

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21

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

Jesper G. Sørensen^{a,b,1}, Craig R. White^{b,c}, Grant A. Duffy^b, and Steven L. Chown^b

^aSection for Genetics, Ecology and Evolution, Department of Bioscience, Aarhus University, Ny Munkegade 116, DK-8000 Aarhus C, Denmark; ^bSchool of Biological Sciences and ^cCentre for Geometric Biology, Monash University, Victoria 3800, Australia

¹ Corresponding author: Jesper G. Sørensen; email: jesper.soerensen@bios.au.dk; phone +45 3018 3160; Address: Section for Genetics, Ecology and Evolution, Department of Bioscience, Aarhus University, Ny Munkegade 116, DK-8000 Aarhus C, Denmark

Short title: Biological rates preserved across biomes

Keywords: ectotherm, optimal temperature, thermodynamic effect, physiological adaptation, metabolic compensation

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.

38

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_{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_{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_{opt} and a measure of environmental temperature (T_{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_{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_{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_{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 1st 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 or 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) λ (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 ± 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_{opt} . In contrast with previous investigations,
222 however, we find this effect (on average an activation energy of 0.37 ± 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 ± 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_{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_{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_{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

299 **ACKNOWLEDGMENTS.** We thank Johannes Overgaard and Lesley Alton for comments on a previous
300 version of the manuscript. Research funding for this project was provided by a Sapere Aude DFF-Starting
301 grant from The Danish Council for Independent Research | Natural Sciences and a sabbatical grant from
302 the Aarhus University Research Foundation (AUFF) to JGS, and by the Australian Research Council
303 through ARC DP170101046 to SLC and FT130101493 to CRW.

304 **References**

- 305 1. Cossins AR, Bowler K. 1987 *Temperature Biology of Animals*. Chapman and Hall, New York.
- 306 2. Gaston KJ. 2009 Geographic range limits: achieving synthesis. *Proc R Soc B* **276**, 1395-1406.
- 307 3. Overgaard J, Kearney MR, Hoffmann AA. 2014 Sensitivity to thermal extremes in Australian
308 *Drosophila* implies similar impacts of climate change on the distribution of widespread and
309 tropical species. *Global Change Biol* **20**, 1738-1750.
- 310 4. Angilletta MJ. 2009 *Thermal Adaptation. A Theoretical and Empirical Synthesis*. Oxford
311 University Press, Oxford.
- 312 5. Atkin OK, Bloomfield KJ, Reich PB, Tjoelker MG, Asner GP, Bonal D, Bönisch G, Bradford
313 MG, Cernusak LA, Cosio EG *et al.* 2015 Global variability in leaf respiration in relation to
314 climate, plant functional types and leaf traits. *New Phytol* **206**, 614-636.
- 315 6. Heskell MA, O'Sullivan OS, Reich PB, Tjoelker MG, Weerasinghe LK, Penillard A, Egerton JGG,
316 Creek D, Bloomfield KJ, Xiang J *et al.* 2016 Convergence in the temperature response of leaf
317 respiration across biomes and plant functional types. *Proc Natl Acad Sci USA* **113**, 3832-3837.
- 318 7. Clarke A. 1980 A reappraisal of the concept of metabolic cold adaptation in polar marine
319 invertebrates. *Biol J Linn Soc* **14**, 77-92.
- 320 8. Gaston KJ, Chown SL, Calosi P, Bernardo J, Bilton DT, Clarke A, Clusella-Trullas S, Ghalambor
321 CK, Konarzewski M, Peck LS *et al.* 2009 Macrophysiology: A Conceptual Reunification. *Am Nat*
322 **174**, 595-612.
- 323 9. Padfield D, Lowe C, Buckling A, Ffrench-Constant R, Student Research Team, Jennings S,
324 Shelley F, Ólafsson JS, Yvon-Durocher, G. 2017 Metabolic compensation constrains the
325 temperature dependence of gross primary production. *Ecol Lett* **20**, 1250-1260.
- 326 10. Hazel JR, Prosser CL. 1974 Molecular mechanisms of temperature compensation in
327 poikilotherms. *Physiol Rev* **54**, 620-677.
- 328 11. Clarke A. 2003 Costs and consequences of evolutionary temperature adaptation. *Trends Ecol Evol*
329 **18**, 573-581.

- 330 12. Clarke A. 2017 *Principles of Thermal Ecology. Temperature, Energy and Life*. Oxford University
331 Press, Oxford.
- 332 13. Krogh A. 1916 *The Respiratory Exchange of Animals and Man*. Longman, London.
- 333 14. Sømme L, Block W. 1991 Adaptations to alpine and polar environments. *Insects at Low*
334 *Temperature*, eds Lee RE, Denlinger DL. Chapman & Hall, London, pp 318-359.
- 335 15. Chown SL, Gaston KJ. 1999 Exploring links between physiology and ecology at macro-scales:
336 the role of respiratory metabolism in insects. *Biol Rev* **74**, 87-120.
- 337 16. Clarke A, Johnston NM. 1999 Scaling of metabolic rate with body mass and temperature in teleost
338 fish. *J Anim Ecol* **68**, 893-905.
- 339 17. Addo-Bediako A, Chown SL, Gaston KJ. 2002 Metabolic cold adaptation in insects: a large-scale
340 perspective. *Funct Ecol* **16**, 332-338.
- 341 18. Steffensen JF. 2002 Metabolic cold adaptation of polar fish based on measurements of aerobic
342 oxygen consumption: fact or artefact? Artefact! *Comp Biochem Physiol A* **132**, 789-795.
- 343 19. White CR, Alton LA, Frappell PB. 2012 Metabolic cold adaptation in fishes occurs at the level of
344 whole animal, mitochondria and enzyme. *Proc R Soc B* **279**, 1740-1747.
- 345 20. Padfield D, Yvon-Durocher G, Buckling A, Jennings S, Yvon-Durocher G. 2016 Rapid evolution
346 of metabolic traits explains thermal adaptation in phytoplankton. *Ecol Lett* **19**, 133-142.
- 347 21. Peck LS. 2016 A cold limit to adaptation in the sea. *Trends Ecol Evol* **31**, 13-26.
- 348 22. Alton LA, Condon C, White CR, Angilletta MJ, Jr. 2017 Colder environments did not select for a
349 faster metabolism during experimental evolution of *Drosophila melanogaster*. *Evolution* **71**, 145-
350 152.
- 351 23. Savage VM, Gillooly JF, Brown JH, West GB, Charnov EL. 2004 Effects of body size and
352 temperature on population growth. *Am Nat* **163**, 429-441.
- 353 24. Pörtner HO. 2002 Climate variations and the physiological basis of temperature dependent
354 biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comp Biochem*
355 *Physiol A* **132**, 739-761.

- 356 25. Araújo MB, Ferri-Yáñez F, Bozinovic F, Marquet PA, Valladares F, Chown SL. 2013 Heat
357 freezes niche evolution. *Ecol Lett* **16**, 1206-1219.
- 358 26. Frazier MR, Huey RB, Berrigan D. 2006 Thermodynamics constrains the evolution of insect
359 population growth rates: "Warmer is better". *Am Nat* **168**, 512-520.
- 360 27. Knies JL, Kingsolver JG, Burch CL. 2009 Hotter is better and broader: Thermal sensitivity of
361 fitness in a population of bacteriophages. *Am Nat* **173**, 419-430.
- 362 28. Angilletta MJ, Huey RB, Frazier MR. 2010 Thermodynamic effects on organismal performance:
363 Is hotter better? *Physiol Biochem Zool* **83**, 197-206.
- 364 29. Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL. 2001 Effects of size and temperature
365 on metabolic rate. *Science* **293**, 2248-2251.
- 366 30. Zhu W, Zhang H, Li X, Meng Q, Shu R, Wang M, Zhou G, Wang H, Miao L, Zhang J *et al.* 2016
367 Cold adaptation mechanisms in the ghost moth *Hepialus xiaojinensis*: Metabolic regulation and
368 thermal compensation. *J. Insect Physiol.* **85**, 76-85.
- 369 31. Clarke A. 2004 Is there a universal temperature dependence of metabolism? *Funct Ecol* **18**, 252-
370 256.
- 371 32. Cavicchioli R. 2016 On the concept of a psychrophile. *ISME J* **10**, 793-795.
- 372 33. Dell AI, Pawar S, Savage VM. 2011 Systematic variation in the temperature dependence of
373 physiological and ecological traits. *Proc Natnl Acad Sci USA* **108**, 10591-10596.
- 374 34. Dell AI, Pawar S, Savage V. 2014 Temperature dependence of trophic interactions are driven by
375 asymmetry of species responses and foraging strategy. *J Anim Ecol* **83**, 70-84.
- 376 35. Dillon ME, Wang G, Huey RB. 2010 Global metabolic impacts of recent climate warming. *Nature*
377 **467**, 704-706.
- 378 36. Seebacher F, White CR, Franklin CE. 2015 Physiological plasticity increases resilience of
379 ectothermic animals to climate change. *Nature Climate Change* **5**, 61-66.
- 380 37. Gilchrist GW. 1995 Specialists and generalists in changing environments. I. Fitness landscapes of
381 thermal sensitivity. *Am Nat* **146**, 252-270.

- 382 38. Huey RB, Bennett AF. 1987 Phylogenetic studies of coadaptation: preferred temperatures versus
383 optimal performance temperatures of lizards. *Evolution* **41**, 1098-1115.
- 384 39. Angilletta MJ, Niewiarowski PH, Navas CA. 2002 The evolution of thermal physiology in
385 ectotherms. *J Therm Biol* **27**, 249-268.
- 386 40. Amarasekare P, Johnson C. 2017 Evolution of thermal reaction norms in seasonally varying
387 environments. *Am Nat* **189**, E31-E45.
- 388 41. Makarieva AM, Gorshkov VG, Li B-L, Chown SL, Reich PB, Gavrillov VM. 2008 Mean mass-
389 specific metabolic rates are strikingly similar across life's major domains: Evidence for life's
390 metabolic optimum. *Proc Natnl Acad Sci USA* **105**, 16994-16999.
- 391 42. Deere JA, Chown SL. 2006 Testing the beneficial acclimation hypothesis and its alternatives for
392 locomotor performance. *Am Nat* **168**, 630-644.
- 393 43. Hester ET, Doyle MW. 2011 Human impacts to river temperature and their effects on biological
394 processes: A quantitative synthesis. *J Am Water Res Assoc* **47**, 571-587.
- 395 44. Dell AI, Pawar S, Savage VM. 2013 The thermal dependence of biological traits. *Ecology* **94**,
396 1205.
- 397 45. Lurling M, Eshetu F, Faassen EJ, Kosten S, Huszar VLM. 2013 Comparison of cyanobacterial
398 and green algal growth rates at different temperatures. *Freshwater Biol* **58**, 552-559.
- 399 46. Ras M, Steyer J-P, Bernard O. 2013 Temperature effect on microalgae: a crucial factor for
400 outdoor production. *Rev Environ Sci Bio/Technol* **12**, 153-164.
- 401 47. Hinchliff CE, Smith SA, Allman JF, Burleigh JG, Chaudhary R, Coghill LM, Crandall KA, Deng
402 J, Drew BT, Gazis R *et al.* 2015 Synthesis of phylogeny and taxonomy into a comprehensive tree
403 of life. *Proc Natnl Acad Sci USA* **112**, 12764-12769.
- 404 48. Chamberlain S. 2017 rgbif: Interface to the Global 'Biodiversity' Information Facility 'API'. R
405 package version 0.9.8. <https://CRAN.R-project.org/package=rgbif>
- 406 49. Chamberlain S, Ram K, Hart T. 2016 spocc: Interface to Species Occurrence Data Sources. R
407 package version 0.5.0. <http://CRAN.R-project.org/package=spocc>

- 408 50. R Development Core Team. 2017 *R: A language and environment for statistical computing*. R
409 Foundation for Statistical Computing, Vienna, Austria.
- 410 51. Hodar JA. 1996 The use of regression equations for estimation of arthropod biomass in ecological
411 studies. *Acta Oecol* **17**, 421-433.
- 412 52. Ganihar SR. 1997 Biomass estimates of terrestrial arthropods based on body length. *J Bioscience*
413 **22**, 219-224.
- 414 53. Lynch M. 1991 Methods for the analysis of comparative data in evolutionary biology. *Evolution*
415 **45**, 1065-1080.
- 416 54. Housworth EA, Martins EP, Lynch M. 2004 The phylogenetic mixed model. *Am Nat* **163**, 84-96.
- 417 55. Hadfield JD, Nakagawa S. 2010 General quantitative genetic methods for comparative biology:
418 phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *J Evol*
419 *Biol* **23**, 494-508.
- 420 56. Gilmour AR, Gogel BJ, Cullis BR, Thompson R. 2009 *ASReml user guide. Release 3.0* (NSW
421 Department of Industry and Investment, Sydney, Australia).
- 422 57. R Development Core Team. 2013 *R: A language and environment for statistical computing*. R
423 Foundation for Statistical Computing, Vienna, Austria.
- 424 58. Hadfield JD. 2010 MCMC methods for multi-response generalized linear models: the
425 MCMCglmm R Package. *J Statistical Softw* **33**,1-22.
- 426 59. Michonneau F, Brown J, Winter D. 2016 *rotl: Interface to the 'Open Tree of Life' API*. R package
427 version 0.5.0. <https://CRAN.R-project.org/package=rotl>.
- 428 60. Hahn MW, Pöckl M. 2005 Ecotypes of planktonic actinobacteria with identical 16S rRNA genes
429 adapted to thermal niches in temperate, subtropical, and tropical freshwater habitats. *Appl Environ*
430 *Microbiol* **71**, 766-773.
- 431 61. Sorokin C, Krauss RW. 1962 Effects of temperature & illuminance on *Chlorella* growth
432 uncoupled from cell division. *Plant Physiol* **37**, 37-42.

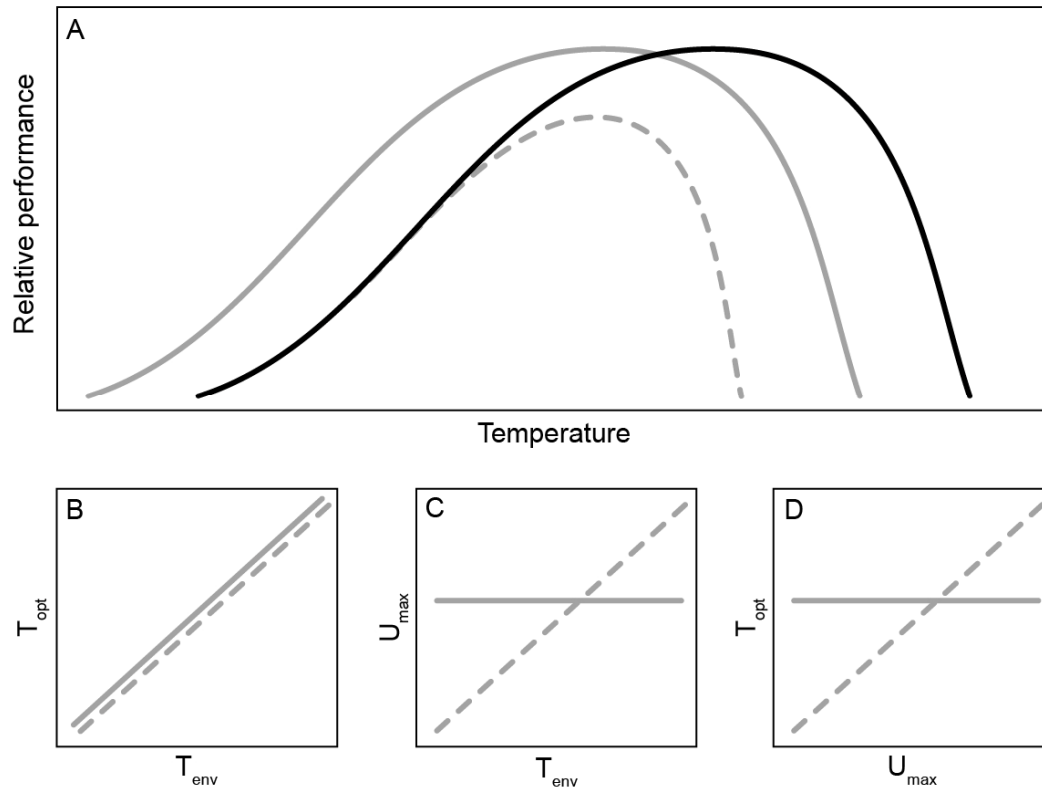
- 433 62. Mattiuzzi M, Detsch F. 2017 *MODIS: Acquisition and Processing of MODIS Products*. v1.1.0.
434 <https://CRAN.R-project.org/package=MODIS>.
- 435 63. Hijmans RJ. 2016 *raster: Geographic Data Analysis and Modeling*. v2.5-8. [http://CRAN.R-](http://CRAN.R-project.org/package=raster/)
436 [project.org/package=raster/](http://CRAN.R-project.org/package=raster/).
- 437 64. Ryan RA, Ulrich J. 2014 *xts: eXtensible Time Series*. v0.9-7. [https://CRAN.R-](https://CRAN.R-project.org/package=xts)
438 [project.org/package=xts](https://CRAN.R-project.org/package=xts).
- 439 65. Felsenstein J. 1985 Phylogenies and the comparative method. *Am Nat* **125**, 1-15.
- 440 66. Grafen A. 1989 The phylogenetic regression. *Phil Trans R Soc B* **326**, 119-157.
- 441 67. Kenward MG, Roger JH. 1997 Small sample inference for fixed effects from restricted maximum
442 likelihood. *Biometrics* **53**, 983-997.
- 443 68. Pagel M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877-884.
- 444 69. White I. 2013 *R pin function*. <http://www.homepages.ed.ac.uk/iwhite//asreml/>.
- 445 70. Hochachka PW, Somero GN. 2002 *Biochemical Adaptation. Mechanism and Process in*
446 *Physiological Evolution*. Oxford University Press, Oxford.
- 447 71. Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, Longino JT, Huey RB. 2014
448 Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and
449 elevation. *Proc Natl Acad Sci USA* **111**, 5610-5615.
- 450 72. Denny MW. 1993 *Air and Water: The Biology and Physics of Life's Media*. Princeton University
451 Press, Princeton.
- 452 73. Michaletz ST, Kerkhoff AJ, Enquist BJ. 2017 Drivers of terrestrial plant production across broad
453 geographical gradients. *Glob Ecol Biogeogr* **27**, 166-174.
- 454 74. Hodkinson ID. 2003 Metabolic cold adaptation in arthropods: a smaller-scale perspective. *Funct*
455 *Ecol* **17**, 562-567.
- 456 75. Irlich UM, Terblanche JS, Blackburn TM, Chown SL. 2009 Insect rate-temperature relationships:
457 environmental variation and the metabolic theory of ecology. *Am Nat* **174**, 819-835.

458 76. Heinrich B. 1977 Why have some animals evolved to regulate a high body temperature? *Am Nat*
459 **111**, 623-640.

460

461

462



463

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_{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_{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_{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_{env}) and T_{opt} , (c) T_{env} and U_{max} , (d) U_{max} and T_{opt} , respectively under the

474 temperature compensation (solid lines) and thermodynamic effect (dashed lines) hypotheses. Both

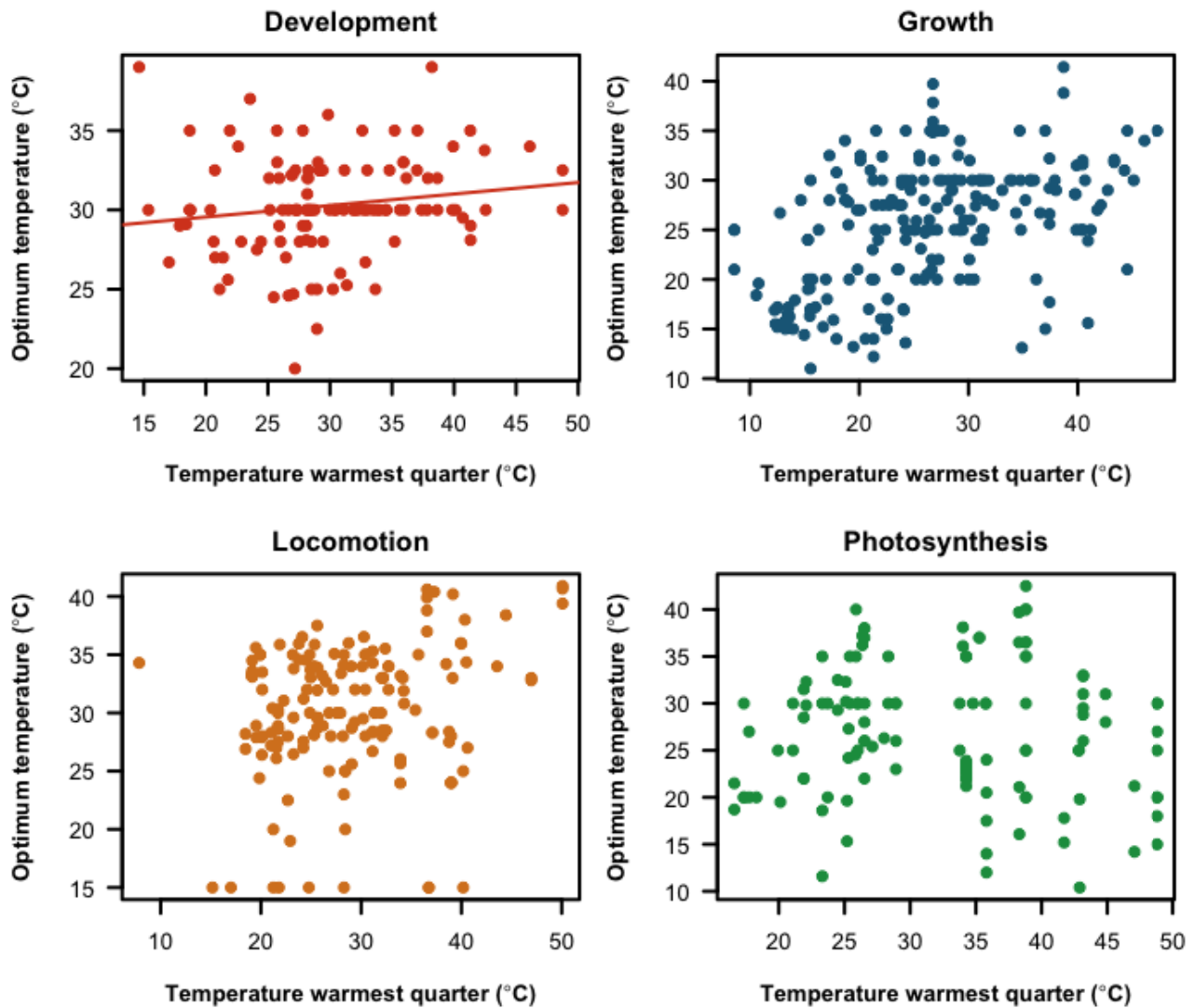
475 hypotheses predict a positive correlation between T_{env} and T_{opt} (b). However, the temperature

476 compensation hypothesis predicts that T_{opt} will be independent of T_{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_{opt} under temperature compensation, while the thermodynamic effect hypothesis predicts a positive
479 relationship (d).

480

481



482

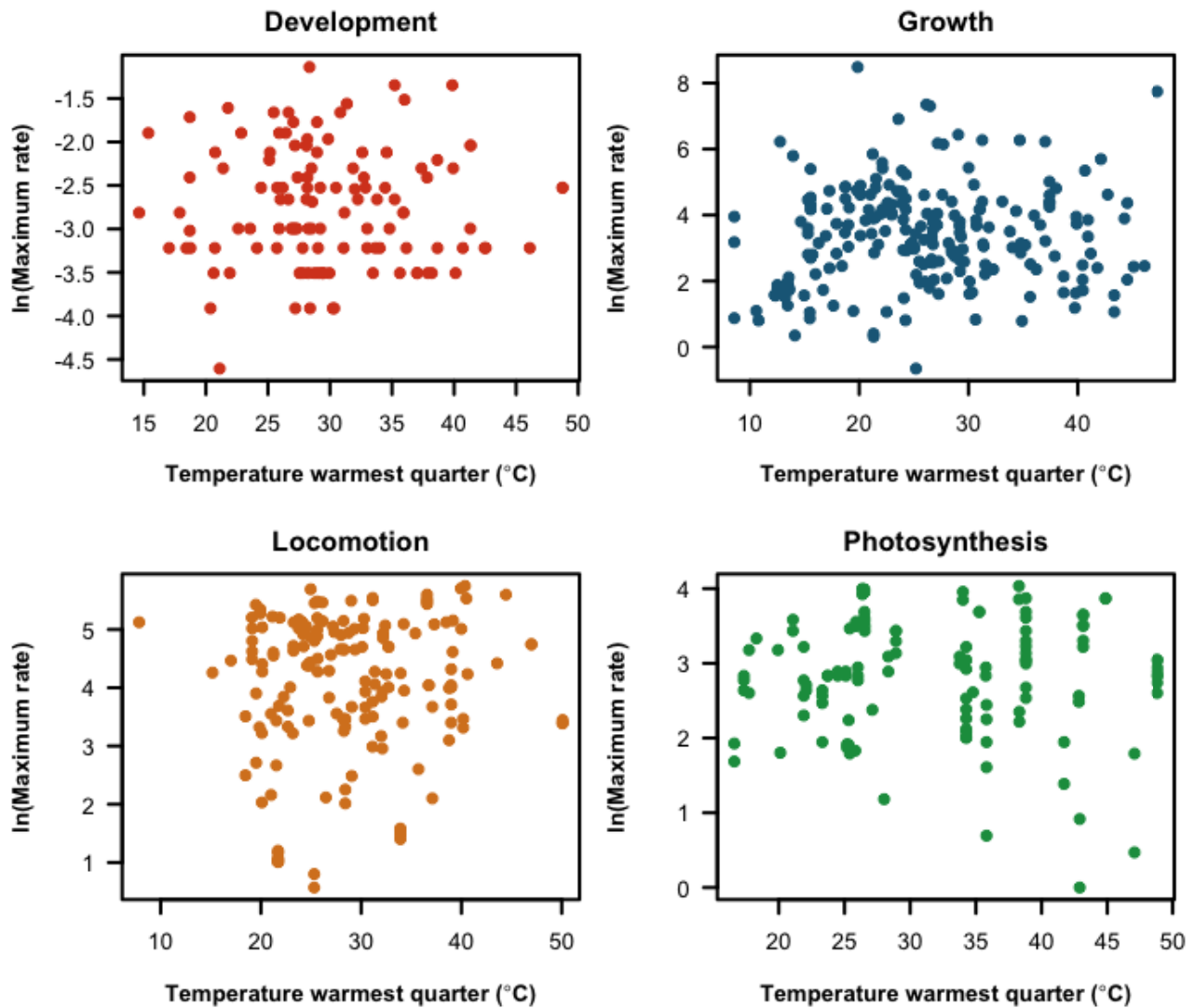
483 **Figure 2. Relationship between mean temperature of the warmest quarter of the year (as a measure**
484 **of T_{env} , °C) and the optimum temperature (T_{opt} , °C) for rates of development (d^{-1}), growth ($\% d^{-1}$),**
485 **locomotion ($cm s^{-1}$) and photosynthesis ($\mu mol m^{-2} s^{-1}$), 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).**

488

489

490

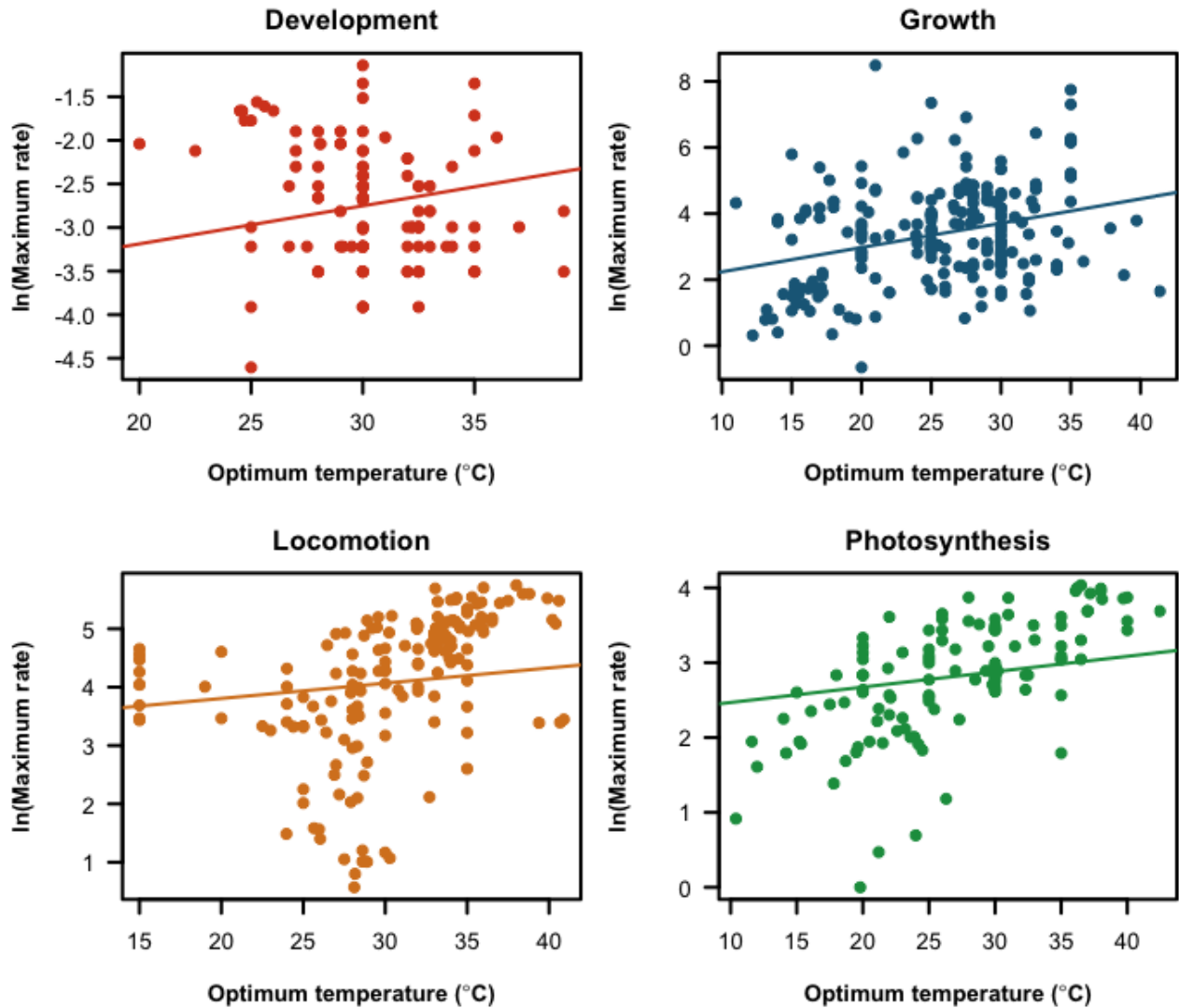
491



492

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.**

497



498
499
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).**