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# Intraspecific variance

“The response of species to global warming depends on how different populations are affected by increasing temperature throughout the species’ geographic range.” (Gardiner et al., 2010, p. 1)

Incorporation of the evolutionary history into any analysis follows from the ‘‘unarguable premise that species are not independent biological units that are devoid of history and genealogical affinities’ (Sinclair 2016)

Intraspecific variation in key traits such as tolerance of warming can have profound effects on ecological and evolutionary processes, notably responses to climate change. (Mckenzie 2021)

There is also strong evi- dence of structured variation in tolerance of warming within species, which may have ecological and evolutionary significance irrespective of whether it reflects plasticity or adaptation (mckenzie) ; Geographic variation in temperature tolerance, or differences in the average individual tolerances between geographically distinct populations, arises due to individual variation. This variation in temperature tolerance of an organism represents both adaptation (a distinct genotype) and phenotypic plasticity, or the range of phenotypes possible for a single genotype, which can be either fixed or variable over an individual's lifespan (sorte 2013)

“These collective effects of individual variation in thermal tolerance can, therefore, have important implications for vulnerability of populations and species to both short-term extreme heatwaves and long-term gradual warming (Bennett et al., 2019)” (McKenzie et al., 2021, p. 1537)

“The effect of higher temperatures on species’ distribution and abundance includes range shifts, population collapses, local extinctions, and phase shifts [5–11” (Gardiner et al., 2010, p. 1); “These patterns emerge from the combined responses of populations to increasing temperature throughout the species’ geographic range” (Gardiner et al., 2010, p. 1)

“Consequently, comparing the effects of temperature increases in different populations is essential for generating robust predictions about the impact of global warming on animal communities at large spatial scales” (Gardiner et al., 2010, p. 1); “Understanding the ecological effects of intraspecific variation is important for models predicting the consequences of biodiversity loss and rapid trait change19,2” (Des Roches et al., 2018, p. 57)

“For example, geographic range size is often assumed to be inversely correlated with extinction risk from climate change, because large geographic ranges are assumed to stem from a broad environmental tolerance at the species level. But in some species, genetic subdivision may produce a collection of locally adapted populations whose environmental niches are narrower than the species as a whole” (Kelly and Griffiths, 2021, p. 33); “A 10-generation selection experiment revealed that heattolerant phenotypes observed in low-latitude populations could not be achieved in high-latitude populations, through either acclimation or selection; and many populations plateaued in their responses to selection, suggesting that standing variation had already been depleted. These experiments demonstrated that broad geographic ranges do not necessarily imply low extinction risk in every population of a widely distributed species.” (Kelly and Griffiths, 2021, p. 33)

As mean and extreme temperatures increase in marine systems, the likelihood that a given population persists is partly related to the physiological capacity of organisms to tolerate elevated temperatures (sorte 2011)

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“At a geographic scale, variation in thermal tolerance is expected to be structured by large-scale environmental gradients and may reflect both plastic responses and underlying genetic diversity (Bennett et al., 2019).” (McKenzie et al., 2021, p. 1548); **“Local adaptation to thermal gradients could cause populations in different parts of the range to respond differently” (Gardiner et al., 2010, p. 1)**

Natural environments are often heterogeneous, characterized by strong spatial variation in both abiotic and biotic factors. Persistent environmental gradients may impose divergent selection, such that populations evolve differences in morphology, physiology, behavior, or life history that provide a fitness advantage under those local conditions. (Sanford and Kelly)

For species with broad geographic ranges, adaptive differentiation among populations can generate a variety of spatial patterns, ranging from countergradient variation across a latitudinal gradient (Conover et al. 2006, 2009) to more complex geographic mosaics ofadaptation (Thompson 1999).

Local adaptation to thermal gradients can cause populations in different parts of the geographic range to exhibit different responses to temperature variation [12–18].” (Gardiner et al., 2010, p. 1); “nature, the generation of intraspecific variation can occur through a variety of mechanisms, including, local adaptation, artificial selection, parental conditions and phenotypic plasticity4” (Des Roches et al., 2018, p. 57)

“When generated by evolutionary mechanisms, intraspecific trait variation can reflect microgeographic adaptation, divergent selection and even incipient speciation26.” (Des Roches et al., 2018, p. 57)

## Regions/edges

The temperature tolerances of individuals in geographically separated populations of a single species can be used as indicators of each population's potential to persist or become extinct in response to climate change. (sorte 2011)

Adaptation to local environmental conditions plays a fundamental role in the generation and maintenance of biodiversity (Levene 1953; Gavrilets 2003), the contraction and expansion of species geo- graphical ranges (Kirkpatrick & Barton 1997) and the ecological and evolutionary dynamics of species interactions (Kaltz & Shykoff 1998).

In addition, because local adaptation measures the match between adaptive genetic variation and environmental variation, its magnitude depends on the interaction among evolutionary forces such as selection and gene flow (Kawecki & Ebert 2004) such that quantifying levels of local adaptation may provide important insight into the relative strengths of these evolutionary forces (Blanquart 2013)

Because ectotherms can acclimate (phe- notypically) and adapt (genetically) to different tempera- tures (Angilletta 2009), there is a general expectation that optimal and critical temperatures will reflect, to some extent, the environmental temperatures an ectotherm expe- riences throughout its geographical range (payne 2016)

Comparative and experimental studies support this expectation, with Topt shown to correlate positively with mean environmen- tal temperatures (Frazier, Huey & Berrigan 2006; Deutsch et al. 2008; Huey et al. 2012), and critical temperatures to correlate with latitude (Addo-Bediako, Chown & Gaston 2000; Sunday, Bates & Dulvy 2011). (payne 2016).

“At a geographic scale, variation in thermal tolerance is expected to be structured by large-scale environmental gradients and may reflect both plastic responses and underlying genetic diversity (Bennett et al., 2019).” (McKenzie et al., 2021, p. 1548);

“Tropical species also live closer to their upper thermal limits (Comte & Olden, 2017), such that there would be less thermal margin for standing variation in tolerance to persist in tropical latitudes.” (McKenzie et al., 2021, p. 1548)

“For example, the optimal thermal temperature of Pacific salmon populations varies in direct relationship with their historically experienced river temperatures [15]. (Gardiner); “Geographic range differences among the study species may also contribute to differences in thermal tolerance” (Gardiner et al., 2010, p. 11)

Such macro-ecological patterns are hypothesized to reflect both genetic adaptation to higher temperatures characteristic of lower latitude, and/or plastic adaptation to broader temperature ranges experienced at higher latitudes (termed the climatic variability hypothesis; [25]). 2.

Innate genetic responses should correlate with mean environmental temperature [23], while phenotypic plasticity (or performance breadth) should correlate with the amplitude of thermal variability [24] (following the climatic variability hypothesis [25]).

Studies of porcelain crabs [26,27] and tropical lizards [28] have shown some support for these hypotheses.

Those results imply that warm-adapted taxa from lower latitudes, particularly ectotherms, are most threatened by further increases in temperature because (i) their innate acute thermal limits (LD50 values) lie close to current environmental thermal maxima, and (ii) they have only limited ability to modify heat tolerance through plasticity [6]. 2.

The two critical assumptions of the climate variability hypothesis are that there is a gradient between latitude and thermal variability, and that there is a match between this cline and thermal physiological breadth of a taxon [25].

he climate variability hypothesis (CVH; Janzen, 1967; Stevens, 1989) posits that thermal tolerance, the ability of an organism to withstand exposure to high temperatures, should correspond to the mean temperature experienced by a population whereas phenotypic plasticity should evolve in response to variability in the thermal environment.

This hypothesis has accumulated support over time, especially in terrestrial and freshwater systems (Deutsch et al., 2008; Sunday, Bates, & Dulvy, 2010), but still lacks robust experimental validation in the marine realm. 7.

Other studies where genetic and plastic factors could be separated also did not show a correlation between latitude and thermal breadth (e.g. in amphibians [50] and in fruit flies [51]), suggesting that the climatic variability hypothesis might not explain the evolution of latitudinal gradients in thermal tolerance in all species and that its generalization to explain such a strong macro-ecological pattern is premature. 2.

The *climate variability hypothesis* suggests that thermal tolerance breadths of populations are correlated with climatic variability (Janzen 1967; Gaston et al. 2009). Therefore, populations that experience a narrow range of climatic conditions are expected to have narrow thermal tolerance breadths optimized to perform under a limited range of conditions (i.e. thermal specialists, stenotherms); whereas species that experience increased climatic variability are expected to contain widened thermal tolerance breadths (i.e. thermal generalists, eurytherms; Gaston et al. 2009; Rummer et al. 2014). Alternatively, the *climate extremes hypothesis* suggests that extreme climatic events are more important agents of selective pressures than overall temperature variability (Pither 2003).

it has long been recognized that geographically separated populations of animals can exhibit similar rates of respiration or growth in their native environments, despite experiencing vastly different temperatures (Bullock 1955). However, when animals from distant portions ofa geographic range are acclimated at a common temperature in the laboratory, populations from cooler environments often exhibit higher rates of respiration. Although such metabolic compensation may often reflect physiological acclimatization (i.e., phenotypic plasticity), in other cases, fixed genetic differences among populations appear to make a major contribution to this countergradient pattern (Somero 2005, 2010).

“At a larger spatial scale, dispersal drives colonisation of novel habitats and impacts biogeography2. Dispersal within meta-populations determines rates of gene flow between individual populations and influences genetic variation and adaptation to different environments3” (Wu and Seebacher, 2022, p. 2)

“Greater variation within and among populations can buffer negative effects of climactic stressors and reduce the overall risk of negative effects on stability of the species.” (McKenzie et al., 2021, p. 1549); “This effect does not require that variation is heritable, just that structured variation exists (Bolnick et al., 2011; Moran et al., 2016).” (McKenzie et al., 2021, p. 1549)

“Thermal optima could be locally adapted to match the thermal environment, such that populations from warmer locations outperform populations from cooler locations at higher temperatures, but populations from cooler locations outperform populations from warmer locations at cooler temperatures” (Gardiner et al., 2010, p. 1).

Recent studies suggest tropical species may be more vulnerable to climate warming because average or maximum temperatures in their natural habitat are already closer to those that maximize physiological performance in the lab- oratory than are those of species from higher latitudes (Deutsch et al. 2008; Huey et al. 2009; Rummer et al. 2014). ; Species living at extreme latitudes (equator and poles) may be particularly sensitive to global warming because they evolved in a relatively stable thermal environment and are expected to exhibit narrow ther- mal tolerance ranges (Tewksbury et al., 2008). The ther- mal range for optimum aerobic performance (thermal optima; Topt) in such species may only span a few degrees, whereas temperate species need to perform over a much wider range of temperatures(Deutsch et al., 2008; Somero, 2010; Nguyen et al., 2011; Sunday et al., 2011).

many species also have large geographi- cal ranges that span temperature ranges that are greater than the projected increase in ocean tempera- ture due to global warming (Munday et al., 2008b). This suggests that populations are acclimatized or adapted to their local thermal environment along a latitudinal gradient. Adaptation to the very narrow equatorial temperature range may cause equatorial populations of reef fishes to be far more sensitive to global warming than populations of the same species from higher latitudes (Rummer 2014)

### Transition statement

**Most marine species have traditionally been viewed as a collection of demographically open populations that are interconnected by high gene flow. This expectation followed from the apparent lack of dispersal barriers in marine systems and the fact that most marine invertebrates and fishes have planktonic larvae that spend days to months in the water column (Grosberg & Cunningham 2001). However, this paradigm of well-mixed marine populations has changed considerably in recent decades as mul- tiple lines of evidence now suggest that many marine populations are less connected than once thought (reviewed by Palumbi 2004, Levin 2006). ;** Restricted connectivity among marine populations may arise from life history, larval behavior, and/or oceanographic features that lead to the retention of offspring near their natal habitats (Dawson 2001, Sherman et al. 2008, Morgan et al. 2009); **The idea that a few successful migrants per generation may be sufficient to maintain genetic homogeneity between two populations is a useful guideline that has been repeated frequently in the literature (e.g., D´ıaz-Viloria et al. 2009, Goldstien et al. 2009, Hellberg 2009). Although this is likely true for neutral molecular markers (the focus of most population genetic studies), it is unlikely to be true for loci under selection (Hedgecock 1986, Slatkin 1987);** This may contribute to the misconception that a few larvae traveling between sites during each generation may be sufficient to maintain homogeneity across the entire genome, thus precluding adaptive divergence.

A growing awareness of restricted connectivity among marine populations has been accompa-nied by a parallel realization that environmental gradients in the sea may be more fine-grained than has been traditionally appreciated

Moreover, there may be no selection pressure to tolerate temperatures outside of what the populations are regularly experiencing. Equatorial populations of marine species are predicted to be especially sensitive to rising temperature because they experience an even narrower temperature range than equatorial populations of terrestrial species (due to the large heat storage capacity of water). In addition, their geographical ranges more closely conform to organismal thermal tolerance limits than the geographical ranges of terrestrial species, especially near equatorial boundaries (Sunday et al., 2011, 2012)

# Marine environments + temperature

**Most marine species occur over broad geographic ranges and exhibit considerable spa- tial variation in key traits.**

“Fishes may be especially vulnerable to global warming because, as ectotherms, their physiology is determined by thermodynamic effects of the surrounding water temperature, which sets their body temperature” (McKenzie et al., 2021, p. 1536); Among abiotic factors that affect living organisms, temperature plays a unique role because of its profound effect on the organisms’ biochemistry and physiology through fundamental physical and chemical constraints [1,2].

Such macro-ecological patterns are hypothesized to reflect both genetic adaptation

“Secondly, there are latitudinal shifts in species distributions, notably a poleward invasion by temperate and sub-tropical species” (Lefevre et al., 2021, p. 1)

While some tropical species appear to live close to their upper thermal limits [23,24], the capacity to acclimate may increase species flexibility to succeed in warmer temperatures [20].

With tropical ocean temperatures predicted to increase up to 3uC over the next 100 years [3,4], investigating the response of tropical marine taxa to higher temperatures has become increasingly important” (Gardiner et al., 2010, p. 2)

It has been suggested that species with higher temperature tolerances will be better able to cope with global warming (Calosi et al., 2008) or, conversely, that more warm-adapted species will be at a disadvantage because they tend to live closer to their absolute tolerance limits (Stillman and Somero, 2000; Somero, 2005, 2010; Compton et al., 2007; Bonebrake and Mastrandrea, 2010) and have lower acclimation potentials (Stillman, 2003; Somero, 2005; Stenseng et al., 2005; Ghalambor et al., 2006). (sorte 2011)

At the species level, latitudinal distribution is often positively related to thermal tolerance range, although the implications for responses to climate change are equivocal given that this pattern is often driven by greater variation in lower, rather than upper, tolerance limits (Goto and Kimura, 1998; Gaston and Chown, 1999; Addo-Bediako et al., 2000; Kimura, 2004). (sorte 2011).

## Physiology

“The energetic demands of ectothermic organisms increase with temperature and activity, and must be met by an adequate supply of oxygen (O2) and food” (Deutsch et al., 2020, p. 557)

As mean and extreme temperatures increase in marine systems, the likelihood that a given population persists is partly related to the physiological capacity of organisms to tolerate elevated temperatures (Hutchins, 1947; Newell, 1969, 1979). Temperature clearly affects species' distribution patterns: a strong relationship between upper temperature tolerance and maximum habitat temperature has been demonstrated for many species (sorte 2011)

At a minimum, physiological survival requires that the supply of energy matches the maintenance costs of an organism in a resting state (Deutsch et al., 2020, p. 557); “Metabolism shapes the ecosystem role of organisms by dictating their energy demand and nutrient recycling potential.” (Moffett et al., 2018, pp. -)

“Additional energetic costs are incurred by the growth and activity required for ecological survival, which depend on lifestyle and ecological niche and typically increase energy expenditure several-fold above resting rates8,” (Deutsch et al., 2020, p. 557); “A third component of the energetic balance of an organism is the O2 needed to fuel growth and essential ecological activities” (Deutsch et al., 2020, p. 557)

For coral reef fishes, rising ocean temperatures may not be immediately lethal (Mora & Osp?ına, 2001), but could have significant impacts on individual perfor- mance that will ultimately affect population demogra- phy and biogeographic distributions (Munday et al., 2008b; Nilsson et al., 2009). For example, an increase in average temperature of 2–3 °C significantly com- promises growth and reproduction of some species (Munday et al., 2008a; Donelson et al., 2010; Pank- hurst & Munday, 2011; Rushworth et al., 2011; Zarco- Perell?o et al., 2012). (Rummer 2014)

Teasing apart the relative demand of cellular repair and growth would require measurements of the proportion of SMR spent by separate physiological processes.” (Wootton et al., 2022, p. 1185)

“These observations appear to support the life-history-based ‘optimisation’ explanation for TSR with a reproduction-growth trade-off at its core” (Wootton et al., 2022, p. 1185); “Higher temperatures lead to faster developmental rates and earlier maturation in many ectotherms (Berrigan & Charnov, 1994; Forster & Hirst, 2012). Naturally, an earlier onset of reproductive allocation is expected to divert energy away from growth” (Wootton et al., 2022, p. 1185); “We note that this reproductive allocation is not only a direct expenditure on gonads but also includes other indirect costs of reproduction such as migration, reproductive behaviours and competition (Watson et al., 1998).” (Wootton et al., 2022, p. 1185)

“All else being equal, an earlier onset of reproduction is advantageous because it increases an individual's chance to reproduce (Cole, 1954). However, earlier reproduction and a resultant smaller adult body size typically means lower fecundity later in life. One explanation for TSR-type growth could be that size-specific fecundity increases later in life at colder temperatures and hence the risks of delayed maturation are compensated for by higher overall reproductive output in these conditions (Arendt, 2011).” (Wootton et al., 2022, p. 1185)

“Another adaptive pathway could lie in evolved responses to shorter lifespans in warmer waters. Reductions to longevity at higher temperature can occur through direct (e.g. oxidative stress: Monaghan et al., 2009) and indirect (e.g. increased predation: Walker et al., 2020) processes, and involve the expression of early maturation or increased reproductive allocation in response to reduced lifetime reproductive opportunity (Kozlowski, 1992” (Wootton et al., 2022, p. 1185)

Rather, they more likely reflect an adaptive metabolic response to temperature-induced changes in community structure due to shifting predation rates or faster developmental rates (Clarke & Fraser, 2004).” (Wootton et al., 2022, p. 1185)

“Physiology can underlie movement, including short-term activity, exploration of unfamiliar environments, and larger scale dispersal, and thereby influence species distributions in an environmentally sensitive manner.” (Wu and Seebacher, 2022, p. 1)

## Thermal performance curves

In studies with ecological applications, TPCs typically quantify whole-organism perfor- mance (e.g. speed, stamina, feeding rate, or growth) or some- times fitness proxies (e.g. reproductive output) because such integrative, higher level, traits are more directly related to eco- logical performance than are lower level ones such as enzyme activity. (Sinclair 2016)

for ectotherms, environmental temperature has a profound influence on physiology and fitness. The thermal sensitivity of ectotherm performance is often described by a thermal performance curve, which increases with temperature to a maximum (the temperature at maximum performance is defined as the optimum temperature, Topt), and declines at higher temperatures.

“A TPC can then identify a thermal optimum, the thermal range over which performance is near to optimal (thermal breadth), and temperature thresholds for alterations in performance (Figure 1) (Currie & Schulte, 2014; Pörtner et al., 2010; Schulte et al., 2011; Wang & Overgaard, 2007).” (McKenzie et al., 2021, p. 1538).

“In water breathing animals, such as fish, a key mechanism affecting performance with increasing temperatures is aerobic capacity.” (Gardiner et al., 2010, p. 2)

“Thermal optima of some ectotherms are finetuned to their local thermal environment” (Gardiner et al., 2010, p. 11)

“Performance curves based on AAS have been used to interpret declines in species population abundance (Pörtner & Knust, 2007), failures of reproductive migrations (Eliason et al., 2011), how optimal habitats change with warming (Deutsch et al., 2015), and why particular species may be invading new areas (Marras et al., 2015” (McKenzie et al., 2021, p. 1539)

“Whether warming oceans will shift the distributions of tropical marine species polewards depends strongly on the metabolic capacity of populations to keep pace with increased oxygen demand” (Gardiner et al., 2010, p. 12)

# Conservation importance – move most to discussion

Characterizing patterns of thermal adaptation and determining their underlying causes are, therefore, directly related to our ability to predict vulnerability and responses of the biota to climate change (Moran, Hartig, & Bell, 2016; Sorte, Jones, & Miller, 2011) 7.

These models assume that every population ofa species has the same environmental niche and may underestimate extinction risk in species with strong local adaptation, where individual populations have a narrower range of tolerances than the species as a whole (Figure 5). (Sanford and Kelly); Such models typically assume that the association between the environment and a species’ abundance (i.e. its niche) does not vary across the species’ geographical range and will remain stable in the future (but see Kear- ney et al., 2009). However, spatial variation in environ- mental tolerances is observed across many species’ ranges, demonstrating local niche differentiation (Banta et al., 2012; Kelly et al., 2012) (O’Brien 2017)

Ignoring variation in a species’ ecological niche within populations, or between populations across its geographical range, will have two contrasting conse- quences: (i) we may overestimate the geographical dis- tribution of a species if tolerances are assumed to be constant throughout the species’ range (i.e. that all pop- ulations can tolerate all currently occupied conditions: Hampe, 2004; Kelly et al., 2012); and (ii) we may under- estimate the potential for species to persist through evolutionary change, where extinction would be pre- dicted based on current distributions (Davis et al., 2005; Kearney et al., 2009; Hoffmann & Sgr?o, 2011).

Understanding and incorporating variation in traits is therefore important for basic science, for making predictions about global change impacts, and for managing species affected by global change (Sinclair 2016)

**Addressing spatial patterns of local adaptation in the sea is central to advancing our un- derstanding ofcommunity ecology, climate change impacts, and the spatial management of marine populations.**

“This then has far-reaching consequences. If broad functional variation among individuals increases the stability and resilience of a species in the face of environmental stressors, such as warming, this can stabilize the species’ ecological functions and, in turn, stabilize overall community and ecosystem function (Bolnick et al., 2011; Mimura et al., 2017; Pacifici et al., 2015).” (McKenzie et al., 2021, p. 1537)

“The effect of higher temperatures on species’ distribution and abundance includes range shifts, population collapses, local extinctions, and phase shifts [5–11” (Gardiner et al., 2010, p. 1)

“Their [Nilsson GE, Crawley N, Lunde IG, Munday PL (2009) Elevated temperature reduces the respiratory scope of coral reef fishes. Global Change Biol 15: 1405–1412.] results predict rising sea temperatures will alter reef fish community structure by causing more substantial declines in cardinalfish populations than in the damselfish populations. Deleterious effects of rising temperature on aerobic performance has already led to population collapses and ecosystem shifts in polar and temperate regions [9], and similar effects might be expected to occur in tropical marine systems” (Gardiner et al., 2010, p. 2)

“Much of our current approach to making these predictions is based on studies that take subsets of communities from a single ecosystem, expose them to elevated temperature over relatively short periods of time (i.e., within the lifespan of some constituent organisms), and gauge ecological responses (Shurin et al. 2012, Yvon-Durocher et al. 2012)” (Moffett et al., 2018, p. 2318)

“Regardless of the mechanisms underlying the trait change, the ecological outcome suggests that ignoring predictable variation in metabolic scaling traits can vastly overestimate consumer population energy demand and nutrient cycling and may ultimately underestimate the scope for persistence under future warming” (Moffett et al., 2018, p. 2323)

In aquatic systems, comparisons of geographic variation amongst conspecific populations has predominantly focused on polar and temperate climates, and counter-gradient patterns have often been detected [22,23].

Valladares,

# Methods

“Energetics and aerobic energy (ATP) production are the most frequently recognised physiological constraints of movement1” (Wu and Seebacher, 2022, p. 2)

“The AAS is proposed to be of ecological significance because it defines the upper limit for oxygen allocation by a fish to sustain aerobic activities such as foraging, digestion, tissue deposition, migration, reproduction (Claireaux & Lefrançois, 2007; Farrell, 2009; Fry, 1971; Pörtner, 2010; Schulte, 2015)” (McKenzie et al., 2021, p. 1538)