1   **Title: A global synthesis of phenological responses to climate change**

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8   **Author Contributions:** J.M.C., M.J.L., and J.R.R. contributed ideas and devised the analyses,

9   J.M.C. assembled the database of phenological time-series, J.M.C. collected climate data, M.J.L.

10   designed and conducted the analyses, J.M.C., M.J.L., and J.R.R. wrote the paper.

11

12   **Phenology, or the timing of seasonal activities, is shifting with climate change, resulting**

13   **in disruptions to the timing of migration and breeding and in emerging asynchronies**

14   **between interacting species[1-5]. Recent syntheses have concluded that trophic level[1],**

15   **latitude[6], and how phenological responses are measured[7] are key to determining the**

16   **strength of phenological responses to climate change. However, despite these insights,**

17   **researchers still lack a comprehensive framework that can predict responses to climate**

18   **change globally and across diverse taxa. For example, little is known about whether**

19   **phenological shifts are driven by different climatic factors across regions or which**

20   **ecologically important species characteristics (e.g., body size) predict the strength of**

21   **phenological responses. Here, we address these questions by synthesizing hundreds of**

22   **published time series of animal phenology from across the planet. We find that**

23   **temperature drives phenological responses at mid-latitudes, but precipitation is more**

24   **important at lower latitudes, likely because these climate factors often drive seasonality in**

25   **each of these regions. Body size is also negatively associated with the strength of**

26   **phenological shift, suggesting emerging asynchronies between interacting species that differ**

27 **in size, such as hosts and ectoparasites and predators and prey. Finally, although there are**

28 **many compelling biological explanations for spring phenological delays, some examples of**

29 **delays are associated with short annual records prone to sampling error. As climate change**

30 **intensifies, our findings arm biologists with predictions concerning which climatic variables**

31 **and organismal traits drive phenological shifts.**

32   Global climate change has significant ecological consequences[4,8] and perhaps the best-

33 studied are advancements in the timing of seasonal activities, or phenology, of organisms[1-3,5,7,9-

34 [13]. Understanding the factors influencing phenological shifts are critical because these shifts can

35 impact the fitness of organisms by altering the availability of resources[2-4]. In addition,

36 phenological shifts can cause species declines by generating asynchronies or "mismatches"

37 between plants and pollinators[12], plants and herbivores[14], migrant birds and their prey[11] or floral

38 resources[15], and hosts and parasites[16]. Several recent syntheses have made significant inroads to

39 understanding how the phenology of species is shifting with climate change[1,5-7,13]. For example,

40 primary consumers were demonstrated to be shifting their phenology faster than other species in

41 the U.K.[1], species are shifting their phenology faster in spring than in autumn in China[5], and the

42 strength of phenological responses to climate change is dependent on the way responses are

43 measured e.g., type of behavior observed or number of observations [7].

44   Despite these insights, several critical knowledge gaps preclude accurate predictions on the

45 sensitivity of organisms to climate change on a global level. First, although many phenological

46 syntheses assume climate change as an important driver, few explicitly test for effects of climate

47 (but see[1,5,6]), and among those that do, climate data that has been standardized among studies is

48 rarely used to confirm the link between changes in phenology and climate. As a consequence, it

49 remains unclear which climatic variables, such as temperature or precipitation, are driving shifts

50   in phenology, and whether the broad geographical heterogeneity in these climate variables

51   impacts the power of these variables to explain and predict ecological trends. Second, recent

52   syntheses have relied on country-level data, and no synthesis in over a decade has addressed

53   phenological responses to climate change across the globe. Global analyses greatly improve

54   sample sizes and statistical power to detect drivers of phenological shifts. In addition, local-scale

55   syntheses may miss important broad-scale spatial heterogeneity in climate factors. For example,

56   global syntheses are critical to test broad-scale latitudinal hypotheses about phenological shifts,

57   such as the hypothesis that climatic factors driving seasonality across latitudes also drive

58   phenological changes. Third, it is unclear why some species show delayed spring phenologies

59   despite an overall trend towards advancement[10,17]. Finally, it is also unclear whether certain

60   ecologically important characteristics of organisms are predictive of strong phenological

61   responses. For example, body size may be an important factor determining the magnitude of

62   phenological response to climate change because smaller organisms acclimate more quickly to

63   changing conditions than larger organisms[18]. In addition, ectotherms may exhibit stronger

64   phenological responses than endotherms because they cannot thermoregulate independent of

65   their environments and are therefore more sensitive to changes in environmental conditions.

66   Because of these knowledge gaps, a general global framework is still missing for predicting the

67   direction and magnitude of phenological shifts based on ecological context and organismal traits.

68   To address these gaps, we conducted a global synthesis of phenological time series of

69   animals from 127 studies (Table S1; Table S2), spanning five continents and 15 classes of

70   animals including insects, mammals, reptiles, and birds. We focused on spring phenological

71   events in animals because phenological responses to climate change in plants have recently been

72   synthesized[19], some of our primary questions could only be answered using animal data, and the

73   evidence for advancement in animal phenology is more conflicting and controversial than it is

74   for plants[9] (see Supplement). Here, we synthesize the multivariate effects of climate change on

75   phenology, as well as test predictors of this complex phenomenon (e.g., latitude, endo- or

76   ectothermy), with a unique meta-analysis approach that jointly models phenological shifts, the

77   effects of climate on phenology, and climate change (the 50 year correlation between climate and

78   year) using a trivariate mixed-effects model[20,21] (see Extended Data Fig. 1; see Methods). Unlike

79   previous univariate meta-analyses that strictly synthesize phenological shifts[2,3], our trivariate

80   approach assesses whether phenology is dependent on climate and climate change and whether

81   the magnitude and direction of these relationships is dependent on 10 climate variables (e.g.,

82   mean, minimum and maximum temperature, precipitation, snowfall[22], see Methods). All climate

83   variables were standardized across all time series by accessing a single source of historical point-

84   based climate data (NOAA's NCDC-3 data[23]) with data that were specific to the region and time

85   of each study, reliably allowing us to identify which aspects of climate were driving

86   phenological shifts. Importantly, this approach facilitated evaluation of whether climate change

87   (the 50 year slope between climate and year), rather than just long-term climate means, was

88   associated with changes in phenology. Further, our trivariate mixed-effects meta-analysis also

89   accounted for dependencies of effects among related taxa due to their shared phylogenetic

90   history[24] (see Supplementary Code). We were able to compare relationships between phenology

91   and year for 1,011 time series and relationships between phenology, year and climate for a subset

92   of these including 321 time series.

93   The meta-analysis revealed that, on average, animals have advanced their phenology

94   significantly since 1950 ($\bar{\beta}$=-0.318, df=937, p=0.01; Fig. 1a; Table S3), advancing by 2.88

95   days/decade and 3.08 days/°C. Across all species and sites, mean temperature increased

96   significantly over time (Fig. 1a; Table S4). The meta-analysis also revealed that temperature is

97   closely related to phenological date independent of year, and that phenology is more closely

98   linked with mean temperature in areas with more climate change (Extended Data Fig. 2),

99   suggesting that climate change is indeed the driver of these shifts (Fig. 1a; Table S4).

100   Phenological shifts were not heavily biased by the phylogenetic history of taxa, which accounted

101   for only about 4.5% of the variance (phylogenetic τ^2) between phenology and year, and 0-6%

102   between phenology and climate (Tables S3-8). Between-study variance accounted for 8-9% of

103   the total variance accounted for in all models (Tables S3-8).

104   The direction of phenological shifts may differ among taxa, with some species showing

105   delays rather than advances of spring phenology[5,10,13,17,19]—such as delays in seabird egg laying

106   as a consequence of reduced sea ice[10] or delays in phenology (e.g., flowering) after short winters

107   that fail to induce vernalization[17]. To test whether a similar phenomenon might be responsible

108   for phenological delays (positive relationships between phenological date and year), we

109   examined whether the magnitude of the delay could be predicted by the increase in winter

110   temperatures (defined here as the relationship between year and average temperature during the

111   year's three coolest consecutive months), controlling for latitude. We found no support for the

112   hypothesis that winter temperatures predicted phenological delays, instead finding that they

113   predicted advancements (β=-0.296, df=321, p<0.001 in models with all time series) or were not

114   predictive (β=-0.125, df=68, p=0.32 among time-series with delays only). In fact, winter

115   temperatures were positively correlated with spring temperatures that are well documented to

116   drive phenological advancements (β=0.298, df=321, p<0.0001 for all time series, β=0.202,

117   df=68, p=0.03 among delays). Alternatively, many apparent spring delays might be sampling

118   artifacts of short annual records. Indeed, a funnel plot revealed that many studies based on short

119   time series (e.g., small sample sizes) had both delays and strong advances in phenology, but

120   when sample sizes were large, phenology advanced more uniformly (Flinger-Killeen test for

121   homoscedasticity: χ^2=112.72, p<0.0001; Fig. 1b; see Extended Data Fig. 3 for comparisons of

122   effect sizes with variance). In addition, there was no evidence of funnel plot asymmetry (Egger's

123   test: z=-0.724, p=0.47), suggesting that phenological delays are appropriately represented in our

124   dataset. While this result does not exclude true and biologically relevant spring delays in

125   phenology (see examples above), it suggests that reports of delays are likely sensitive to

126   sampling error; in fact, duration of time series has previously been found to influence observed

127   phenological trends in marine species[7]. These findings also indicate that previous phenological

128   syntheses[1-3] may have underestimated phenological advancements since they did not statistically

129   account for differences among studies emerging via sampling error[25].

130   We also hypothesized that phenological shifts would be associated with the climatic variables

131   that drive seasonality locally—such as temperature at mid-latitudes (i.e. temperate zones) and

132   precipitation at low latitudes (i.e. tropical and subtropical zones). Moreover, because climate

133   change is resulting in greater changes in temperature than precipitation[26], we hypothesized

134   greater phenological shifts in temperate than tropical zones. In support of these hypotheses, as

135   absolute value of latitude increased, changes to temperature became more predictive of the

136   magnitude of phenological shifts, and as latitude decreased, precipitation was a stronger

137   predictor of phenology (test for different slopes[27]: t=7.89, df=1650, p<0.0001; Fig. 1c; Table S5).

138   Further, there was a greater increase in temperature than precipitation through time (Extended

139   Data Fig. 4), and the correlation between phenology and temperature in the temperate zones was

140   stronger than the correlation between phenology and precipitation in the tropics (Fig. 1c). These

141   results indicate that different climatic variables are triggering phenology in temperate and

142   tropical regions. While past syntheses have hypothesized that species should shift their

143   phenology faster at higher latitudes in response to greater warming in these regions[2,3,6], low-

144   latitude species may also be shifting their phenology at high rates in response to changes in

145   rainfall. Given that the majority of phenological studies are from northern temperate climates[7]

146   (especially North America and Europe; Fig. 2), and emphasize temperature over precipitation,

147   additional phenological time series from low latitudes are needed to quantify the full effects of

148   precipitation shifts on tropical phenology. However, the effects of precipitation on phenology

149   may be less closely associated with latitude than the effects of temperature simply because

150   latitude is more strongly correlated with temperature than precipitation.

151   Given that temperature and precipitation drive phenology unequally across the globe and

152   particular taxa exhibit differential sensitivities to extreme temperatures and moisture levels, we

153   hypothesized that the phenology of specific taxonomic groups might be more strongly associated

154   with temperature than precipitation. For example, we expected amphibians to respond to

155   precipitation more strongly than any other taxonomic group because of their considerable

156   reliance on moist conditions for survival and reproduction. Across all taxa synthesized,

157   phenology was associated more strongly with temperature than with precipitation (temperature,

158    $\bar{\beta}$=-0.310, df=1579, p=0.02; precipitation, $\bar{\beta}$=-0.054, df=1579, p=0.54; Extended Data Fig. 5;

159   Table S4), and different components of temperature (mean, minimum and maximum) did not

160   significantly differ from one another at predicting phenology. As predicted, amphibians

161   exhibited the strongest association between precipitation and phenology among all taxa ($\bar{\beta}$=-

162   0.172, df=1564, p=0.16; Extended Data Fig. 5b; Table S6).

163   Next, we sought to identify general ecologically-important characteristics of taxa that might

164   predict the strength of phenological responses to climate change. Here, we hypothesized that

165   ectotherms and smaller organisms should be more sensitive to shifts in climate than endotherms

166   and larger organisms (because thermal inertia is positively associated with body size[18,28]).

167   Indeed, body size was a significant negative predictor of phenological shifts alone (β=-0.0221,

168   df=921, p<0.01; Table S7) and as a covariate alongside other species traits in most statistical

169   models (Fig. 1d; Table S7). Among taxa, invertebrate groups tracked their phenology to

170   temperature more closely than birds and mammals (Fig. 3a; Table S7), and as a whole,

171   invertebrates tended to track temperature better than vertebrates (Fig. 3b; Table S7). As

172   predicted, the phenology of ectotherms was more strongly correlated with temperature than the

173   phenology of endotherms (Fig. 3c; Table S7). Finally, herbivore phenologies tracked

174   temperature more closely than carnivore phenology (Fig. 3d; Table S7) when accounting for

175   body size, possibly because herbivores are also responding to shifts in the timing of plant

176   phenology[29], supporting conclusions by Thackeray *et al.* based on phenological shifts in the

177   U.K.[1]. Additionally, we did not observe a difference between the phenological responses of

178   terrestrial and aquatic species (Extended Data Fig. 6; Table S7), although there are admittedly

179   few aquatic species in the dataset (18 total) and all are marine.

180   Finally, we posited that the type of phenological responses, such as peak seasonal abundance,

181   arrival (migration), and breeding/rearing (calling, nesting, laying, hatching, or weaning), may

182   differ in their sensitivities to climate change, as recently concluded by synthesis on marine

183   systems[7]. We predicted that arrival would be least correlated with climatic factors because

184   migrants are likely reacting to climatic conditions where they left from rather than conditions

185   where they are arriving[30]. Phenological responses related to arrival tracked climate the most

186   poorly (Extended Data Fig. 7; Table S8), and those based on peak abundance tracked

187   temperature changes the most closely—possibly because peak abundance is more often

188   documented with smaller invertebrates that phenologically respond strongly to climate.

189   Unfortunately because there are very few phenological time series from equatorial regions, and

190   arriving species often come from multiple departure locations, we could not test whether the

191   timing of departures for spring migrations tracked temperature better than arrivals (but see[31]).

192   Our findings add to the growing evidence of direct ecological consequences of climate

193   change on ecological systems and provide strong evidence linking climate change to

194   phenological shifts. Our synthesis unveiled previously unidentified generality in the phenological

195   responses of organisms to climate, indicating that the phenology of species at high and low

196   latitudes most strongly respond to temperature and precipitation, respectively, and thus different

197   components of climate drive phenology in different regions of the globe. We also found that

198   different taxa respond to the same climatic signals but do so at different rates, and that the

199   strength of these phenological shifts is predictable based on two easily measured traits,

200   thermoregulation and body size. As climate change intensifies in the next century, our results

201   suggest that advances in phenology are likely to become more exaggerated, potentially further

202   desynchronizing interactions between species that vary considerably in their body sizes, such as

203   mutualistic, predator–prey, and host–parasite interactions. However, the synthesis presented here

204   now arms climate biologists with knowledge regarding the specific components of climate and

205   the traits of interacting species that can drive phenological shifts, providing new opportunities to

206   forecast mismatches and mitigate their adverse effects.

207

208

209   **Materials and methods:**

210   *Literature survey and data requirements.* We conducted a literature search in September 2012

211   on Web of Science for the term "phenology AND climate" within the following fields:

212   environmental sciences and ecology, zoology, developmental biology, reproductive biology, life

213   sciences (other), entomology, behavioral sciences, physiology, biodiversity and conservation,

214   fisheries, evolutionary biology, parasitology, marine and freshwater biology, infectious diseases,

215   and oceanography. This search generated 6,989 studies which were examined for phenological

216   time series. References in these papers and the USA National Phenology Network (usanpn.org)

217   database were also examined for time series. Time series were not used if they (1) contained data

218   from a span of <10 years; (2) contained data for fewer than seven individual years; (3) described

219   autumn migrations; or (4) described data that were redundant with data we had already compiled

220   from another paper. We also eliminated raw data from before 1950, because this is considered to

221   be before significant global climate change[32]. Our exclusion criteria are similar to those from

222   previous meta-analyses[2,3].

223

224   *Data extractions.* We extracted raw time series data from figures plotting day of year of

225   phenological event (including date of first or median arrival, first calling, nesting, laying, peak

226   abundance, oestrus, or weaning) against year using Datathief III Version 1.6 (© Bas Tummers).

227   Correlation coefficients between phenological date and year, standard errors or surrogates, and

228   slopes were also calculated for each time series when they were not reported in the original text

229   (All analyses were conducted in R 3.1.0; stats package, glm function). Correlation coefficients

230   (*r*) and standard deviations were available for 1,011 of these time series (representing 127

231   studies) which were used in the meta-analysis examining the relationship between phenology and

232   year. Approximately 400 time series from about 100 papers provided raw data and were used in

233   the meta-analyses examining the relationships between phenology, year, and climate (the actual

234   numbers varied between different climate variables because some variables were not available at

235   certain geographic locations). Sampling variances (used as weights) were derived from all

236   correlation coefficients, and coefficients and variances were standardized using Fisher's z-

237   transformation before all meta-analysis modeling.

238

239   ***External climate data.*** Climate data were from the NOAA National Climatic Data Center

240   (NCDC; www.ncdc.noaa.gov) worldwide database of "monthly observational data"

241   corresponding to the nearest location (within 100km) and full time span of every time series that

242   provided raw data and geographic coordinates. Ten climate variables were used in our meta-

243   analysis (see Extended Data Fig. 6), and they generally were related to temperature or

244   precipitation. Climate variables were used individually in models instead of as covariates (see

245   below). Yearly averages of climate variables were compiled for all variables in all locations and

246   for the years in all time series only when data were available for all 12 months. Within each time

247   series, correlation coefficients and standard errors were compiled for all correlations between all

248   annual climate variables year, all climate variables and phenology, and phenology and year (stats

249   package, glm function). We did not have any climate data for marine species and did not include

250   these time series in any analyses testing the effects of climate.

251

252   ***Independent fixed-effects variables.*** Independent variables collected for each time series

253   included taxonomic classification of the focal species, absolute value of latitude, elevation, form

254   of thermoregulation (ectothermy or endothermy), trophic level, habitat (terrestrial or marine),

255   country (to control for geography), log-transformed body mass (see Supplementary Methods)

256   and type of phenological event (endpoint measured). Taxonomic classification was assessed to

257   the class level. Elevation specific to the locations where time series were observed was extracted

258   from Worldclim elevation rasters (www.worldclim.org) (raster package, extract function).

259   Trophic levels were assigned categorically as "herbivore", "omnivore", or "carnivore". If a

260   species typically eats plants and animals it was designated an omnivore, but if it mostly relies on

261   either prey or plants and only occasionally ate the other, it was assigned to "carnivore" or

262   "herbivore" respectively. Phenological events were categorized as either "arrival" (migrations),

263   "breeding/rearing" (calling, nesting, laying, hatching, or weaning), or "peak abundance" (peak

264   population abundance).

265

266   *Meta-analysis models.* A trivariate mixed-effects meta-analysis was used to analyze three effect

267   sizes per study that jointly quantify the pairwise relationships among phenology, time, and a

268   single climate variable. Preserving the trivariate structure of effect sizes has the advantage of

269   accounting for the correlations within the three non-independent effect sizes (because of

270   sampling variability and covariances), while also explicitly accounting for any existing

271   correlations among these three effect size groups (via a multivariate random-effects model). Our

272   overall model had a hierarchical structure in which we modeled the sampling variances and

273   covariances among the three effect sizes (within-study weighting to account for study sampling

274   error; see Supplementary Methods), between-study random-effects for each effect size triplicate

275   that were allowed to be correlated but differ among groups (i.e., a multivariate version of the

276   between-study variance component typically included in traditional random-effects meta-

277   analysis), and finally an unstructured random-effect modeling the phylogenetic correlations

278   among taxa (see Supplementary Methods and Code). For all models, the *rma.mv* function from

279   the R package *metafor* was used (see Supplement), with the variance-covariance matrix as the

280   variance-covariance matrix of the sampling errors, and all random effects (trivariate between-

281   study variances, and phylogenetic) were based on restricted maximum likelihood estimator using

282   a nlminb numerical optimizer. However, we did not include phylogenetic random-effects in our

283   analyses of the relationship between phenology and body size because phylogeny and body size

284   are highly correlated and thus controlling for phylogeny also indirectly eliminates much of the

285   body size variation (see Supplement). Please see Supplementary Code for the R script used in

286   these analyses.

287

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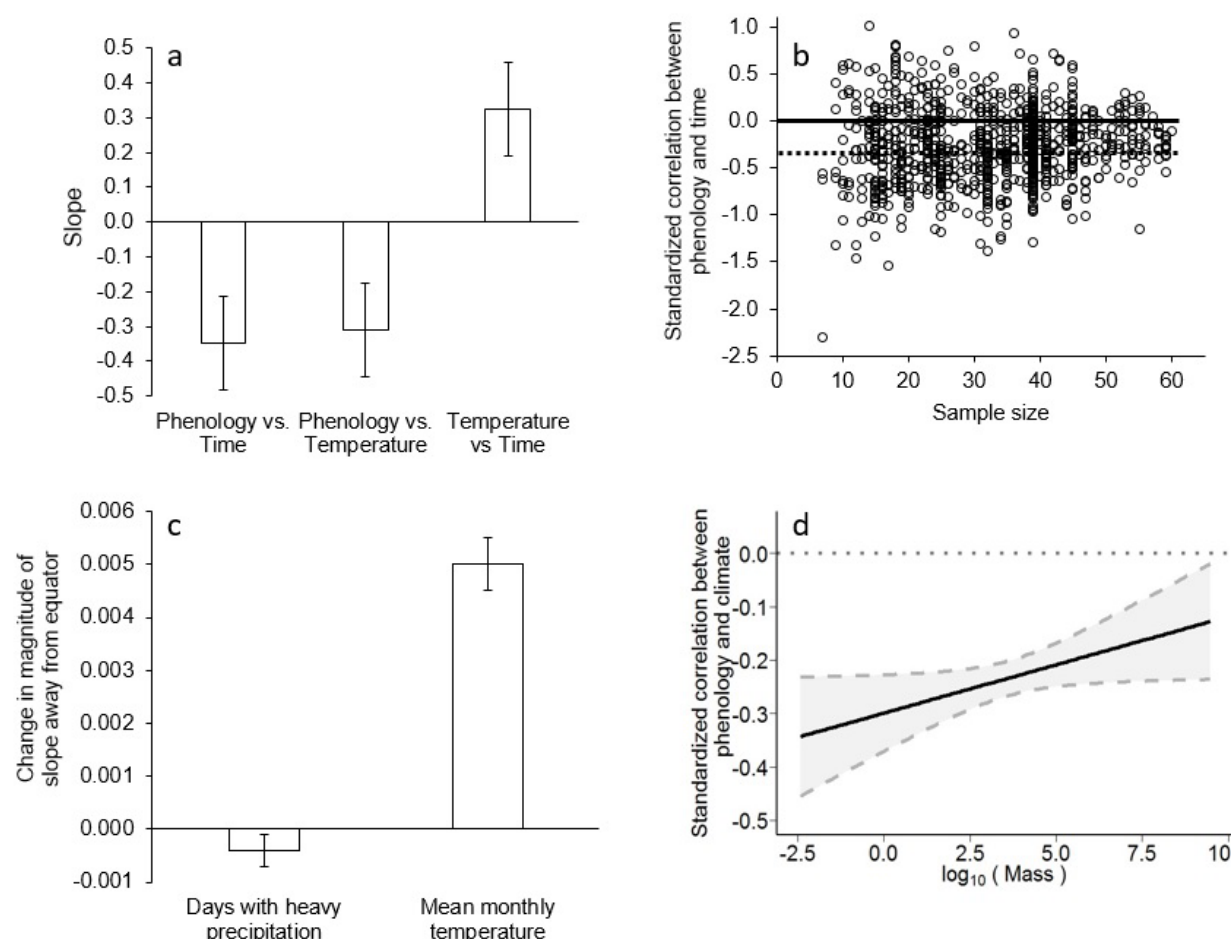390   **Figures:**

391

392   **Fig. 1. Improving how we understand advancements in phenology due to climate change.**
393   (a) Across 1,011 time series, phenology became earlier through time as temperature increased
394   through time and the detrended increases in temperature were negatively correlated with
395   phenology (see Extended Data Fig. 4 for precipitation). Error bars represent SEM. (b) A funnel
396   plot comparing sample sizes (total years in time series) with standardized effect sizes (correlation
397   between phenology and time quantified via Fisher's Z effect sizes) reveals that studies with small
398   samples sizes have large variation with both the positive and negative shifts, suggesting that
399   species appearing to delay their phenology in spring might sometimes be spurious products of
400   sampling error. The solid line is the zero line and the dotted line represents the grand mean
401   correlation (-0.349). (c) The slope between temperature and phenology became steeper as the
402   absolute value of latitude (or distance from the equator) increased (bar, $p<0.0001$), while the
403   slope between rainfall and phenology became less steep ($p<0.01$). Thus, temperature became
404   more predictive of phenology further from the equator, whereas rainfall became more predictive
405   of phenology closer to the equator, suggesting that the phenology of species is driven by the
406   climatic factor that drives seasonality locally. Error bars represent SEM. (d) The slope between

407   log-transformed body mass and the correlation between phenological date and mean temperature
408   is positive in the trivariate meta-analysis model, indicating that smaller organisms track their
409   phenology with temperature more closely than larger organisms. Data points are not shown to
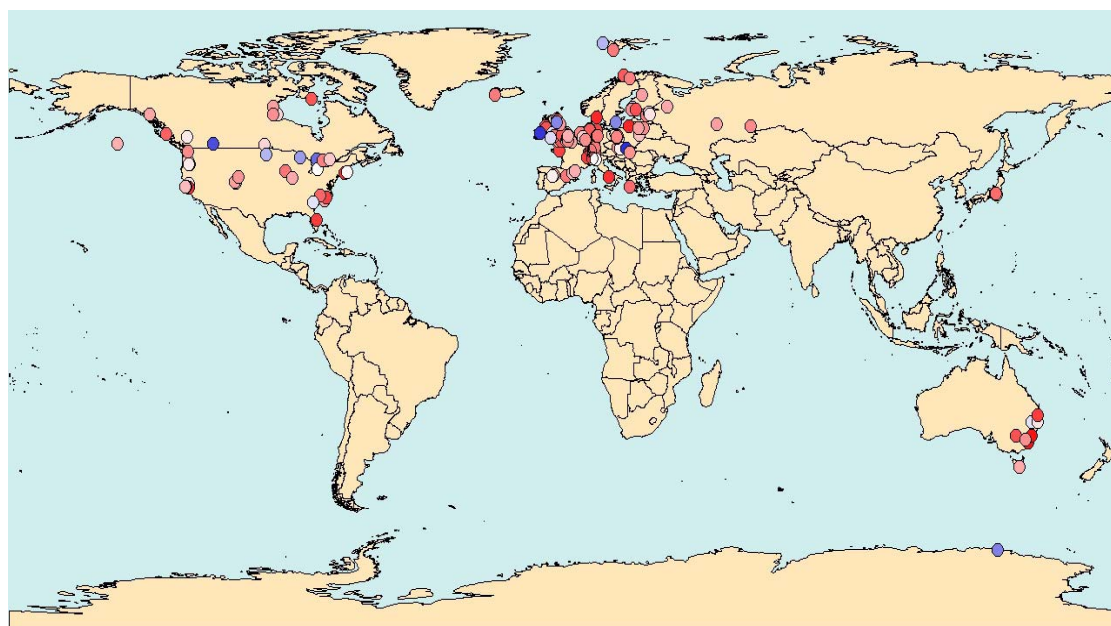410   reduce clutter and 95% confidence intervals are provided in gray.

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Fig. 2. The uneven global distribution of published studies exploring the phenology of animals. There are hundreds of published phenology time series from North America and Europe, but much less is known about phenology on the other five continents with particularly large gaps in the tropics and marine systems. Red points indicate advancements in phenology over time and blue points indicate delays. The strength of the color indicates the magnitude of the relationship between phenology and time (as quantified with a Fisher's Z effect size).
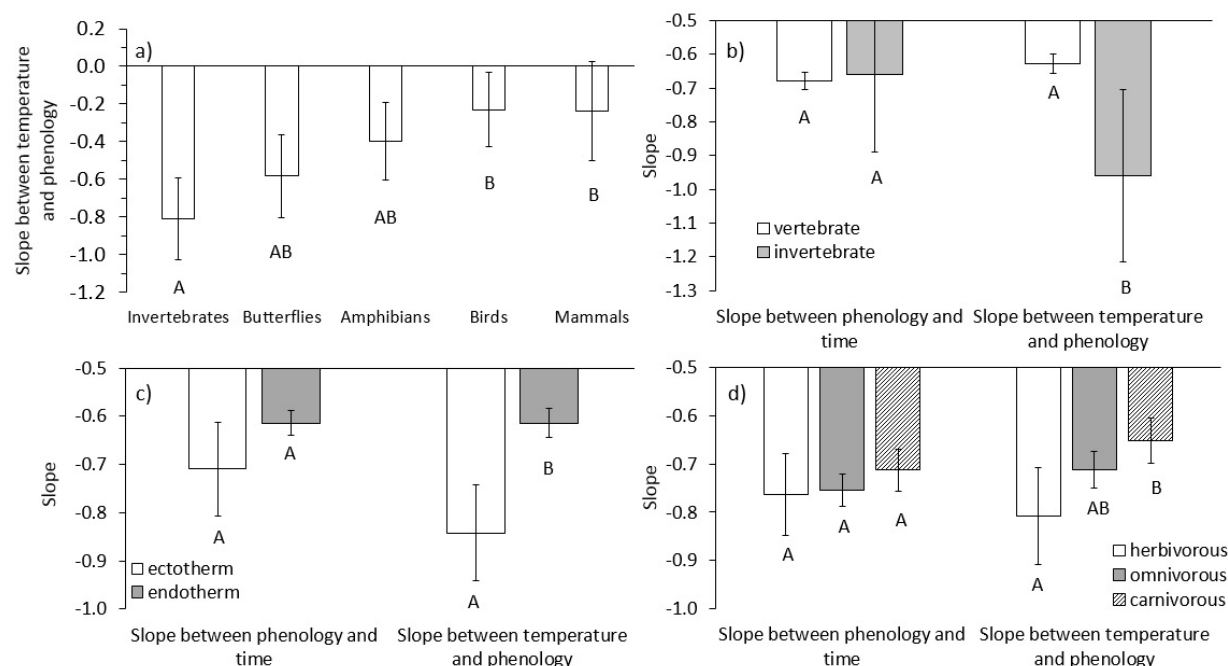
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Fig. 3. The ability of phenology to track temperature varies among taxonomic classes of animals, ecto- or endothermy, and trophic level. In models including body size as a covariate, (a) smaller taxa, such as (b) invertebrates, and (c) ectotherms tracked temperature closer than larger animals and endotherms. (d) Herbivores had a greater association between temperature and phenology than carnivores, possibly because herbivores were reacting to shifts in plant phenology associated with temperature. We report relationships between phenology and both temperature and time to highlight that even if groups are apparently advancing their phenology at similar rates, they could be responding to changing climates at dissimilar rates if they come from regions experiencing different rates of climate change. Error bars represent SEM for the slope parameters from trivariate mixed-model meta-regressions. Different letters denote statistically significant differences in effect sizes.