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The universal evolutionary and ecological significance of 20 °C

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Abstract

We connect evidence that 20 °C is the most stable temperature for cellular processes with macroecological observations. Examples show that temperatures warmer than ~20 °C result in decreases in: aquatic species' tolerance to low oxygen; marine pelagic and benthic algal productivity; pelagic and benthic predation rates; global species richness in pelagic fishes, plankton and benthic invertebrates; and genetic diversity; but increased extinctions in the fossil record. The realised thermal niche of reef fishes and invertebrates globally is narrowest among species with distributions centred on 20 °C, as also seen in microbes. While many species have evolved to live at warmer and colder temperatures, most species live at, and extinctions in the fossil record across seven phyla were lower at, 20 °C. The mathematical "Corkrey" model, which predicts that thermal breadth should be minimized and species richness maximised at 20 °C across all Domains of life, provides an explanation for this "20 °C effect". A literature search found highest species richness at ~20 °C across life in air and water, including animals, plants and microbes. That life seems centred around ~20 °C implies fundamental constraints that compromise the ability of extant tropical species to adapt to higher temperatures.

Highlights

- 20°C is the most stable temperature biochemically and for most species.
- The optimal temperature for a species survival is below its optimum for growth.
- Temperatures above 20°C are increasingly suboptimal for marine species.
- Marine species guilds and productivity–biomass relationships overlap around 20–22°C.
- 20°C is significant from biochemical to ecosystem levels of biodiversity.

Keywords: Biodiversity, freshwater, marine, rate-limiting enzyme reaction, species richness, temperature-dependence, temperature optima, terrestrial, thermal guilds, 20 °C effect.

Introduction

Biological importance of temperature

Temperature is a primary environmental variable driving biological processes because of its direct effects on life at biochemical, cellular, metabolic, individual, species, and ecosystem levels, e.g., Loeb and Northrop (1916), Martin and Palumbi (1993), Gillooly (2001), Allen (2002), Clarke (2004), Allen et al. (2006), Munch and Salinas (2009), Brown (2013), Puurtinen et al. (2016), Arroyo et al. (2022). The fact that most species occur in the tropics suggests that tropical temperatures may be ideal for life on Earth. This tropical species richness arises from enhanced speciation opportunities due to the absence of a cold-season, higher mutation rates, shorter generation times, more sunlight driven productivity, structurally complex rainforest and coral reef habitats, and increased ecological opportunities and competition, all feasibly leading to an increase in biodiversity over time (e.g., Wright and Rohde 2013, Costello and Chaudhary 2017).

Are endotherm and/or tropical temperatures optimal?

A second reason warmer temperatures may be often considered optimal for life is that endotherm body temperatures are generally above average environmental temperature in the tropics. Additionally, the thermal limit for marine tropical ectotherms reaches 35 °C and higher (Pörtner 2002; Sunday et al. 2012). Indeed, endotherms and ectotherms gain energetic advantages (e.g., faster response times and greater mobility for foraging and predator avoidance) at warmer body temperatures. These advantages increase evolutionary fitness despite higher metabolic costs, which can be sustained by air-breathers because of higher oxygen in air than water (Clarke and Pörtner 2010). Mammal, bird and thermoregulating reptile body temperatures range between 30–45 °C (Clarke and Pörtner 2010). These maximum body temperatures of endotherms in different evolutionary lineages imply a common upper prolonged physiological limit for multicellular eukaryotes from 30 to 45 °C and no higher. Why this is a limit is unclear and may be due to fundamental biochemical constraints at a molecular level, including temperature affecting the molecular properties of water (Drost-Hansen 1967, Dougherty and Howard 1998), particularly within the cell and in close proximity to proteins (Wiggins 2008). O'Brien (2006) explained how water mediates the effect of temperature on life because liquid water is essential for life to evolve, and thus argues how water-energy dynamics restrict life on Earth.

Biological complexity and temperature

For most species, metabolism depends on the ambient external environmental temperature (i.e., most species are ectotherms), and most species live in the tropics where environmental temperatures are generally warm (Costello and Chaudhary 2017); endotherms comprise just 1% of all species, primarily mammals and birds (Costello et al. 2013). Observations

across the kingdoms of life (from Archaea to Bacteria to unicellular and multicellular eukaryotes) indicate that thermal tolerances decline with increasing complexity (Storch et al. 2014). Indeed, (a) increasing cellular structural complexity (Lane and Martin 2010), (b) greater cell specialisation in multicellular species, and (c) multiple species in ecosystems may suggest greater resilience and adaptability to changing environmental conditions (the portfolio effect). However, perhaps because the realised niche of organisms appears to narrow with greater organismal complexity, most eukaryote species cannot function optimally at the high temperatures where some Bacteria and most Archaea can persist (Corkrey et al. 2019). We may thus expect an optimal environmental temperature for most Eukarya species to be below endotherm body temperatures but within the range of tropical temperatures (i.e., between 15 °C and 45 °C).

A thermodynamic growth model

A mathematical model, distinguished here as the Corkrey model (Box 1), described temperature-dependent growth rates by assuming that a cell contains a master reaction system that depends on a single rate-limiting mechanism, process or enzyme (Corkrey et al. 2012). While the suggestion that growth rates can be attributed to a single limiting process is simplistic, the Corkrey model obtained highly accurate fits to temperature-dependent growth rates of 230 diverse unicellular and multicellular taxa in all three domains of life ranging from psychrophilic ($T_{opt} < 17$ °C) to the highest temperature so far observed for growth. The fits for all 230 taxa in Corkrey et al. (2014) were excellent, even including those cases with few data, and across a large (-4 to +122 °C) temperature range, and the model fits were attained with only three species-specific parameters. Some examples of plots of the growth curves are shown in Supplementary Fig. S1, including microbes, insects, plankton, fungi, and plants. The underlying mechanism may be more complex than a single rate-limiting enzyme process, such as a ribosome limitation (Corkrey et al. 2019), but single enzymes have been shown to control growth rates (Ron et al. 1990, Gur et al. 2002), while a complex network of enzymes sharing the same thermal responses would require equally complex feedback mechanisms (Ruoff et al. 2007) and involve multiple supervisory genes (Bruggeman and Westerhoff 2007, Klumpp et al. 2009). Apart from excellent fits to data, which many models can produce, the Corkrey model also obtained estimates of thermodynamic parameters consistent with the published literature, as previously identified from protein chemistry experiments. As explained below, this advance in modelling temperature dependencies in growth rates leads to a hypothesis that 20 °C is a pivotal temperature for life on Earth. However, the generalised contribution of 20 °C to other aspects of biodiversity remains to be investigated.

Here, we summarise examples of relationships between temperature and a variety of biological features of species and communities in the context of recent

Box 1. A more detailed explanation of the Corkrey model.

<p>For simplicity, the rate-limiting process controlling organism growth rates was considered to be a single enzyme system in the Corkrey model (Corkrey et al. 2012, 2014). Mathematically, the Corkrey model assumed a single rate-limiting, enzyme-catalysed ‘master reaction’ using an Arrhenius form modified by terms that describe the temperature-dependent hot and cold denaturation of that enzyme. The modelled properties of the enzyme include three specific-parameters, the number of amino acid residues, heat capacity of denaturation, energy required (enthalpy) for activation, and four ‘global’ parameters, the convergence entropy and enthalpy for protein unfolding with associated temperatures.</p>
<p>The model estimated the number of amino acid residues to be largest in Eukarya, intermediate in Bacteria, and least in Archaea, which matched that expected for proteins in the three domains (Zhang 2000). The estimate of the heat capacity for protein denaturation was found to be contained within the range expected for Bacteria and mesophilic Eukarya and thermophilic Archaea (McCrary et al. 1996), and, as expected, there was also an increasing trend in heat capacity from psychrophiles to mesophiles, thermophiles and hyperthermophiles ($T_{opt} > 80$ °C) consistent with experimental findings (Hobbs et al. 2013).</p>
<p>The estimated enthalpy of activation of the rate-limiting enzyme was consistent with measured data (Ng et al. 1962, Shaw 1967, Menett and Nakayama 1971, Billing 1974, Coultate and Sundaram 1975, Price and Sowers 2004). The interpretation of the model results was also consistent with considerations of there being a trade-off between enzyme activity and stability such as observed between psychrophiles, mesophiles and thermophiles (Corkrey et al. 2014, D’Amico et al. 2003, Luke et al. 2007, Cherry 2010, Bloom et al. 2006, Wang et al. 2002, Hollien and Marqusee 1999).</p>
<p>In addition, the Corkrey model found that: (1) the enthalpy of activation and heat capacity change increased with temperature and the number of amino acid residues declined, as has been reported (Das and Gerstein 2000, Brocchieri and Karlin 2005); (2) the number of non-polar residues per amino acid residue increased with temperature, as has been observed experimentally (Feller 2013); and (3) heat capacity was negatively correlated with the number of non-polar residues, confirming a previously proposed relationship (Graziano et al. 1998). The Corkrey model also predicted that the enzyme rate limiting process in thermophiles and hyperthermophiles would be stabilized over a broader temperature range than in mesophiles and psychrophiles, as has been observed (Collins et al. 2003). Finally, estimates of thermodynamic properties of globular proteins, such as the convergence temperatures for enthalpy and entropy, were consistent with those reported decades earlier by experiment (Privalov and Gill 1988, Privalov and Makhatazde 1993).</p>
<p>It is important to emphasize that these results were obtained by modeling the rate of organism growth only, and without the incorporation of protein information (Corkrey et al. 2014). In doing so, the good fits and the successful estimation of previously determined experimental thermodynamic data, supported the idea that the temperature-dependent growth rate of poikilothermic life is controlled by a single-enzyme system. More generally, the Corkrey model suggested that the thermal stability of proteins is a fundamental property in the evolution and adaptation of life on Earth.</p>
<p>The modeled growth curve (Fig. 1A) has a low rate at the minimum temperature for growth (T_{min}) rising almost linearly to the “optimum” at T_{opt}. It should be noted that this temperature only represents the fastest growth rate and not a physiological or evolutionary optimum. Above T_{opt} the growth rate reduces until the temperature reaches T_{max}, beyond which death occurs or growth ceases. In the model, rates increase with temperature until T_{opt} is reached, above which they decline due to hot denaturation of the rate-limiting enzyme. While the identity of the rate-limiting enzyme or enzymes is unknown, recent research into the rate-limiting process has identified 17 proteins that may be involved in the process (Cameron Macdonald, personal communication, 27 May 2022). Further development of this methodology may further reduce this number and explore the nature of the process.</p>
<p>The model estimates the lower (L_{mes}) and upper (U_{mes}) temperatures within which enzyme stability is still 90% of the maximum possible value (Corkrey et al. 2019); the subscripts refer here to ‘maximum enzyme stability’. This range of temperatures, $U_{mes} - L_{mes}$, was termed the Thermal Stability Range (TSR), and was found to itself to be temperature-dependent (Fig. 1B). We propose that temperature-dependent variation of the TSR has implications for processes at the level of ecosystems because the range of temperatures over which growth is efficient for particular species will vary systematically with temperature. Of course, this tendency will be also influenced by ecological adaptations, evolutionary history, and palaeo-climates. For example, a species living in a variable or cold climate may be inactive at cold temperatures and only grow within a narrow temperature range, such as during summer in seasonal climates. Thus, a species living in a seasonal environment with a large temperature range is not necessarily eurythermal, i.e., able to function over a wide range of temperatures. Even Arctic fish species, while adapted to a cold environment, have compromised growth rates at both low and high temperatures (Lavin et al. 2022).</p>
<p>With a wider TSR, as is predicted will occur below or above 20 °C, a species can grow efficiently over a wider temperature range than a species with a narrower TSR living at 20 °C. Thus, all else being equal, we postulate that the number of potential thermal niches will be larger in an ecosystem containing species with narrower TSRs than in one with wider TSRs. To see the effect of the TSR on species richness we can examine the theoretical degree of overlap in TSR for species with varying T_{opt}. For example, given two species, one with a T_{opt} of 25 °C and another of 30 °C, any overlap in their TSRs can be estimated. In other words, we can calculate the expected species richness based on the overlapping ranges. If the TSRs are narrower, the overlap would be less and hence the species richness would be greater, while wider TSRs would result in lower species richness. Using data from Corkrey et al. (2019) we find the largest proportion of species have overlapping TSRs at around 20 °C (Fig. 1D). It should be noted that we chose to use a heuristic approach in calculating this proportion since the Corkrey model is mathematically complex. If a more extensive approach were possible it would presumably require the use of assumptions additional to those in the Corkrey model. Further, the predicted distribution of TSRs should be interpreted as a general tendency that may be modified by environmental factors such as pH, oxygen, and water activity (McMeekin et al. 1993).</p>

theoretical advances regarding temperature optima for life on Earth. We first summarise the findings of a theoretical model that 20 °C is the most stable and biochemically efficient temperature across all domains of life, and then explore whether a signal for this effect exists at more complex levels of biodiversity in the literature and independent datasets held by the authors. We find evidence that temperatures above 20 °C become increasingly suboptimal for all domains of life, including animals, plants, and prokaryotes. We term this phenomenon the “20 °C effect”. These examples illustrate the importance of 20 °C to life from

field and laboratory data across individual species, past and present species richness patterns at global and local scales, fish and invertebrate abundance, oxygen tolerance, predation intensity, and productivity–biomass relationships. Finally, we conducted a systematic literature search to quantify the response of species richness to temperature. Our findings suggest that the pace of climate change is too fast for new species to evolve to replace those lost within the lowest latitudes. Warming will have strong energetic consequences that are likely to shift the energy supply and demand pathways structuring food webs in the tropics.

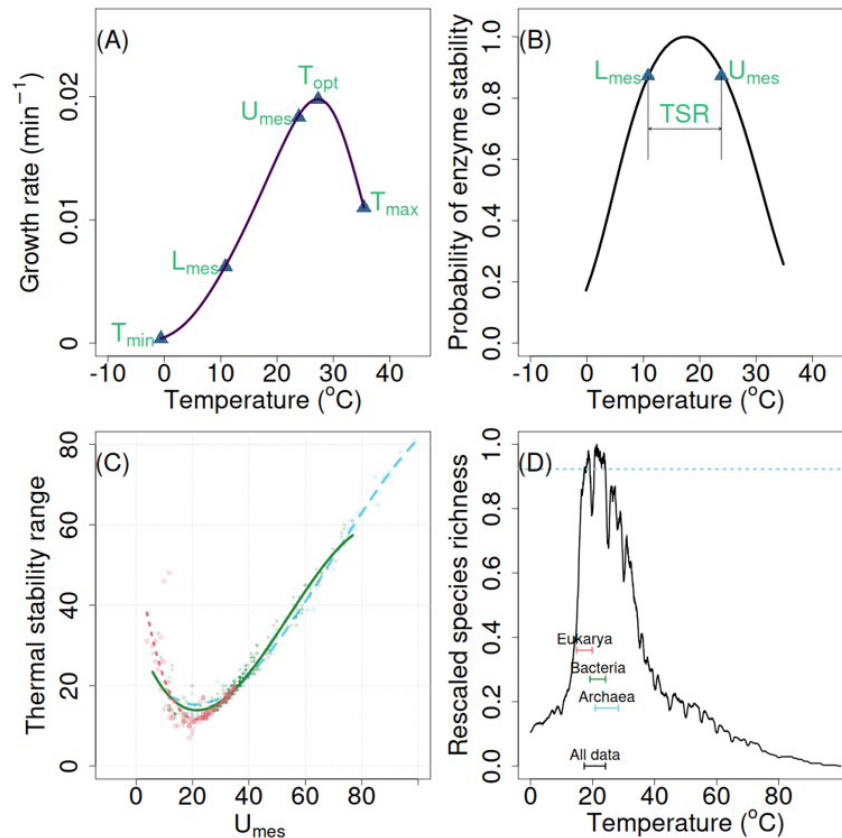


Figure 1. (A) An example of a temperature-dependent specific growth rate curve for a single species (*Pseudomonas fluorescens*) fitted using the Corkrey model. (B) The modelled enzyme stability curve for the species in (A) showing the L_{mes} , U_{mes} , and Thermal Stability Range (TSR). (C) The TSR versus temperature for species in the three domains of life: Bacteria, unicellular and multicellular Eukarya, and Archaea; data from Corkrey et al. (2017)). The minimum TSR, greatest stability, occurs at almost the same temperature in the three domains: Bacteria, green dots, 20°C (95% CI 18, 24); Eukarya, pink dots, 19°C (17, 21); Archaea, blue dots, 22°C (18, 25). (D) The predicted species richness estimated at each temperature with the 95% quantile shown as a dotted horizontal line for all data. The temperature interval that corresponds to the quantiles is shown as brackets for all data and each domain.

Materials & Methods

Corkrey Model

Model estimates and data for the Corkrey model were obtained from Corkrey et al. (2019), which should be consulted for details. Data on the posterior distributions of the upper and lower maximum enzyme stability estimates, U_{mes} and L_{mes} , were extracted for Bacteria (356 species from 12 phyla), unicellular and multicellular Eukarya (108 fungi, algae, chromistan, protozoan, insect and mite species) and Archaea (65 Euyarchaeota and Crenarchaeota species), and the Thermal Stability Range (TSR) calculated as $U_{mes} - L_{mes}$. The TSR was plotted against U_{mes} . The minima of the TSR by domain (Bacteria, Archaea, Eukarya) were summarised by means and bootstrapped 95% CI using the boot library (Canty and Ripley 2021). The proportional overlaps of species' TSR were calculated and plotted against temperature to obtain a predicted species richness. Note that this is equivalent to calculating how many ways a resource, temperature, can be subdivided; i.e., more species

with narrow TSRs can share a given temperature range compared to species with wide TSRs, since the overlap in the former is less than in the latter. The maximum overlap corresponds to the temperature at which the TSRs are narrowest. The 95% quantiles of the TSRs were calculated and the corresponding temperature ranges shown on the plot as brackets for all data and by domain (Figs. 1D and 2).

Literature search

A literature search was conducted between 6th March and 28th July 2020 to locate papers that described the temperature dependence of species richness in nature. Searches using Google Scholar were conducted by two PhD students under supervision. The search terms used were (“species richness” or “biodiversity”) and (“temperature” or “temperature dependence”). Only papers published in peer-reviewed journals were retained, but there was no limitation on publication date. The reference lists of the located papers were searched for additional relevant papers. Only observed data of measures of the dependence

of species richness on temperature were retained with modelled estimates being discarded. Data were extracted from tables or digitised from plots using the open-source program g3data (available from <https://github.com/pn2200/g3data>) and saved in electronic format. Data sets were categorised according to the source environment (freshwater, marine, terrestrial) and the reported organism type (animals, bacteria, fungi, plants). Where possible, studies of animals were further categorised as ectothermic or endothermic.

A total of 54 papers were located, of which 41 contained data. Of these, 39 were found to contain sufficient data for analysis, resulting in 77 separate datasets (Supplementary Table S1). The measures of species richness in the studies may not always have been in compatible units, but this was not important since only the temperatures of peak species richness were of interest.

Plots of species richness versus temperature were calculated, which indicated that the majority possessed a peak at a single temperature. There were also a small number of datasets where peak species richness occurred at the highest observed temperature, which indicated that the supra-optimal temperatures may not have been reached. To obtain estimates with and without peaks a nonlinear curve was fitted to the data so as to obtain a consistent estimate of the peak temperature. After examination of the data plots the curve selected was an inverse quadratic model:

$$R = \frac{1}{(C \cdot T^2 - 2 \cdot C \cdot P \cdot T + 1) \cdot A}$$

In the model, species richness is denoted R and temperature (°C) by T . The A controls the height of the fitted curve, C modifies its curvature, and P is the peak temperature. To simplify model fitting, the data were scaled first so that R ranged between 0 and 1. Since this is a nonlinear model, the 'nls' function in R software was used (R Core Team 2018). Residuals plots were calculated using the 'nlsResiduals' function from the 'nlstools' library (Baty et al. 2015) and, if needed, the data were transformed by taking logs or square roots to correct for heteroscedasticity. Successful fits were obtained in all but 10 cases that were discarded and not used in further calculations. Lack of fit in these cases was due to insufficient sample sizes or a lack of a clear trend (confirmed by visual examination). The function 'nlsBoot' from the nlstools library (Baty et al. 2015) was used to calculate 95% bootstrapped confidence limits for the peak temperature based on 1000 bootstraps.

From the model statistics, the proportions of the datasets with overlapping confidence intervals were calculated at $T = 0, 1, \dots, 100$ °C. A correction was needed to allow for uneven sampling effects because some temperatures were more heavily sampled than others, such as due to a preference for organisms that grow at room temperature. Therefore, the proportions were weighted by the inverse square root of the number of data sets that contributed to each temperature. The 95% quantile of the proportions and the lower and upper temperatures that bracketed the

quantile were calculated. The proportions were plotted against temperature along with the 95% quantile and the bracketing temperatures. These two temperatures thus determined the temperature range within which the maximum species richness was found.

The calculation was repeated for subsets of the data: environment (freshwater, marine, terrestrial), organism type (ectothermic animals, fungi, and plants). There were insufficient data in the case of endothermic animals and bacteria, which were therefore omitted from the plot.

The biochemical basis for temperature-dependent growth rates

Studies of homologous proteins from psychrophilic ($T_{\text{opt}} < 17$ °C), mesophilic ($T_{\text{opt}} 17$ to 45 °C), and thermophilic ($T_{\text{opt}} > 45$ °C) microbes have found that the maximum stability of the 20 out of 26 proteins examined was at 20 °C (Kumar et al. 2001, 2002), raising questions about mechanisms that facilitate growth of species at different preferred temperatures. These suggested that all organisms should prefer 20 °C, since less protein maintenance would be required at that temperature, and hence energetic efficiency would be greater. Furthermore, while proteins tend to be most stable at about 20 °C (Puurtinen et al. 2016), homologous proteins were also found to be about equally stable between species when assessed at the living temperatures of the organisms (Kumar et al. 2001). Thus, the constituent proteins that make up species' proteomes have been selected to function best across the temperatures in which the species typically lives, i.e., its thermal niche. From this, one may argue that there is no advantage for a species living at 20 °C. But, as we show below, the temperature range over which proteins are stable is itself temperature-dependent, which provides the clue to understanding the observed data and the 20°C effect.

Temperature governs the rate of chemical reactions, including those enzymic processes controlling the development of life from cells to complex populations and temperatures from below freezing to above the boiling point of water (Rothschild and Mancinelli 2001, O'Brien 2006). Of particular relevance here is the growth rate dependence on temperature, as growth rates are determined by the rate of chemical reactions within the cell (Stegelmann et al. 2009) and can refer to the rate of cell division through to population growth rate. The former is usually quantified by specific growth rate (McMeekin et al. 1993, 2013) and the latter by intrinsic growth rate as derived by life table analysis (Birch 1948). The two rates, referred to here as growth rates, are comparable since both describe the maximum growth rate after allowing for mortality. At higher levels than the cell, ecosystem function depends on a range of processes at the species level, including temperature-dependent cellular growth rates (Beveridge et al. 2010). For ectotherms, growth rate has a temperature-dependency that is asymmetric and unimodal (Fig. 1A), which is seen across all three domains of life, Bacteria, Archaea and Eukarya (Woese et al. 1990). This uniformity of

response suggests that growth curves have a natural shape (Angilletta 2006), which implies a physiological commonality.

Here we highlight the Corkrey model (Box 1), which predicts that the range of temperatures within which the rate-limiting process is active, called here the Thermal Stability Range (TSR), is narrowest (i.e., most stable) at 20 °C (Figs. 1B, C). The model results indicate that TSR is itself temperature-dependent and narrowest at 20 °C (Fig. 1C). This means that 20 °C is the temperature at which the rate-limiting enzyme has the narrowest range over which it is functional and stable. This outcome can be interpreted as arising from the temperature-dependent balance of the hydrophobic forces (Kumar et al. 2001) that affect the denaturation status of the rate-limiting molecular process. Rather than the emphasis now being on the maximum rate of biological response with temperature, which is conditional on the cell or organisms having sufficient resources, which may not be available in nature, this model emphasises the temperature at which processes are most stable. If all life is indeed limited by a single rate-limiting process, or if multiple processes are most stable at 20 °C, then the footprint of 20 °C should emerge across a diverse range of cells, taxa and higher-level processes. The Corkrey model also predicts that species whose distribution centres at 20 °C should have the narrowest thermal niche, being more stenothermal than species living at much higher and lower temperatures.

Ecological significance of 20 °C

Systematic review

In addition to the examples from our own and other published datasets described below, we conducted a systematic literature search to objectively assess the relationship between temperature and estimates of species richness. A summary of the data, including peak temperatures, is detailed in the Supplementary Materials Table S1. A total of 7,618 observations were used in this analysis and data were not restricted by environment, habitats or taxa. The range of minimum environmental temperatures was -17.5 to 29.2 °C, and the range of maximum environmental temperatures was 7.5 to 92.1 °C. There were more studies of land-based life: terrestrial ($n = 62$), freshwater ($n = 9$), and marine ($n = 14$). There were also more studies of animals than other taxa: bacteria ($n = 3$), ectothermic animals ($n = 40$), endothermic animals ($n = 2$), unspecified animals ($n = 1$), fungi ($n = 3$), microbial eukaryotes ($n = 1$), plants ($n = 27$). The mean number of responses found per study was 97.3 (median 42).

The temperature interval ranges for each taxonomic and environmental group that bracketed the 95% quantile overlapped at 20 °C (Fig. 2). The interval for 'all data' estimated in the Corkrey model (18.5 °C, 23.5 °C; Fig. 1) also overlapped the temperature interval ranges for the literature search data (19.3 °C, 26.3 °C). The ectothermic interval (12.0 °C, 20.4 °C) agreed well with Corkrey model estimate for Eukarya (14.9 °C, 19.9 °C; Fig. 1). Endothermic animals' intervals

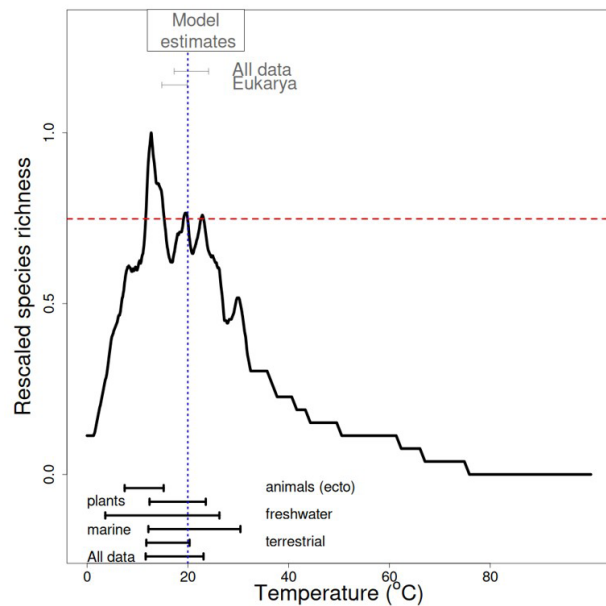


Figure 2. The weighted distribution of species richness, rescaled to between 0 and 1, based on 7,618 samples in 77 datasets from papers that reported the number of species at particular temperatures (see systematic Literature Search in Methods). The unweighted distribution is shown in Fig. S12. Beneath the peak is shown the 95% quantile of the species richness as a dashed horizontal red line. The temperature intervals that correspond to the 95% quantile for all data, and also for subsets of the data (environments and taxa), are shown as brackets. A vertical blue dotted line indicates 20 °C. Also shown in grey bars are the predicted temperature interval ranges for peak species richness from the Corkrey model (as in Fig. 1D).

were not estimated due to insufficient data. Thus, for species richness, the 20 °C effect emerged from the systematic literature data. Whether the differences in thermal intervals between species' groups are a sampling effect or not warrants further investigation.

Species optima

For over 1,000 species, Dell et al. (2011) found that mean physiological optima were 19 °C and 21 °C for marine and freshwater organisms, respectively, but 30 °C for air-living organisms, which included endotherms and insects (Table 1). However, their estimate of the terrestrial habitat temperature was due mostly to ants, including *Pogonomyrmex occidentalis*, which alone added about 5 °C to the mean (Dell et al. 2013). The high temperature reflected its habitat conditions, not endothermy. The optimal temperature for growth across species of multicellular marine eukaryotes is 22.5 °C, but 30 °C in unicellular organisms; and only Bacteria and Archaea and some fungi grow above 45 °C (including hydrothermal vent microbes) (Clarke 2004, Storch et al. 2014, Corkrey et al. 2016). Thus, except in what are arguably extreme cases, an optimum of ~20 °C is evident in aquatic phyla,

Table 1. A list of examples where temperature optima have been reported for guilds or communities of species, presented in chronological order.

Temperature °C	Phenomenon	Reference	No. of observations or samples
19	Separation of warm and cold guilds on North American freshwater fishes	Reist et al. 2006	99 species
20	Maximum gross primary production of phytoplankton	López-Urrutia et al. 2006	164 species
21-22	Maximum species richness of tuna and billfish (large pelagic fish)	Boyce et al. 2008	18 species
19	Mean temperature optimum for marine organisms	Dell et al. 2011	78 species
21	Mean temperature optimum for freshwater organisms	Dell et al. 2011	89 species
30	Mean temperature optimum for terrestrial organisms	Dell et al. 2011	205 species
15 to 20	Temperature at which richness peaked and then declined (using 16S rRNA)	Stratil et al. 2013	4,341 OTU
20	Threshold of rapidly increasing risk of oxygen stress in marine animals	Vaquero-Sunyer and Duarte 2011	147 species
30	Optimal growth temperature for unicellular marine eukaryotes	Storch et al. 2014	162 species
22.5	Optimal growth temperature for multicellular marine eukaryotes	Storch et al. 2014	52 species
22	Maximum richness of bacteria and archaea	Sharp et al. 2014	165 samples
19.9 and 21.2	Median and mean niche breadth of reef fish and invertebrates	Stuart-Smith et al. 2015	7,040 transects, 3,920 species
~20	Separation of warm and cold temperate guilds of reef fish and invertebrates	Stuart-Smith et al. 2015	7,040 transects, 3,920 species
20	Temperature at which OTU richness decreased for three size classes of marine bacteria	Milici et al. 2016	359 seawater samples
28	Peak richness of razor clams in coastal sediments	Saeedi et al. 2016	77 species
20 to 25	Maximum terrestrial soil respiration	Carey et al. 2016	3,800 observations in 27 studies
10	Maximum tag sequence richness marine bacteria	Thompson et al. 2017	6,976 samples
20	Global phytoplankton species richness peaked at 20 °C	Righetti et al. 2019	540,000 observations of 536 species
20	Composition of tree fungal symbionts changes	Steidinger et al. 2019	1.1 million plots with 28,000 tree species
20	Highest predation pressure by pelagic fish	Roesti et al. 2020	42,050 samples
20	Highest predation pressure by fish in benthic bait experiments	Whalen et al. 2020	42 study sites
20	Maximum species richness for planktonic foraminifera	Yasuhara et al. 2020	34 species
20	Preferred temperature across 84 species North American freshwater fishes	Bates and Morley 2020	84 species
20	Maximum species richness for all marine taxa, invertebrates, and pelagic fish	Chaudhary et al. 2021	48,661 species
26	Maximum species richness for benthic, demersal and reef fish	Chaudhary et al. 2021	10,167 species
18.3 (linear) 21.1 (GAM)	Maximum generic diversity of (fossil) molluscs since Jurassic	Boag et al. 2021	196 observations
20	Maximum gross primary production intertidal benthic algae	Díaz-Acosta et al. 2021	4 species
22	Maximum biological response rates "around 25 °C" and a peak for species richness at 22 °C (95% CI 17-22 °C)	Arroyo et al. 2022	128 responses from 65 studies
21.1	Extinction odds lowest, 95% CI 18.8 to 22.5 °C. Rapid elevation in extinctions above 21 °C.	Reddin et al. 2022	16,732 fossil benthic genera in 7 phyla
20	All 95% confidence intervals of animal, plant, microbial, ecto- and endotherm species' thermal ranges across terrestrial, freshwater and marine environments overlapped 20 °C	Present systematic review	53 papers, 7,618 observations

including the earliest evolved taxa. However, because these compilations of thermal optima may have been biased by the species studied, typically in laboratory conditions, and may not reflect community-level optima or the species pool on Earth, we sought further evidence to test this generality.

Species richness

Plots of species richness against annual average sea temperature illustrate the macroecological

importance of temperature to this most popular measure of biodiversity. Comparisons of marine species richness in 5° latitudinal bands with annual sea surface temperature show declines from 20 °C for invertebrate benthos, pelagic fishes, and planktonic foraminifers (patterns that extend at least from the last glacial maximum), and from 26 °C for benthic (demersal and reef) fishes (Fig. 3). Herbivorous marine fishes are rare below 20 °C (Floeter et al. 2005). Trends can vary between taxa, for example the species richness of tunas

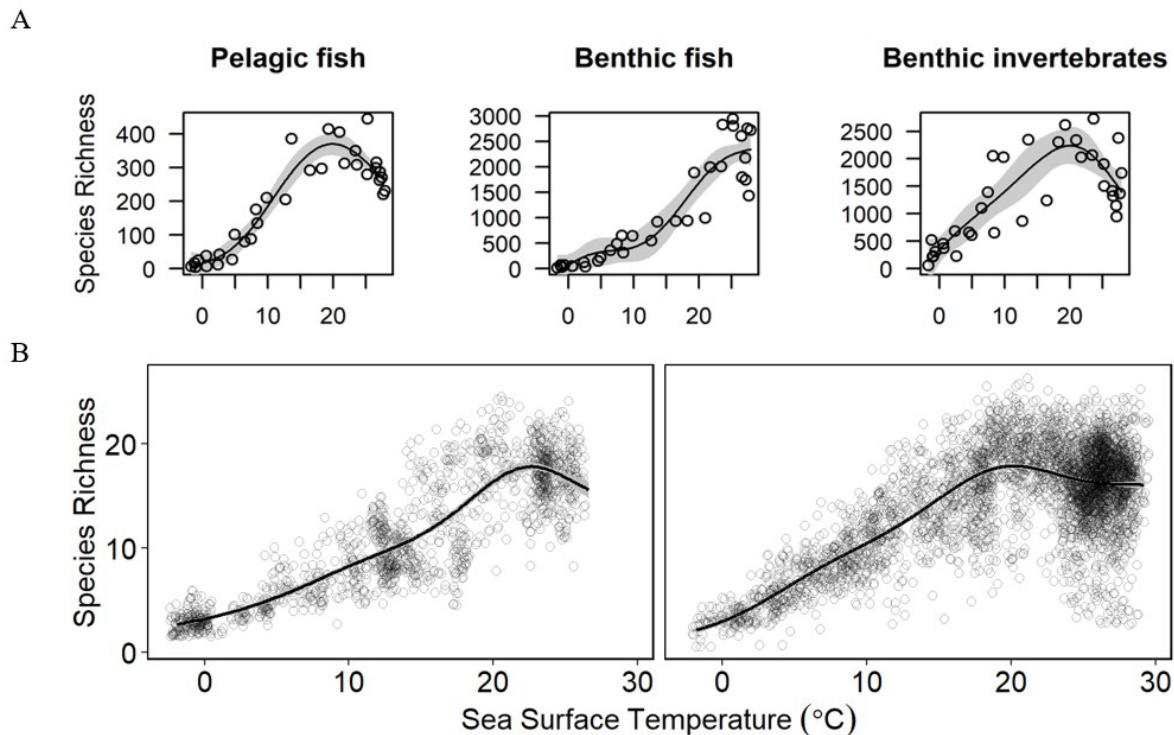


Figure 3. The relationship of global marine species richness to sea surface temperature for (A) pelagic fishes (1,308 species), benthic fishes (9,599 species, including demersal and reef-associated), benthic arthropods and molluscs (18,310 species); and (B) planktonic foraminifera counted from sediment cores during the last glacial maximum (34 species, 1,141 samples, left) and present (34 species, 4,119 samples, right); data from Yasuhara et al. (2020). In (A) the estimated total number of species (GAM using the natural log of the number of samples as an offset) in each 5° latitudinal band was plotted against the average sea surface temperature in each 5° latitude band; data from Chaudhary et al. (2021).

and other large pelagic fishes drops above 21–22 °C (Boyce et al. 2008) (Fig. 4A) and of benthic razor clams above 28 °C (Saeedi et al. 2016). An examination of the latitudinal distribution of 536 species of phytoplankton (Righetti et al. 2019) found that species richness reached a maximum and mean individual species thermal ranges a minimum (i.e., were narrowest) at about 20 °C (Fig. 4B). The authors suggested these results were explained by competitive exclusion mediated by temporal environmental variability, but they did not exclude other possibilities.

Latitudinal bands integrate variation at local scales to produce a more generalized pattern correlated with temperature, suggestive of long-term evolutionary origins. However, annual latitudinal average sea surface temperatures approximate the actual temperatures experienced by the species during the year, and mobile species may avoid locally unsuitable temperatures, e.g., by swimming to cooler, deeper waters (Burrows et al. 2019). Furthermore, spawning fish and embryos, and younger life-stages of invertebrates, can have lower and narrower thermal tolerances (Pandori and Sorte 2018, Bates and Morley 2020, Dahlke et al. 2020). Nevertheless, these macroecological patterns notably show 20 °C as a significant temperature for species richness across many pelagic and benthic taxa.

Boag et al. (2021) estimated the maximum generic diversity of marine molluscs through geological time (upper Jurassic through to modern) to be found at 18.3 °C (± 3.2) using a disjoint linear regression model (Fig. 4C). By fitting a Bragg equation to identify the peak of the curve (Ratkowsky 1990) on their data, we estimated the maximum to be at 23 °C (95% bootstrap CI: 20.5, 27.2); where $R = \alpha + \beta \cdot \exp\left[-\gamma(T - \delta)^2\right]$, and α , β , and γ are parameters to be estimated, T is temperature, and R is species richness. Boag et al. (2021) found richness increased with temperature and decreased as aerobic habitat declined.

Sharp et al. (2014) estimated the diversity in microbes (Bacteria and Archaea) living in aquatic habitats between 7.5–99 °C to reach a maximum at 22 °C. Fitting a Bragg equation to these data obtained a peak richness at 22.6 °C (95% bootstrap CI: 17.5, 26.3) (Fig. 4D). A study of genetic diversity in marine microbes found a distinct peak in observed tag sequences between 0–20 °C (Thompson et al. 2017). However, Milici et al. (2016) found peak operational taxonomic unit (OTU) richness for free-living marine bacteria at 19.1 °C (99% CI 18.2, 20.1) and that it decreased above 20 °C (Table 1). While genetic diversity is not the same as species richness, it is notable that these studies found distinct peaks at or near 20 °C.

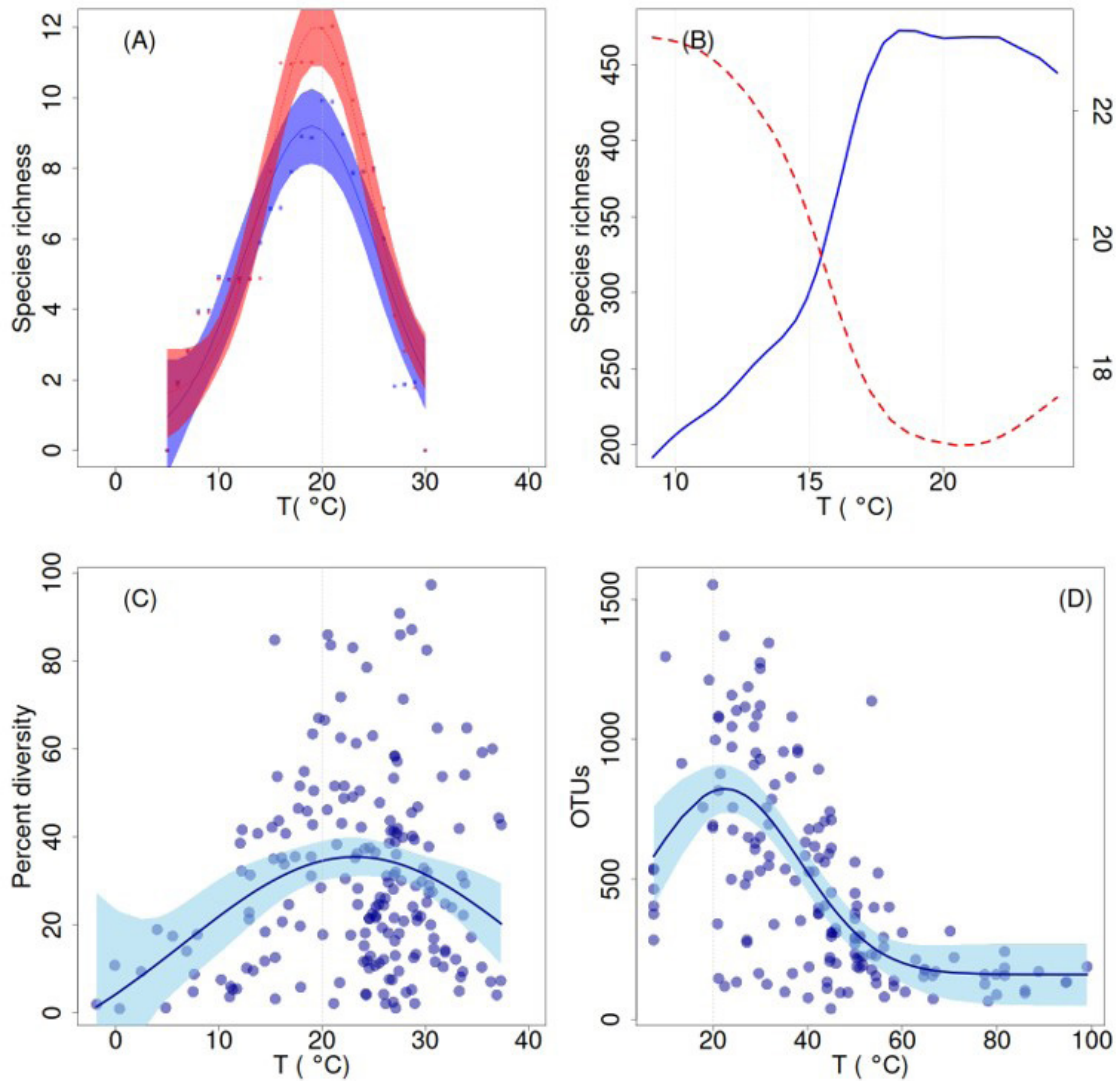


Figure 4. Examples of temperature relationships across taxa. (A) Global tuna and billfish species richness predicted from in situ temperatures where species were observed versus annual average temperature for the Atlantic (red, dashed line, squares) and Indo-Pacific (blue, solid line, circles); data from Boyce et al. (2008). (B) Global phytoplankton species richness (blue line, left axis) and mean species thermal range (red dashed line, right axis) versus temperature based on 0.5 million observations and niche models of 536 species; data from Righetti et al. (2019). (C) Percent global genus diversity of fossil marine molluscs versus temperature spanning the upper Jurassic to the late Pliocene; data from Boag et al. (2021). (D) OTU diversity of microbial species in geothermal environments in Canada and New Zealand versus temperature; data from Sharp et al. (2014).

Thermal guilds

While a species' thermal niche spans a range of temperatures, the mode of its geographic distribution is not necessarily at its optimal temperature. Rather, thermal models and overlap in thermal ranges of species suggest that the optimum across many species in air and aquatic environments remains close to 20 °C, and species may have widened their niche in response to ambient temperatures (Huey and Kingsolver 2011). Standardised scuba surveys of coral and rocky reefs around the world showed distinct tropical, temperate and subpolar guilds of fish and large mobile invertebrates (Stuart-Smith et al. 2015). When plotted

against the midpoint of the thermal range of each species (as an indication of the relative position of their geographic distribution along the thermal gradient of the oceans), the thermal niche breadth was narrowest at a median of 19.9 °C and mean of 21.2 °C (Fig. 5A). The decline in niche breadth at higher temperatures (above 25 °C) is probably limited to some extent by the lack of warmer seas available to spread out into (i.e., realised niche breadth is truncated by geography and contemporary sea temperatures). However, the decline in niche breadth may also be related to the often-observed tendency for species' upper thermal limits to be more evolutionarily conserved than lower

limiting temperatures (Floeter et al. 2005, Araújo et al. 2013). For those species with distributions that are centred around 19 to 22 °C (i.e., warm-temperate and the ‘true’ subtropical species), their realized thermal niche breadth is narrowest of all reef species examined, other than those restricted to the warmest seas (Stuart-Smith et al. 2017). A narrower thermal niche of species whose distribution is centred around 20 °C was also predicted by the Corkrey model.

When the realized thermal range is considered for all reef species together, providing an indication of the number of species that can theoretically occupy

each degree of sea temperature (ignoring dispersal and ecological constraints), peaks in ‘richness’ occur at ~28 and 21 °C for reef fishes and invertebrates respectively (Fig. 5C, 5D). Such peaks generated from overlapping thermal ranges of systematically surveyed reef species correspond remarkably well to the independent data on accumulated species richness for the same taxonomic groups aggregated from occurrence records from thousands of independent datasets (Fig. 3).

Similar to patterns in reef fishes, cold and warm water guilds of freshwater fishes in North America

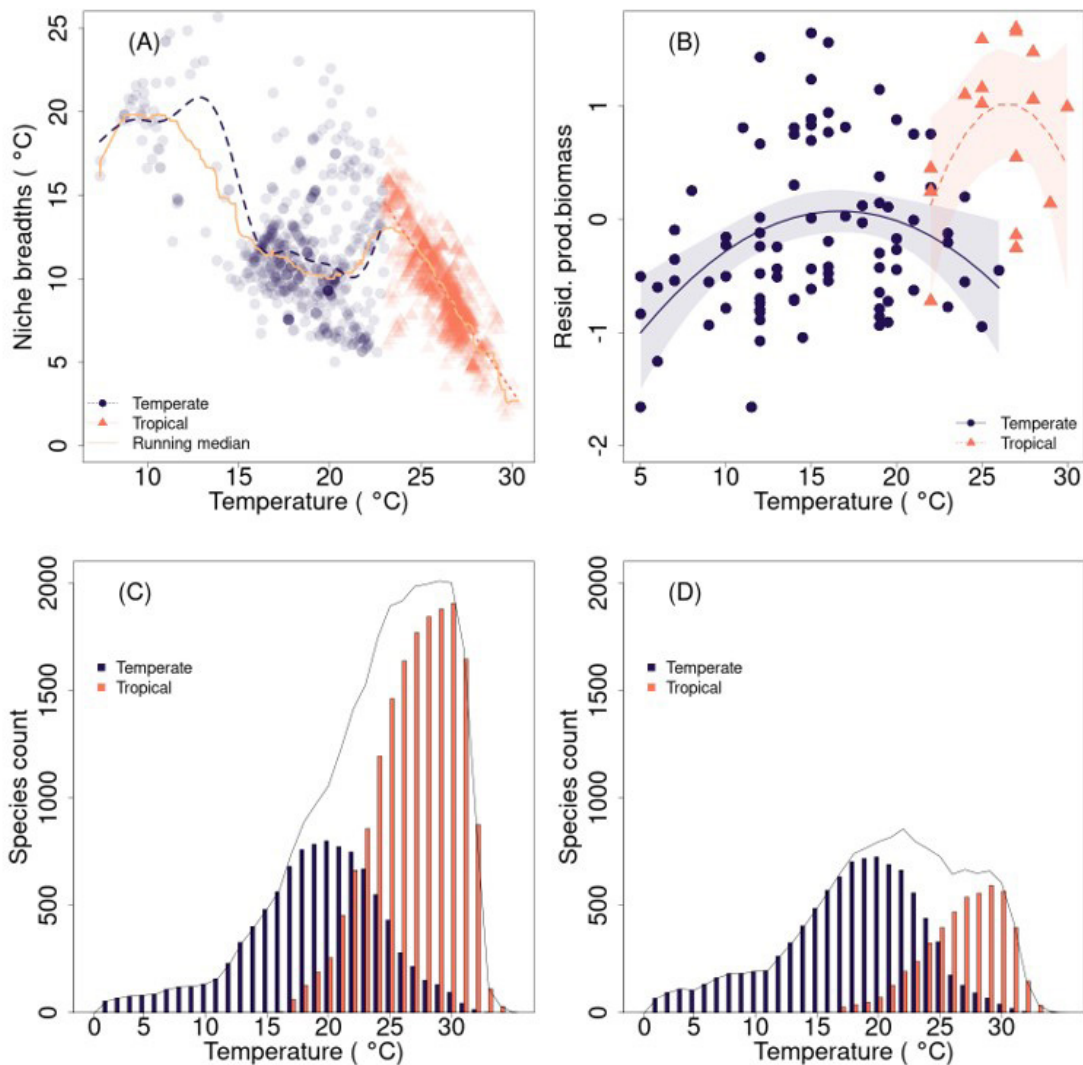


Figure 5. (A) Coral and rocky reef fish and invertebrate species’ realised thermal niche breadth against the midpoint of each species’ thermal range (x-axis) derived from the geographic range of each species’ annual mean Sea Surface Temperatures occupied, with separate trends for species in temperate and tropical guilds. Points represent individual species. Data ($n = 1,790$ species) re-plotted from Stuart-Smith et al. (2017). (B) Residuals derived from linear regression relating log production (P ; mg/d) to log biomass (B ; mg) for fishes ($\log P = 4.34 + 0.704 \cdot \log B$, $R^2 = 0.89$, $n = 62$) and invertebrates ($\log P = 2.39 + 0.840 \cdot \log B$, $R^2 = 0.92$, $n = 41$) plotted against temperature for species categorised within tropical and temperate guilds; best fit parabolic curves: tropical $R^2 = 0.21$, $n = 15$; temperate $R^2 = 0.14$, $n = 88$; field data for fishes from Table 1 of Edgar and Shaw (1995), and for invertebrates from Table 1 in Edgar (1990). (C, D) The number of reef (C) fish and (D) invertebrate species from temperate and tropical guilds (bars) and in total (line) from (A) in each one degree of sea temperature.

similarly separate at 18–20 °C (Reist et al. 2006). Moreover, the preferred temperature across 84 species of freshwater fish in Canada was 20 ± 2 °C (mean \pm 95% confidence limits), with a cooler 15 ± 2 °C optimal for spawning and egg development, and up to 30 ± 2 °C tolerated (Bates and Morley 2020). Thus, 20 °C could be considered an optimum from the perspective that more species (tropical and temperate) can feed, grow, reproduce and maintain populations in these temperatures than any other temperature range in the world's shallow seas, and North American freshwaters, at least.

In addition to temperature relationships with species richness and density, we found strong positive relationships between productivity and biomass for both temperate and tropical guilds of marine fish and invertebrates. When plotted against temperature, ~ 20 °C is midway between the two guilds (Fig. 5B). Thus, 20 °C is a point at which biodiversity changes at latitudinal and local scales, and in terms of productivity–biomass relationships. In addition, primary production of phytoplankton and intertidal benthic algae declines above 20°C as the rate of respiration exceeds the rate of photosynthesis (Fig. 6A, D) (López-Urrutia et al. 2006, Díaz-Acosta et al. 2021). These empirical observations indicate that 20 °C is significant for species richness at global and local scales, and for fundamental ecosystem processes.

In terrestrial ecosystems, soil respiration is maximal between 20 and 25 °C in all biomes except deserts (Carey et al. 2016). Furthermore, an abrupt change in fungal symbionts of trees occurs at 20 °C (Steidinger et al. 2019). That the temperature ranges of most terrestrial species also overlapped 20 °C (Fig. 3) suggests that further examination of terrestrial biodiversity, including ecosystem processes, may find more examples of the significance of 20 °C.

Oxygen limitations

As water warms, the solubility and concentration of oxygen decreases while demand for oxygen by marine organisms increases (Pauly 2019, Seibel and Deutsch 2020). A review of lethal oxygen concentrations in laboratory studies indicates that their relationship with temperature is not linear. Below 20 °C, oxygen needs to be as low as 3 mg L^{-1} to be lethal, whereas mortality has been reported at oxygen concentrations above 3 mg L^{-1} if temperature exceeds 20 °C (Fig. 6B) (Vaquer-Sunyer and Duarte 2011). These observations suggest trade-offs between thermal optima and oxygen supply in aquatic environments, and a metabolic model indicates that oxygen limits marine species richness above 21 °C (Boag et al. 2018).

Ecological and evolutionary fitness

At the level of an individual organism, fitness is often assumed to be maximised at the thermal optimum (Martin and Huey 2008). However, theoretical advances regarding temperature optima across all domains of life on Earth indicate that what has conventionally been called 'optimal temperature' (T_{opt} , the temperature at which a rate function is maximal), is suboptimal

in terms of energetic efficiency (Corkrey et al. 2019). For example, for some terrestrial reptiles that prefer temperatures in the range of 30–35 °C, fitness is maximised below their apparent physiological thermal optimum (Martin and Huey 2008). In addition, an organism living near its thermal maximum risks death if this is exceeded for even a short time (Martin and Huey 2008). Thus, the optimal temperature for evolutionary survival should be below the maximum at which an organism may grow fastest. Scale transition theory also predicts that performance will be lower in a more variable rather than a stable environment (Dowd et al. 2015), and organisms will have a lower optimal temperature in a more variable environment, as has been observed in standardised experiments (Bates et al. 2010).

Predator–prey interactions

The optimal temperature for an individual organism will depend on its history, physiology and ecology. Together these comprise its evolutionary fitness. Dell et al. (2011) found support for the "life-dinner principle" whereby death has more evolutionary pressure than going hungry. Accordingly, prey have a generally lower activation temperature than their ectothermal predators, thereby enabling prey to react sooner and escape predation. Thus, maximizing rates to survive, even when not energetically favourable, is a strong evolutionary selective force. Mammals and birds have overcome this temperature constraint, so they have the advantage over ectothermal prey and predators in colder waters and dominate food webs in polar latitudes (Grady et al. 2019).

At least in the ocean, field and experimental evidence increasingly suggests that predation pressure decreases with latitude (e.g., Rodemann & Brandl 2017, Freestone et al. 2021, Ashton et al. 2022). Benthic and pelagic studies have found an inflexion in predation pressure above 20 °C (Ashton et al. 2022) and that it peaked at 30° latitude, where mean annual temperature is ~ 20 °C, including higher capture rates of pelagic fish on long line hooks (Roesti et al. 2020). A globally replicated field experiment on predation pressure in 33 seagrass beds and 31 nearby non-vegetated areas found consumption rates peaked at 20 ± 2 °C in both habitats (Fig. 6C) (Whalen et al. 2020). The authors proposed that this was due to these latitudes being a transition zone between temperate and tropical guilds as discussed above. We suggest that the reason is because both guilds function well at this temperature. It supports our proposition that 20 °C is where ecological interactions will be strongest because of the underlying physiological and biochemical thermal stability and associated energetic efficiency.

Adaptations

Species may adapt to unsuitable temperatures through changes in their body size, such as occur in warmer and colder conditions, or by behaviours that include seeking shade, basking in the sun, hibernating, nocturnal activity, movement, and laying down fat reserves for periods of unsuitable temperature

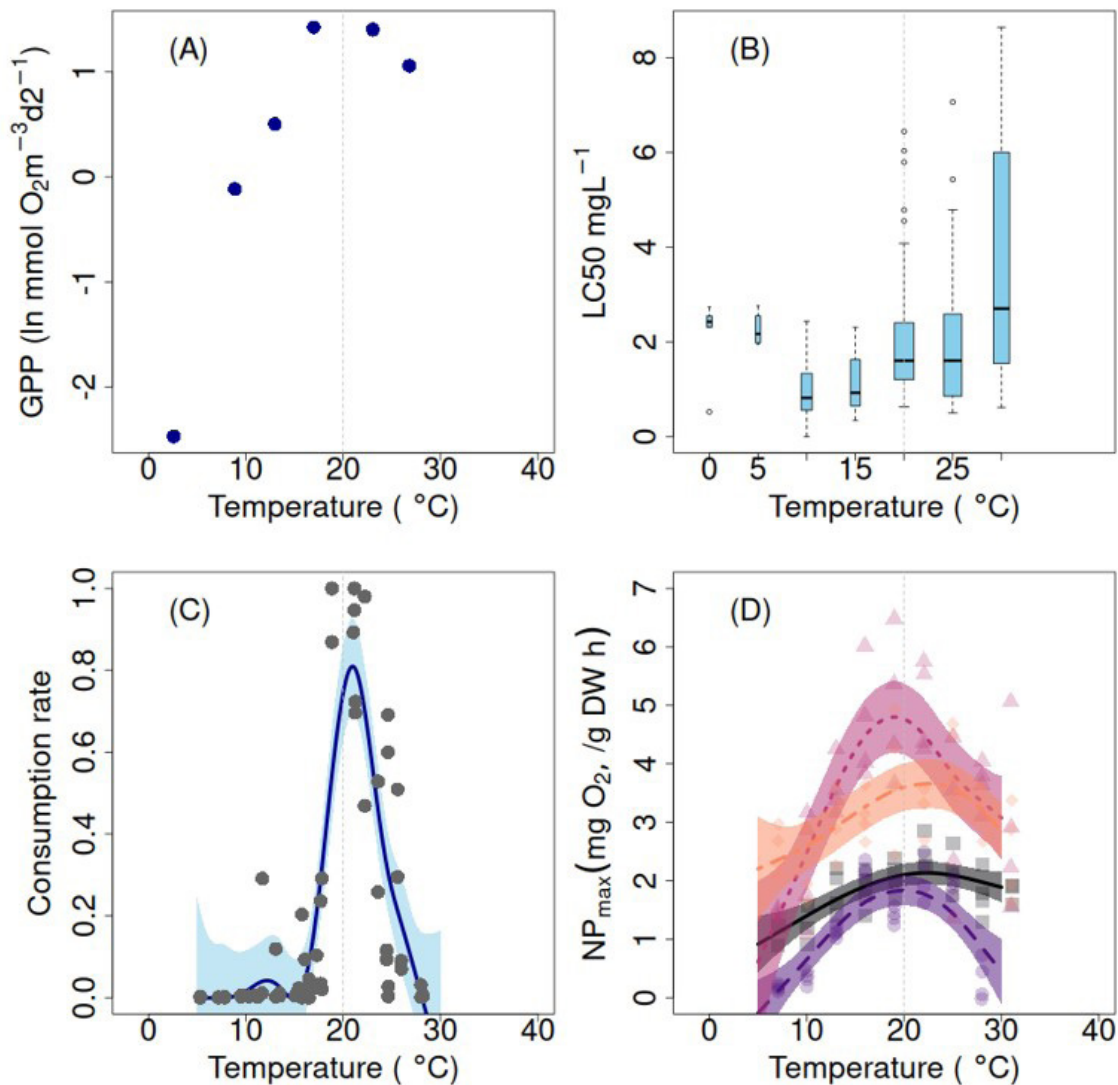


Figure 6. (A) Gross primary production (GPP) of the global ocean versus temperature. Data from López-Urrutia et al. (2006). (B) Boxplots of LC50, the mean lethal concentration of oxygen in which 50% of organisms die: median (heavy horizontal line), the box contains the middle 50% of the data, 1.5 times the interquartile distances (whiskers), and statistical outliers (circles). Above 20°C more species of marine fishes, benthic crustaceans and molluscs ($n = 149$) are intolerant of dissolved oxygen levels above 3 mg/l. Data from Vaquer-Sunyer and Duarte (2011). (C) Generalised additive model fit with 95% confidence intervals for fish consumption rate versus temperature. Data from Whalen et al. (2020). (D) Net productivity of the intertidal macroalgae *Padina panonica* (mauve shading, triangles), *Vertebrata lanosa* (orange shading, dots), *Fucus serratus* (grey shading, squares), and *Gigartina pistillata* (purple shading, circles), versus temperature. Data from Díaz-Acosta et al. (2021).

and/or when food is scarce. Physiological adaptations include thermoregulation and reducing metabolism (Pörtner 2002, Deutsch et al. 2015). Animals living in cold temperate climates may have reduced efficiency below 20°C and limit their activity. For example, in the North-East Atlantic, labrid fishes are inactive and retire to crevices when temperatures are below 8°C and show a linear increase in activity and thus apparent abundance to at least 18°C (Darwall et al. 1992, Costello et al. 1995).

Temperature ‘performance’ curves for individuals, populations and ecosystems have similar asymmetric unimodal shapes, gently increasing to a maximum and

then precipitously declining, e.g., Fig. 1A, (Angilletta 2006). This shape in an ecological setting is due to slower metabolism and evolutionary processes (mutation rates, generation times, ecological competition) at lower temperatures, and the deadly consequences when the maximum tolerable temperature is reached. Thus, a species may live in colder climates, vary its activity with the seasons, and find less ecological competition. In contrast, tropical animals may have wider thermal ranges, but they also need to grow, reproduce, and compete for food while escaping predators at temperatures above 20 °C. This evolutionary pressure will drive genetic

and phenotypic adaptations at warmer temperatures leading to more species in the tropics. Thus, other factors than temperature limit growth, including food availability and foraging costs and risks. Future research into how the 20 °C effect applies in nature should consider other limiting factors.

Benefits of mobility

At high temperatures, and certainly above 20 °C, individuals have elevated metabolic demands and thus must obtain more oxygen and food. Feeding, especially if it requires movement to find food, increases the risk of predation (Dell et al. 2011). However, mobility also increases potential access to food and allows individuals to avoid unfavourable conditions, such as extreme temperatures and areas with low oxygen. For example, three species of marine snails actively select their preferred temperature range by adjusting their distance from hydrothermal vents which are acidic and rich in reduced sulphur (Bates et al. 2005). This balance between the advantages and risks of mobility creates opportunities for adaptive speciation, a likely contributing factor to the far higher species richness of species that are mobile rather than sessile on land and sea (e.g., over 70% of all species on Earth are either arthropods, molluscs, vertebrates, or worms) (Costello et al. 2013, Costello and Chaudhary 2017, Costello 2023). The evolution of endothermy is probably driven by these selective advantages, but its high energy and oxygen demand means that full endothermy is only fully achieved by air breathing mammals and birds (Clarke and Pörtner 2010).

Generally, we may expect pelagic species to be more mobile than benthic species. However, while peak species richness at 20 °C is observed for pelagic, planktonic, benthic invertebrates (Fig. 3), and all invertebrates combined (Fig. 5), two independent datasets and analyses indicated that demersal (seabed associated) fish richness peaks around 26 to 28 °C (Fig. 5). Perhaps some of these fish species find temporary thermal refugia in cooler depths and thus avoid extreme temperatures.

Terrestrial life

In contrast to aquatic environments, heat is more readily lost through evaporation in air, and more thermal refugia options exist (shade, burrows, nocturnal) in terrestrial environments. An analysis of species vulnerability to climate warming found such thermal refugia, including forest cover, important in enabling terrestrial species to survive hot temperatures (Pinsky et al. 2019). Only mobile marine species have the option to swim to cooler deeper water to avoid extreme heat events. Thus, most marine organisms are more sensitive to warming than terrestrial species, in part because they lack comparable refugia options. However, marine organisms may shift their geographic ranges more easily than terrestrial species because the latter often inhabit environments fragmented by human land use and/or on geographically isolated islands or mountain tops. Thus, local extirpation may be more rapid in the ocean than on land, but

global extinction is less likely for those marine species with sufficient mobility to track changing isotherms (Pinsky et al. 2019, Chaudhary et al. 2021, Gordó-Vilaseca et al. 2023).

Evolutionary history

In the Triassic ~200–250 million years ago, the fossil record shows a flattening of the latitudinal gradient in marine species richness, with shifts in species richness to high latitudes coincident with temperatures 6 to 15°C warmer than present and associated anoxia (Song et al. 2020). This suggests that oceans significantly warmer than they are now did not harbour more species. Most extant species have diverged from ancestral species in the last 66 million years (the Cenozoic). The major part of the Cenozoic was characterized by warmer temperatures than now, and also by gradual cooling throughout, with a few exceptional warm peaks. For example, the tropical early Eocene temperature was ~34°C, much warmer than the present-day tropics (Norris et al. 2013). Mid-Pliocene tropical temperatures were up to 2 °C higher than the present day some 3 million years ago (Dowsett et al. 2013). Thus, numerous species may once have adapted to higher temperatures than in the present-day tropics. However, during the Eocene, Oligocene and Plio-Pleistocene cooling, most of these (hypothetically) hot adapted tropical species – if they existed – would have become extinct (Yasuhara et al. 2012, Lam and Leckie 2020, Reddin et al. 2022). The 20 °C effect that we now see (Fig. 3B) may be, in part, the result of this evolutionary consequence of warm-adapted species extinction in the tropics, which would explain the recent tropical dip of species richness (Chaudhary et al. 2016, 2017, Yasuhara et al. 2020, Chaudhary et al. 2021). On the other hand, the 20 °C effect may always have limited biodiversity, because genus richness of fossil marine molluscs was highest at 21.1 ± 3.2 °C over the past 145 million years (Boag et al. 2021), and extinction rates across seven benthic marine phyla were lowest at 21 °C (Reddin et al. 2022). Thus, species richness in the fossil record declined above 21 °C, as the case for most taxa today and during the last glacial maximum (Fig. 3).

Conclusions

The Corkrey model produced an estimate of the Thermal Stability Range (TSR) that has a minimal range at about 20 °C in Bacteria, Archaea and Eukarya, implying that energetic efficiency has a common temperature span across all Domains of life (Box 1). Most field studies are concerned with larger organisms than were used to develop the Corkrey model, but the generality of the model implied that it should be broadly applicable. It was therefore satisfying that numerous examples obtained estimates of the peak species richness temperature that were consistent with predictions (Table 1). Most importantly, our literature search, which was conducted independently of the other studies, concurred with a previous review (Dell et al. 2011) and supported the theoretical

approach as well as the examples of species richness (Fig. 2).

The primary assumption of the Corkrey model is that a single rate-limiting process is most efficient within a range (the TSR) that is predicted to be narrowest at 20 °C, resulting in greater species richness and narrower thermal widths at that temperature. This is proposed as the source of the 20 °C effect. Thus, at 20 °C organisms tend towards narrower niche widths, as seen in coral and rocky reef fishes and invertebrates (Stuart-Smith et al. 2017), and in phytoplankton (Righetti et al. 2019), and show greater diversity, such as in pelagic fish and benthic invertebrates (Chaudhary et al. 2021), phytoplankton (Righetti et al. 2019), fossil molluscs (Boag et al. 2021) and foraminifera (Yasuhara et al. 2020). Righetti et al. (2019) and Sharp et al. (2014) explained unimodal temperature responses for biodiversity by means of an exponential dependence on temperature combined with environmental heterogeneity or hypoxia respectively. Both of these hypotheses may be correct, but a single rate-limiting process could explain these results with temperature alone. While species can survive at higher or lower temperatures, the range of temperature for maximum metabolic efficiency will tend to be narrowest and protein stability greatest near 20 °C, and as noted earlier, proteins are about equally stable at the temperature to which a species has evolved to live, allowing endotherms to thrive with a high body temperature. Evolution will select for species that can live at, above and below 20 °C, by ecological, physiological and/or behavioural adaptations, and because the pace of evolution is faster at warmer temperatures (Wright and Rohde 2013), we see more species above (tropical) than below (temperate, polar) 20 °C.

We have shown multiple lines of evidence that evolutionary pressures become increasingly acute for most species in both directions from 20 °C, which is most of the time for species presently living in the tropics. Tropical species are more likely to be near their upper thermal limits and are therefore more sensitive to the effects of warming. Living at their thermal limits may also reduce their ability to genetically adapt to a new climate. Thus, rather than the tropics being a stable and ideal “Goldilocks zone” (not too hot and not too cold), species living in low latitudes may already be living beyond their optimal biological efficiency. Our literature search only turned up a few datasets for endotherms, but the 20 °C effect remains important since they must lose heat and this becomes more difficult at higher ambient temperatures. For example, a prolonged wet bulb temperature of 35 °C is fatal to people (Sherwood and Huber 2010), and outdoor labour productivity declines above 20 °C (Burke et al. 2015).

Coral bleaching and shifts in species' ranges away from the equator can thus be viewed as symptoms of temperature-induced stress which manifests at individual levels (Stuart-Smith et al. 2018). Marine species richness does not now peak at the equator, as occurred at the last glacial maximum (Chaudhary et al. 2017, Yasuhara et al. 2020). During

Earth's recent glaciations annual average equatorial sea temperatures were 25 °C (2 °C colder than today) and species richness of corals (Mihaljević et al. 2017) and planktonic foraminiferans (Yasuhara et al. 2020) were higher at the equator. Now, while still high in the tropics, species richness dips at the equator, and this dip has predictably deepened and widened during the past century in concert with ocean warming, and is predicted to decline further (Yasuhara et al. 2020, Chaudhary et al. 2021, Yasuhara and Deutsch 2022). While species can evolve at a wide range of temperatures, as evident from half of Antarctica's marine species being endemic (Costello et al. 2010, 2017), if any species have evolved to live in warmer Cenozoic temperatures then it seems that they have largely gone extinct. Indeed, this seems to be the case, with high extinction rates found across a diverse range of marine phyla in the fossil record when average temperature went above 20 °C (Reddin et al. 2022). Thus, evidence from the fossil record indicates that the present equatorial temperatures are excessive for many marine species.

A lack of attention to the importance of 20 °C in studies on temperature relationships amongst species and ecosystems probably reflects different study aims and data sets with limited temperature ranges. What we find in this review is that when multiple empirical observations are taken together along with the results of an objective literature search, and considered in the context of thermal models and theory, 20 °C is indeed a significant temperature in both biochemical, ecological and evolutionary contexts where the stability of biomolecules and cellular processes also have a narrower temperature range. For aerobic life, the primary limiting factor below 20 °C is temperature, and above 20 °C is food, oxygen (especially in water), and heat stress. Endotherms have escaped these limitations to some extent, especially below 20 °C, where they use metabolic activity to generate heat and maintain insulative layers. Our findings add to recent evidence that the trend for reduced biodiversity above 20 °C is further compounded by global warming, leading to a simplification of ecosystems and increasing competition effects restricting the area of thermal ‘habitat’ for species now extant on Earth.

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Author Contributions

All authors contributed to the writing of the paper. Writing was led and coordinated by the first author. Authors MJC, RC, AEB, MTB, GJE and RDSS conceived the paper, and MJC, RC, CC, GJE, RDSS, MY and CLW contributed figures. RC conducted the systematic review.

Data Accessibility Statement

New data provided in this article is available in the Supplementary Material section.

Supplementary Material

The following materials are available as part of the online article at <https://escholarship.org/uc/fb>

Figure S1. Examples of growth across temperatures of species in various kingdoms.

Figure S2. Unweighted distribution of species richness based on data from the systematic literature search.

Table S1. Summary of data and estimates of species' thermal ranges.

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