%IC]
A	Intercept	**168.73** [158.93; 178.83]
β	Temperature anomaly	**-2.18** [-2.82; -1.56]
δ	Mean site temperature	**-1.73** [-2.59; -0.76]
φ	Thermal predictability	0.01 [-0.22; 0.22]
θ	Warming rate	2.20 [-1.59; 5.80]
γ_1	Temperature anomaly * mean site temperature	**-0.13** [-0.24; -0.02]
γ_2	Temperature anomaly * Thermal predictabilty	**0.03** [0.01; 0.06]
γ_3	Temperature anomaly *Warming rate	**-1.70** [-3.27; -0.01]

Table 2: Species traits models

Table 2: Effects of species traits on mean fledging plasticity (β), and on between-species variation in between-site dependence of fledging plasticity on site thermal properties (γ1, γ2, γ3). These effects were estimated independently for each parameter across the 50 species, after adjusting for phylogenetic distance between species. Bold term terms correspond to estimates for which their 95% posterior distribution do not cross zero.

	β median[95%IC]	γ_1 median[95%IC]	γ_2 median[95%IC]	γ_3 median[95%IC]
	Temperature anomaly	Mean site temperature*Temperature anomaly	Predictability* Temperature anomaly	Warming rate* Temperature anomaly
Intercept	**-1.7 [-2.92;-0.39]**	-0.15 [-0.5;0.19]	0.06 [-0.03;0.15]	0.66 [-4.17;5.57]
Broods per year	-0.06 [-0.55;0.4]	-0.04 [-0.16;0.09]	**-0.03 [-0.06;0]**	1.48 [-0.07;2.99]
Trophic Niche: Invertivore	-0.3 [-1.16;0.52]	0.04 [-0.2;0.29]	0.01 [-0.05;0.08]	-1.88 [-7.17;3.33]
Trophic Niche: Omnivore	-0.7 [-1.53;0.1]	0.11 [-0.13;0.35]	0.02 [-0.04;0.09]	-2.72 [-8.14;2.57]
Migration distance	**0.33 [0.1;0.55]**	**0.07 [0;0.13]**	-0.01 [-0.03;0.01]	0.68 [-0.59;1.96]
Thermal maximum	-0.07 [-0.26;0.13]	0.07 [-0.01;0.15]	**0.02 [0;0.04]**	-0.95 [-2.36;0.46]
Phylogeny (sd)	0.1 [0.04;0.15]	0.01 [0;0.03]	0 [0;0.01]	0.2 [0.02;0.49]

Author contributions

PC led the formal analysis and writing of the original draft. PC, CT, PYH shared conceptualization, planning the analysis and editing drafts. TB helped with the analysis and interpreting the results. RR is responsible for ensuring data consistency (as head of EuroCES) and gathered datasets provided by organisers from each country who coordinated and supported the efforts of hundreds of volunteer ringers: PL, JA, JvR, AL, KT, ZK, HvdJ, IH, CH, OG and WF. All authors commented on the manuscript.

Acknowledgements

We thank the thousands of volunteers, ringers and assistants, who contributed to CES-based long-term monitoring of European passerines. We thank BNP Paribas Foundation for funding PC’s salary and supporting this project. A special thanks to Catriona Morrison who helped with data preparation, Noa Rigoudy, Anne Charmantier and Luis-Miguel Chevin for useful discussions. We also thank Paul Dufour who helped providing and interpreting the phylogeny.

Conflict of interest

Authors declare no conflict of interest.

Supporting information

Appendix 1: Post-breeding truncation

Because age-specific post-breeding movements and migration phenology affect the seasonal pattern in juvenile/adult ratio in some species, we removed capture sessions late in the season. In general, the breeding period can be considered to end on August 1st but for some species and/or biogeographic regions an earlier temporal truncation was required to avoid the confounding effects of juvenile dispersal and/or early adult migration. For each species per region (see Capture data), we examined the overall pattern of juvenile proportion between April and September using generalized additive mixed models (package mgcv). If a marked secondary decrease (adult-biased movements) or increase (juvenile-biased movements) in the proportion of juveniles before August 1st (day 213) was observed, we adjusted the end date so that it was set before the direction shift in the curve (Figure S1).

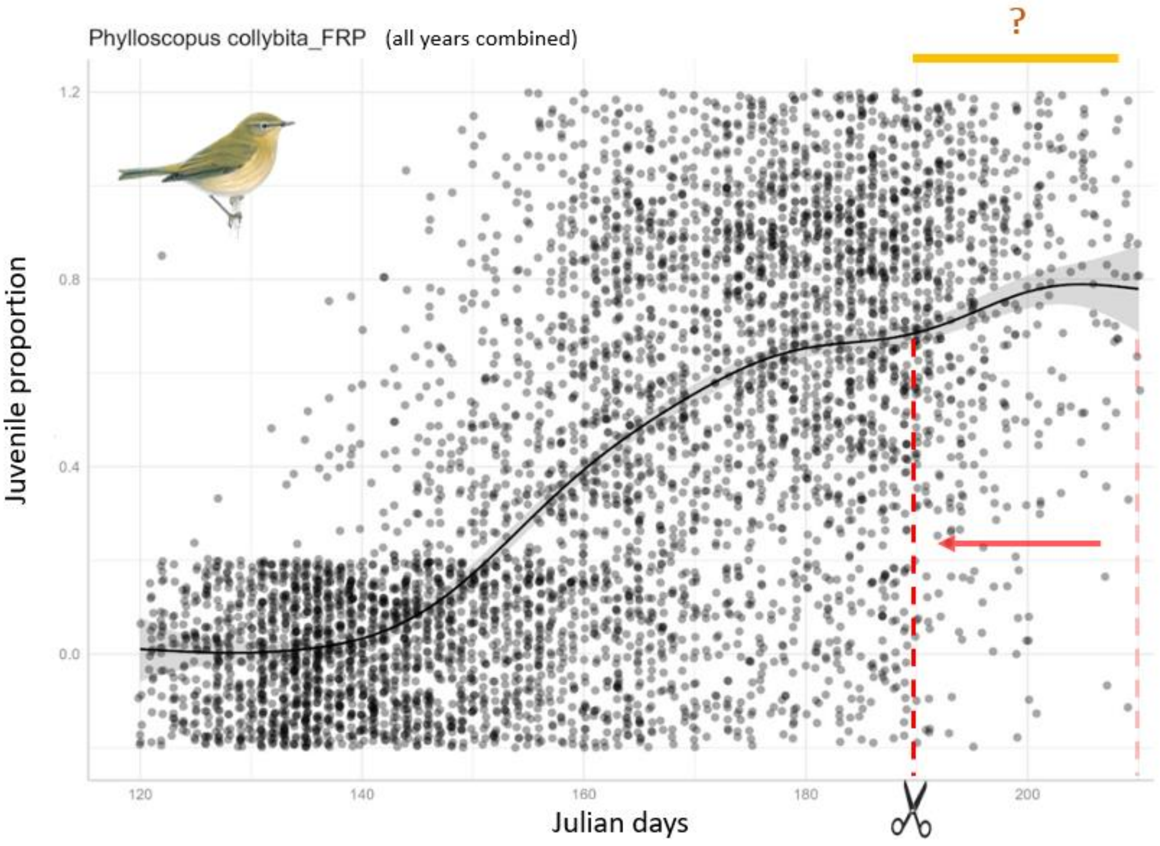


Figure S1: Juvenile proportion of the common chiffchaff Phylloscopus collybita in France. We can identify a bump in juvenile proportion which starts after day 190 (10th July) and can be due to either 1) a reduced capturability of adults, e.g., due to moulting or 2) an earlier dispersal of juvenile (relative to adults). In this situation, we removed all captures sessions that occurred after the 10th of July (right truncation on julian day = 190)

Appendix 2: Fledging time assessment

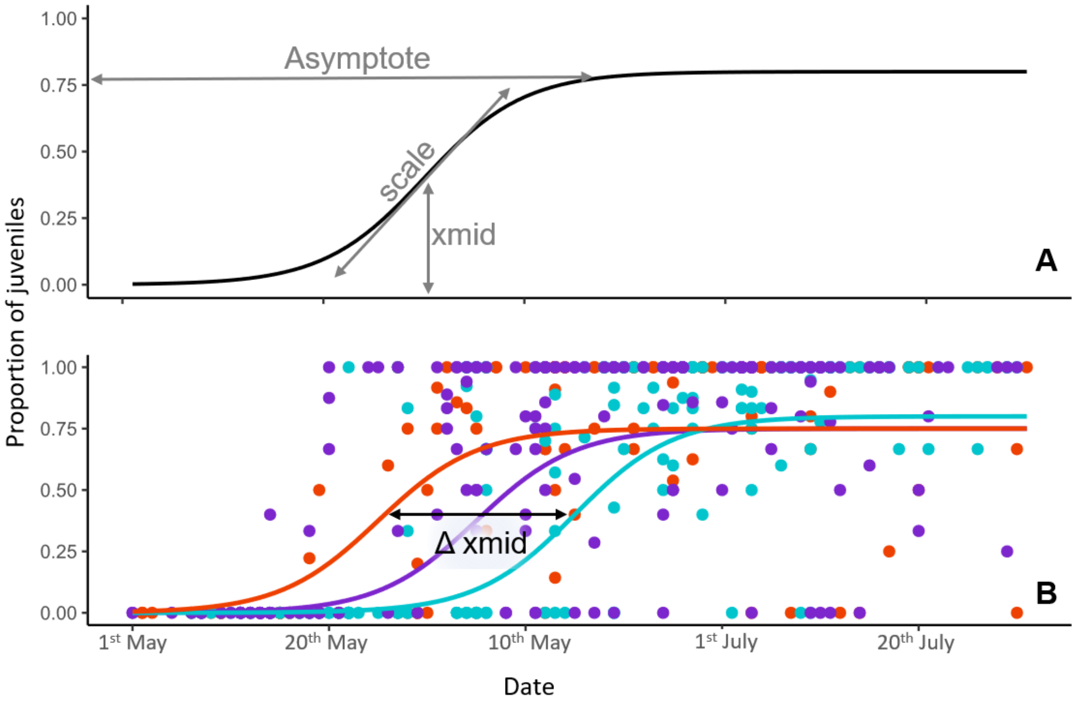


Figure S2: Modelling the pattern of temporal emergence of juveniles throughout a breeding period. A) In early spring the proportion of juveniles is 0: juveniles are still in the egg or in the nest. A plateau is reached in June, when most chicks have fledged. B) Examples of change of the proportion of juveniles of blue tits in France (102 capture sites) during the breeding season for 3 years (2009 in orange, 2010 in blue and 2011 in purple). Each dot represents a capture session at a site. Phenological changes between years are documented by the change in estimates of xmid. Extracted from Cuchot et al. (2024).

Appendix 3: Temperature window

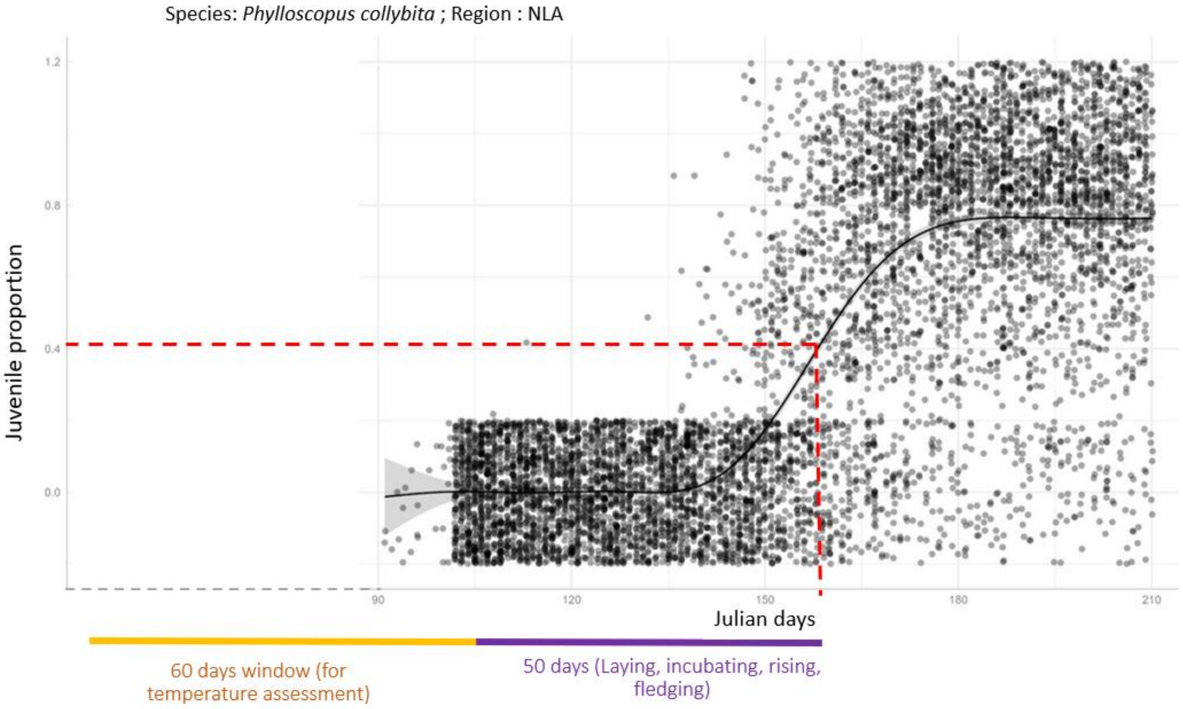


Figure S3: Juvenile proportion of the Common Chiffchaff Phylloscopus collybita in the Netherlands. On average across years, mean fledging peak is estimated to occur at the beginning of June (julian day = 160). For the Chiffchaff model, the 60-days temperature window of each site located in the Netherlands will end on April 10th (julian day = 110).

Appendix 4: Temperature unpredictability – Calculation and correlation with other temperature metrics

Temperature unpredictability

We computed a metric of temperature unpredictability, for each site, representative of between-day variance in mean temperature. To do so, we first estimated the between-year average temperature profile, i.e., how the temperature increases throughout spring, using a General Additive Model (GAM; Figure S4). Then, for each year, we averaged daily temperature deviation to this GAM and subtracted this yearly mean to each daily residual values to discard the signal of differences in mean temperature among years (i.e., warm vs. cold years, eq.1).

$$\overline{Deviation}_{j,k} = \frac{1}{D}\sum_{d=1}^{D_k}\left(Temp_{d,j,k} - \widehat{Temp}_{d,k}\right) \tag{1}$$

Eventually, we computed the between-day variance in these yearly centered temperature deviations from the GAM (eq.2) along the temperature window, for the 1950-2022 period (eq.3).

$$Temp^{*}_{d,j,k} = Temp_{d,j,k} - \overline{Deviation}_{j,k} \tag{2}$$

$$Unpredictability_{k} = \sum_{d=1}^{D}(Temp^{*}_{d,j,k} - \overline{Temp}_{d,k})^{2} \tag{3}$$

This metric of unpredictability indeed corresponds to a residual variance, higher values indicating lower between-day temperature predictability.

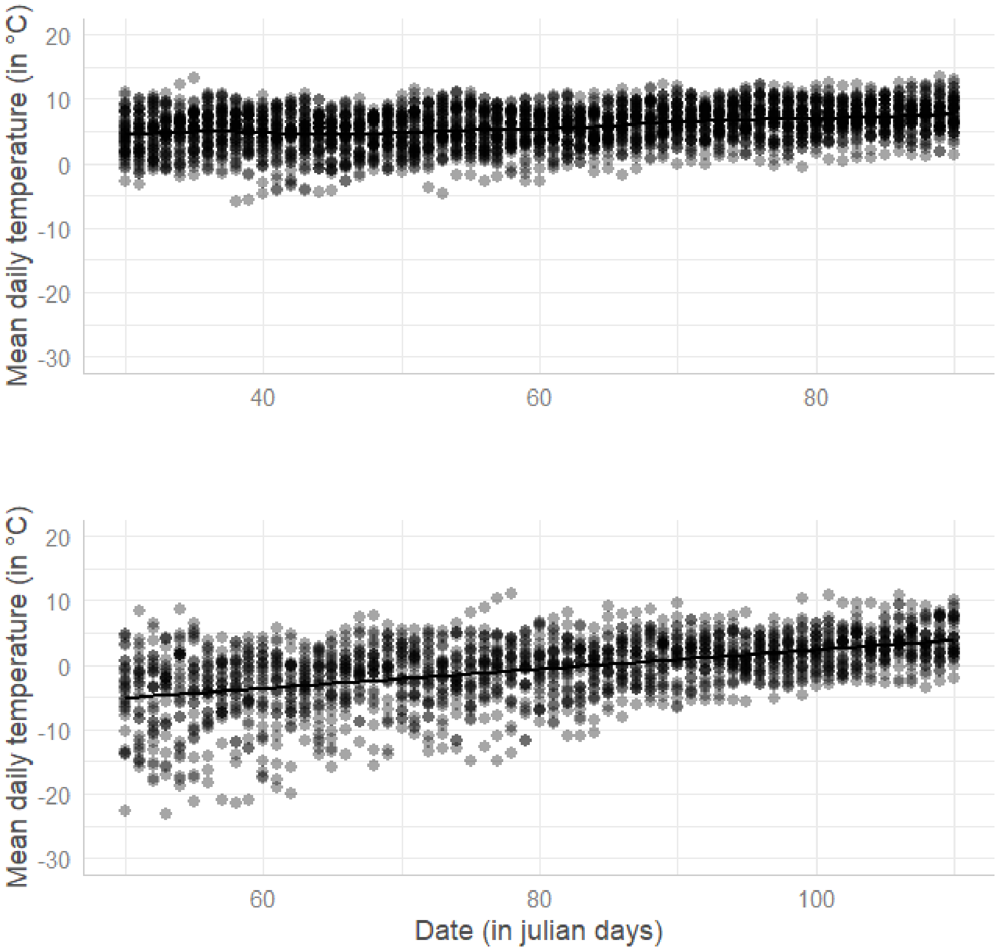


Figure S4: Spring temperature profiles defined using GAM, for two distinct sites, one very predictable (upper panel) and less predictable (lower panel).

Correlations

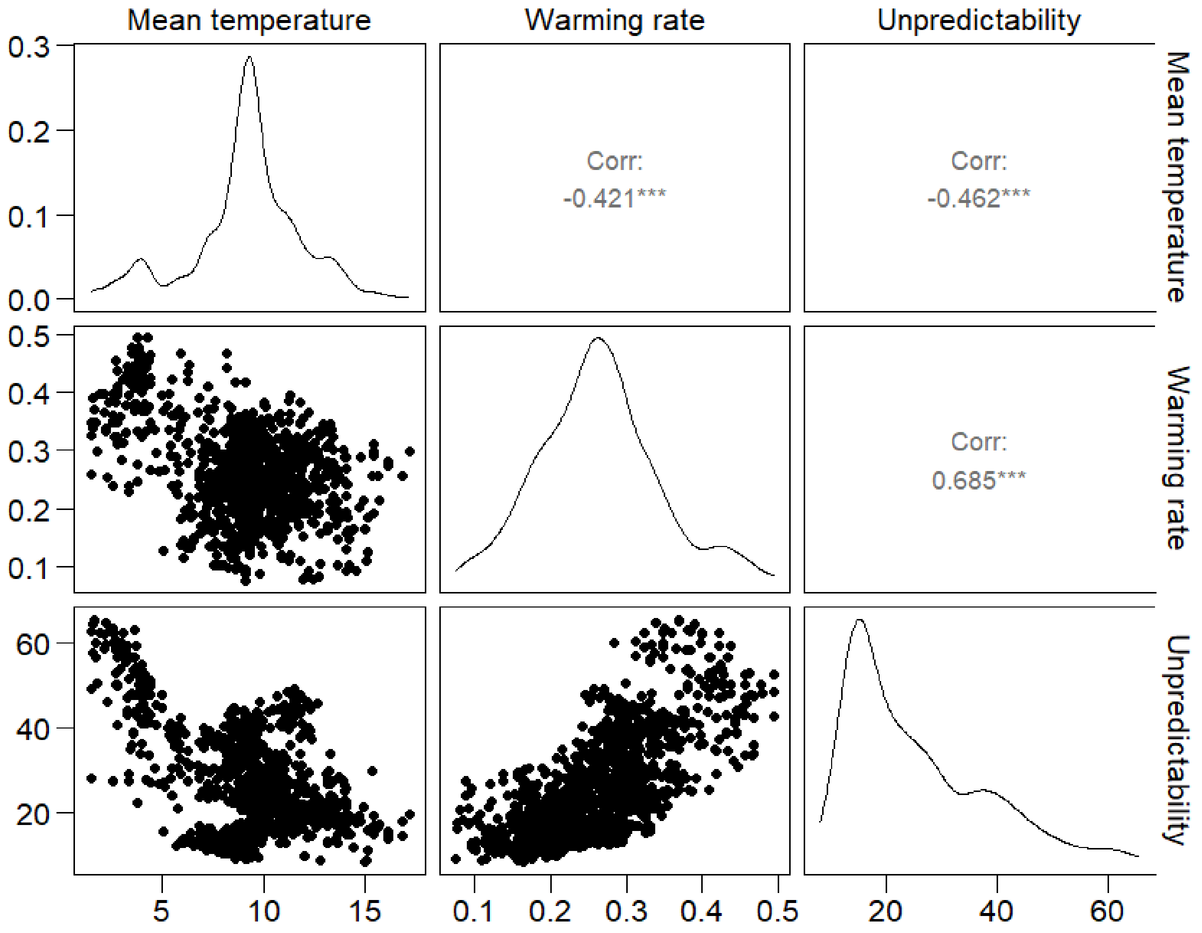


Figure S5: Correlation plot between the three site-level temperature characteristics: Mean temperature, warming rate and unpredictability.

Appendix 5: Phylogeny

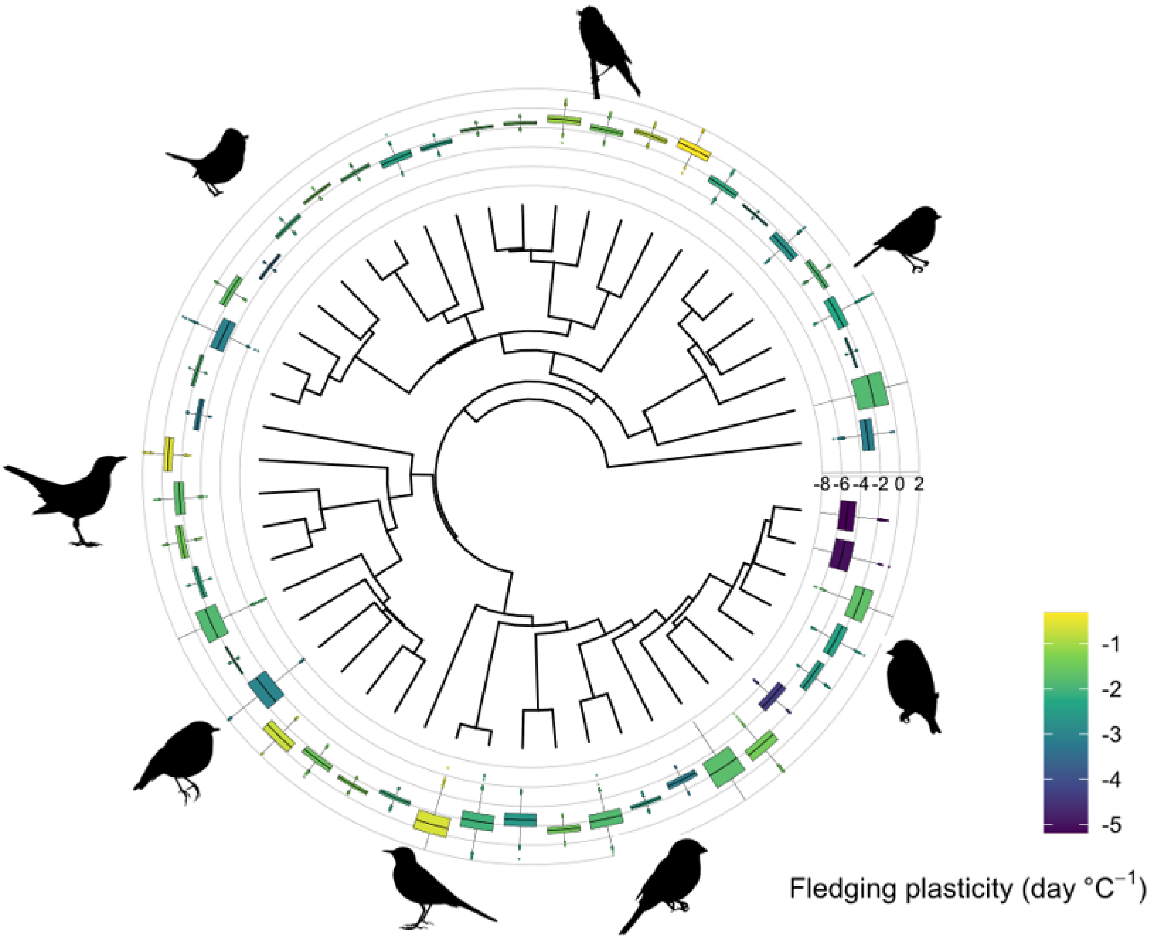


Figure S6: Estimates of mean fledging plasticity for 50 European passerine species. Histograms are representative of the posterior distributions of the β estimate, i.e., the mean response to spring temperature anomaly. Phylogeny explains only 1.2 percent of the between species variation in fledging plasticity.

Appendix 6: Data summary

Table S1: Table summarizing capture monitoring designs per country. Spain and Germany have two and three codes as capture data are managed at the regional scale. CONT_ID corresponds to grouping we did for some countries that depends on capture designs and biogeographical similarities. ***M_num_sess*** *refers to the mean number of sessions per year and capture site,* ***mean_n_year*** *to the mean number of years monitored per site,* ***mean_time_btw_sess*** *to the mean number of days between two capture sessions,* ***mean_start*** *to the mean date of the first session, and* ***mean_end*** *to the mean date of the last session.* ***First_year*** *indicates the first year of recorded data,* ***N_sites*** *the total number of capture sites, and* ***N_birds*** *the total number of captured birds.*

Code	Country	CONT_ID	m_num sess	mean_n year	mean_time btw_sess	mean_start	mean_end	First year	N_sites	n_birds
CZP	Czech Republic	EUR_CONT	8.9	8.1	10.6	3-may	26-jul	2004	48	116149
DEH	Hiddensee (Germany)	EUR_CONT	11.8	5.3	10.2	4-may	22-aug	1999	103	172768
DER	Radolfzell (Germany)	EUR_CONT	11.6	3.8	10.3	5-may	22-aug	2000	24	20936
DEW	Helgoland (Germany)	EUR_CONT	11.6	4.3	10.3	4-may	22-aug	2001	41	69056
DKC	Danemark	SCAND	11.9	5.7	10	5-may	22-aug	2004	9	17593
ESA	San Sebastian (Spain)	SP	6.7	4.9	15.4	8-may	4-aug	2010	36	38287
ESI	Madrid (Spain)	SP	10.5	5.7	9.8	15-apr	16-jul	1999	144	212106
FRP	France	FR	3.8	7	16.6	18-may	4-jul	1988	412	357806
GBT	UK+Ireland	UK	10.9	7.5	11.3	3-may	23-aug	1983	583	1378587
HES	Switzerland	EUR_CONT	7.5	4	14	4-may	3-aug	2013	1	781
HGB	Hungary	EUR_CONT	9.4	9.7	10	18-apr	6-jul	2004	54	155952
NLA	Netherlands	NL	11.2	11.4	10.6	17-apr	3-aug	1994	97	436858
SFH	Finland	SCAND	10.1	6.1	11.2	12-may	22-ug	1986	196	290498
SPC	Catalunya (Spain)	SP	7.6	6.8	12	12-may	30-jul	1991	130	155127
SVS	Sweden	SCAND	11.4	5.6	10.3	8-may	23-aug	2004	59	80763

Appendix 7: Species model coefficients

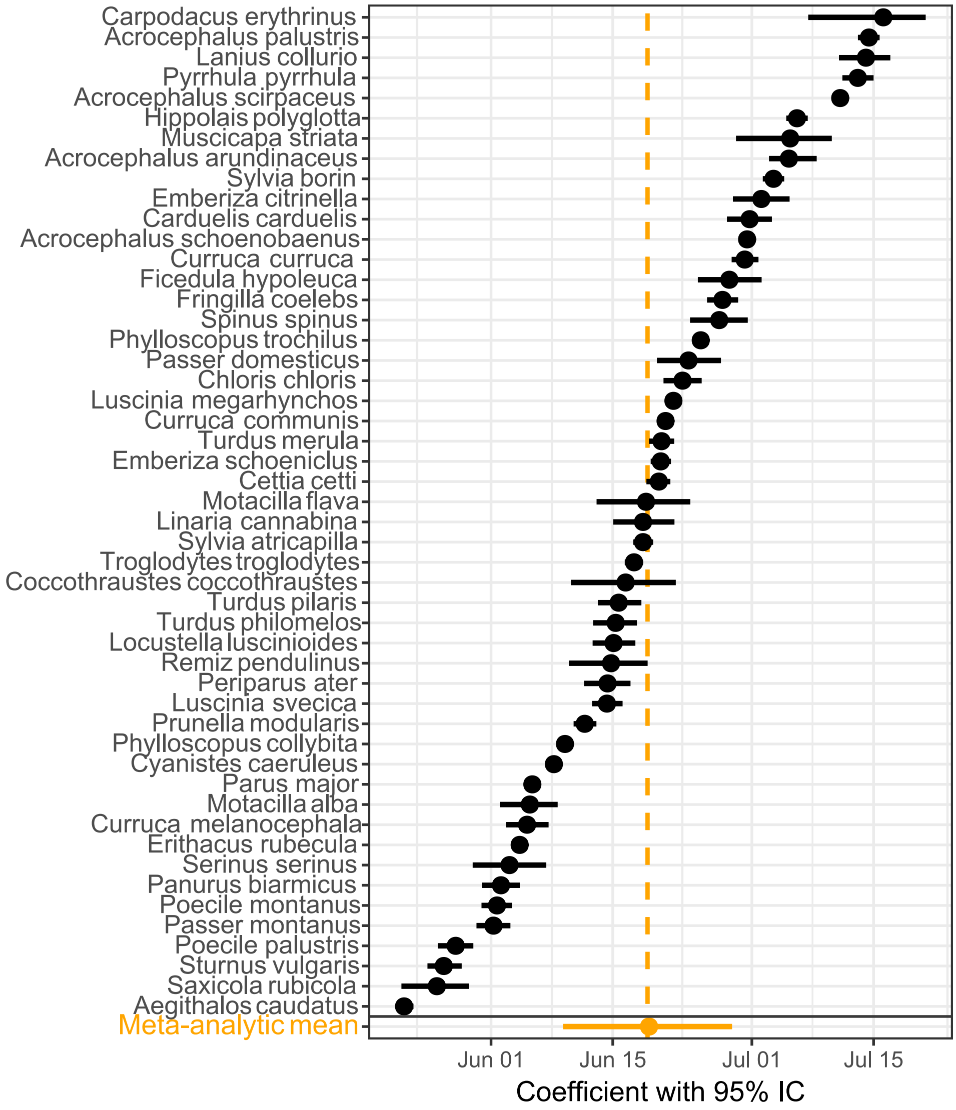


Figure S7: Posterior distributions of estimates of mean fledging date (α parameter, i.e., model intercept) per species, across all European sites. Meta-analytic mean takes species posterior distributions (as a measure of uncertainty) and phylogeny into account.

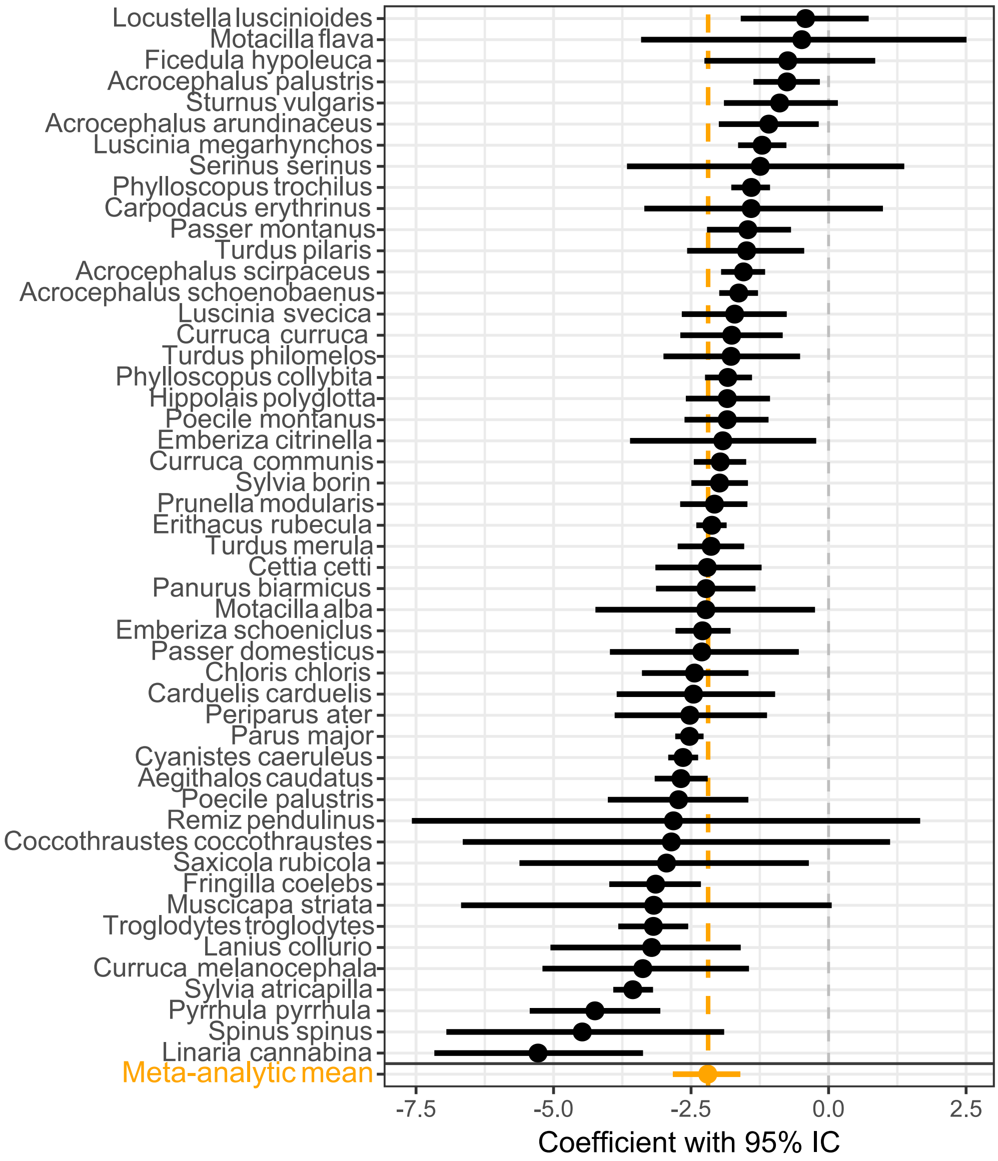


Figure S8: Posterior distributions of estimates of phenological response to spring temperature anomaly (β *parameter, i.e., fledging plasticity) per species, across all European sites. Meta-analytic mean takes species posterior distributions (as a measure of uncertainty) and phylogeny into account.*

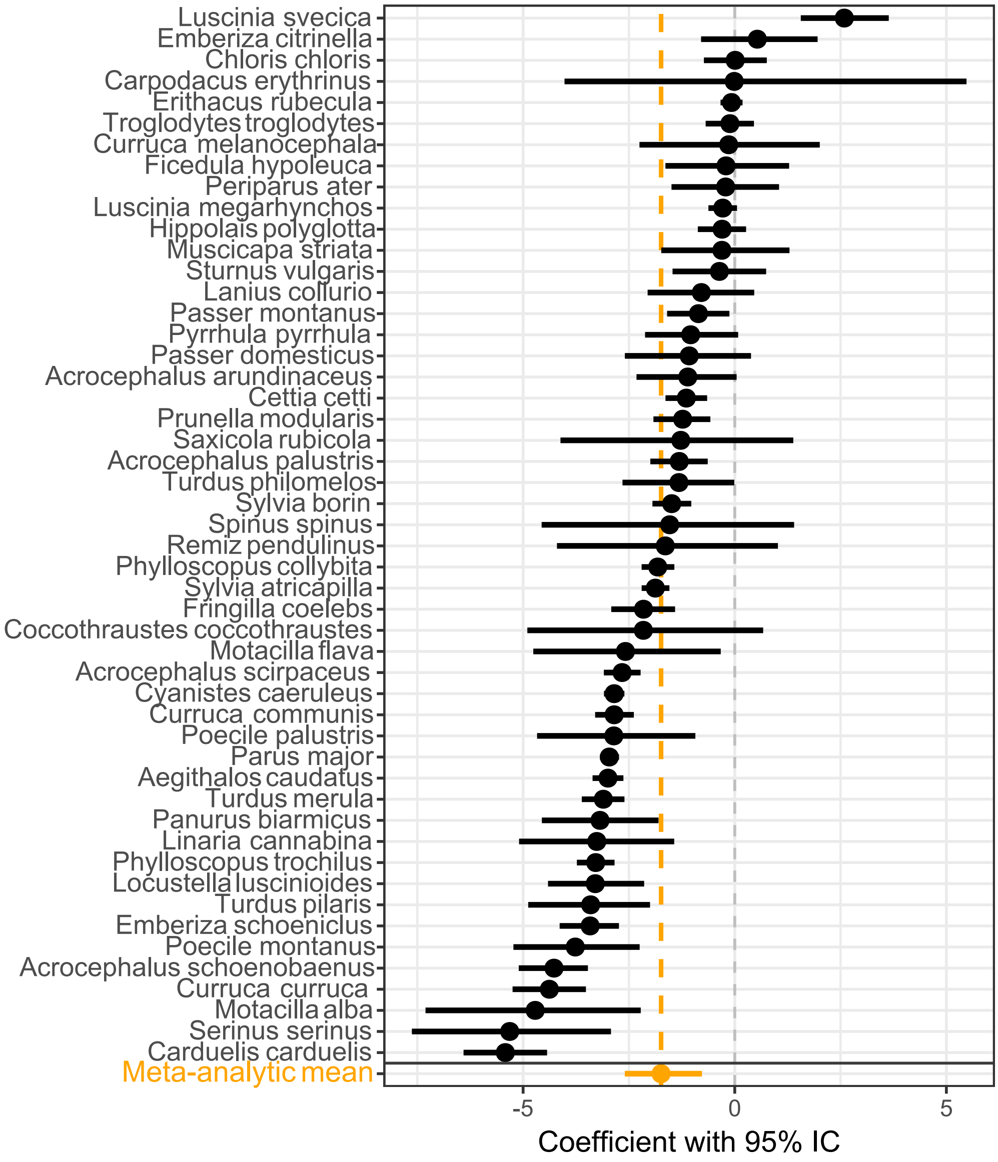


*Figure S9: Posterior distributions of estimates of phenological response to mean site temperature (**δ** parameter) per species, across all European sites. Meta-analytic mean takes species posterior distributions (as a measure of uncertainty) and phylogeny into account.*

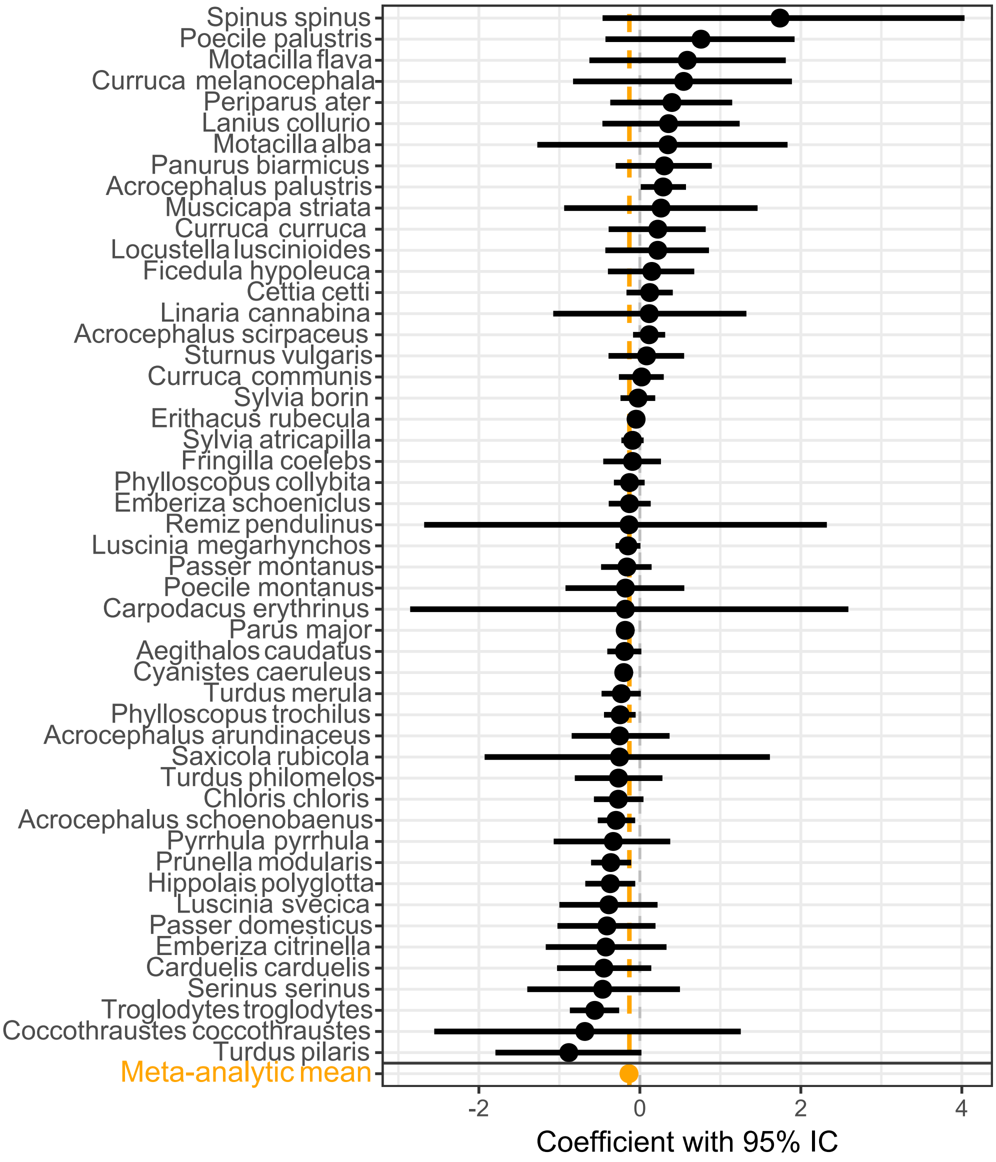


*Figure S10: Posterior distributions of estimates of the effect of mean site temperature on fledging plasticity (**γ_1** parameter) per species, across all European sites. Meta-analytic mean takes species posterior distributions (as a measure of uncertainty) and phylogeny into account.*

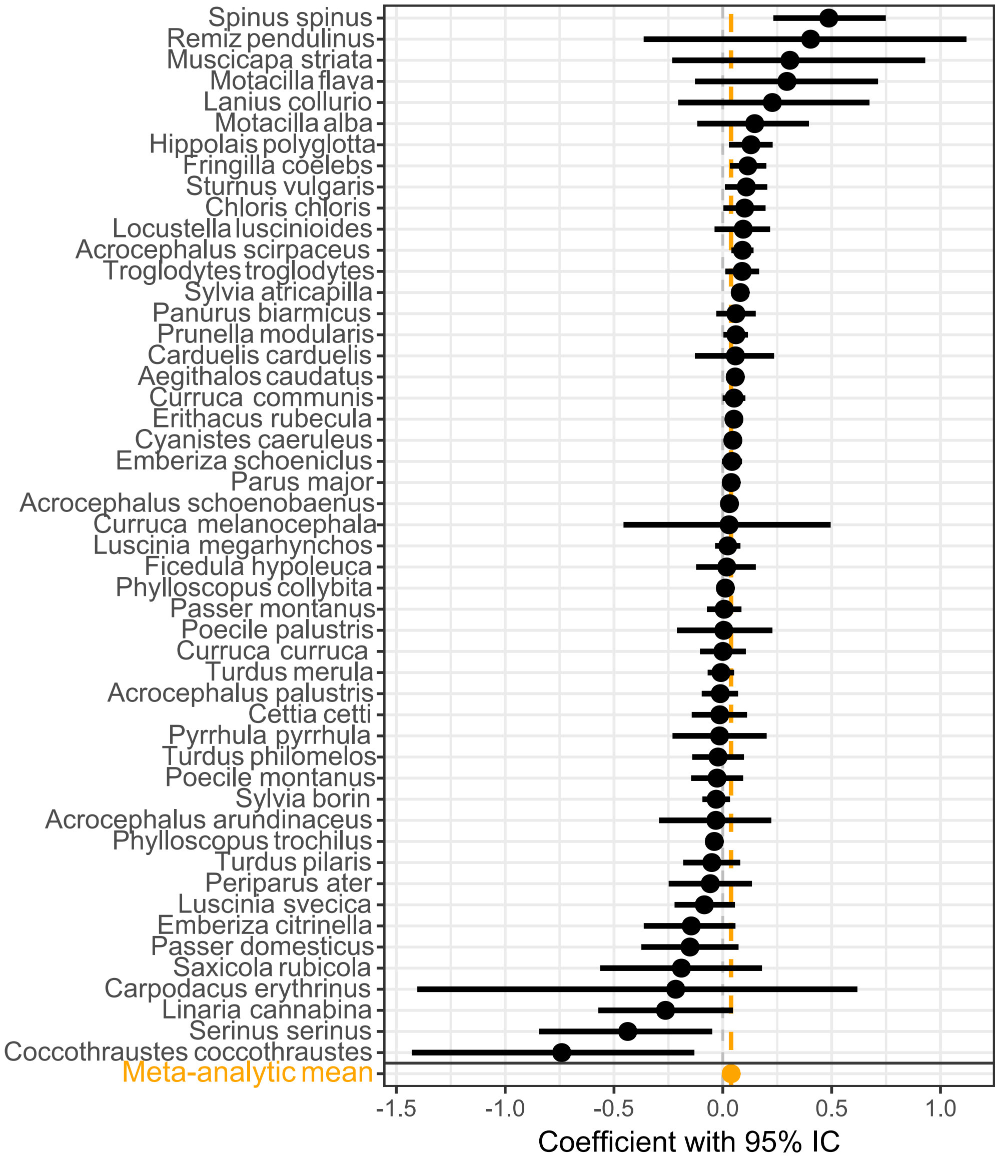


Figure S11: Posterior distributions of estimates of the effect of thermal predictability on fledging plasticity (γ_2 parameter) per species, across all European sites. Meta-analytic mean takes species posterior distributions (as a measure of uncertainty) and phylogeny into account.

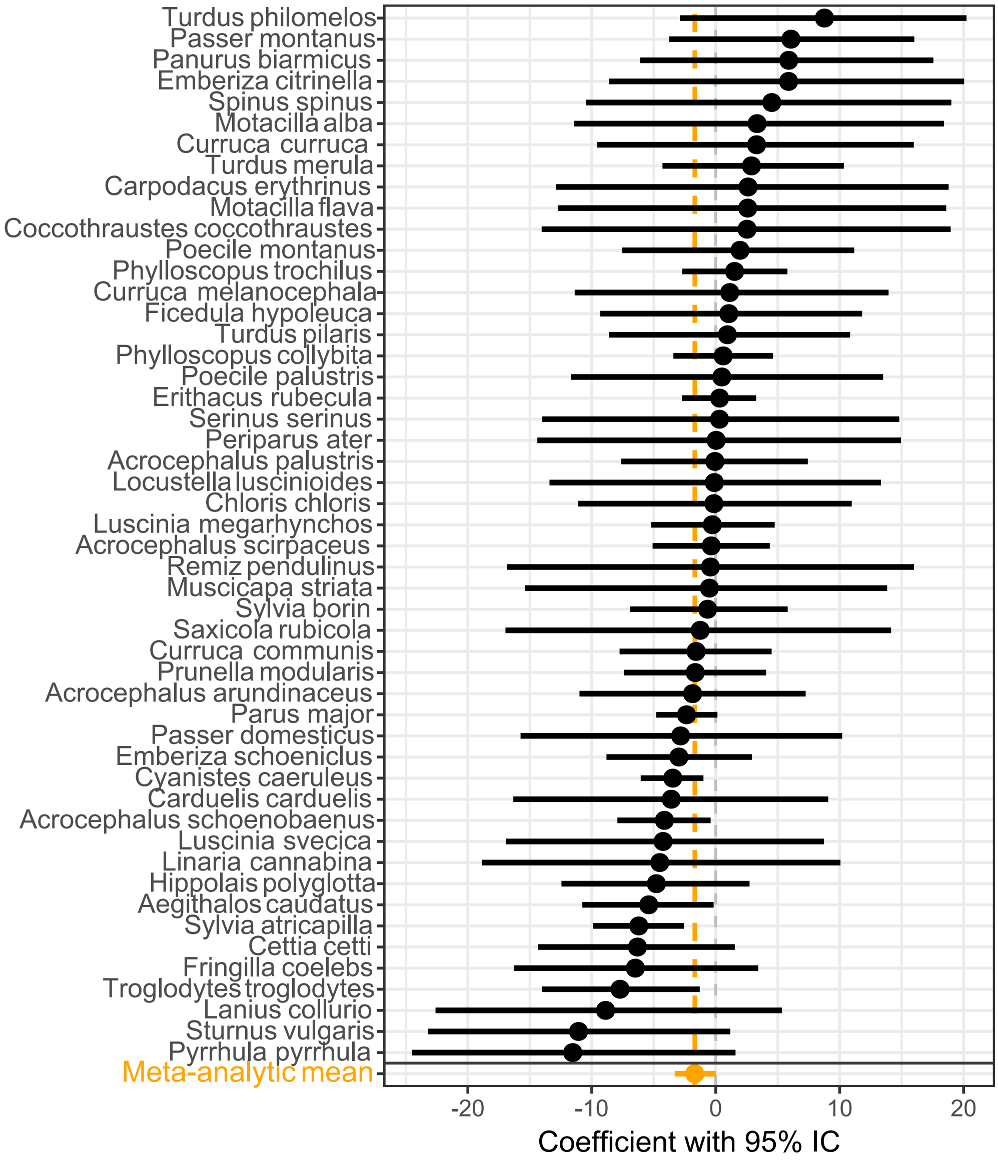


Figure S12: Posterior distributions of estimates of the effect of warming rate on fledging plasticity (γ_3 *parameter) per species, across all European sites. Meta-analytic mean takes species posterior distributions (as a measure of uncertainty) and phylogeny into account.*

Table S2: Posterior distributions and their 95% confidence interval of the species model parameters that explain variations of fledging date in response to spring temperature anomaly (ß), mean site temperature (δ), thermal predictability (φ), warming rate (ϑ) and these last three variable in interaction with spring temperature anomaly (γ1, γ2 and γ3) to assess their effect on fledging plasticity (γ1, γ2 and γ3).

Aegithalos caudatus	*Acrocephalus scirpaceus*	*Acrocephalus schoenobaenus*	*Acrocephalus palustris*	*Acrocephalus arundinaceus*		
141 [140;142.08]	191.16 [190.24;192.1]	180.45 [179.5;181.37]	194.47 [193.2;195.69]	185.26 [182.97;188.46]	Intercept	α
-2.68 [-3.16;-2.2]	-1.55 [-1.95;-1.15]	-1.63 [-1.99;-1.28]	-0.76 [-1.37;-0.16]	-1.09 [-2;-0.18]	Temperature anomaly	β
-2.99 [-3.36;-2.63]	-2.66 [-3.09;-2.22]	-4.27 [-5.1;-3.47]	-1.31 [-1.99;-0.64]	-1.11 [-2.32;0.04]	Mean site temperature	δ
-0.41 [-0.49;-0.34]	-0.09 [-0.2;0.02]	0.22 [0.11;0.33]	0.13 [-0.06;0.32]	0.75 [0.26;1.23]	Thermal predictability	φ
13.37 [4.76;22.1]	0.13 [-9.44;9.98]	26.28 [15.67;36.93]	-2.38 [-14.79;10.3]	0.74 [-13.03;14.03]	Warming rate	θ
-0.19 [-0.4;0.02]	0.12 [-0.08;0.31]	-0.3 [-0.52;-0.06]	0.29 [0.01;0.57]	-0.25 [-0.85;0.37]	Temperature anomaly* Mean site temperature	γ_1
0.06 [0.01;0.1]	0.09 [0.04;0.14]	0.03 [0;0.07]	-0.01 [-0.1;0.07]	-0.03 [-0.29;0.22]	Thermal predictability* Temperature anomaly	γ_2
-5.4 [-10.76;-0.17]	-0.36 [-5.09;4.36]	-4.14 [-7.93;-0.41]	-0.07 [-7.63;7.43]	-1.87 [-10.99;7.26]	Warming rate* Temperature anomaly	γ_3
4.99 [4.48;5.56]	8.28 [7.67;8.93]	9.12 [8.51;9.78]	4.83 [4.05;5.82]	5.57 [3.98;7.28]		Random int (sd)
0.71 [0.05;1.51]	1.06 [0.56;1.56]	0.23 [0.03;0.51]	0.41 [0.07;0.88]	0.8 [0.02;2.15]		Random slope (sd)

Curruca communis	*Coccothraustes coccothraustes*	*Chloris chloris*	*Cettia cetti*	*Carpodacus erythrinus*	*Carduelis carduelis*
171.07 [170.14;172.04]	166.48 [160.18;172.25]	173.03 [170.84;175.23]	170.3 [168.87;171.63]	196.12 [187.48;200.99]	180.74 [178.13;183.3]
-1.97 [-2.45;-1.5]	-2.86 [-6.65;1.12]	-2.44 [-3.39;-1.46]	-2.21 [-3.15;-1.22]	-1.41 [-3.35;0.99]	-2.46 [-3.85;-0.97]
-2.85 [-3.3;-2.38]	-2.16 [-4.9;0.67]	0.01 [-0.73;0.76]	-1.14 [-1.64;-0.65]	-0.01 [-4.02;5.48]	-5.42 [-6.41;-4.43]
0.3 [0.22;0.39]	1.43 [0.55;2.37]	-0.1 [-0.32;0.13]	-0.32 [-0.54;-0.1]	0.9 [-0.3;3.25]	-0.15 [-0.46;0.17]
-2.18 [-11.45;7.35]	-0.57 [-16.97;15.78]	3.27 [-12.03;18.24]	4.07 [-6.95;14.5]	0.92 [-15.56;17.23]	-8.02 [-22.86;7.09]
0.02 [-0.26;0.3]	-0.68 [-2.55;1.25]	-0.27 [-0.57;0.05]	0.12 [-0.17;0.41]	-0.18 [-2.85;2.59]	-0.45 [-1.03;0.14]
0.05 [0;0.1]	-0.74 [-1.43;-0.13]	0.1 [0;0.2]	-0.01 [-0.14;0.11]	-0.22 [-1.4;0.62]	0.06 [-0.13;0.24]
-1.58 [-7.76;4.51]	2.53 [-14.04;18.96]	-0.14 [-11.09;10.98]	-6.31 [-14.34;1.54]	2.61 [-12.9;18.79]	-3.59 [-16.33;9.08]
4.02 [3.45;4.58]	10.34 [5.51;15.46]	17.43 [15.58;19.3]	5.41 [4.46;6.46]	4.32 [0.15;16.08]	14 [11.85;16.24]
0.67 [0.19;1.27]	4.19 [0.11;9.03]	1.23 [0.18;2.82]	1.01 [0.32;1.88]	1.81 [0.13;4.58]	1.51 [0.41;3.04]

Erithacus rubecula	*Emberiza schoeniclus*	*Emberiza citrinella*	*Cyanistes caeruleus*	*Curruca melanocephala*	*Curruca curruca*
154.29 [153.51;155.06]	170.52 [169.36;171.69]	182.09 [178.82;185.34]	158.23 [157.42;159.06]	155.14 [152.72;157.62]	180.18 [178.67;181.76]
-2.12 [-2.4;-1.85]	-2.29 [-2.78;-1.78]	-1.92 [-3.61;-0.22]	-2.65 [-2.92;-2.37]	-3.38 [-5.2;-1.45]	-1.76 [-2.7;-0.83]
-0.08 [-0.34;0.18]	-3.42 [-4.14;-2.74]	0.53 [-0.8;1.96]	-2.85 [-3.09;-2.61]	-0.14 [-2.25;2.01]	-4.38 [-5.25;-3.52]
0.56 [0.5;0.62]	-0.19 [-0.31;-0.07]	-0.26 [-0.64;0.12]	-0.22 [-0.28;-0.17]	0.42 [-0.43;1.29]	0.02 [-0.11;0.16]
-1.48 [-9.96;6.6]	-1.71 [-13.46;9.85]	2.75 [-12.96;18.3]	2.5 [-4.24;9.02]	5.09 [-9.79;19.7]	13.01 [-0.96;26.51]
-0.05 [-0.14;0.04]	-0.13 [-0.39;0.14]	-0.42 [-1.17;0.33]	-0.2 [-0.3;-0.1]	0.54 [-0.83;1.89]	0.22 [-0.39;0.82]
0.05 [0.03;0.07]	0.04 [0;0.09]	-0.15 [-0.36;0.06]	0.05 [0.03;0.06]	0.03 [-0.46;0.5]	0 [-0.11;0.11]
0.32 [-2.73;3.26]	-2.97 [-8.81;2.91]	5.88 [-8.62;20.04]	-3.46 [-6.05;-0.99]	1.13 [-11.38;13.95]	3.3 [-9.55;15.98]
7.46 [7.05;7.89]	7.52 [6.79;8.26]	11.32 [8.81;14.14]	5.68 [5.36;6.02]	7.08 [5.2;9.18]	3.84 [2.25;5.39]
0.6 [0.36;0.87]	0.57 [0.03;1.31]	1.41 [0.37;3.07]	0.31 [0.07;0.55]	1.11 [0.1;2.61]	1.01 [0.12;1.96]

Locustella luscinioides	*Linaria cannabina*	*Lanius collurio*	*Hippolais polyglotta*	*Fringilla coelebs*	*Ficedula hypoleuca*
165.1 [162.68;167.6]	168.48 [165.06;172.1]	194.12 [191.02;196.93]	186.19 [184.96;187.43]	177.62 [175.84;179.42]	178.41 [174.78;182.12]
-0.42 [-1.6;0.73]	-5.28 [-7.17;-3.37]	-3.22 [-5.06;-1.6]	-1.84 [-2.6;-1.06]	-3.14 [-3.99;-2.32]	-0.74 [-2.26;0.85]
-3.3 [-4.41;-2.14]	-3.26 [-5.1;-1.43]	-0.79 [-2.06;0.46]	-0.3 [-0.87;0.27]	-2.16 [-2.92;-1.41]	-0.21 [-1.64;1.28]
-0.3 [-0.52;-0.09]	0.62 [0.14;1.13]	0.11 [-0.56;0.73]	0.2 [-0.02;0.41]	0.36 [0.2;0.52]	0.45 [-0.16;1.03]
1.89 [-13.51;17.28]	-1.54 [-17.42;14.06]	5.5 [-10.1;21.21]	4.47 [-6.91;15.76]	1.54 [-12.99;15.54]	1.73 [-14.04;17.16]
0.22 [-0.43;0.86]	0.12 [-1.08;1.32]	0.36 [-0.47;1.24]	-0.37 [-0.68;-0.06]	-0.09 [-0.46;0.26]	0.15 [-0.4;0.68]
0.09 [-0.04;0.22]	-0.26 [-0.57;0.05]	0.23 [-0.21;0.67]	0.13 [0.03;0.23]	0.11 [0.03;0.2]	0.02 [-0.12;0.15]
-0.11 [-13.41;13.33]	-4.51 [-18.86;10.07]	-8.89 [-22.61;5.34]	-4.79 [-12.45;2.73]	-6.49 [-16.26;3.43]	1.06 [-9.32;11.81]
4.89 [3.11;6.83]	11.18 [8.23;14.48]	5.6 [3.32;8.08]	5.22 [4.17;6.32]	11.77	14.87
1.52 [0.5;2.81]	3.74 [1.22;6.57]	1.37 [0.12;3.21]	0.45 [0.02;1.14]	2.14 [1.18;3.34]	1.05 [0.02;2.32]

Panurus biarmicus	*Muscicapa striata*	*Motacilla flava*	*Motacilla alba*	*Luscinia svecica*	*Luscinia megarhynchos*
152.14 [149.97;154.3]	185.41 [179.17;190.2]	168.83 [163.14;173.92]	155.46 [152;158.66]	164.33 [162.61;166.13]	171.98 [171.03;172.95]
-2.23 [-3.14;-1.33]	-3.18 [-6.68;0.06]	-0.49 [-3.41;2.51]	-2.23 [-4.24;-0.25]	-1.71 [-2.67;-0.76]	-1.21 [-1.65;-0.77]
-3.18 [-4.56;-1.8]	-0.3 [-1.74;1.29]	-2.58 [-4.76;-0.33]	-4.71 [-7.31;-2.22]	2.59 [1.56;3.64]	-0.28 [-0.62;0.05]
-0.67 [-0.92;-0.42]	0.87 [0.23;1.61]	-0.52 [-1.36;0.32]	0.01 [-0.42;0.44]	0.29 [0.04;0.52]	-0.1 [-0.23;0.02]
1.86 [-13.41;17.38]	-2.46 [-18.31;13.55]	1.05 [-14.6;16.94]	0.27 [-15.51;16.42]	-2.33 [-18;13.04]	-14.22 [-24.06;-4.45]
0.3 [-0.3;0.89]	0.26 [-0.94;1.46]	0.59 [-0.63;1.81]	0.35 [-1.27;1.84]	-0.38 [-1;0.22]	-0.15 [-0.3;0.01]
0.06 [-0.03;0.15]	0.31 [-0.23;0.93]	0.29 [-0.13;0.71]	0.15 [-0.12;0.4]	-0.08 [-0.22;0.06]	0.02 [-0.04;0.08]
5.89 [-6.1;17.56]	-0.51 [-15.39;13.83]	2.58 [-12.72;18.6]	3.34 [-11.41;18.42]	-4.25 [-16.94;8.73]	-0.27 [-5.2;4.76]
7.76 [6.01;9.68]	6.08 [0.74;12.64]	13.28 [8.39;19.35]	6.36 [2.77;9.96]	3.71 [0.07;6.84]	5.01 [4.42;5.63]
1.05 [0.14;2.1]	2.34 [0.04;6.51]	3.69 [0.69;6.93]	1.49 [0.16;3.41]	0.84 [0.16;1.83]	0.33 [0.03;0.94]

Phylloscopus trochilus	*Phylloscopus collybita*	*Periparus ater*	*Passer montanus*	*Passer domesticus*	*Parus major*
175.12 [174.45;175.81]	159.51 [158.62;160.42]	164.4 [161.69;167.04]	151.28 [149.32;153.23]	173.71 [170.08;177.44]	155.75 [154.88;156.63]
-1.4 [-1.77;-1.06]	-1.83 [-2.25;-1.39]	-2.52 [-3.89;-1.12]	-1.47 [-2.21;-0.68]	-2.31 [-3.98;-0.54]	-2.53 [-2.79;-2.27]
-3.28 [-3.73;-2.84]	-1.82 [-2.2;-1.43]	-0.21 [-1.49;1.05]	-0.86 [-1.6;-0.13]	-1.08 [-2.6;0.38]	-2.96 [-3.18;-2.73]
0.15 [0.06;0.23]	-0.11 [-0.17;-0.05]	0.78 [0.42;1.13]	-0.35 [-0.56;-0.13]	-0.62 [-1.14;-0.09]	-0.23 [-0.28;-0.18]
12.49 [4.03;20.63]	0.65 [-7.59;8.64]	-6.26 [-21.39;9.64]	-1.64 [-16.15;12.97]	3.11 [-12.63;18.54]	12.34 [5.84;18.84]
-0.25 [-0.45;-0.05]	-0.13 [-0.32;0.06]	0.4 [-0.37;1.15]	-0.16 [-0.48;0.15]	-0.41 [-1.02;0.19]	-0.18 [-0.27;-0.09]
-0.04 [-0.08;0]	0.01 [-0.02;0.04]	-0.06 [-0.25;0.13]	0.01 [-0.07;0.09]	-0.15 [-0.37;0.07]	0.04 [0.02;0.06]
1.52 [-2.7;5.79]	0.6 [-3.42;4.63]	0.04 [-14.39;14.95]	6.07 [-3.75;16.02]	-2.83 [-15.75;10.2]	-2.36 [-4.8;0.14]
5.88 [5.35;6.52]	4.74 [4.31;5.2]	8.73 [6.3;11.64]	8.21 [6.37;10.09]	21.38 [18.37;24.7]	6.11 [5.78;6.44]
0.3 [0.08;0.75]	0.46 [0.22;0.83]	1.63 [0.19;3.69]	0.47 [0.01;1.41]	1.51 [0.21;3.68]	0.3 [0.19;0.43]

Saxicola rubicola	*Remiz pendulinus*	*Pyrrhula pyrrhula*	*Prunella modularis*	*Poecile palustris*	*Poecile montanus*
144.77 [140.69;148.47]	164.8 [159.95;169.01]	193.18 [191.41;195]	161.78 [160.5;163.12]	146.94 [144.88;148.97]	151.69 [149.9;153.4]
-2.95 [-5.62;-0.36]	-2.82 [-7.58;1.67]	-4.25 [-5.43;-3.06]	-2.07 [-2.7;-1.48]	-2.73 [-4.01;-1.46]	-1.84 [-2.62;-1.09]
-1.28 [-4.12;1.38]	-1.64 [-4.2;1.02]	-1.04 [-2.12;0.08]	-1.23 [-1.92;-0.58]	-2.86 [-4.67;-0.93]	-3.77 [-5.23;-2.25]
-0.32 [-0.98;0.3]	0.53 [-0.3;1.41]	-0.68 [-0.94;-0.4]	0.5 [0.37;0.63]	-0.64 [-0.97;-0.29]	-0.3 [-0.54;-0.06]
-0.18 [-16.3;15.79]	-1.42 [-17.37;14.86]	10.45 [-4.18;24.66]	-7.82 [-19.44;4.4]	2.03 [-12.87;16.03]	1.47 [-12.35;15.31]
-0.25 [-1.93;1.62]	-0.13 [-2.68;2.32]	-0.33 [-1.07;0.38]	-0.36 [-0.61;-0.11]	0.76 [-0.43;1.92]	-0.18 [-0.92;0.55]
-0.19 [-0.56;0.18]	0.4 [-0.36;1.12]	-0.02 [-0.23;0.2]	0.06 [0;0.12]	0 [-0.21;0.23]	-0.03 [-0.15;0.09]
-1.25 [-16.96;14.15]	-0.43 [-16.85;15.99]	-11.54 [-24.52;1.6]	-1.65 [-7.41;4.06]	0.5 [-11.69;13.5]	1.96 [-7.56;11.18]
6.48 [0.71;13.09]	3.05 [0.06;9.91]	9.4 [7.93;10.9]	8.5 [7.8;9.22]	2.67 [0.5;5.59]	4.48 [2.95;6.23]
3.16 [0.32;9.42]	4.85 [0.71;10.81]	1.63 [0.32;3.18]	0.5 [0.19;1]	1.2 [0.07;3.53]	0.56 [0.04;1.42]

Troglodytes troglodytes	*Sylvia borin*	*Sylvia atricapilla*	*Sturnus vulgaris*	*Spinus spinus*	*Serinus serinus*
167.45 [166.38;168.48]	183.49 [182.25;184.72]	168.48 [167.36;169.65]	145.57 [143.69;147.62]	177.25 [173.88;180.53]	153.12 [148.89;157.36]
-3.18 [-3.82;-2.55]	-1.98 [-2.5;-1.47]	-3.56 [-3.91;-3.19]	-0.89 [-1.9;0.17]	-4.48 [-6.95;-1.9]	-1.24 [-3.67;1.38]
-0.11 [-0.69;0.45]	-1.49 [-1.94;-1.03]	-1.88 [-2.2;-1.54]	-0.36 [-1.47;0.74]	-1.54 [-4.56;1.4]	-5.32 [-7.63;-2.92]
-0.28 [-0.44;-0.13]	0.77 [0.65;0.89]	-0.11 [-0.17;-0.04]	0.35 [0.17;0.54]	0.34 [0.02;0.66]	0.45 [-0.56;1.5]
-4.27 [-14.74;5.92]	7.38 [-3.7;18.68]	15.51 [7.1;23.88]	-10.15 [-24.95;4.62]	5.73 [-9.33;20.58]	1.75 [-14.28;17.75]
-0.56 [-0.87;-0.26]	-0.02 [-0.24;0.19]	-0.09 [-0.23;0.05]	0.08 [-0.39;0.55]	1.74 [-0.46;4.03]	-0.46 [-1.4;0.5]
0.09 [0.01;0.17]	-0.03 [-0.09;0.03]	0.08 [0.05;0.11]	0.11 [0.01;0.2]	0.49 [0.23;0.75]	-0.44 [-0.84;-0.05]
-7.72 [-14.04;-1.29]	-0.65 [-6.9;5.81]	-6.21 [-9.9;-2.57]	-11.07 [-23.21;1.18]	4.53 [-10.45;19.01]	0.31 [-13.99;14.81]
5.58 [5.03;6.16]	7.55 [6.85;8.29]	7.81 [7.35;8.27]	8.68 [5.92;11.66]	7.3 [2.38;11.87]	19.79 [16.39;23.7]
0.42 [0.11;0.85]	0.37 [0.08;0.8]	0.53 [0.19;0.94]	1.46 [0.14;3.4]	1.44 [0.19;3.75]	2.47 [0.52;4.96]

Turdus pilaris	*Turdus philomelos*	*Turdus merula*
165.68 [163.28;168.29]	165.34 [162.74;167.78]	170.61 [169.16;172.07]
-1.49 [-2.57;-0.44]	-1.77 [-3;-0.52]	-2.14 [-2.74;-1.53]
-3.4 [-4.88;-2]	-1.32 [-2.65;-0.01]	-3.1 [-3.61;-2.61]
0.08 [-0.2;0.38]	-0.13 [-0.43;0.16]	-0.33 [-0.46;-0.2]
-4.32 [-18.42;10.19]	2.8 [-11.88;17.92]	6.01 [-5.37;17.23]
-0.88 [-1.79;0.02]	-0.27 [-0.81;0.28]	-0.23 [-0.48;0.01]
-0.05 [-0.18;0.08]	-0.02 [-0.14;0.1]	-0.01 [-0.07;0.05]
0.95 [-8.63;10.84]	8.77 [-2.89;20.24]	2.89 [-4.29;10.34]
5.18 [3.1;7.62]	10.8 [9.02;12.67]	10.87 [10.1;11.63]
0.93 [0.14;1.95]	0.75 [0.12;1.91]	1.17 [0.75;1.77]

Appendix 8: Temperature maps

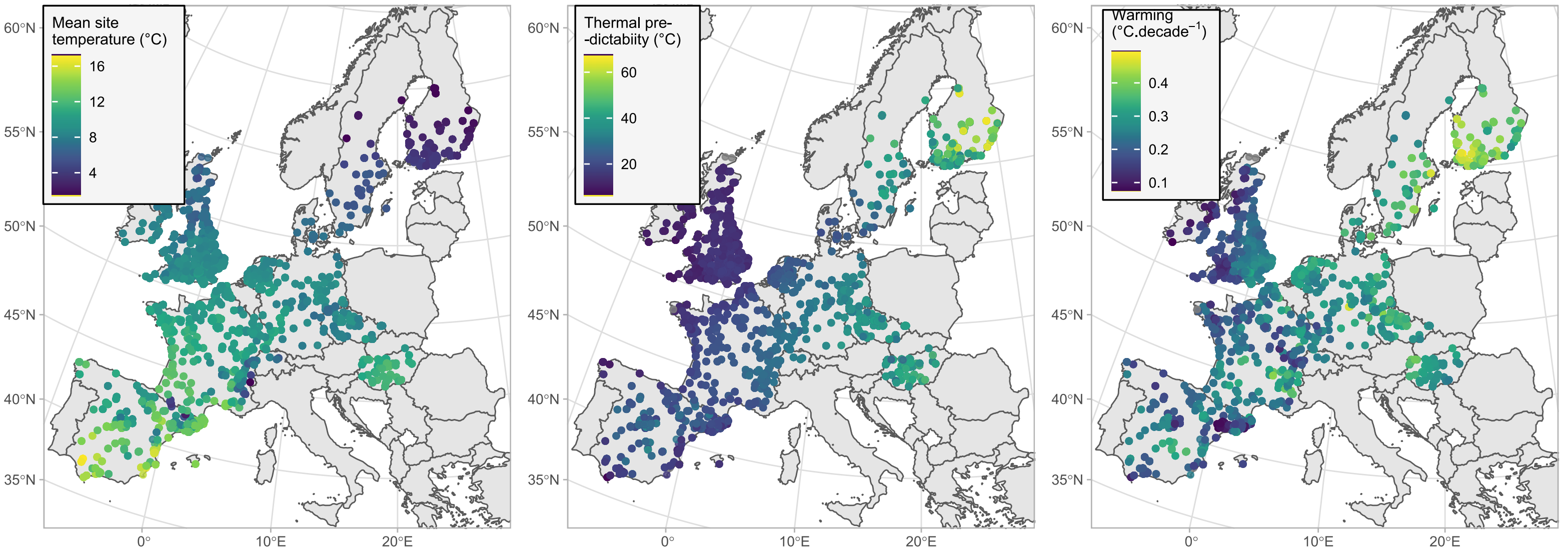


Figure S13: Maps representing each of the three site temperature characteristics: warming rate, temperature variance (thermal predictability) and mean site temperature across CES sites in Europe.

Appendix 9: Supplementary results

As showed in Table 2, interaction terms γ_1, γ_2 and γ_3 depended on species traits. In this section, we present the predictions made out of this table.

γ_1~ Standardized migration distance + Number of broods

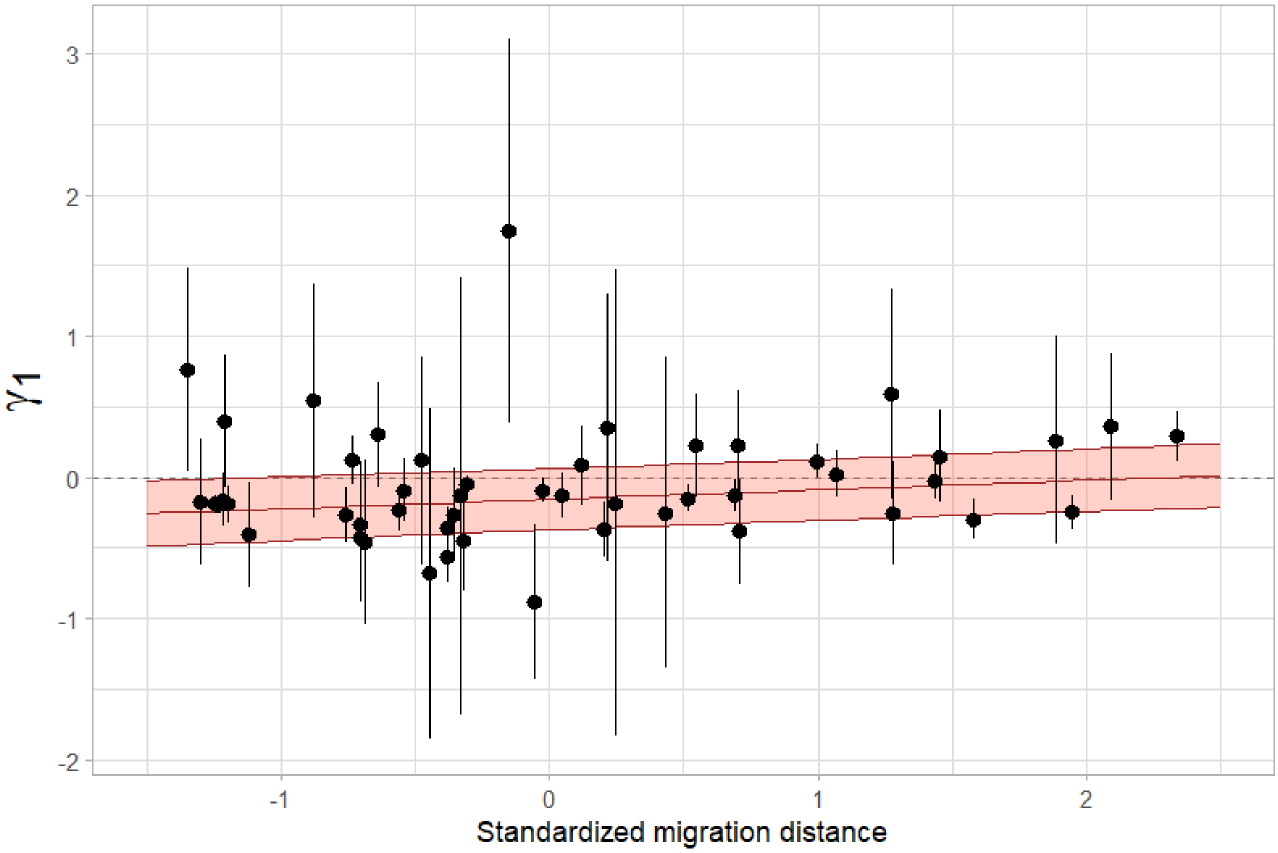


Figure S14: Posterior distributions of estimates of the effect of mean site temperature on fledging plasticity (γ_1 *parameter) according to standardized migration distance, across all European sites. Points represent the mean of the posterior distribution and the associated range corresponds to the 95% of the distribution.*

γ_2~ Thermal maximum + number of broods

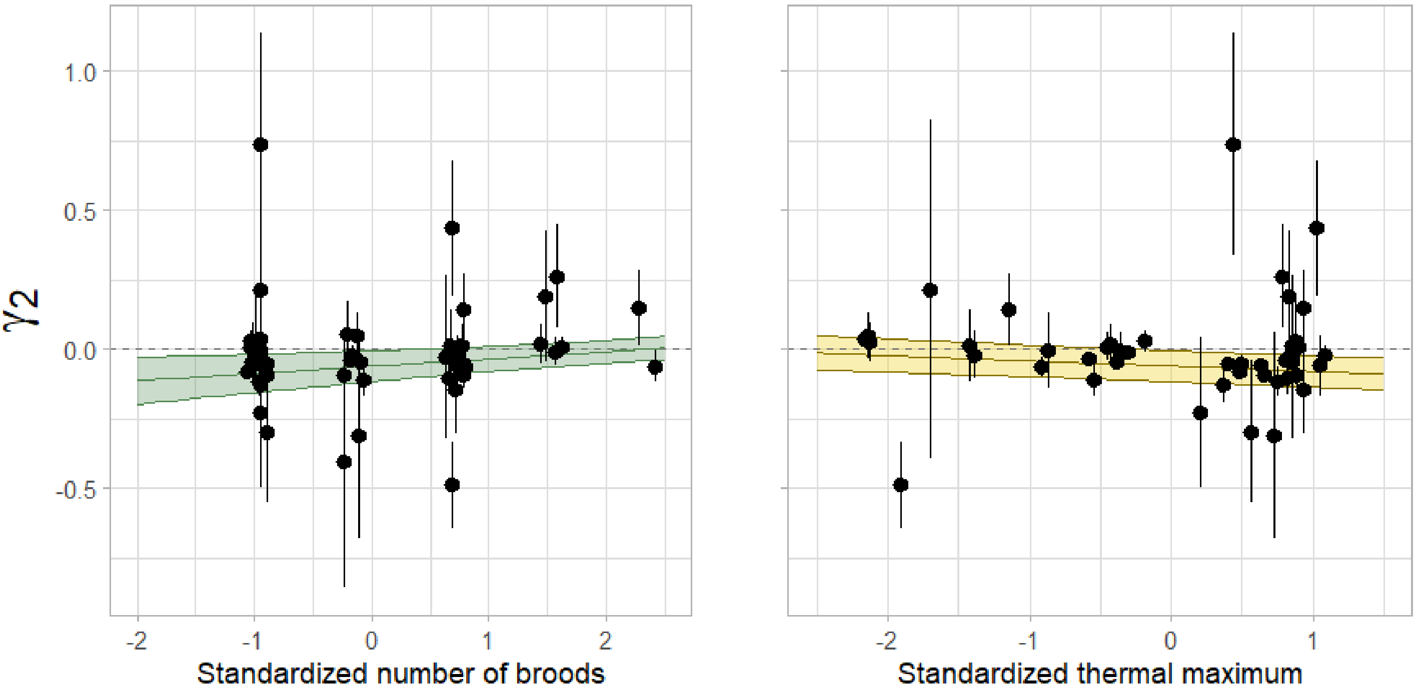


Figure S15: Posterior distributions of estimates of thermal predictability on fledging plasticity (γ_2 *parameter) according to standardized number of broods (left panel) and standardized thermal maximum, across all European sites. Points represent the mean of the posterior distribution and the associated range corresponds to the 95% of the distribution.*

Appendix 10: β-δ correlation

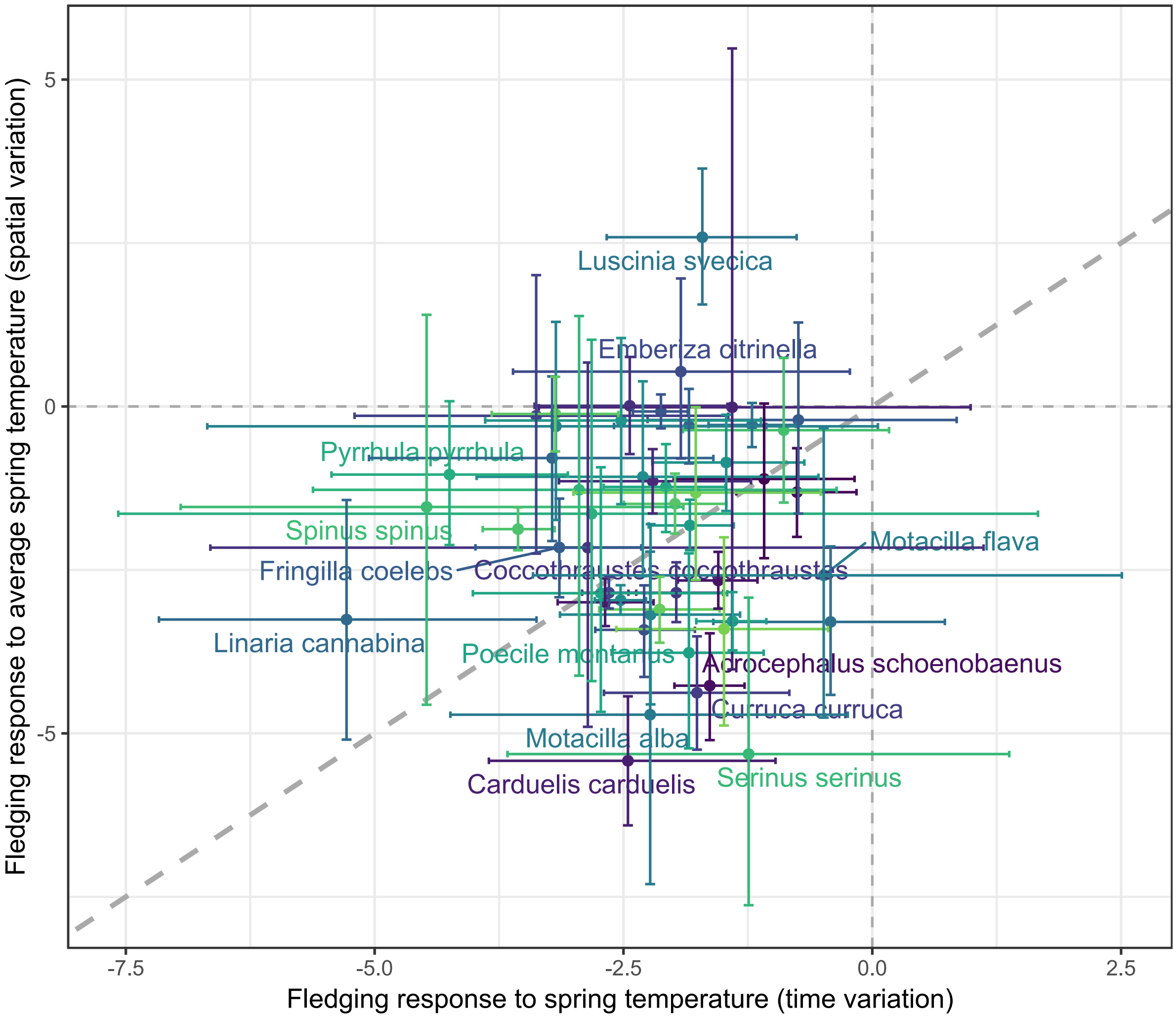


Figure S16: Correlation between the effects of temperature anomaly (β parameter; i.e., time variation) and mean site temperature (δ parameter, i.e., spatial variation) on fledging time. Both effects are expressed in °C.day^{-1}.