

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 species¹⁻⁵. Recent syntheses have concluded that trophic level¹,**
15 **latitude⁶, and how phenological responses are measured⁷ 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 resources²⁻⁴. In addition,
36 phenological shifts can cause species declines by generating asynchronies or “mismatches”
37 between plants and pollinators¹², plants and herbivores¹⁴, migrant birds and their prey¹¹ or floral
38 resources¹⁵, and hosts and parasites¹⁶. 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 China⁵, 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 observations⁷.

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 organisms¹⁸. 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 synthesized¹⁹, 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 plants⁹ (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, snowfall²², 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 data²³) 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 history²⁴ (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 ice¹⁰ or delays in phenology (e.g., flowering) after short winters
107 that fail to induce vernalization¹⁷. 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 ($\beta=-0.296$, $df=321$, $p<0.001$ in models with all time series) or were not
114 predictive ($\beta=-0.125$, $df=68$, $p=0.32$ 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 ($\beta=0.298$, $df=321$, $p<0.0001$ for all time series, $\beta=0.202$,
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: $\chi^2=112.72$, $p<0.0001$; 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 species⁷. These findings also indicate that previous phenological
128 syntheses¹⁻³ may have underestimated phenological advancements since they did not statistically
129 account for differences among studies emerging via sampling error²⁵.

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 precipitation²⁶, 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 slopes²⁷: $t=7.89$, $df=1650$, $p<0.0001$; 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 climates⁷
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 ($\beta=-0.0221$,
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 phenology²⁹, 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 systems⁷. 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 arriving³⁰. 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 see³¹).

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 change³². 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 Tummars).
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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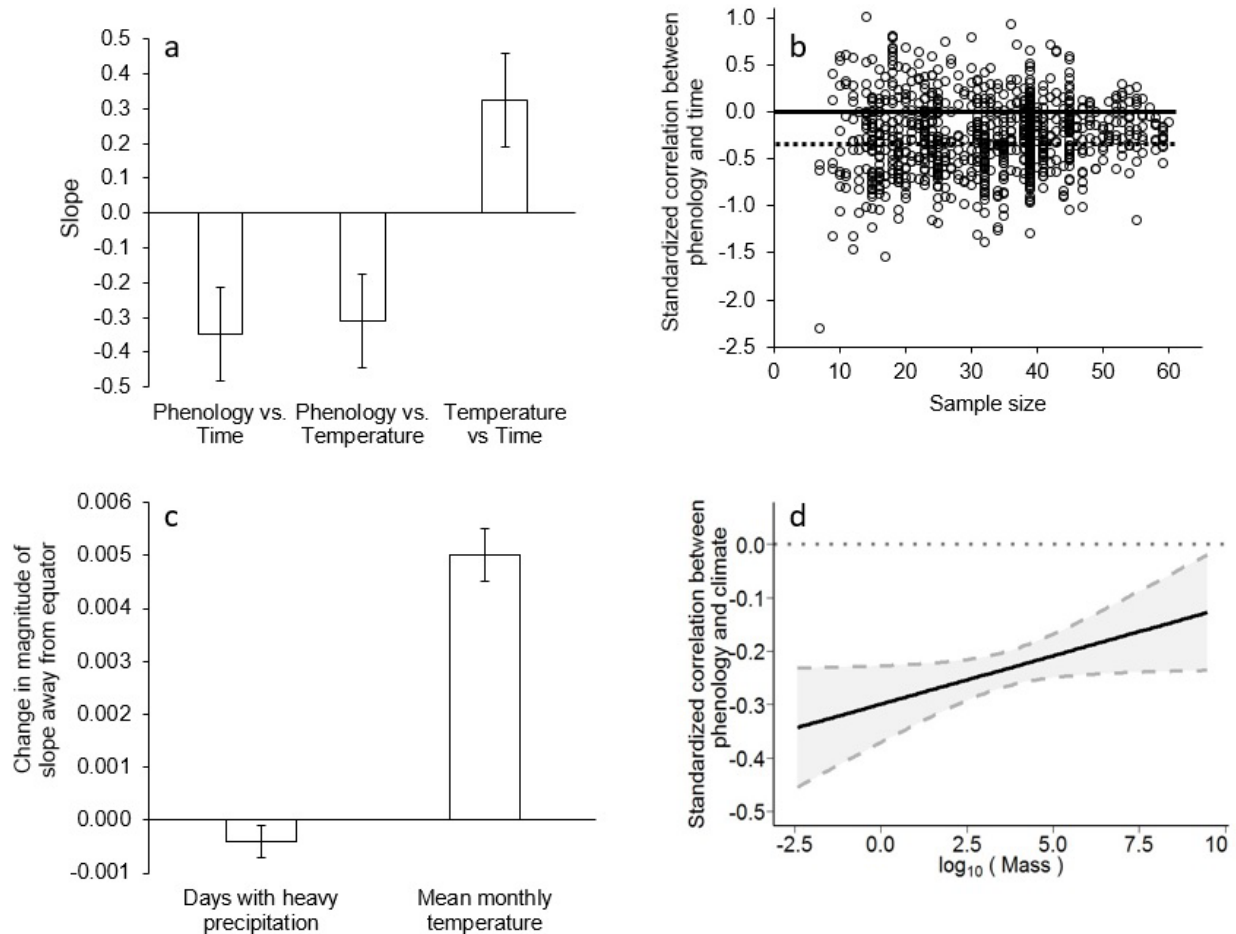
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388 and requests for materials should be addressed to J.M.C. (jcohen9@mail.usf.edu).

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390 **Figures:**

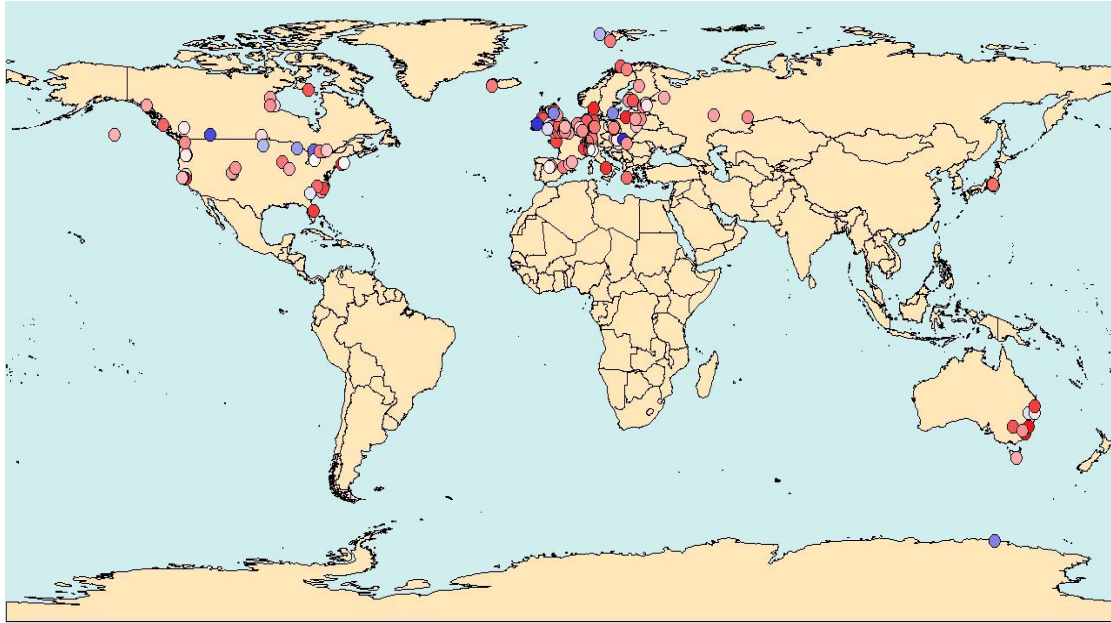


391

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

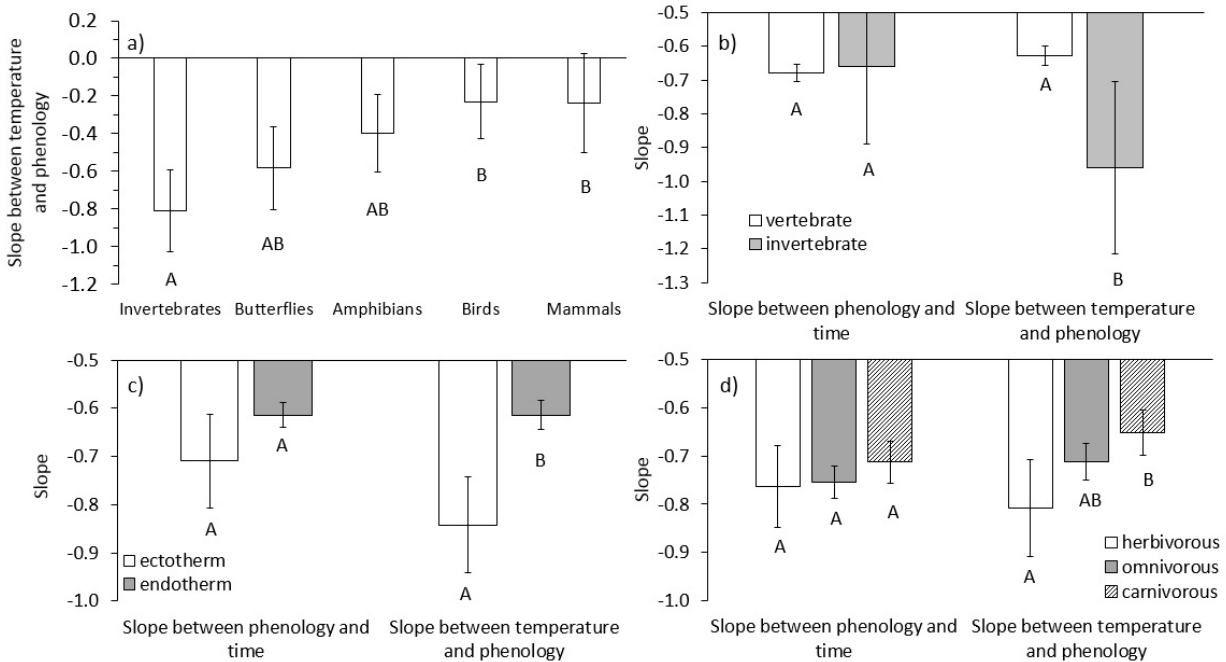
407 log-transformed body mass and the correlation between phenological date and mean temperature
408 is positive in the trivariate meta-analysis model, indicating that smaller organisms track their
409 phenology with temperature more closely than larger organisms. Data points are not shown to
410 reduce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



411

412 **Fig. 2. The uneven global distribution of published studies exploring the phenology of**
413 **animals.** There are hundreds of published phenology time series from North America and
414 Europe, but much less is known about phenology on the other five continents with particularly
415 large gaps in the tropics and marine systems. Red points indicate advancements in phenology
416 over time and blue points indicate delays. The strength of the color indicates the magnitude of
417 the relationship between phenology and time (as quantified with a Fisher's Z effect size).

418



419

420 **Fig. 3. The ability of phenology to track temperature varies among taxonomic classes of**
 421 **animals, ecto- or endothermy, and trophic level.** In models including body size as a covariate,
 422 (a) smaller taxa, such as (b) invertebrates, and (c) ectotherms tracked temperature closer than
 423 larger animals and endotherms. (d) Herbivores had a greater association between temperature
 424 and phenology than carnivores, possibly because herbivores were reacting to shifts in plant
 425 phenology associated with temperature. We report relationships between phenology and both
 426 temperature and time to highlight that even if groups are apparently advancing their phenology at
 427 similar rates, they could be responding to changing climates at dissimilar rates if they come from
 428 regions experiencing different rates of climate change. Error bars represent SEM for the slope
 429 parameters from trivariate mixed-model meta-regressions. Different letters denote statistically
 430 significant differences in effect sizes.