

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

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Abstract

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

Introduction

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

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

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

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

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

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

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

Methods

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

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

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

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

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

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

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

Results

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

Competing interests

The authors declare no competing interests.

Authors' contributions

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

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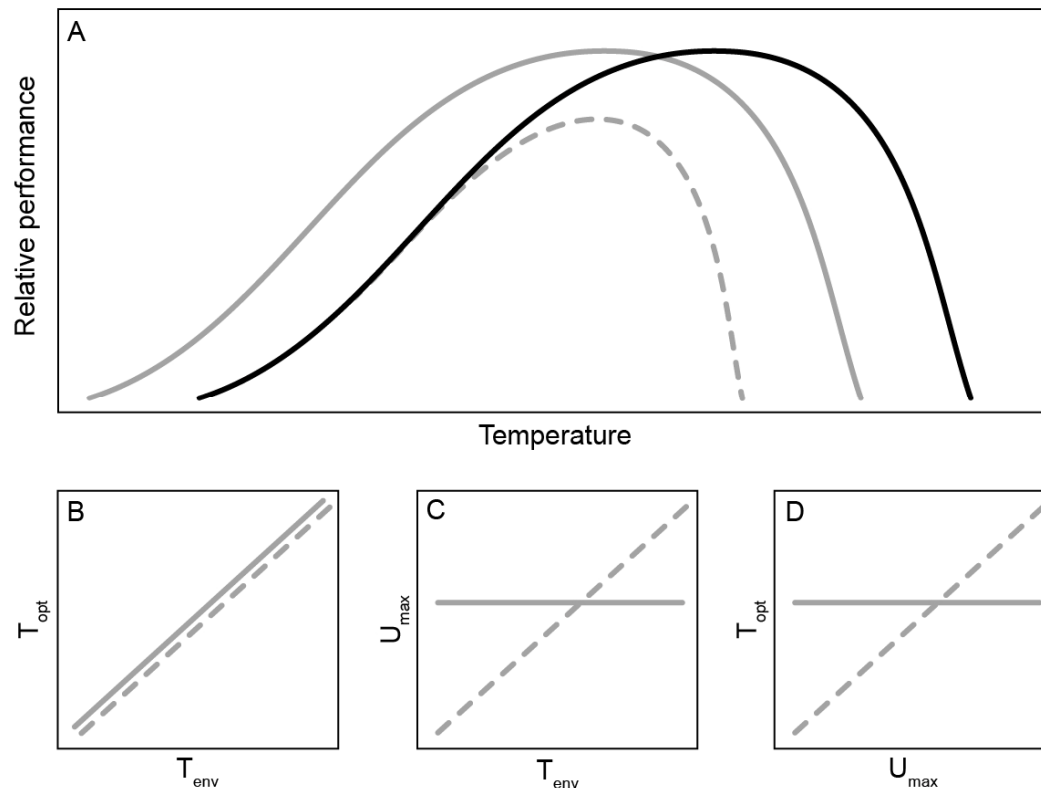


Figure 1. Conceptual figure showing expected relationships under either the temperature compensation or thermodynamic effect hypothesis. The relative performance of a given trait (a) is expected to increase with temperature until peak performance (U_{max}) is achieved at the optimum temperature (T_{opt}),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

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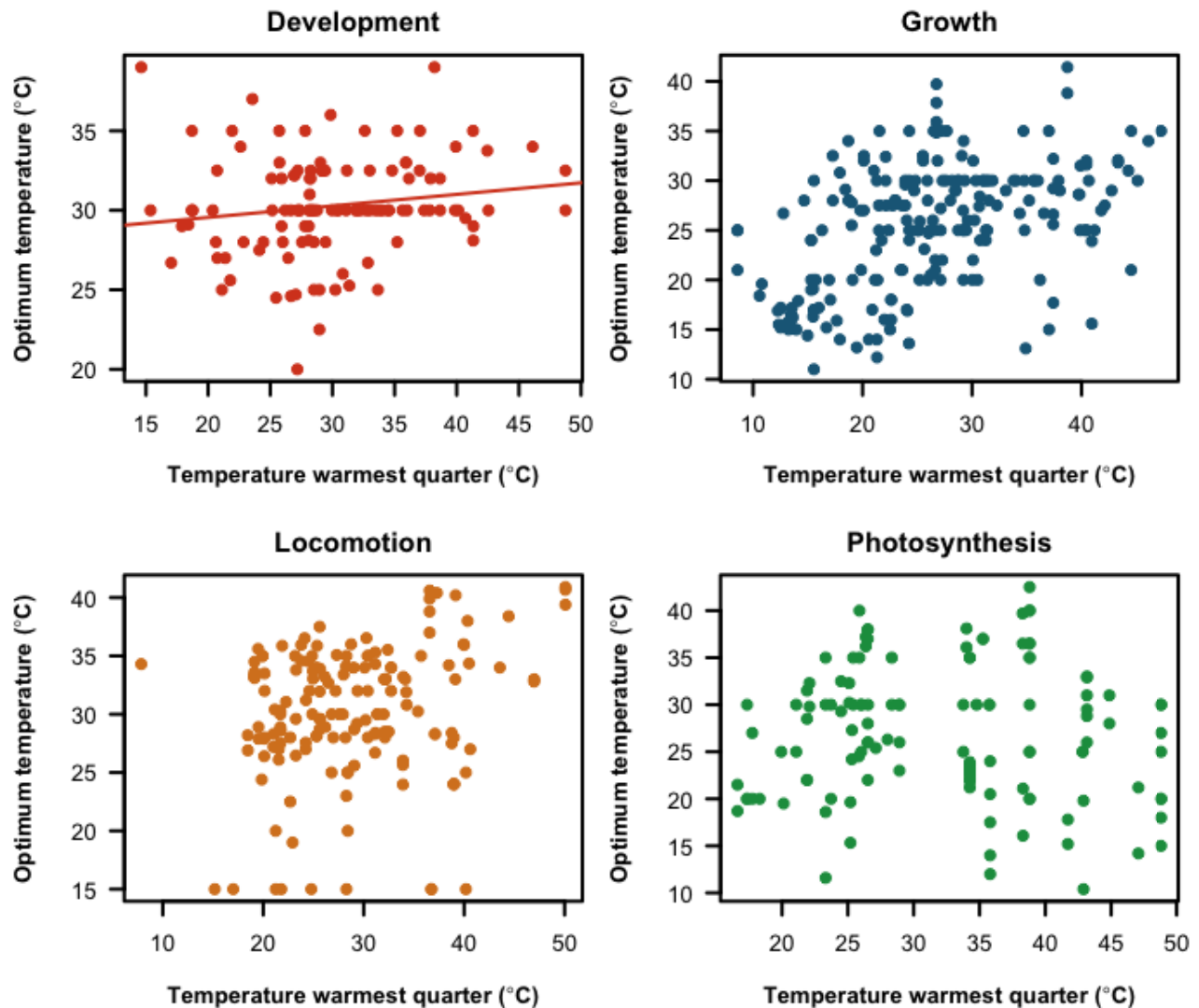


Figure 2. Relationship between mean temperature of the warmest quarter of the year (as a measure of T_{env} , °C) and the optimum temperature (T_{opt} , °C) for rates of development (d^{-1}), growth ($\% d^{-1}$), locomotion ($cm s^{-1}$) and photosynthesis ($\mu mol m^{-2} s^{-1}$), respectively. Statistical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

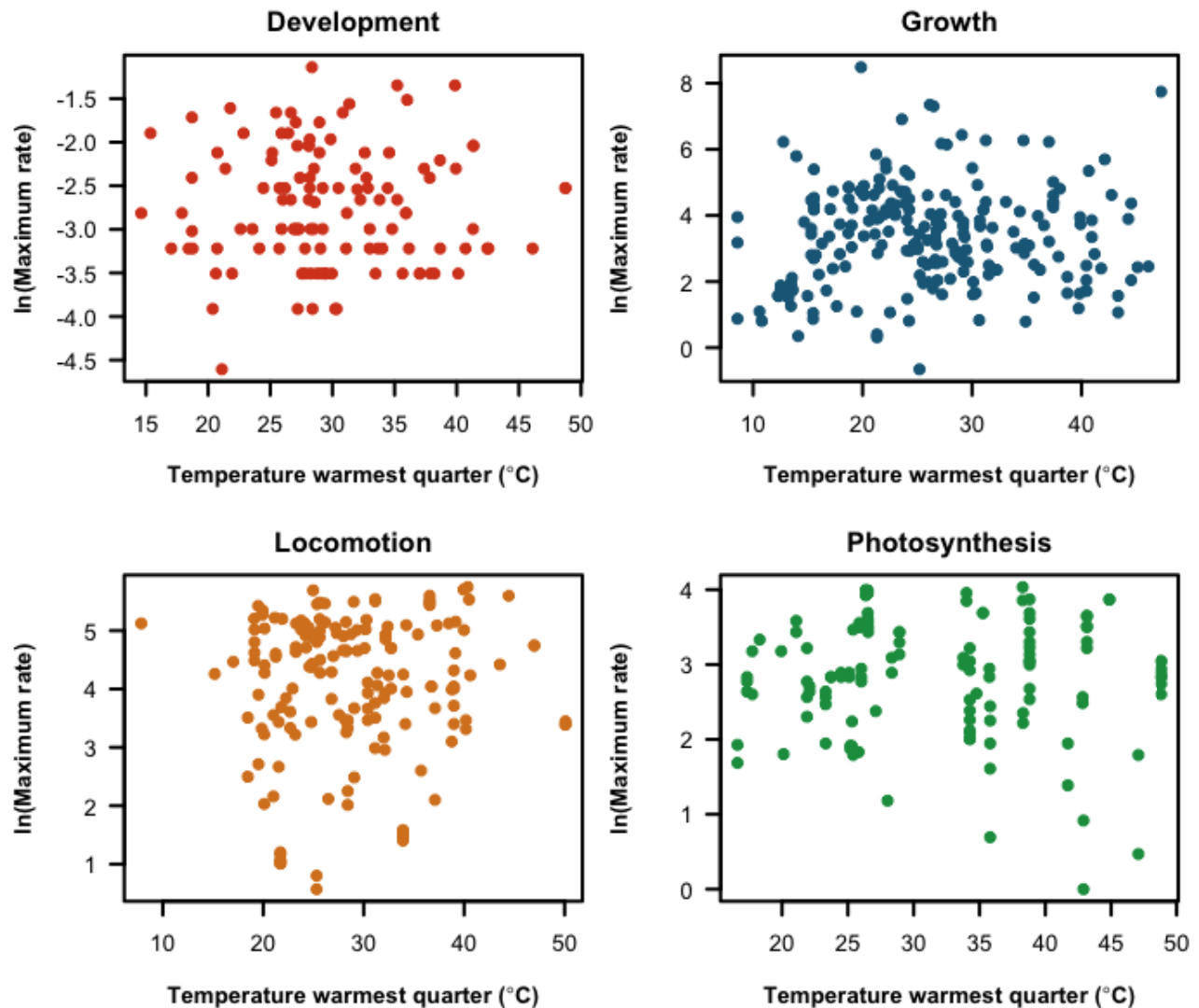


Figure 3. Relationship between mean temperature of the warmest quarter of the year (as a measure of T_{env} , °C) and the natural log-transformed maximum rate (U_{max}) for rates of development (d^{-1}), growth ($\% d^{-1}$), locomotion ($cm s^{-1}$), and photosynthesis ($\mu mol m^{-2} s^{-1}$), respectively.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

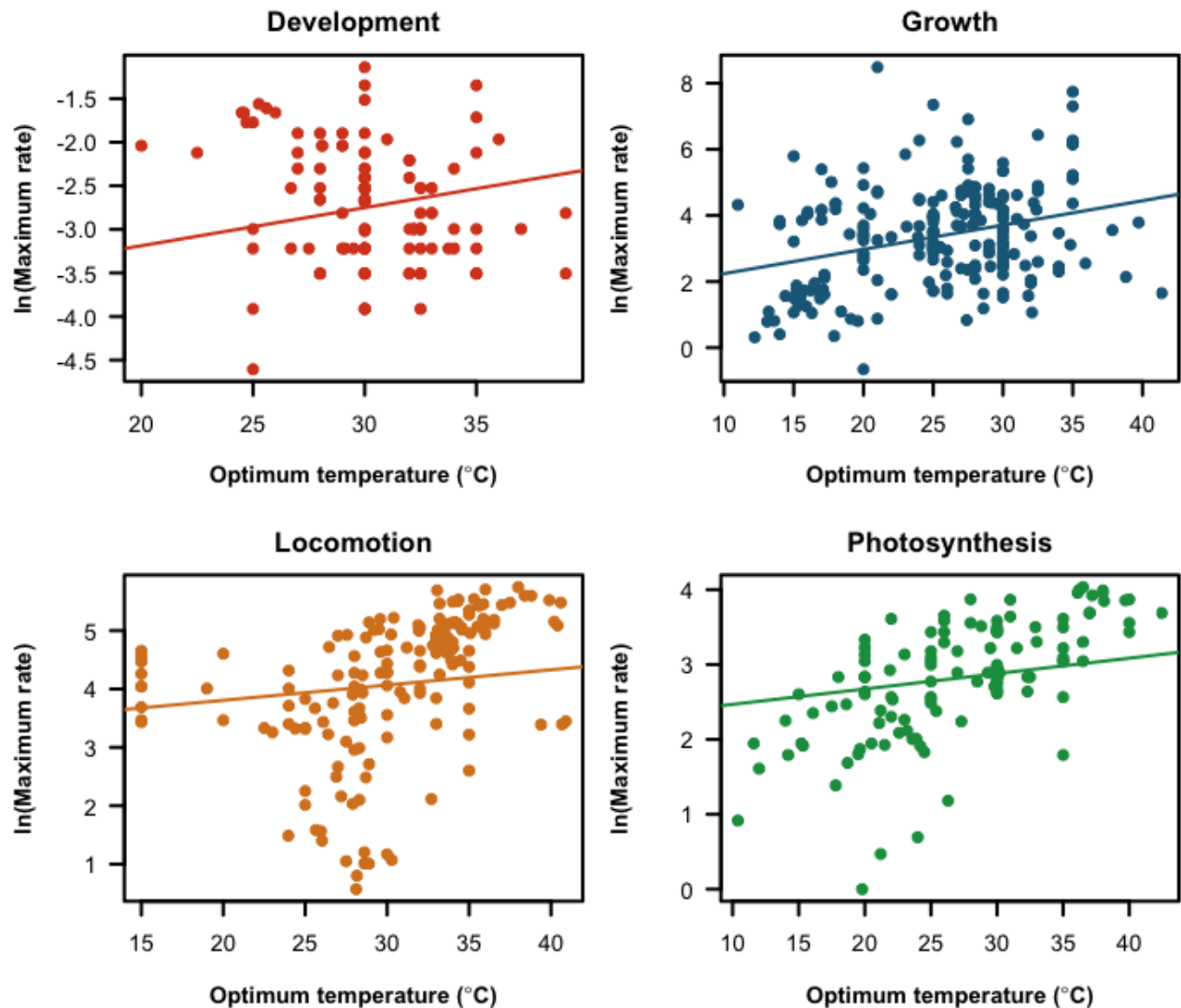


Figure 4. Relationship between optimum temperature (T_{opt} , °C) and the natural log-transformed maximum rate (U_{max}) for rates of development (d^{-1}), growth ($\% d^{-1}$), locomotion ($cm s^{-1}$), and photosynthesis ($\mu mol m^{-2} s^{-1}$), respectively. Solid lines depict significant relationships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