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**A widespread thermodynamic effect, but maintenance of biological rates through space across life's major domains**

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Short title: Biological rates preserved across biomes

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## 22 **Abstract**

23 For over a century, temperature compensation (maintenance of biological rates with changing  
24 temperatures) has remained controversial. An alternative idea, that fitness is greater at higher  
25 temperatures (the thermodynamic effect), has gained increasing traction, and is being used to understand  
26 large-scale biodiversity responses to environmental change. Yet evidence in favour of each of these  
27 contrasting hypotheses continues to emerge. In consequence, the fundamental nature of organismal  
28 thermal responses and its implications remain unresolved. Here we investigate these ideas explicitly using  
29 a global dataset of 619 observations of four categories of organismal performance, spanning 14 phyla and  
30 403 species. In agreement with both hypotheses, we show a positive relationship between the temperature  
31 of maximal performance rate ( $T_{opt}$ ) and environmental temperature ( $T_{env}$ ) for all traits. Next we  
32 demonstrate that relationships between  $T_{env}$  and the temperature of maximal performance rate ( $U_{max}$ ) are  
33 rarely significant and positive, as expected if a thermodynamic effect predominates. By contrast, a  
34 positive relationship between  $T_{opt}$  and  $U_{max}$  is always present, but markedly weaker than theoretically  
35 predicted. These outcomes demonstrate that while some form of thermodynamic effect exists, ample  
36 scope is present for biochemical and physiological adaptation to thermal environments in the form of  
37 temperature compensation.

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39

## 40 **Introduction**

41 All organisms are exposed to variation in ambient temperature. Such variation typically has direct effects  
42 on the physiology and population dynamics of ectotherms, ultimately exerting a marked influence on  
43 range size and dynamics (1-3). In consequence, ectothermic animals and plants exhibit a wide range of  
44 responses to modulate the effects of ambient temperature variation (4-6). Among their adaptive  
45 responses, temperature compensation has proven especially controversial. Also known as metabolic cold  
46 adaptation (7), the Krogh effect (8), or metabolic compensation (9), temperature compensation refers to  
47 the maintenance of biological rates in the face of a temperature change (10-12). Initially proposed on the  
48 basis of empirical evidence and the theoretical notion that rate maintenance, especially under low  
49 temperature conditions, would result in maintenance of fitness (13-15), the idea has become controversial  
50 on both theoretical and empirical grounds. The controversy has been most prominent for metabolic rate  
51 conservation, with the theoretical counterargument being that because metabolic rate represents a cost (of  
52 maintenance) to an organism, conservation thereof, in the face of an opportunity for reduction, should not  
53 be beneficial (11). Empirical evidence, typically from measurements of standard or resting metabolic  
54 rates across a range of biological levels, has come out both in favour of and against temperature  
55 compensation (3, 5, 9, 15-22).

56 One line of evidence that has been especially effective in questioning the temperature  
57 compensation hypothesis is the discovery and description of a thermodynamic effect (23). Sometimes  
58 also known as the ‘warmer is better’ hypothesis, the idea encompasses both sound theoretical reasons and  
59 evidence for a relationship between the optimum temperature of a process and the maximal rate of that  
60 process (Figure 1). In other words, because rates proceed faster at higher ambient, and therefore by  
61 association for many ectotherms, higher organismal temperatures, fitness should always be higher at  
62 higher temperatures, acknowledging that upper thermal limits to performance exist for all organisms (24-  
63 25). The strongest evidence for the thermodynamic effect comes from population growth rates in insects,  
64 with suggestions that it applies to performance traits in ectotherms generally (26-28). Across the 65 insect  
65 species examined by Frazier et al. (26), the thermodynamic effect was found to be even stronger than

66 predicted by theory (29), suggesting that relatively warm environments have the highest fitness benefits  
67 for organisms. In turn, these findings have also been used to explain the slow life histories of polar  
68 organisms (21).

69 Despite this evidence for a thermodynamic effect, several studies continue to find empirical  
70 support for temperature compensation. For example, in plants, much evidence has been found for  
71 maintenance of respiration rate across a broad range of temperatures (5-6, 9). In other groups, contrasting  
72 empirical outcomes continue to be published (22, 30), with little indication of a developing consensus (8,  
73 21). In consequence, despite the existence of the idea of temperature compensation for a century (13), and  
74 strong theoretical and empirical bases for the thermodynamic effect (29, 31), how these contrasting ideas  
75 are related, and which might provide the strongest explanation for the evolution of biological rates in  
76 response to temperature variation across the globe remains at best unclear. Moreover, explanations also  
77 seem to differ in their support across different groups of organisms and from different environments (11),  
78 and often with little comparison among taxa (compare e.g. 17, 21, 32), though with notable exceptions (9,  
79 33). Yet at the same time, the expectations from these competing hypotheses are variously being used as  
80 the basis to understand diversity variation globally (34) and the extent to which changes in this diversity  
81 might occur as a consequence of anthropogenic warming (35-36).

82 Here we seek to resolve these long-standing and important (11) contrasting ideas by examining  
83 optimum temperature and rates at those optima for a suite of biological functions across much of life's  
84 ectotherm diversity and at a global scale. Rather than treating major taxa and organisms from terrestrial  
85 and aquatic habitats separately, we use phylogenetic mixed models to investigate the extent to which both  
86 habitat and phylogenetic signal influence the relationships between optimum temperature and rates of  
87 biological functions at that temperature, and subsequently the ways in which both optimum temperature  
88 and maximum rates vary with temperature across the planet. We focus on rates of development, growth,  
89 locomotion and photosynthesis, which are expected to be correlated with fitness (26), but we avoid  
90 investigation of metabolic rates (or respiration rate for plants, e.g. 9). We do so because few animal

91 ectotherm metabolic rate investigations provide measured values for maximal rates and the temperatures  
92 thereof ( $U_{\max}$  and  $T_{\text{opt}}$  in the terminology of 37).

93 Our analysis uses information from 619 observations, spanning 14 phyla, 75 orders, 300 genera  
94 and 403 species. By contrast with previous comprehensive analyses of the slope of the relationship  
95 between rate and temperature (e.g. 33), we are concerned here with optimum rates ( $U_{\max}$ ) and the  
96 temperatures at which they occur ( $T_{\text{opt}}$ ). We test explicitly three predictions of the temperature  
97 compensation and thermodynamic effect hypotheses. First, if either of these hypotheses holds, a positive  
98 relationship between  $T_{\text{opt}}$  and a measure of environmental temperature ( $T_{\text{env}}$ ) during the maximal activity  
99 period of the organism should be found (Figure 1), assuming that some form of thermal adaptation (or  
100 coadaptation) is typical of ectotherms (38-40). Absence of a relationship might indicate some form of  
101 performance constraint (41). Second, the relationship between  $U_{\max}$  and  $T_{\text{env}}$  should be positive in the  
102 case of the predominance of a thermodynamic effect, but absent or weak in the case of temperature  
103 compensation (40, 42). Third,  $U_{\max}$  and  $T_{\text{opt}}$  should be positively related in the case of a pronounced  
104 thermodynamic effect, but weak or absent where temperature compensation predominates (26). More  
105 specifically, when  $U_{\max}$  is plotted against the inverse of optimum body temperature, the thermodynamic  
106 effect hypothesis suggests that the slope of the line should provide an estimate of activation energy of 0.6  
107 to 0.7 eV or perhaps steeper (23, 26, 29).

108

## 109 **Methods**

110 We compiled data from published literature on optimal temperature and maximal performance ( $T_{\text{opt}}$  and  
111  $U_{\max}$  (*sensu* 37) for whole organismal traits expected to be closely related to fitness including rates of  
112 photosynthesis, growth, development and locomotion performance. Many published studies are available  
113 for these traits, making it possible for the database to cover the majority of the world and a diverse range  
114 of taxonomic groups and habitats to gain general insight. In addition to original papers, recent  
115 compilations of data and their reference lists were also searched (26, 28, 32, 43-46). The search ended on  
116 January 1<sup>st</sup> 2016. We only accepted records where measured estimates of performance were undertaken

117 beyond the measured maximal performance (i.e.  $T_{opt}$  and  $U_{max}$ ). Performance curves where maximal  
118 performance was only estimated by models were not included. For development rates, however, high  
119 temperatures leading to no development were accepted as a data point above maximal performance. We  
120 included the full taxonomy of all organisms as given by the primary publication, and adjusted for  
121 synonymy where appropriate based on online repositories (such as [www.algaebase.org](http://www.algaebase.org) or [www.gbif.org](http://www.gbif.org)).  
122 The analyses were done according to the species lists as generated by the online tree of life (47). The  
123 geographical origin of the investigated population of each species (and for each trait where the locations  
124 differed among traits) was taken from the primary literature whenever possible. When the origin of an  
125 investigated population was not available from primary literature, the origin was estimated using data  
126 from the Global Biodiversity Information Facility (GBIF). Median latitude and longitude was extracted  
127 from GBIF occurrence records using the ‘*rgbif*’ (48) and ‘*spocc*’ (49) packages in R (50) and used for that  
128 species. In cases where GBIF records were lacking the origin was estimated from other sources  
129 (described for each record in the database, Table S17). For locomotion we included ln-transformed body  
130 length as a covariate, and for developmental rates we included ln-transformed dry mass as a covariate  
131 because of significant allometry of these traits (see results). Snout-vent length (for reptiles and anurans)  
132 and body length (for fish and invertebrates) were obtained from the original literature or estimated from  
133 other sources when not available (described for each record in the database, Table S17). Dry mass  
134 estimates were sourced from the original literature when given or inferred from length or fresh mass  
135 measured available using specific relationships given by Hodar (51) and Ganihar (52). In all cases the  
136 sources and relationships used to generate dry mass estimates are given in the database.

137  
138 Data were analysed using phylogenetic mixed models (53-55), which were implemented in the ‘ASReml-  
139 R’ v3.0 (56) package of R v3.0.2 (57), with inverse relatedness matrices calculated from phylogenetic  
140 covariance matrices using the ‘MCMCglmm’ package v2.21 (58). The phylogeny used for analysis was  
141 drawn from a comprehensive tree of life, accessed using the ‘rotl’ v0.5 package of R v3.2.2 (47, 59). In  
142 addition to the 619 observations that were analysed, a further 319 records for 80 species were excluded

143 from the analysis; some of these could not be matched to the online tree of life, and so were not  
144 considered further. Six extremely high maximum rates for growth of Actinobacteria from the Luna-2  
145 cluster (60) and one extremely high growth rate for *Chlorella pyrenoidosa* (61) exerted high leverage on  
146 the data and were excluded on these grounds. Twenty-two records were removed because they could not  
147 be matched to climate data, one record was removed because the temperature of the warmest quarter was  
148 less than 0 °C; the remaining records were excluded because they data were presented in units that could  
149 not be reasonably converted to match the majority of the remaining data.

150  
151 Environmental temperature ( $T_{env}$ ) at the site of geographical origin (see above) for each record was  
152 calculated as the mean temperature of the warmest quarter using monthly (January 2001 – December  
153 2016) daytime data from the MODIS Land Surface Temperature dataset (MOD11C3 v6;  
154 doi:10.5067/MODIS/MOD11C3.006; 0.05° spatial resolution). Seasonality at each site was calculated as  
155 the difference between the mean temperature of the warmest quarter and the mean temperature of the  
156 coldest quarter, also calculated from the MODIS Land Surface Temperature dataset. These data were  
157 downloaded and analysed using the ‘MODIS’ (62), ‘raster’ (63), and ‘xts’ (64) packages in R (50).

158  
159 Phylogenetic mixed models were selected over the more commonly used methods of independent  
160 contrasts (65) and phylogenetic generalised least squares (66) because the former can formally  
161 incorporate non-independence associated with phylogenetic relatedness as well as non-independence  
162 associated with multiple measurements of single species. Multiple measurements were relatively  
163 uncommon in the data sets for locomotion, growth, and development, where 73%, 88%, and 91% of  
164 species were represented by only one measurement, respectively, though a small number of species were  
165 represented by many measurements (up to ten measurements per species for locomotion, up to 14  
166 measurements per species for growth, and up to five measurements per species for development).  
167 Multiple measurements are more common in the data for photosynthesis, where 33% of species have one  
168 measurement, 49% of species have two measurements and the remainder have three-to-eight

169 measurements. Phylogenetic mixed models are an analogue of the animal model from quantitative  
170 genetics, which partitions phenotypes of related individuals into heritable (additive genetic) and non-  
171 heritable components to estimate inter-specific variances and covariances between traits (55). The  
172 significance of fixed effects was tested using Wald-type  $F$ -tests with conditional sums of squares and  
173 denominator degrees of freedom calculated according to Kenward and Roger (67). Phylogenetic  
174 heritability, a measure of phylogenetic non-independence equivalent to Pagel's (68)  $\lambda$  (55), was estimated  
175 as the proportion of variance attributable to the random effect of phylogeny. Approximate standard errors  
176 for the estimate of phylogenetic heritability was calculated using the R 'pin' function (69).

177

## 178 **Results**

179 We used phylogenetic mixed models to investigate the relationship between optimum temperature ( $T_{opt}$ )  
180 and environmental temperature ( $T_{env}$ ), measured here as mean temperature of the warmest quarter  
181 (derived from the Moderate Resolution Imaging Spectroradiometer, MODIS,  
182 <https://modis.gsfc.nasa.gov/>) of the collection locality of the species concerned (see Methods). The results  
183 demonstrated a positive relationship, though with much variation, for development rate, and no  
184 relationship between  $T_{opt}$  and  $T_{env}$  for growth rate, locomotion rate, and photosynthetic rate (Figure 2).  
185 Interaction terms in these models were always non-significant. Thus, only models with additive  
186 combinations of main effects are presented. For all traits a strong phylogenetic signal was detected  
187 (Phylogenetic heritability  $\square$  0.82 – 0.98; Tables S1-S4).

188 In the case of the relationship between natural log-transformed maximal performance ( $U_{max}$ ) and  
189 our measure of  $T_{env}$ , no relationship was found for any of the performance traits (Figure 3). Again,  
190 interaction terms were never significant and the phylogenetic signal was strong (Phylogenetic  
191 heritability  $\square$  0.76 – 0.98; Tables S5-S8).

192 By contrast with these variable outcomes, a positive relationship between maximal performance  
193 ( $U_{max}$ ) and optimal temperature ( $T_{opt}$ ) was characteristic of all the traits examined in models that  
194 considered only main effects without interaction terms: development rate, growth rate, locomotion speed



195 and photosynthetic rate (Figure 4, Tables S9-S12), again with much variation about the central  
196 tendencies. In the full factorial models, however, phylum and  $T_{opt}$  showed significant interactions (Table  
197 S13) for growth rate, as did  $T_{opt}$  and phylum for locomotion rate (Table S14). Data for growth rate were  
198 therefore further subdivided by phylum (Figure S1), but there were locomotion data for too few species of  
199 arthropod to formally estimate model parameters for this phylum alone. Significant positive relationships  
200 between  $U_{max}$  and  $T_{opt}$  characterised the subdivided datasets (Table S15). When converted to activation  
201 energy, values ranged between 0.16 and 0.68 eV, with a mean of  $0.37 \pm 0.08$  [SE] eV, which is  
202 significantly different from the value of 0.60 eV predicted from theory (26) ( $t_5 = -2.93$ ,  $p = 0.03$ ), but not  
203 from 0.54 eV ( $t_5 = -2.16$ ,  $p = 0.08$ ), previously a minimum empirical value (23).

204

## 205 **Discussion**

206 Understanding the nature of and potential limitations characterising physiological and biochemical  
207 adaptation to temperature is a fundamental question in organismal biology (4, 12, 70). Moreover, what  
208 form such adaptation might take, as reflected in the relationship between temperature and biological rates,  
209 has important implications for interpreting the responses of organisms to changing environments,  
210 including the influences of global climate change (6, 20, 35-36, 40). For example, if the thermodynamic  
211 effect predominates in the relationship between  $U_{max}$  and  $T_{opt}$ , rising temperatures might prove largely  
212 beneficial for ectotherms except perhaps in the tropics (though see 44) because biochemical constraints  
213 are reduced. By contrast, if some form of compensation is more common, changing temperature regimes  
214 may have less of an effect on performance (9, 11, 36). Thus, which of these major relationships between  
215  $U_{max}$  and  $T_{opt}$  predominate is of both fundamental and applied significance.

216 Previous examinations of the relationship between  $U_{max}$  and  $T_{opt}$  have come out strongly in favour  
217 of the thermodynamic effect hypothesis (23, 26-28), with activation energies either being within the  
218 predicted range of 0.6 to 0.7 eV (23), or larger, implying a stronger thermodynamic effect than  
219 theoretically predicted (26). Based on a much larger suite of data, spanning a wide range of localities,  
220 habitats and taxa, and several key performance traits, we also find that the thermodynamic effect is

221 generally supported for the relationship between  $U_{\max}$  and  $T_{\text{opt}}$ . In contrast with previous investigations,  
222 however, we find this effect (on average an activation energy of  $0.37 \pm 0.08$  eV) much weaker than  
223 proposed by theory or previously found empirically (i.e. 0.6-0.7 eV, or 0.54 to 0.97 eV) (23, 26). Thus,  
224 while a thermodynamic effect is general, it is not pronounced.

225 The difference between this finding and that of previous studies might owe in part to the inclusion  
226 of a specific plant performance trait, photosynthetic rate, in the current investigation. The activation  
227 energy value for this trait was lowest of all of the significant values (0.16 eV); with the value for  
228 photosynthetic rate excluded, the mean activation energy increases to  $0.41 \pm 0.08$  and is not significantly  
229 different from 0.54 ( $t_4 = -1.57$ ,  $p = 0.19$ ) or 0.60 ( $t_4 = -2.30$ ,  $p = 0.08$ ). This change does, however, point  
230 to a further explanation for the different outcomes between our study and others. The consideration of  
231 organisms from a wide variety of environments, which represent several life history types and trophic  
232 groups is likely to mean much larger variation in the way  $U_{\max}$  and  $T_{\text{opt}}$  are related, and how these traits  
233 are related to environmental temperature (11, 33-34, 40). For example, owing to their restricted  
234 movement capability, plants may be expected to show a much greater level of thermal compensation than  
235 ectotherm animals, which can behaviourally select among a diversity of thermal microenvironments  
236 available to them in any given larger setting (4, 71). Indeed, temperature compensation of respiration  
237 rates in plants of several different groups is commonly found (5, 9, 20). The same preponderance of  
238 compensation might be expected in aquatic versus non-aquatic groups, given the thermal inertia of  
239 aquatic environments (72). In the one case where we were able to draw such an explicit contrast – for  
240 locomotion speed in aquatic versus non-aquatic chordates (Table 1; Figure S1) – the variation is in the  
241 direction predicted, with no significant relationship between  $U_{\max}$  and  $T_{\text{opt}}$  for the aquatic group.  
242 Nonetheless, for metabolic rate variation the reverse seems to be true, with compensation being less  
243 commonly found in aquatic marine groups than in terrestrial species (11-12).

244 The relatively weak relationship between  $U_{\max}$  and  $T_{\text{opt}}$  does point to the fact that some form of  
245 thermal compensation is characteristic of all the organisms we examined, in keeping with long-standing  
246 contentions about the importance thereof (10, 13). The typical absence of a relationship between  $U_{\max}$  and

247  $T_{env}$  here also supports this contention, because the absence of a relationship is predicted by the  
248 hypothesis of temperature compensation (42). For photosynthesis rate, the outcome is clearly in keeping  
249 with findings for plants, and in particular for respiration rate, where compensation is well documented (5-  
250 6, 9, 20). For the other traits, and especially in animal ectotherms, the findings contrast with those from  
251 the broader thermal performance literature (4, 28). The variability around the  $T_{env}$  and  $T_{opt}$  relationship in  
252 the traits excluding photosynthesis is also perhaps surprising, although here positive relationships for  
253 development rate and for locomotion speed are in keeping with previous work (26). Nonetheless, our  
254 results demonstrate that temperature compensation is more commonplace than previously estimated for  
255 animals.

256 Several caveats should be borne in mind, however. First, a mismatch between  $T_{env}$  and the peak  
257 characteristics of the performance curve –  $T_{opt}$  and  $U_{max}$  – might be expected because such differences,  
258 especially between  $T_{env}$  and  $T_{opt}$  could be an adaptive response to environmental seasonality (40). In this  
259 case, the difference between  $T_{env}$  and  $T_{opt}$  should be strongly related to a measure of environmental  
260 seasonality, with a potential difference between tropical and non-tropical organisms. We tested for such  
261 an effect of seasonality and found that the strength of the effect varied among traits and phyla, with  
262 significant relationships between seasonality and the difference between  $T_{env}$  and  $T_{opt}$  found only for  
263 locomotion and photosynthesis rates (Table S16, Figure S2). The latter accords well with recent finding  
264 that terrestrial net primary production is better predicted by growing season length than by latitude or  
265 temperature (73). Thus, some adaptive response to seasonality may be occurring in these traits, and  
266 deserves further consideration. Second, we calculated  $T_{env}$  as mean temperature of the warmest quarter  
267 from the collection locality of the population investigated (see Methods). This may not fully represent the  
268 thermal environment typical of the organisms collected, though it is likely a better estimate of  
269 temperature when most organisms are actively growing and developing than mean annual temperature  
270 (74). Moreover, the temperature estimate used can have an effect on the form of the relationship between  
271 a trait and temperature (75). The estimates of relationships between  $T_{env}$  and performance-related traits  
272 provided here differ, however, from those made for activation energy of traits in other studies (e.g. 33-

273 34). In those studies, the temperature dependence of the traits is estimated not from comparisons of  $T_{opt}$  or  
274  $U_{max}$  across species from different environments, but rather from trait values at a given range of  
275 experimental temperatures leading up to and moving away from  $T_{opt}$  within a given species.

276 Given these outcomes, it is clear that while some form of thermodynamic effect exists, ample  
277 scope is present for biochemical and physiological adaptation in the form of temperature compensation.  
278 Indeed, the overriding influence seems to be one of biochemical and physiological adaptation, at least for  
279 the traits examined here, so vindicating earlier views on the significance of such adaptation (10, 13, 70,  
280 76). Much variation exists, however, within and among traits, and among taxa and environments. Such  
281 variation would have to be considered when using these general relationships to forecast the broader  
282 implications of environmental change, as has become clear from related studies of the thermal  
283 dependence of performance-related traits (33-34). To some extent the variation seen may also explain the  
284 many contrary findings in the literature to date. In the case of assessments based on metabolic rate of  
285 animal ectotherms, which have often dominated the animal literature, much of the debate on the existence  
286 of compensation (5, 11, 15-19, 21-22) might, however, be overcome by trait assessments which include  
287 the full performance curve providing empirical estimates of  $T_{opt}$  and  $U_{max}$ , as is done for plants (e.g. 9),  
288 rather than just on the increasing side of the curve.

289

## 290 **Competing interests**

291 The authors declare no competing interests.

292

## 293 **Authors' contributions**

294 JGS and SLC designed the study and collected the data from the literature. GAD provided input to the  
295 design of the study, and prepared environmental data and the conceptual figure. CRW performed the  
296 analyses and associated figures. JGS and SLC prepared the first draft of the ms, and all authors  
297 contributed to the final version.

298

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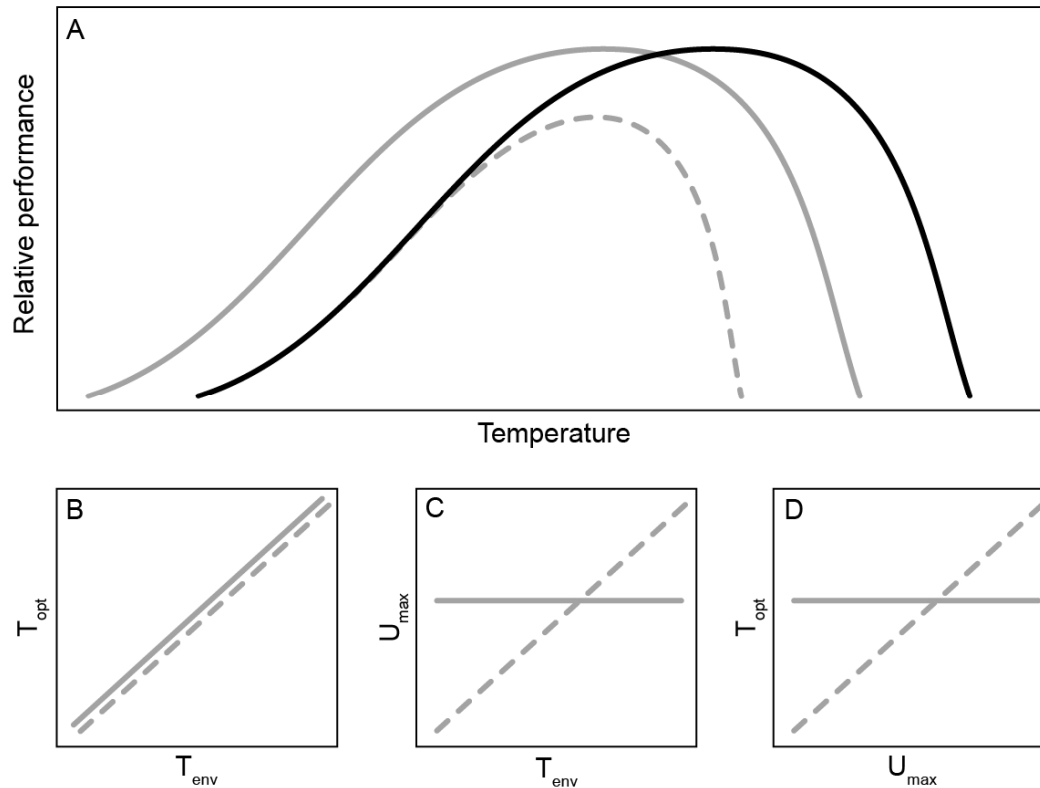
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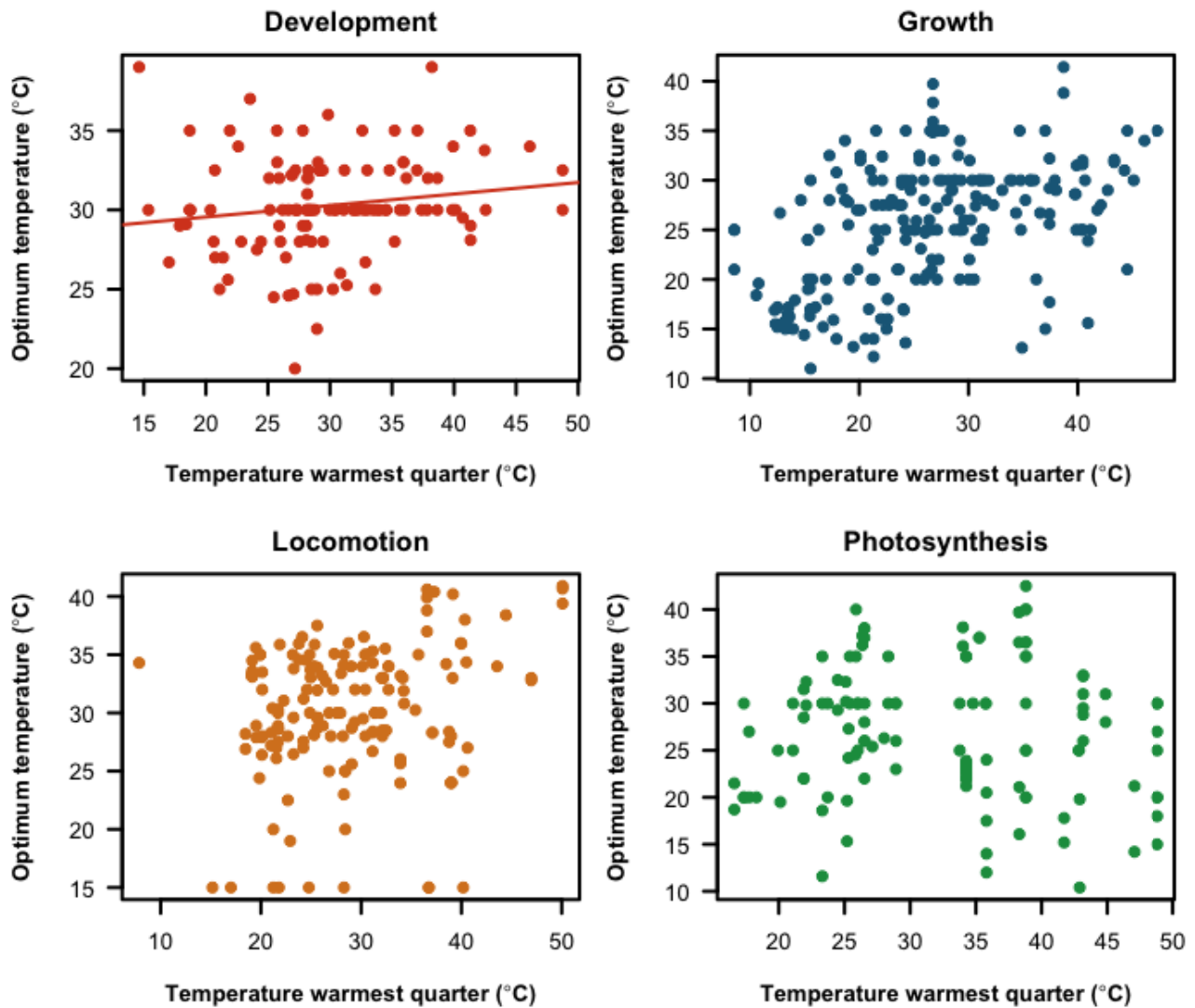


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464 **Figure 1. Conceptual figure showing expected relationships under either the temperature**  
465 **compensation or thermodynamic effect hypothesis.** The relative performance of a given trait (a) is  
466 expected to increase with temperature until peak performance ( $U_{\max}$ ) is achieved at the optimum  
467 temperature ( $T_{\text{opt}}$ ), after which performance declines (solid black line). In colder climates, the temperature  
468 compensation hypothesis predicts that the relationship between relative performance and temperature will  
469 shift such that  $U_{\max}$  occurs at a lower  $T_{\text{opt}}$ , but remains equal to that observed in warmer climates if full  
470 compensation is achieved (solid grey line). Alternatively, the thermodynamic effect hypothesis predicts  
471 that in colder climates  $U_{\max}$  will not only occur at a lower  $T_{\text{opt}}$ , but will also be lower than that observed in  
472 warmer climates (dashed grey line). Panels below show the expected relationships between (b)  
473 environmental temperature ( $T_{\text{env}}$ ) and  $T_{\text{opt}}$ , (c)  $T_{\text{env}}$  and  $U_{\max}$ , (d)  $U_{\max}$  and  $T_{\text{opt}}$ , respectively under the  
474 temperature compensation (solid lines) and thermodynamic effect (dashed lines) hypotheses. Both  
475 hypotheses predict a positive correlation between  $T_{\text{env}}$  and  $T_{\text{opt}}$  (b). However, the temperature  
476 compensation hypothesis predicts that  $T_{\text{opt}}$  will be independent of  $T_{\text{env}}$  while a positive relationship is

477 expected under the thermodynamic effect hypothesis (c). Likewise,  $U_{\max}$  is expected to be independent of  
478  $T_{\text{opt}}$  under temperature compensation, while the thermodynamic effect hypothesis predicts a positive  
479 relationship (d).

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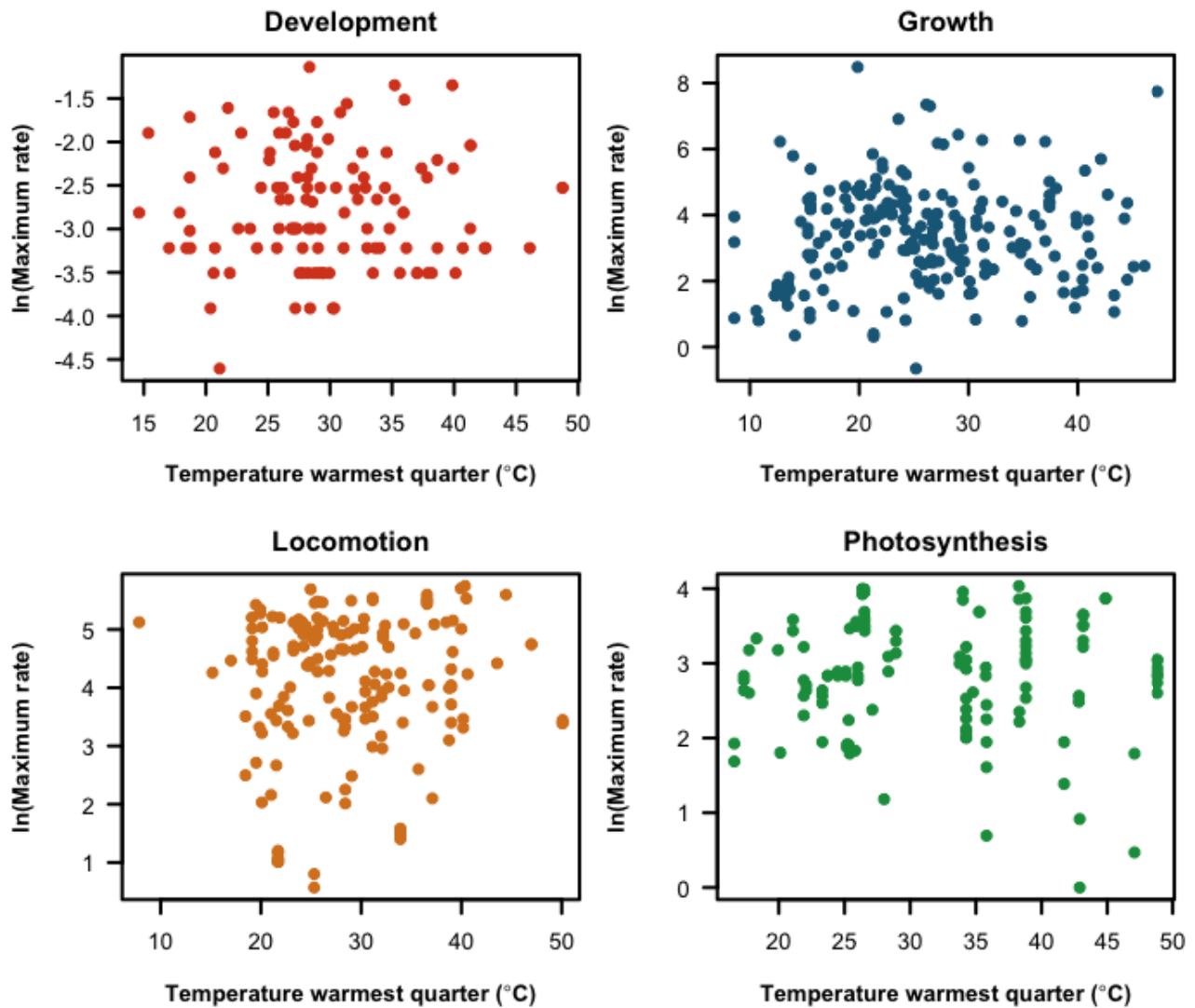
483 **Figure 2. Relationship between mean temperature of the warmest quarter of the year (as a measure**  
484 **of  $T_{env}$ , °C) and the optimum temperature ( $T_{opt}$ , °C) for rates of development ( $d^{-1}$ ), growth ( $\% d^{-1}$ ),**  
485 **locomotion ( $cm s^{-1}$ ) and photosynthesis ( $\mu mol m^{-2} s^{-1}$ ), respectively. Statistical outcomes are provided**  
486 **in Tables S1-S4. Solid lines depict significant relationships from phylogenetic mixed models testing for**  
487 **effects of  $T_{env}$  on  $T_{opt}$  (Table S1).**

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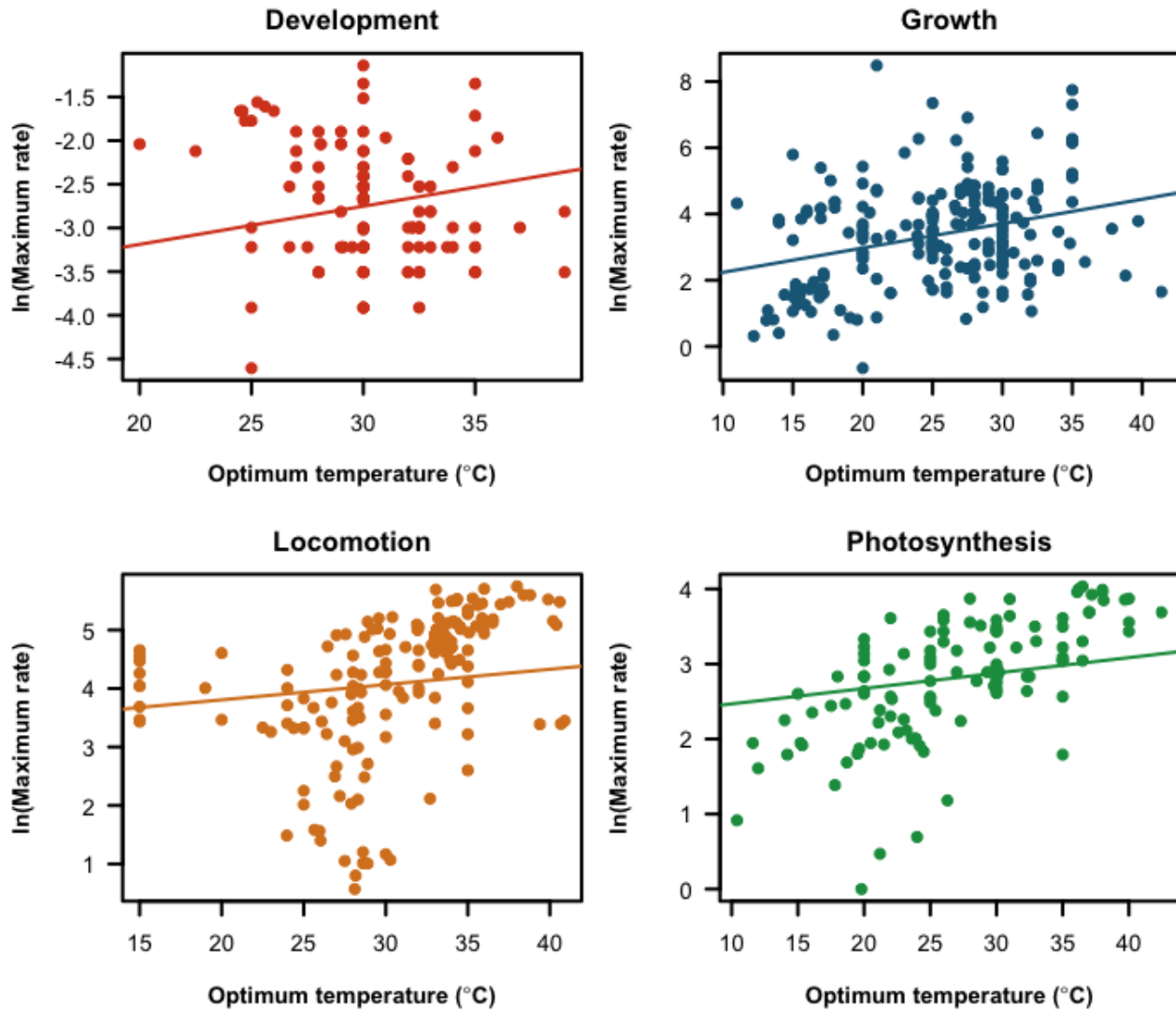


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493 **Figure 3. Relationship between mean temperature of the warmest quarter of the year (as a measure**  
494 **of  $T_{env}$ , °C) and the natural log-transformed maximum rate ( $U_{max}$ ) for rates of development ( $d^{-1}$ ),**  
495 **growth ( $\% d^{-1}$ ), locomotion ( $cm s^{-1}$ ), and photosynthesis ( $\mu mol m^{-2} s^{-1}$ ), respectively. Statistical**  
496 **outcomes are provided in Tables S5-S8.**

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500 **Figure 4. Relationship between optimum temperature ( $T_{opt}$ , °C) and the natural log-transformed**  
501 **maximum rate ( $U_{max}$ ) for rates of development ( $d^{-1}$ ), growth ( $\% d^{-1}$ ), locomotion ( $cm s^{-1}$ ), and**  
502 **photosynthesis ( $\mu mol m^{-2} s^{-1}$ ), respectively. Solid lines depict significant relationships from**  
503 **phylogenetic mixed models testing for significant effects of  $T_{opt}$  on  $U_{max}$  (Tables S9-S12).**