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Phenological Plasticity and Its Temperature-Related Drivers in Common Songbirds Across Europe

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ABSTRACT

Phenological plasticity—the ability of organisms to adjust the timing of life-history events in response to environmental variability—is the primary adaptive mechanism for many organisms to changing seasonality (e.g., earlier spring). By enabling alignment between life-history events and resource availability, it helps to maintain fitness despite changing environmental conditions. Theory predicts that phenological plasticity should vary among populations because of heterogeneity in environmental variability, and among species because of differences in life-history (e.g., migration distance) 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 temperature 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 sites with predictable temperature profiles 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 temperature conditions drive phenological plasticity. By demonstrating that the interplay between local environmental conditions and life-history traits

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underpins variation in breeding phenological responses, our study refines the current framework for predicting adaptive potential across populations and species under climate change.

1 | Introduction

Many seasonal vertebrates respond to climate change by shifting their phenology (Parmesan 2006; Thackeray et al. 2016), that is, their timing of critical life-history events. Phenotypic plasticity—the ability of a single genotype to produce different phenotypes depending on environmental conditions—has been identified as a predominant mechanism underlying these phenological shifts (Charmantier and Gienapp 2014; Merilä and 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). In contrast, evolutionary responses are often undetectable (e.g., Biquet et al. 2021) or contribute significantly less to phenological shifts than plasticity (e.g., Moiron et al. 2023; Bonnet et al. 2019).

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 and Both 2005; Visser and Gienapp 2019) so that the ability of organisms to track optimal environmental conditions over time through phenological plasticity determines their reproductive success (Chevin et al. 2013, 2010; Phillimore et al. 2016; Reed et al. 2010; Taff and Shipley 2023; Vedder et al. 2013; Youngflesh et al. 2023). 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 (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 emphasizes 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 and 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 anticipate the timing of peak food availability, and fine-tune their breeding time (Visser and Both 2005; Visser and Gienapp 2019). Such impact of environmental predictability has been evidenced experimentally, in an alga, in response to salinity under different regimes of salinity variation (Leung et al. 2020). Second, some studies suggest that shorter favorable seasons, typically in high-latitude/altitude regions (Martin and Wiebe 2004), constrain the ability of organisms to adjust their phenology by limiting the available time for adjusting critical life events, such as breeding, including lower phenological plasticity (Chmura et al. 2019; Gutiérrez and Wilson 2021; Iler et al. 2013). Third, under ongoing climate change phenological plasticity may reach its limits, potentially leading to less plasticity (Iler et al. 2013). This is in line with recent empirical studies, such as Bailey et al. (2022), having shown that blue and great 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 and Møller 2014; Moussus et al. 2011; Youngflesh et al. 2021). In birds, the life-history trait most tightly linked to environmental seasonality is the migratory strategy: long-distance migrants exhibit weaker phenological responses to variation in spring phenology than short-distance migrants (Youngflesh et al. 2023). 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. 2006; 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 and Møller 2014). Species inhabiting warmer environmental conditions are also expected to exhibit steeper plasticity (Moussus et al. 2011). 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 and Møller 2014).

In the present study, we analyzed within and among-species variation in phenological plasticity in response to spring temperature for 50 passerine bird species across Europe. We tested whether the temperature 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, predictability and warming rate. Using a meta-analysis, we then investigated how variation in fledging time plasticity across these temperature characteristics differed among species and tested whether such variation was explained by differences in life history/ecological traits (migration distance, number of broods per year, thermal maximum in the breeding range, diet).

2 | Materials and Methods

2.1 | 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

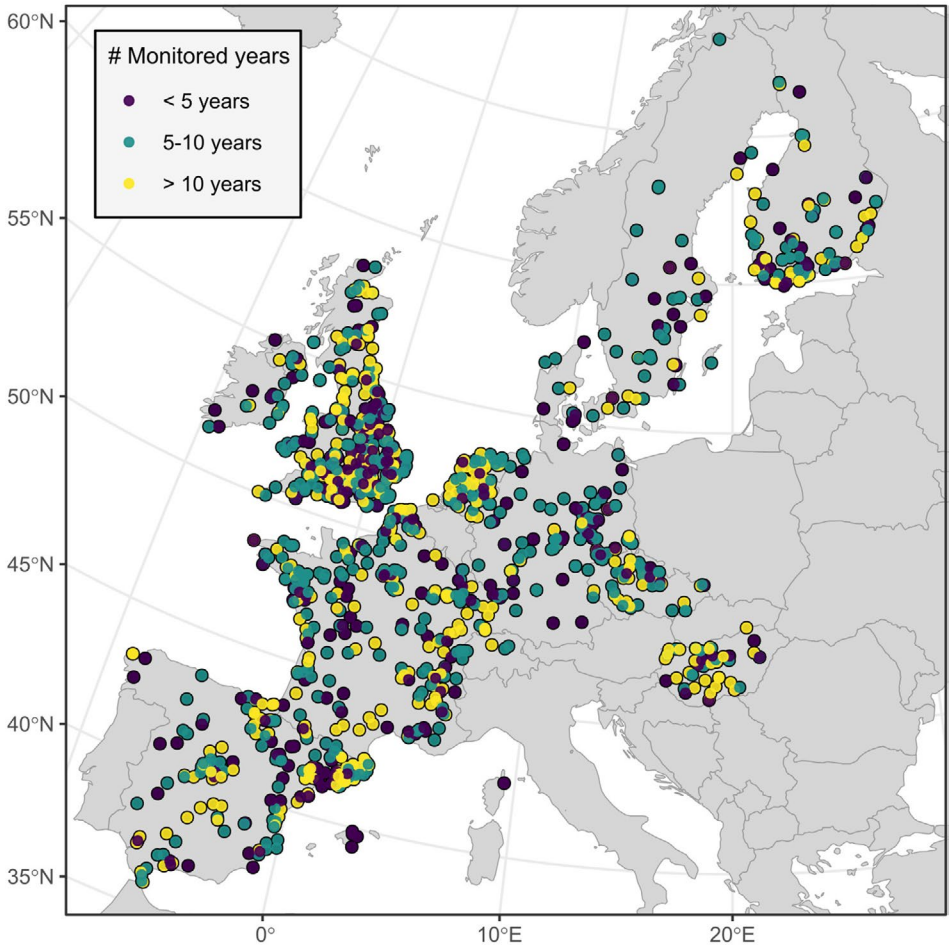

FIGURE 1 | Locations of constant capture effort sites (CES). Colors represent the number of years of monitoring per site. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

capture sessions (day of ringing), typically between April and May and July and August (the season starts and ends later at higher latitudes). Although the number of capture sessions and the number of mist-nets per site vary between countries, it remains constant within site over the years (Table S1). Capture sessions are to occur on the same date each year, but the actual date is determined by suitable weather (no rain) and the ringer's availability. 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 S1), 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).

2.2 | Data Filtering

For each species, we selected sites where data were collected (i) during at least three consecutive years, (ii) with at least five sessions per spring (minimum set to three sessions for French sites, see Table S1), and (iii) where on average at least three birds were captured per session. 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). To avoid detecting phenological patterns due to post-breeding or 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 S1.

2.3 | 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 and 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/).

2.4 | 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 the average laying date. This duration of the temperature window 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 2 months before the egg-laying date (Bailey et al. 2022; Hanzelka et al. 2024). We inferred the average egg-laying dates for the 50 studied species, which defined the end date of the 2-month window (since Bailey et al. 2022 showed that, on average, for tits, the mean egg-laying date occurs 26.5 days after the mid-date of the time window). To do this, we 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). By assuming that the average egg-laying date occurs *ca*. 50 days before the estimated fledging peak (Appendix S3; Storchová and Hořák 2018), we inferred the average (across years) peak of laying date for each region and species. Using this approach, windows were defined for each species and region, and were assumed to be constant across years.

2.5 | Sites' Temperature Characteristics

Mean site temperature was calculated for each site and species over the previously defined time window for the 1950–2022 period. We assessed temperature predictability at the site level by calculating the average variance of daily temperature residuals, obtained by subtracting the long-term mean temperature profile (1950–2022) from the observed daily temperatures (see Appendix S4 for details). We applied a sign change after mean-centering to ensure that highly predictable sites correspond to low intra-spring variance. Our measurement is akin to a measure of temporal autocorrelation, as lower variance in residuals implies higher consistency, and thus predictability, of daily temperatures over time (Bitter et al. 2021). 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 temperature characteristics of sites is plotted in Appendix S9 (Figure S17). Each of these three temperature characteristics was mean centered separately in the species models.

2.6 | 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 and Yajima 2021).

For each species, the number of juveniles on day t, year j and site k, follows a binomial distribution (Equation 1) 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 $N_{t,j,k}$.

$$Njuv_{t,j,k} \sim \mathrm{Bin}\left(p_{t,j,k}, N_{t,j,k}\right) \quad (1)$$

Cuchot et al. (2024) assumed that during the breeding period (April and July), $p_{t,j,k}$ follows a sigmoid curve (Figure S2). We thus modeled p separately for each species with a 3-parameter function (Equation 2).

$$p_{t,j,k} = \frac{asymptote_{j,k}}{1 + e^{\frac{xmid_{j,k} - t}{scale_{j,k}}}} \quad (2)$$

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, which 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 among sites or years), *xmid* can be considered as the peak of fledging phenology. The last parameter, *scale*, corresponds to a shape parameter and is related to the inverse of the slope of the curve at the inflection point and to the asymptote. These three parameters were assumed to vary independently, following normal distributions. For each species, we fit a three-parameter model to the full species dataset. The assumptions of additive random among-site and among-year variations, and the structural constraints imposed by the continuous explanatory variables ensure that the parameters of interest (primarily xmid) are identifiable and correctly estimated, even with a low number of capture sessions per breeding season (average of 3 capture sessions in Cuchot et al. 2024). All priors were set to be weakly informative. We ran this Bayesian hierarchical model for each species with three chains of 6000 iterations each and a burn-in of 1000, and no thinning. The Gelman-Rubin convergence diagnostics (Brooks and 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, that is, fledging phenology, as a linear function of spring temperature anomaly (spring temperature deviation from mean site temperature; van de Pol and Wright 2009). This linear reaction norm is usually considered as the measure of breeding phenological plasticity to temperature (Charmantier et al. 2008; Nussey et al. 2005). Nonlinearity of this reaction has been tested for the 50 species (see Appendix S12 for details), by incorporating quadratic terms of

spring temperature. We show that for the six species with significant quadratic effects, the effect is weak and the relationship mainly linear (Figure S21). The phenological plasticity can vary across sites depending on three principal temperature characteristics; mean site temperature (calculated over the 1950–2022 period), temperature predictability and warming rate (Equation 3). We introduced two-way linear interaction terms between spring temperature anomaly and respectively mean site temperature γ_1, temperature predictability γ_2 and warming rate γ_3.

$$\begin{aligned} fledge\ date_{k,j} = {} & \alpha + \mu_{0,j} + \mu_{0,k} + \left(\beta + \mu_{1,k}\right) * T^{\circ}\mathrm{C}_{k,j} \\ & + \delta * \overline{T}^{\circ}\mathrm{C}_k + \varphi * pred_k + \theta * warming_k \\ & + \gamma_1 * T^{\circ}\mathrm{C}_{k,j} * \overline{T}^{\circ}\mathrm{C}_k + \gamma_2 * pred_k * T^{\circ}\mathrm{C}_{k,j} \\ & + \gamma_3 * warming_k * T^{\circ}\mathrm{C}_{k,j} + \varepsilon_{k,j} \end{aligned} \quad (3)$$

with α corresponding to the species intercept (average phenology across sites and years), μ_{0k} to the random site intercept, μ_{0j} to the random year intercept, β to the mean slope across sites, u_{1k} to the random site slope, δ to the additive effect of mean site temperature, φ to the additive effect of temperature predictability, γ_1 to the interaction between mean site temperature and temperature anomaly, γ_2 to the interaction between temperature 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 among these parameters.

Plasticity for a given species at the site level can then be expressed as $\beta + \gamma_1 * T^{\circ}\mathrm{C}_{k,j} + \gamma_2 * pred_k + \gamma_3 * warming_k$. These multiplicative terms can be interpreted as varying regression coefficients, indicating how the strength of the temperature–phenology relationship changes depending on local temperature characteristics. To visualize these interactions, we plotted predicted relationships at the 0.1 and 0.9 quantiles of each site-level predictor ("cold" vs. "warm" for mean temperature or "low" vs. "high" for temperature predictability and "fast" vs. "slow" for warming rate).

2.7 | 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 was available in Storchová and 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.

2.8 | 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, temperature predictability, warming rates, and mean site temperatures within species. First, for each of the regression parameters (Equation 3, 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 among-species variation respectively in: average plasticity (β), mean site temperature effect on plasticity (γ_1), temperature 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. The predictive checks for these models are shown in Appendix S8 (Figure S16). 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).

3 | Results

Most studied species (42 out of 50) fledged 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 (i.e., the relationship between fledging time and temperature anomaly, β_1) differed across species. Savi's warbler (*Locustella luscinioides*) was the least plastic (−0.42 day°C^{-1}), and the common linnet (*Linaria cannabina*) was the most plastic species (−5.28 day°C^{-1}, Table S2; Figure S9). Across species, only long-distance migrants exhibited 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 S8), suggesting that the observed variation in plasticity was 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). The European goldfinch (*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, the bluethroat's (*Luscinia svecica*) fledgling phenology was positively affected by mean site temperature (2.59 day°C^{-1}), meaning that the population located at warmer sites bred later (Table S2). The effect of mean site temperature (spatial variability: −1.73 [−2.59;

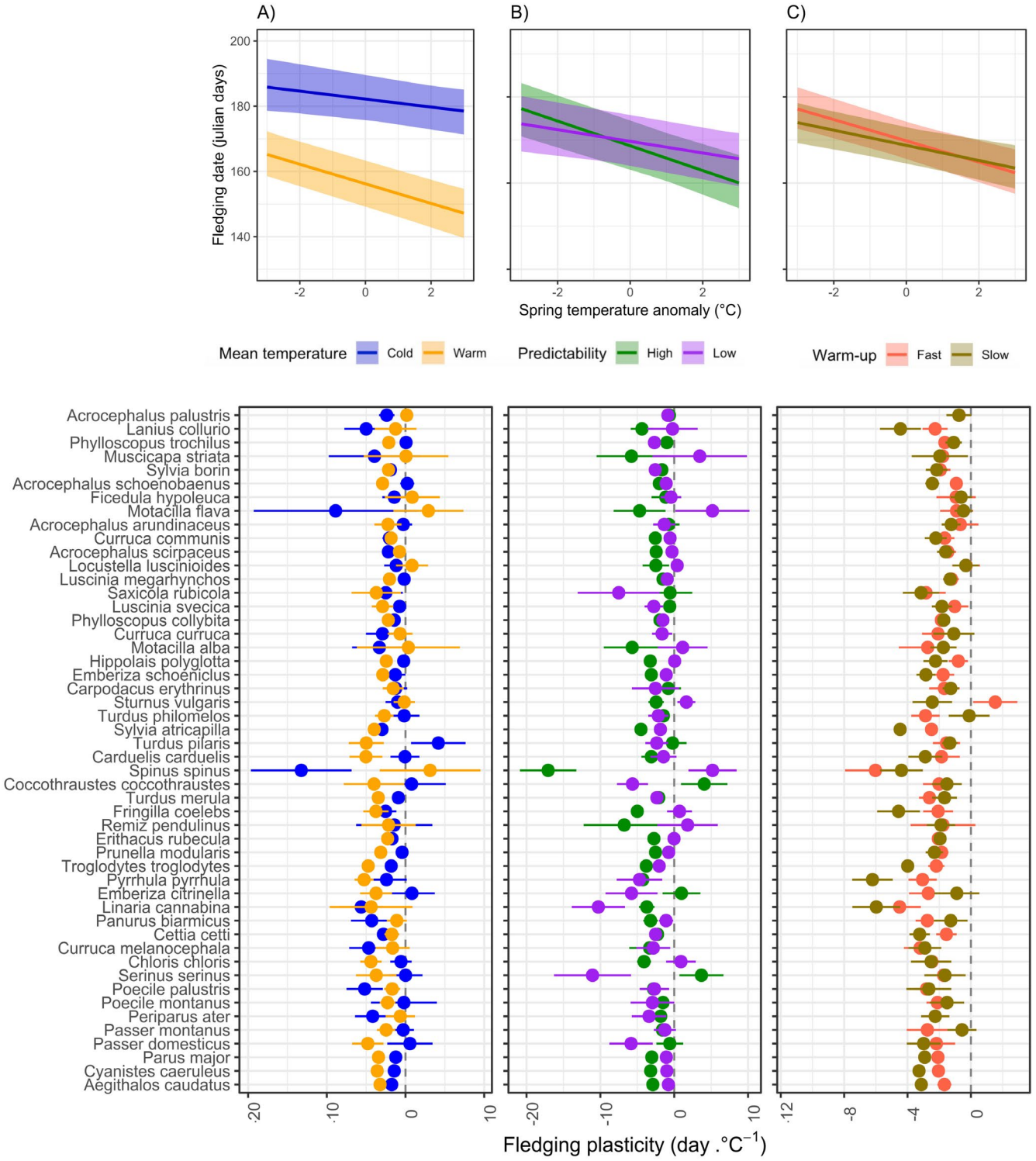

FIGURE 2 | Within-species variation in fledging plasticity in response to spring temperature anomaly and (A) mean site temperature, (B) temperature predictability and (C) warm-up among-species (upper panel) and within-species (lower panel). Predictions were calculated 100 times per category and for 100 values of spring temperature anomaly, by picking in the posterior distributions of the estimates of the intercept models for each parameter (Table 1). Species are arranged according to their migration distance (the species at the top are those that migrate the furthest). 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 for each species.

−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 temperature dependencies were not correlated: the species' responsiveness to yearly fluctuations in temperature was independent of its sensitivity to site mean temperature (Figure S20).

TABLE 1 | Mean effects.

Parameters	Variables	Median [95% CI]
α	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	Temperature predictability	00.01 [−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 * temperature predictability	**−0.03** [−0.06; −0.01]
γ_3	Temperature anomaly * warming rate	**−1.70** [−3.27; −0.01]

Note: Meta-analytic mean (i.e., cross-species) effects of temperature anomaly, mean site temperature, temperature predictability, and warming rate on fledging date. Interactions between temperature anomaly and mean site temperature, temperature predictability or warming-rate characterize the effects site of the temperature properties 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.

Phenological plasticity varied across populations, along the three gradients of site temperature properties. First, on average across species, phenological plasticity depended negatively on mean site temperature (γ_1 meta-analytic mean with 95 CI: −0.13 [−0.24; −0.02]; Table 1; Figure S12): populations inhabiting warmer sites were more plastic. The intensity of this dependence decreased with migration distance until it became null in long-distance migrants (Table 2; Figure S18). 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 [−0.06; −0.01]; Figure 2B; Table 1; Figure S13). In general, species with a higher thermal maximum and those producing fewer clutches per year displayed steeper plasticity in response to temperature predictability at a site (Table 2; Figures S18 and S19). On the contrary, there was no effect of temperature predictability in species with low thermal maximum and multi-brooded species. We found a positive effect of predictability on plasticity for two species: The European serin (*Serinus serinus*; 0.46 [0.04; 0.88]) and the Hawfinch (*Coccothraustes coccothraustes*; 0.76 [0.13; 1.40]). 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 S14), and this did not depend on any of the tested life history traits (Table 2). Predictive checks for the γ_3 parameter (i.e., the interaction between warming rate and temperature anomaly) however reveal a slight mismatch between the distribution of the posterior predictive samples between simulated and observed data, suggesting that this parameter may be less reliable than others and should be interpreted with caution. Finally, although non-significant, we found that multi-brooded species tended to exhibit the opposite pattern, that is, less phenological plasticity in sites that warmed up the fastest (Table 2).

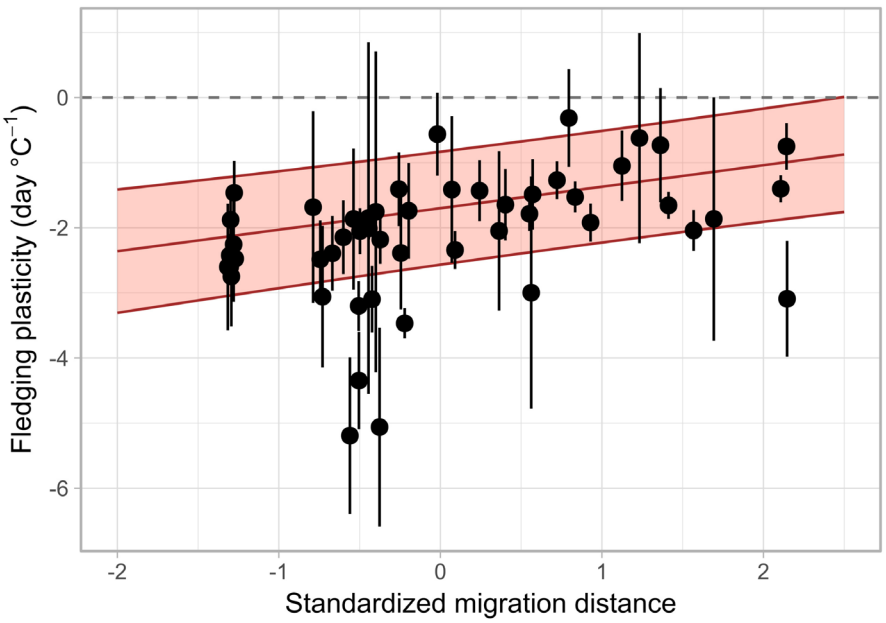

FIGURE 3 | Mean fledging plasticity in response to local temperature anomaly according to standardized species migration distance. Points represent the mean of the posterior distribution and the associated range corresponds to the 95% of the distribution. We verified that the reported relationship remained statistically significant after excluding three granivorous species (*Spinus spinus*, *Pyrrhula pyrrhula*, *Linaria cannabina*) which exhibited particularly high phenological plasticity (< −4 days°C^{-1}; Figure S15).

TABLE 2 | Species traits models.

	β median [95% CI]	γ_1 median [95% CI]	γ_2 median [95% CI]	γ_3 median [95% CI]
	Temperature anomaly	**Mean site temperature * temperature anomaly**	**Temperature predictability * temperature anomaly**	**Warming rate * temperature anomaly**
Intercept	**−1.7 [−2.92; −0.39]**	−0.22 [−0.46; 0.02]	−0.01 [−0.08; 0.05]	0.66 [−4.17; 5.57]
Broods per year	0.03 [−0.27; 0.3]	−0.04 [−0.16; 0.09]	**0.02 [0; 0.03]**	1.48 [−0.07; 2.99]
Trophic niche: Invertivore	−0.3 [−1.16; 0.52]	0.04 [−0.2; 0.29]	−0.02 [−0.08; 0.05]	−1.88 [−7.17; 3.33]
Trophic niche: Omnivore	−0.7 [−1.53; 0.1]	0.11 [−0.13; 0.35]	−0.03 [−0.10; 0.04]	−2.72 [−8.14; 2.57]
Migration distance	**0.33 [0.1; 0.55]**	**0.07 [0; 0.13]**	0.01 [−0.01; 0.03]	0.68 [−0.59; 1.96]
Thermal maximum	−0.07 [−0.26; 0.13]	0.07 [−0.01; 0.15]	**−0.02 [−0.04; 0]**	−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]

Note: Effects of species traits on mean fledging plasticity (β), and on among-species variation in among-site dependence of fledging plasticity on site temperature properties ($\gamma_1, \gamma_2, \gamma_3$). These effects were estimated independently for each parameter across the 50 species, after adjusting for phylogenetic distance among species. Bold term terms correspond to estimates for which their 95% posterior distribution do not cross zero.

4 | 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 temperature predictability exhibit greater fledging plasticity (Figure 2A,B; Table 1). We also found no evidence that populations experiencing higher warming rates display less plasticity. In birds, earlier breeding in warmer 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 and Møller 2014; McLean et al. 2022; Neate-Clegg et al. 2024; 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 (temperature predictability) and interspecific (migrant vs. resident) levels.

4.1 | Among 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 S8). 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 among 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 and 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. 2006; 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 and 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), led us to expect stronger plasticity in granivorous than insectivorous

species. However, we are lacking information on chick diet for most of the species, for which diet is probably insectivorous during nestling stages. Future comparative studies need to integrate more precise data on diet and the degree of diet specialization at the nestling stage.

4.2 | Within Species 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 and Winkler (1999) showed that populations at higher latitudes (i.e., colder environments) exhibited lower laying date plasticity in response to spring temperature. Similarly, horned larks *Eremophila alpestris* which are found in alpine and high-latitude habitats (de Zwaan et al. 2022), exhibit phenological plasticity that is likely weaker than that observed in most of the 50 passerine species from the present study (fig. 5 in de Zwaan et al. 2022). 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). Another hypothesis is that rather than a constraint on plasticity, the optimal reaction norm in colder environments is shallower. In support of this, 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 among-year temperature variation (Gutiérrez and 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 explaining the fact that migratory species are the most vulnerable to climate change, declining faster than other groups (e.g., Morrison et al. 2013). In this study, we demonstrated this pattern only at the species level; however, migration distance also varies within the distribution range of widespread species (such as some of those examined here), primarily according to latitude (and eastern longitude, for example, in Robins: Ambrosini et al. 2016).

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. 2020; 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 allows 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 tracking as well the optimal breeding phenology, likely increasing the probability of phenological mismatch.

Populations from sites with the strongest spring warming rates may be slightly more plastic, but in any case, not less. This pattern characterized by 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 S14) 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 was 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 in 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 and Hoffmann 2017). Further work is needed to understand the origin and implications for breeding success of this increased plasticity.

5 | Conclusion

Our study highlights the importance of temperature conditions and species specificities in shaping phenological plasticity in common songbirds, with minimal influence from phylogenetic inertia. Populations from more 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.

Author Contributions

Paul Cuchot: conceptualization, formal analysis, investigation, methodology, visualization, writing – original draft, writing – review and editing. **Timothée Bonnet:** methodology, validation, writing – review and editing. **Robert A. Robinson:** data curation, validation, writing – review and editing. **Juan Arizaga:** data curation, validation, writing – review and editing. **Wolfgang Fiedler:** data curation, validation, writing – review and editing. **Olaf Geiter:** data curation, validation, writing – review and editing. **Ian Henshaw:** data curation, supervision, writing – review and editing. **Christof Herrmann:** data curation, validation, writing – review and editing. **Henk van der Jeugd:** data curation, validation, writing – review and editing. **Zsolt Karcza:** data curation, validation, writing – review and editing. **Arantza Leal:** data curation, validation, writing – review and editing. **Petteri Lehikoinen:** data curation, validation, writing – review and editing. **Jan A. C. von Rönn:** data curation, validation, writing – review and editing. **Kasper Thorup:** data curation, validation, writing – review and editing. **Céline Teplitsky:** conceptualization, investigation, project administration, resources, supervision, validation, writing – review and editing. **Pierre-Yves Henry:** conceptualization, investigation, supervision, validation, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code are available via the Zenodo Repository: https://doi.org/10.5281/zenodo.14674521.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** gcb70600-sup-0001-AppendicesS1-S12.docx. **Appendix S2:** gcb70600-sup-0001-AppendicesS1-S12.docx. **Appendix S3:** gcb70600-sup-0001-AppendicesS1-S12.docx. **Appendix S4:** gcb70600-sup-0001-AppendicesS1-S12.docx. **Appendix S5:** gcb70600-sup-0001-AppendicesS1-S12.docx. **Appendix S6:** gcb70600-sup-0001-AppendicesS1-S12.docx. **AppendixS7:**gcb70600-sup-0001-AppendicesS1-S12.docx.**AppendixS8:** gcb70600-sup-0001-AppendicesS1-S12.docx. **Appendix S9:** gcb70600-sup-0001-AppendicesS1-S12.docx. **Appendix S10:** gcb70600-sup-0001-AppendicesS1-S12.docx. **Appendix S11:** gcb70600-sup-0001-AppendicesS1-S12.docx. **Appendix S12:** gcb70600-sup-0001-AppendicesS1-S12.docx.