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Global phenological insensitivity to shifting ocean temperatures among seabirds

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Abstract

Reproductive timing in many taxa plays a key role in determining breeding productivity[1] and is often sensitive to climatic conditions[2]. Current climate change may alter timing of breeding at different rates across trophic levels, potentially resulting in temporal mismatch between the resource requirements of predators, and their prey[3]. This is of particular concern for higher trophic-level organisms, whose longer generation times confer a lower rate of evolutionary rescue than primary producers or consumers[4]. However, the disconnection between studies of ecological change in marine systems makes it difficult to detect general patterns of timing of reproduction[5]. Here, we use a comprehensive meta-analysis of 209 phenological time series from 145 breeding populations to show that on average, seabird populations worldwide have not adjusted their breeding seasons over time (-0.020 days yr^{-1}) or in response to sea surface temperature (SST) (-0.272 days °C^{-1}) between 1952 and 2015. However, marked between-year variation in timing observed in resident species and some Pelecaniformes and Suliformes (cormorants, gannets and boobies), may imply that timing, in some cases, is affected by unmeasured environmental conditions. This limited temperature-mediated plasticity of reproductive timing in seabirds potentially makes these top predators highly vulnerable to future mismatch with lower trophic-level resources[2].

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138   The effects of rising global temperatures are having a profound impact on terrestrial

139   and aquatic biota, including species abundance, distributions, behaviours, and interactions[6].

140   Changes in phenology - the timing of seasonally recurring life-history events - are one of the

141   most apparent responses to rising global temperatures; at higher latitudes many spring and

142   early summer events are advancing over time across a suite of terrestrial, freshwater and marine

143   ecosystems[3,2]. As timing of breeding affects the abiotic conditions and biotic interactions to

144   which parents and their offspring are exposed[7], breeding phenology is expected to play a key

145   role in mediating the relationship between environmental temperature and fitness[1].

146   Globally, many species at higher trophic levels have poor conservation status[8]. Current

147   evidence indicates that the phenology of species occupying higher trophic levels is less

148   responsive to environmental change than that of primary producers and consumers[3,2,4], making

149   them particularly susceptible to trophic mismatch and the associated negative demographic

150   consequences[3,9]. However, previous studies which have combined estimates of phenological

151   sensitivity (i.e. phenological change over time or in response to temperature) of multiple high

152   trophic-level species to global change[3,2,9–13] have typically included few species or focused

153   primarily on mean responses within taxa, trophic levels, or regions. Moreover, most earlier

154   multi-species analyses have ignored sampling error in estimates of phenological sensitivity[9,11–

155   14] (but see [2] for an alternative approach) or sources of statistical non-independence, such as

156   phylogeny (but see [15]). As such, it is not clear whether the variation in rates of phenological

157   sensitivity reported in the literature is simply the result of the sampling error variance that is

158   characteristic of regression using short time series[16,17], or represents true variation. If true

159   variation in phenological sensitivity exists, this may arise where the strength of plasticity

160   covaries with attributes of particular species (e.g. body size, feeding ecology, migration

161   strategy), biogeography (e.g. upwelling, latitude, hemisphere or ocean basin), or an interaction

162   between two or more of these effects. Testing the influence of these variables on variation in

163   phenological sensitivity at a global scale across multiple populations will help to ascertain

164   general patterns and highlight those taxa and regions most likely to be vulnerable to climate

165   change.

166   Seabirds are one of the best-studied groups of higher trophic level organisms, and are

167   considered here to include species from the orders Sphenisciformes, Procellariiformes,

168   Suliformes, Pelecaniformes and Charadriiformes. Found throughout the world's oceans, they

169   range in size from ~20g to ~30kg, and generally exhibit long generation times and slow,

170   inflexible life histories. They are more threatened than any other comparable avian group, with

171   the conservation status of many species rapidly deteriorating[18]. Seabirds exhibit considerable

172   interspecific variation in feeding strategies, with breeding season foraging ranges varying from

173   <10 to >1000 km and foraging depths from <1 m to 100s of metres deep. Outside the breeding

174   season, some species remain close to their colony while others undertake the longest migrations

175   known in the animal kingdom[19].

176   Studies of seabird breeding phenology have reported a variety of different trends over

177   time[20]. Among the local environmental drivers of phenology that have been identified, sea

178   surface temperature (SST) is widely reported to correlate with the distribution, abundance and

179   phenology of both local and migratory prey populations[21], of which the effects on higher

180   trophic level organisms can be compared at global scales. Therefore, changes in temperature

181   driven by climate change could be critical, generating a mismatch with prey availability (see

182   further discussion below)[22]. Directional SST changes and fluctuations have been recorded in

183   the waters surrounding many seabird breeding sites (Figure 1a, b, Supplementary Figure 1),

184   with both metrics of change varying geographically. Large-scale climatic variables, such as the

185   North Atlantic Oscillation and the Southern Oscillation Index may also explain annual

186   variation in reproductive phenology (reviewed in [13]). However, using large-scale proxies

187   instead of data on specific climate drivers (e.g. SST) may lead to spurious and simplistic

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188 assumptions of climate-ecology dynamics[23]. Furthermore, proxies at this scale are not

189 amenable to global analyses, since regional proxies are not equivalent or comparable in a single

190 analysis[23]. Thus, variation in the sensitivity in timing of breeding across species and regions

191 remains unclear (but see [17]). Due to their trophic position, global distribution and the numerous

192 long-term studies available, seabirds constitute a tractable and powerful group for a global

193 meta-analysis of breeding phenology. Such an analysis allows us to not only make general

194 inferences about the degree to which breeding phenology has changed both over time and in

195 relation to SST, but also about the life history traits underpinning variation in phenological

196 responsiveness (Table 1). Finally, it allows us to examine predictors of between-year

197 phenological variation, with high variance potentially indicative of phenological sensitivity to

198 one or more unspecified environmental drivers.

199 　　　　We applied a phylogenetic mixed model meta-analysis to a global dataset comprising

200 209 phenological time series of breeding dates obtained from 145 seabird populations (Figure

201 1c. Median number of years/time-series = 18; min = 5; max = 48. Median sample size/year

202 /time-series = 72; min = 6; max = 936), covering 61 species from five main orders. These

203 taxonomic groups exhibit a wide variety of life-history, migration and foraging strategies, and

204 are distributed from equator to poles across all principal oceanographic regimes. Meta-analyses

205 provide a robust approach for identifying average effect sizes across studies, and for identifying

206 predictors of variation around the average[24]. Here, we (i) characterised latitudinal trends in the

207 mean and between-year variance of seabird breeding phenology (laying and hatching dates),

208 (ii) estimated the mean sensitivity of breeding phenology over time and in relation to SST in

209 the waters around the sampled colonies, and (iii) identified predictors (body size,

210 biogeography, phylogeny) of inter- and intra-specific variation around the mean response

211 (mean, variance and both sensitivity measures) of each species/population (for specific

212 predictions see Table 1 & Methods).

213   With increasing latitude, we found that breeding occurred later in the calendar year and

214   that between-year variance in phenology decreased (Supplementary Table 1, Figure 2a, b),

215   which concurs with earlier results obtained from regional studies[25,26]. The low variance at high

216   latitudes may arise due to the shortened period of favourable conditions and the strong seasonal

217   cue that photoperiod provides, whereas the much greater variance at lower latitudes may relate

218   to the reduction of seasonality and the relatively weaker cue from day length[27].

219   Overall, the between-year variance in lay date among populations in our dataset ranged

220   from < 1 in the black-browed albatross (*Thalassarche melanophris*) at New Island, Falklands,

221   consistent with 95% of annual means occurring within a three-day period, to 1573 in the blue-

222   footed booby (*Sula nebouxii*) at Isla Isabel, Mexico, consistent with 95% of annual means

223   occurring within a five-month period. Examination of life history traits potentially explaining

224   this variation (Supplementary meta-data) indicated that resident species were more variable

225   than migrants (Supplementary Table 2, Figure 3b). This result is in accordance with results for

226   terrestrial birds[28] and may arise if the laying dates of resident species are more sensitive to local

227   foraging conditions as a cue to initiate breeding in anticipation of the timing of future resources.

228   Controlling for biogeographic trends, we find that between-year variance in laying date was

229   highly phylogenetically conserved ($H^2 = 0.84$, 95% Credible Interval [CI]: 0.508 – 1, $n = 208$,

230   Supplementary Table 2). From inspection of the best linear unbiased predictors (BLUPs) for

231   the phylogenetic effects, the most threatened order[18], Procellariiformes, particularly giant

232   petrels and fulmars (Procellariidae), and albatrosses (Diomedeidae), stood out as least variable

233   in timing of breeding. This response is consistent with a strong reliance on photoperiod as a

234   cue[29]. In contrast, we find that Pelecaniformes and Suliformes (cormorants, gannets and

235   boobies) vary substantially among years in timing of breeding, suggesting that these species

236   may adjust egg laying in relation to some aspect of the local environment (weather,

237   oceanographic conditions or food availability) in the lead-up to the breeding season[30].

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238   On average, seabirds showed no tendency to advance or delay breeding phenology over

239   time (-0.020 days yr^{-1}, 95% CI: -0.160 – 0.129, n = 209, Figure 3a). This is in agreement with

240   previous studies of this species group[9,20], but the overall slope was much less steep than those

241   from similar analyses of UK birds[3] (mean = -0.19 days yr^{-1}), terrestrial and marine vertebrates[3]

242   (terrestrial mean = ~-0.25 days yr^{-1}, marine mean = ~-0.35 days yr^{-1}) or global estimates of

243   marine species in general[9] (mean = ~-0.4 days yr^{-1}). We found limited evidence for true

244   variation around the mean response (Supplementary Table 3), with 83% of the variation in raw

245   slope estimates of phenology over time attributable to sampling error arising from linear

246   regressions based on small datasets (Supplementary Table 4). Of the remaining true variation,

247   we found that the mean slope estimates did not differ significantly among oceans

248   (Supplementary Table 3). This result runs counter to previous studies of seabird breeding

249   phenology, which have reported variation in long-term trends among biogeographic

250   realms[11,20]. However, we found some evidence that temporal response may vary among species

251   at shared breeding sites (Supplementary Table 3), although sampling covariance between the

252   different phenological measures is likely to inflate this variance estimate. Among-population

253   variation makes it difficult to predict which species and sites will be most phenologically

254   responsive to changing environments, as it implies that the degree of environmental sensitivity

255   in seabird breeding may be determined by a combination of intrinsic and extrinsic factors[31]. Of

256   the environmental or life history variables we considered, body mass was the only significant

257   positive predictor of the temporal trend (Supplementary Table 3), with larger-bodied species

258   responding at a slower rate over time than smaller species, in accordance with our predictions

259   (Table 1).

260   Globally we found no evidence that seabirds as a group have shifted their laying date

261   in relation to SST in waters around the breeding site in the three months preceding egg laying

262   (mean = -0.272 days $°C^{-1}$, 95% CI: -4.896 – 4.482, n = 108, Figure 3b, Supplementary Table

9

263 5). The average response is much shallower than the average response of lay date to air

264 temperature reported for 27 UK terrestrial birds (mean = -3.8 days $^\circ C^{-1}$ (air temperature))[32]. In

265 broad agreement with the temporal analysis we found no evidence that true variation in the

266 slope of the covariation with SST is predicted by phylogeny, species, biogeographic region, or

267 life-history traits. We did, however, find significant variation in slopes among sites, and the

268 lowest BLUP was -2.96 days $^\circ C^{-1}$ (95% CI: -6.00 – 0.13) at Skomer Island, Wales, where SST

269 in the focal time period has increased significantly by $0.6^\circ C$ decade^{-1} since 1982

270 (Supplementary meta-data 1). In contrast, the most positive BLUP was 7.32 days $^\circ C^{-1}$ (95% CI:

271 4.96 – 9.73) at Southeast Farallon Island, California, which is located in a highly variable

272 upwelling zone, where inter-annual variance in SST is higher than average (Figure 1b,

273 Supplementary meta-data), a condition that might select for plasticity. So, although on average,

274 seabirds appear to be unresponsive to SST, we cannot rule out the possibility some populations

275 are temperature-sensitive in either direction.

276   That we could detect no trend in seabird phenology over time or in relation to SST

277 (Supplementary meta-data), suggests that if lower trophic levels are shifting in parallel with

278 changing SST, seabirds, in general, may be at risk from increasing levels of trophic mismatch[33].

279 To date, there are very few studies that have reported the slope of the phenology of

280 poikilothermic seabird prey and lower trophic levels in relation to SST (but see [22]). Differing

281 rates of phenological response between seabirds and their food resources[9] may leave them short

282 of critical prey during the breeding season under future climate regimes. However, there is

283 limited and mixed evidence on the frequency of climate-induced mismatch[17,22], and whether it

284 has an impact on breeding success[34] or population dynamics[35]. Alternatively, any negative

285 fitness consequences of trophic asynchrony may be ameliorated by the ability of some species

286 to alter their behaviour, for example by switching prey or adjusting foraging effort[22,36].

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287   Our study represents the most statistically rigorous and spatially representative meta-

288   analysis to date of the reproductive phenology of a group of upper trophic-level predators,

289   seabirds. Contrary to previous assertions, we find that once sampling error has been taken

290   into account, in most cases the phenology of seabirds shows no trend over time and appears

291   to be largely insensitive to changing SST. While certain populations may be responding,

292   most of the among-species variation in estimates of phenological sensitivity can be attributed

293   to sampling error. Overall, this inflexibility in breeding phenology in relation to temperature

294   may leave seabirds vulnerable to trophic mismatch arising from shifts in timing of their prey.

295

296   **Supplementary Information** is linked to the online version of the paper at

297   www.nature.com/nature.

298   Correspondence and requests for materials should be addressed to KK (k.keogan@ed.ac.uk).

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351 **Author Contributions**

352 KK, SL, ABP, SW, FD and RP conceived the study and wrote the manuscript. KK coordinated

353 the study, compiled the dataset and wrote the first draft of the manuscript. KK conducted the

354 statistical analyses under the guidance of ABP and with advice from SL and CAW. All others

355 provided data and comments on later drafts of the manuscript.

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441

Figure 1. SST trends and map of study sites included in the analyses. a) Across year temporal changes in mean Sea Surface Temperature (SST) in the three months prior to breeding across all biogeographic regions represented by slopes between 1982 (when SST time series' began) and 2015 for each site. Each point represents a slope, with positive slopes indicating warming and negative slopes indicating cooling. b) Standard deviation from the mean SST at each site during the same study period. A = Polar, B = Subpolar, C = Temperate, D = Subtropical, E = Tropical. c) The full dataset comprises 209 time series from 61 seabird species and across 64 locations, collected between 1952 and 2015. The data include slopes for 32 genera, 9 families, and 5 orders (Sphenisciformes (6), Procellariiformes (15), Suliformes (3), Pelecaniformes (5), Charadriiformes (32)) and spans all seven continents. The underrepresentation of tropical time series is due to a combination of a paucity of long-term data for these regions and the asynchronous nature of breeding in many tropical species, which diminishes the informativeness of measuring annual phenological central tendency.

Figure 2. **Mean and between-year variance in phenology separated by hemisphere. a)** represents the differences in latitudinal gradient between Northern and Southern Hemispheres, where each data point (grey or red) represents the median timing of breeding of a population. Lines (grey = lay date, red = hatch date) represent the delay in phenology approaching the poles in days lat $^{-1}$, and were estimated using values from Supplementary Table 1. **b)** represents the between-year standard deviation in mean timing for residents (represented by red dots) and migrants (grey dots). Lines are plotted from the ecological model and represent the median lay date in the mean year of study of an average surface feeding resident bird, weighing 800g, in a region where there is no major upwelling system. The non-linearity in the plot is due to back calculation from the log scale.

Figure 3. Funnel plots of phenological trends in relation to year and sea surface temperature. a) represents year and **b)** represents sea surface temperature. Each point represents a slope estimate from the meta-analysis, with negative slopes indicating an advance and positive slopes indicating a delay, in phenological trends. Positioning of each point on the y-axis indicates the precision (1/S.E) of the estimate. Thus, points with higher precision are expected to converge on the true average response. Lines represent the posterior for the average response or intercept (black) and its 95% credible intervals (dashed red) from the basic model (Tables S3a, S5a).

18

483 **Table 1.** Predictions of the effect of life history and environmental variables on
484 phenology from the four key models. Predictions in bold indicate they are supported
485 by the model.

Prediction		Reason
Mean Phenology		
Phenology will be later:	**at high latitudes**	**due to stronger photoperiodic cues at high latitudes[25,26].**
Between-year variance		
Higher between-year variance will be observed in:	smaller birds	as they are more sensitive to environmental change[37]
	residents & short-distance migrants	**because they may be more sensitive to conditions at the breeding site[28].**
	surface feeders	which are more constrained in the water column, meaning that they can only exploit prey near the water surface[38].
	populations in upwelling zones	**due to high variation in productivity in these areas[39,40].**
Temporal trends		
A steeper negative slope will be observed:	**in birds with smaller body size**	**to avoid incurring fitness costs of thermoregulation when breeding at higher temperatures[37].**
	in birds which feed at the surface	as they may be more sensitive to the timing at which lower trophic level prey are available[38].
	at high latitudes	because polar systems are experiencing warming faster than other areas[41].
Sea Surface Temperature trends		
A steeper negative slope will be observed:	in birds with smaller body size	to avoid incurring fitness costs of thermoregulation when breeding at higher temperatures[37].
	in residents & short-distance migrants	as they are likely to respond to conditions at the breeding site more readily than species which overwinter in different basins[28].
	in birds which feed at the surface	as they are predicted to be more sensitive to the timing at which lower trophic level prey are available[38].
	at high latitudes	as polar systems are experiencing warming faster than other areas[41].

486

Methods

Data collection To prevent an effect of publication bias and to ensure that positive, negative and neutral phenological trends were included, we used only raw time series (see PRISMA checklist). For each time series we used consistent methods to calculate slopes (i.e. rate of phenological change), between-year variance and crucially, standard error. Raw phenological data were compiled from a variety of sources between October 2015 and October 2016. We contacted 120+ known seabird researchers and owners of time series to request annual data on seabird breeding phenology and life history. Furthermore, requests were made via Twitter and at the World Seabird Conference in Cape Town (October 2015); the Pacific Seabird Group Annual Meeting in Oahu (February 2016); The Seabird Group conference in Edinburgh (September 2016); and the International Albatross and Petrel Conference in Barcelona (September 2016).

Data Annual data on breeding phenology during the period 1952 and 2015 were the median or mean date of laying or the median, mean or first date of hatching of the study population, in units of ordinal days. Population was defined as an individual species at a breeding site. We only considered populations that breed seasonally during spring and summer (austral and boreal) months, as measures of phenological central tendency are not informative for species which breed asynchronously or subannually (i.e. many tropical species[19]). Time series' were required to be a minimum of five years for the temporal analysis and ten years for the analysis of SST, although the years did not need to be consecutive. Details of criteria used to choose suitability of time series' are given in Supplementary Table 9, and the field methods used to collect each time series are outlined in the Supplementary Methods.

Monthly means of NOAA Optimum Interpolation (OI) Sea Surface Temperature (SST) V2 for the period 1982 – 2015 were obtained from the NOAA/OAR/ESRL PSD, Boulder,

20

511   Colorado, USA, a resource which provides interpolated *in situ* and satellite SST data on a one-

512   degree grid[42].

513   For each time series we characterised the biogeography at the colony it was located.

514   We collated information on the location (latitude and longitude) and hemisphere of each

515   population, and for our primary fixed effects model we assigned each location to one of the

516   three main oceans: Atlantic, Pacific or Indian. Global climate zones (Equatorial, Tropical,

517   Subtropical, Temperate, Subpolar or Polar) were identified using the classification from

518   Trujillo & Thurman (2014). These zones correspond to latitudinal bands of similar sea surface

519   temperature and are categorized by levels of precipitation, wind and water temperature[43]. We

520   combined hemisphere, ocean and global climate zone to identify 15 Biogeographic Regions

521   (e.g. North Atlantic Temperate; South Pacific Subpolar etc.). Finally, we used the Longhurst

522   Biogeographical Provinces to determine whether each location was situated within an Eastern

523   Boundary (upwelling) zone[44]. These are areas of high productivity within the marine

524   environment, and are also highly variable across seasons, years and decades[40,45].

525   We collated data on several aspects of the ecology and life history of each species that

526   may affect the phenological slope (with year or temperature), mean or between-year variance.

527   These data were provided by authors and supplemented using online resources:

528   www.audubon.org, www.birdlife.org, nzbirdsonline.org.nz, www.bird-research.jp and

529   www.npolar.no (Supplementary meta-data). Feeding strategy was categorised either as surface

530   feeder (feeding <1 metre below the surface), diver (feeding >1 metre below the surface), or

531   kleptoparasite/predator (part-time marine foragers). Species which seek out prey by diving

532   under water may be able to exploit a wider range of prey than those constrained to feeding on

533   the surface (<1 metre depth), thus reducing the necessity to adjust breeding phenology to buffer

534   mismatch[46–48]. We also compiled data on average body mass of every species (Supplementary

535   meta-data), as small-bodied seabird species are predicted to be more sensitive to temperature

21

536   change due to the higher cost of thermoregulation[37,49]. Furthermore, body mass can be used as

537   a proxy for trophic level, which is difficult to classify explicitly in seabirds[50]. We used log

538   body mass in analyses. The migration strategy of individuals from each population was

539   assigned based on the behaviour of the majority (>80%) of individuals. Long distance trans-

540   equatorial migrants, and species which spend the winter outside the sector in which they breed

541   were categorised together as "migrants", and those which remain in the same ocean sector

542   throughout the year were classified as "residents". Sectors were defined as North Atlantic,

543   Mediterranean, South Atlantic, Southern Ocean-Atlantic sector, North Pacific, South Pacific,

544   Southern Ocean-Pacific sector, Indian, Southern Ocean-Indian sector.

545   We took into account phylogenetic relationships among species using 100 samples of

546   the pseudo-posterior species tree[51] using the Hackett *et al.* (2008) backbone[52].

547   **Statistics** We used the *MCMCglmm* package[53] in R (v 3.2.2; R Core Team 2015), to fit

548   Bayesian generalised linear mixed-effects models (GLMMs). We adopted a random effects

549   meta-analytic (REMA) approach, estimating both fixed and random effects, while taking

550   sampling error characteristic or regression using short time series into account[16,24].

551   We included cross-classified random effects to account for and estimate sources of

552   variance, though not every random variable was included in each model (see Tables S1-S5).

553   The model was of the form

554    $$y_i = \mu + \beta x_i + \alpha_{f[i]} + s_{f[i]} + b_{g[i]} + l_{h[i]} + p_{j[i]} + e_i + m_i \qquad \text{eq. 1.}$$

555   where y is the phenological response variable of each time series i, μ represents the global

556   mean response (intercept), and βx_i the fixed effects. For each response variable we also

557   included a null model with the intercept as the sole fixed effect, as this allowed us to infer

558   which random terms captured most of the variance.

22

559    $\alpha_{f[i]}$ is the effect of phylogenetic non-independence due to shared evolutionary

560   history[16] for the fth species. $s_{f[i]}$ is the non-phylogenetic species-specific effect for the fth

561   species. Spatial variation was accounted for via two terms, gth biogeographic region ($b_{g[i]}$)

562   (see Supplementary meta-data) and hth site ($l_{h[i]}$). In certain analyses we included multiple

563   measures/traits for a time series and in these cases we could fit the interaction between site and

564   species (population) ($p_{j[i]}$), which provided us with an estimate of intraspecific geographic

565   variation that is unique to each (jth) population. In these cases the residual term (e_i) captures

566   variation within a site and species (population), and we allowed this variance to be

567   heterogeneous across different phenophases (i.e. median lay date, mean lay date, first hatch

568   date, median hatch date, mean hatch date). In other analyses only a single measure/trait was

569   included and in such instances $p_{j[i]}$ was not estimable. In this case the residual term captured

570   variance both due to intraspecific geographic variation that is unique to each species and

571   differences among phenological measures/traits. Our response variables were themselves

572   estimates that have error associated with them and we incorporated sampling error variances

573   as m_i, which means that the analyses were weighted. For the sampling error term, the among-

574   observation variance was set to 1, and for all other random terms the variance was estimated.

575   The specification of these models assumed that random effects for different measures were

576   perfectly correlated. To test whether this impacted on our estimation of phylogenetic signal we

577   then relaxed this assumption and estimated the covariance between random effects for

578   measures of laying and hatching phenology (Variance Structure of Models section, below).

579   We calculated phylogenetic signal[16,54] in our response variables (H^2), i.e. the tendency

580   of closely related species to resemble each other more than distantly related species, from σ_a^2

581   (the phylogenetic variance), and σ_s^2 (the species variance)

582
$$H^2 = \frac{\sigma_a^2}{(\sigma_a^2 + \sigma_s^2)} \qquad \text{eq. 2.}$$

23

583

584   We considered the following four response variables and clearly identify where analyses are

585   *post hoc* rather than *a priori*:

586   (1) Multi-year mean phenology: we estimated the mean phenology (e.g. average laying date

587   overall) across all years for each time series. Measurement variance in the mean was quantified

588   as the squared standard error. To examine latitudinal trends in mean date we included both

589   absolute latitude and its quadratic term (to test both linear and non-linear effects); hemisphere;

590   and the interaction between latitude and hemisphere as fixed effects. Additional fixed effects

591   were trait (laying and hatching date) and phenological measurement (mean, median, first date).

592   See Table 1 for predictions.

593   *Post hoc tests*: mean phenology is delayed as latitude increases in both hemispheres, with a

594   significant quadratic term, such that the slope appears to reach an asymptote toward the poles

595   (Figure 2, Supplementary Table 1). However, seabirds at low latitudes are underrepresented in

596   this study. When we removed three low latitude data points, there was no support for the

597   quadratic relationship (Supplementary Table 1) but the positive linear relationship between

598   latitude and breeding phenology remained (posterior mean = 0.81 days.lat^{-1}, 95% CI: 0.33 –

599   1.29, $n = 206$, Supplementary Table 1). The intercepts of each measure of phenology (i.e. mean

600   laying date, first hatching date) differed significantly, although a test including the interaction

601   between latitude and phenological measure revealed no difference in their latitudinal slopes

602   (Supplementary Table 1).

603

604   (2) Between-year variance in phenology: the response variable (eq. 3) was based on the natural

605   log of the between-year standard deviation (*s*) of each population ($\ln \sigma$), taking into account

606 the number of years (n). The sampling variance of this measure was quantified as ($s^2{}_{\ln \sigma}$) as in

607 eq. 4[55]:

608
$$\ln \hat{\sigma} = \ln s + \frac{1}{2(n-1)} \quad \text{eq. 3.}$$

609
$$s^2_{\ln \hat{\sigma}} = \frac{1}{2(n-1)} \qquad \text{eq. 4.}$$

610

611 The model included phenological trait and measure, latitude and its quadratic term,

612 hemisphere, presence or absence of upwelling and, to test for decadal patterns, the mean year

613 of each time series as fixed effects. We included body mass, foraging and migration strategies

614 in the same model to investigate the effects of life history traits on between-year variance. See

615 Table 1 for predictions.

616

617 (3) Temporal trend in phenology: we estimated the linear slope (and standard error) of

618 phenological change over time for each measure (median, mean, first date) and trait (laying or

619 hatching date) of a population using Generalised Least Squares (GLS) in nlme[56], fitting an

620 autoregressive model of order 1, AR(1)[57], to take into account temporal autocorrelation in each

621 individual time series. We used these slope estimates in a meta-analysis, and included the

622 squared standard error of the slope to weight the analysis. We included three types of fixed

623 effects: methodology (trait, measure, mean year of time series), life history and ecology (body

624 mass and foraging strategies), and biogeography (ocean basin, hemisphere, latitude). See Table

625 1 for predictions. We did not make predictions about which ocean basins or hemisphere might

626 show the steepest slopes, but allowed the response to differ among ocean basis and hemispheres

627 in our model.

25

628 *Post hoc test:* our primary ecological fixed effects model categorised locations into one of the

629 three main ocean basins (Atlantic, Indian, Pacific), and included the interaction between

630 latitude and hemisphere as an additional parameter. This approach considered the life histories

631 of wide-ranging polar species which may have large foraging ranges. Yet many species forage

632 near to the colony, or may have evolved alongside the unique oceanographic features of polar

633 systems[58]. To consider these species we re-categorised ocean basins into five discrete water

634 bodies (Arctic, Atlantic, Indian, Pacific, Southern) and ran our ecological model again,

635 replacing the three ocean variable with five oceans, and removing the interaction between

636 latitude and hemisphere.

637

638 (4) Phenological response to SST: for each time series we averaged monthly temperature data

639 from the local grid cell for the pre-breeding period (three, two and one month prior to laying,

640 including the month in which laying began) each year. In some cases sea ice cover meant that

641 an average temperature was not estimable and affected time series' were excluded from this

642 analysis. We restricted this analysis to laying dates only, representing each population with a

643 single time series in declining order of preference of measurements: median, mean and first

644 date. In populations for which we only had data on timing of hatching, we back-calculated lay

645 dates using information on the duration of incubation period and average number of eggs.

646 These data were provided by authors and supplemented using online resources:

647 www.audubon.org, www.birdlife.org, nzbirdsonline.org.nz, www.bird-research.jp and

648 www.npolar.no (Supplementary meta-data). Where incubation period was reported as a range,

649 we calculated the central value; this method was used for 70 time series (Supplementary meta-

650 data).

26

651   For each colony we calculated the reaction norms and associated standard errors of

652   phenological response to SST (days $^{\circ}C^{-1}$) using the GLS methods as described for the temporal

653   trends, but retaining year as an additional predictor, in order to de-trend the data and allow us

654   to consider the effects of SST independently of time (Supplementary meta-data). We compared

655   among pre-breeding on the basis of AIC and found very little difference, as expected given the

656   overlap between time periods and month-to-month temporal autocorrelation is SST. Across

657   time series the three-month period had the lowest mean AIC (2 month mean $\Delta AIC = 0.02$, 1

658   month mean $\Delta AIC = 0.50$) and for consistency we used this time period in subsequent analyses.

659   We then passed the slopes of phenology regressed on three-month SST into a meta-

660   analysis, with the squared standard error of the slope included for weighting. We tested similar

661   predictions as in (3) above, predicting that timing of laying would be more sensitive to pre-

662   breeding SST in species with smaller body mass, which feed on the surface, or that remain in

663   the same ocean basin over winter. Measure, trait and mean year of study were also included as

664   fixed effects.

665   All models were run for 30,000 iterations on each phylogenetic tree sample, discarding

666   the first 10,000 as burn-in and sampling every 10th iteration. We repeated this process over 100

667   phylogenetic trees and the pooled posterior distributions take into account both model and

668   phylogenetic uncertainties[59]. Parameter-expanded priors were used for all random effects

669   except the residual, which followed an inverse Wishart distribution. Plots of the mean and

670   variance of the posterior distribution were examined to assess autocorrelation in the posterior

671   samples. Statistical significance of fixed effects was inferred where 95% credible intervals did

672   not span zero.

673   **Variance Structure of Models:**

27

674   Our dataset contains five phenophases: median lay date (1), mean lay date (2), first hatch date

675   (3), median hatch date (4) and mean hatch date (5). The core models (with the exception of

676   temperature) run under the assumption that within the residual term (e_i) the variance would

677   be heterogeneous, with each phenophase varying independently of the other four (eq. S1).

678   We used the idh() variance structure function in the MCMCglmm package[53]. This is

679   consistent with phenophases being uncorrelated at the residual level (i.e. covariance = 0) but

680   at the other random effects the correlation between phenophases is assumed to be 1.

681

682
$$\boldsymbol{V}_{e_i} = \begin{bmatrix} V_{1,1} & 0 & 0 & 0 & 0 \\ 0 & V_{2,2} & 0 & 0 & 0 \\ 0 & 0 & V_{3,3} & 0 & 0 \\ 0 & 0 & 0 & V_{4,4} & 0 \\ 0 & 0 & 0 & 0 & V_{5,5} \end{bmatrix} \quad \text{eq. S1}$$

683

684   These assumptions can be relaxed for each random effect and the covariance between

685   phenophase can be estimated. We used the us() variance structure function (eq. S2), where V

686   = variance, C = covariance and e_i = random effect.

687

688
$$\boldsymbol{V}_{e_i} = \begin{bmatrix} V_{1,1} & C_{1,2} & C_{1,3} & C_{1,4} & C_{1,5} \\ C_{1,2} & V_{2,2} & C_{2,3} & C_{2,4} & C_{2,5} \\ C_{1,3} & C_{2,3} & V_{3,3} & C_{3,4} & C_{3,5} \\ C_{1,4} & C_{2,4} & C_{3,4} & V_{4,4} & C_{4,5} \\ C_{1,5} & C_{2,5} & C_{3,5} & C_{4,5} & V_{5,5} \end{bmatrix} \quad \text{eq. S2}$$

689

690   Allowing slopes of phenophases to covary for every random effect may result in a more

691   informative estimate of phylogenetic signal (i.e. perhaps signal is observed at one stage of

28

692   reproduction but not another), but requires a large amount of data at each level to confidently

693   estimate multiple (co)variances. As our dataset was not large enough to run models with fully

694   unstructured (co)variance, we only estimate the covariance between lay and hatch dates. We

695   restructured the covariance matrix for each random effect (eq. S2) into a 2 x 2 grid (eq. S3).

696

697 $$V_{R.E} = \begin{bmatrix} V_{lay,lay} & C_{lay,hatch} \\ C_{lay,hatch} & V_{hatch,hatch} \end{bmatrix} \quad \text{eq. S3}$$

698

699   Thus, three slopes (lay date, hatch date and the covariance between the two) were estimated

700   for each random effect (phylogeny; species; biogeographic region; location and

701   species:location). We ran the three key models (between year variance, temporal and SST)

702   using this error structure to assess whether any of our key insights were sensitive to the

703   assumption that lay and hatch dates are perfectly correlated.

704   When the assumption of perfect correlation between the two measures was relaxed, we found

705   that phylogenetic signal remained significant for the variance and SST models (Supplementary

706   Tables 6, 8). We also found some evidence for phylogenetic signal in the temporal model

707   (Supplementary Table 7). These results are in agreement with the key findings of our core

708   models.

709   **Data availability** The authors declare that all biological data generated and analysed in this

710   study are available within the article, its supplementary information files and in the following

711   repository: https://github.com/katkeogan/seabird-metaanalysis. The NOAA Optimum

712   Interpolation (OI) Sea Surface Temperature (SST) V2 data that the support the findings of this

713   study are available from NOAA/OAR/ESRL Physical Sciences Division,

29

714 http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html. The phylogenetic trees

715 generated and analysed in this study were obtained from BirdTree, www.birdtree.org.

716

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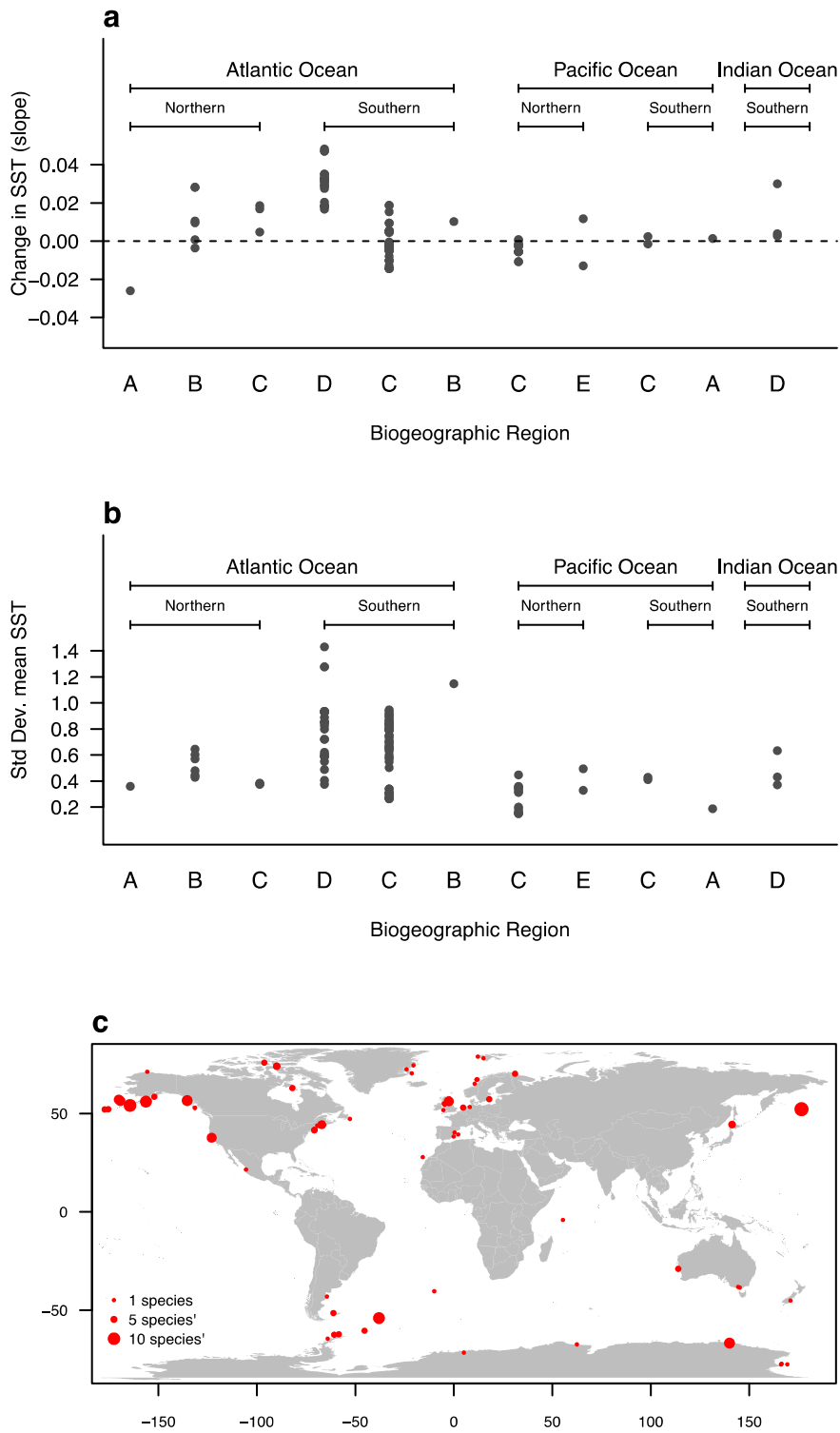
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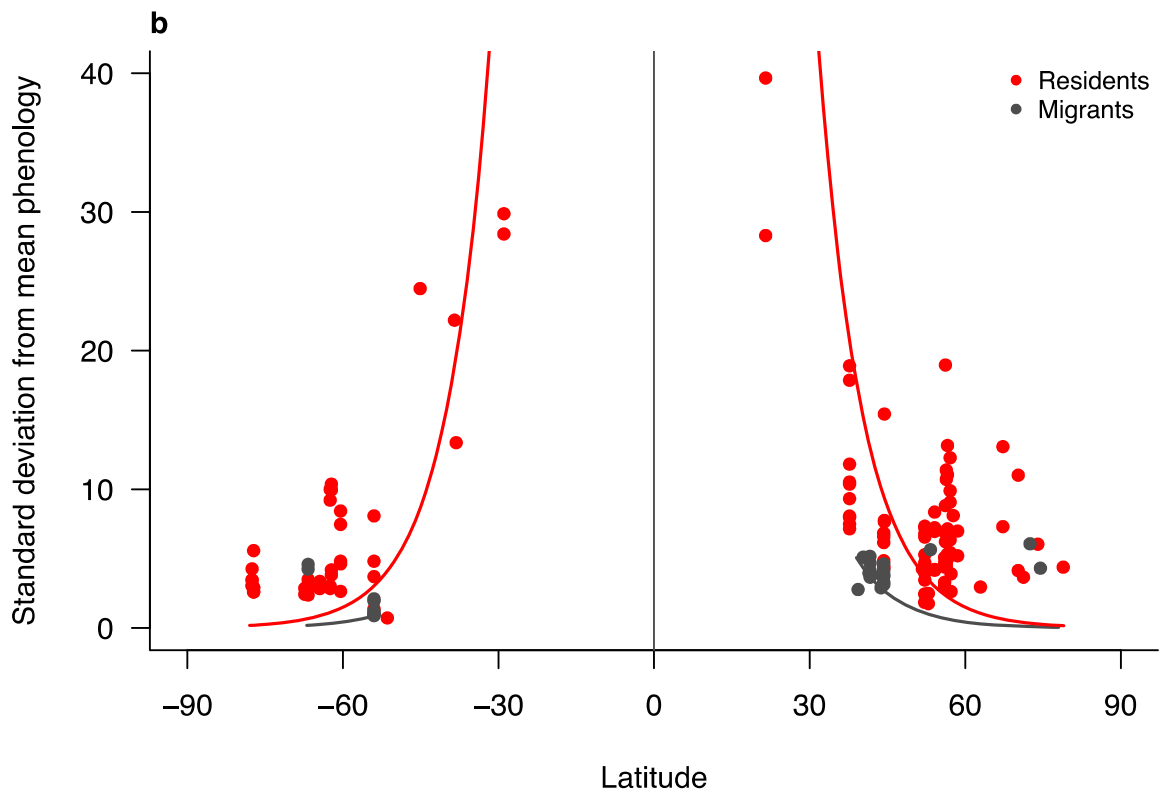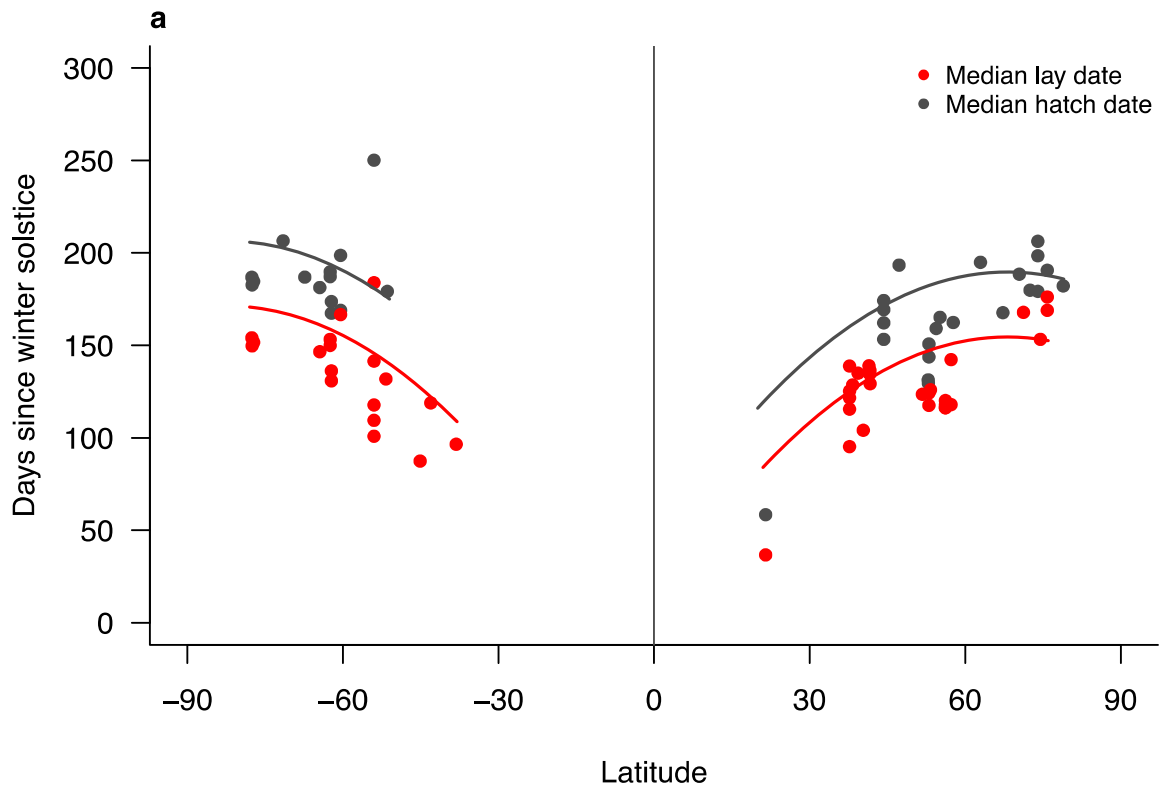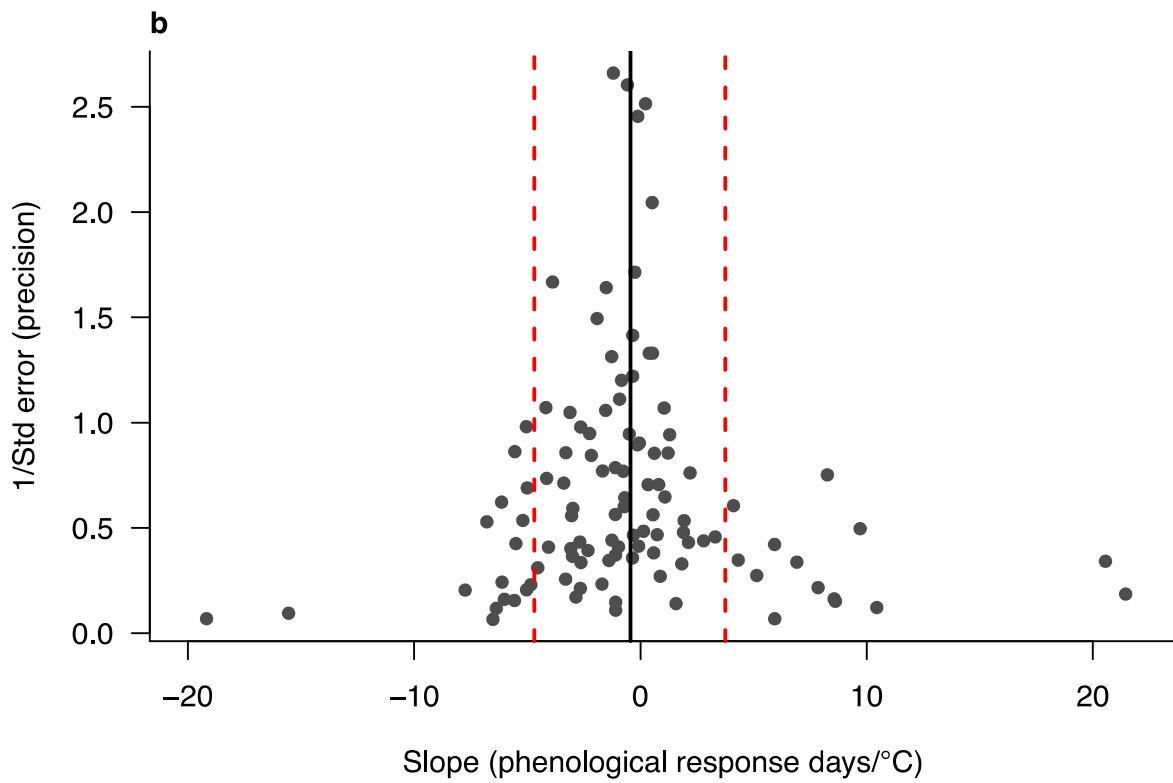764   studies of evolution and adaptation. *Biol. Evol. Stat. Phys.* 148–162 (2002).
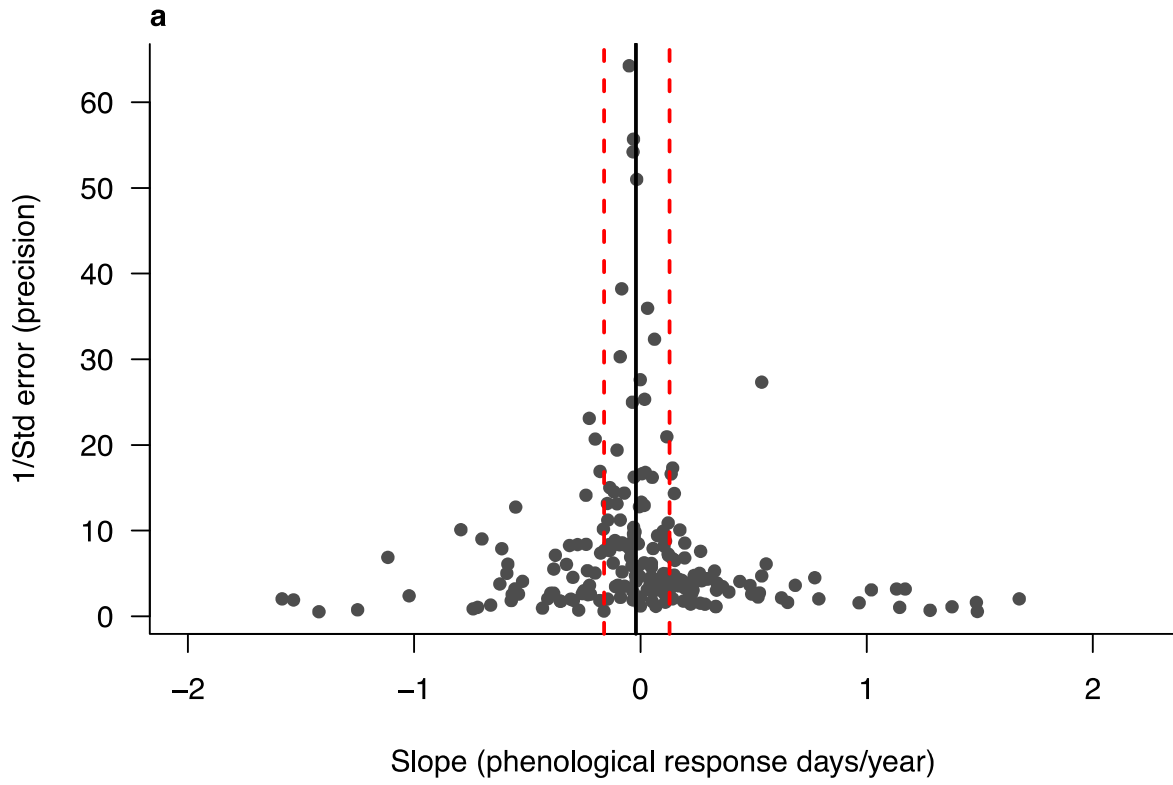
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Figure 1

Figure 3

776   Supplementary materials

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