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COMPLIMENTARY/POSTER SESSION PAPER

Drivers of Intraspecific Variation in Thermal Traits and Their Importance for Resilience to Global Change in Amphibians

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Synopsis Intraspecific variation can be as great as variation across species, but the role of intraspecific variation in driving local and large-scale patterns is often overlooked, particularly in the field of thermal biology. In amphibians, which depend on environmental conditions and behavior to regulate body temperature, recognizing intraspecific thermal trait variation is essential to comprehensively understanding how global change impacts populations. Here, we examine the drivers of micro- and macrogeographical intraspecific thermal trait variation in amphibians. At the local scale, intraspecific variation can arise via changes in ontogeny, body size, and between the sexes, and developmental plasticity, acclimation, and maternal effects may modulate predictions of amphibian performance under future climate scenarios. At the macrogeographic scale, local adaptation in thermal traits may occur along latitudinal and elevational gradients, with seasonality and range-edge dynamics likely playing important roles in patterns that may impact future persistence. We also discuss the importance of considering disease as a factor affecting intraspecific variation in thermal traits and population resilience to climate change, given the impact of pathogens on thermal preferences and critical thermal limits of hosts. Finally, we make recommendations for future work in this area. Ultimately, our goal is to demonstrate why it is important for researchers to consider intraspecific variation to determine the resilience of amphibians to global change.

Introduction

Intraspecific trait variation (phenotypic trait variation within a species) can be more pronounced than variation across species (Albert et al. 2010; Des Roches et al. 2018). Yet, the mechanisms that drive intraspecific variation have historically received little attention in comparison to research that explores phenotypic differences between species (Des Roches et al. 2018). This is notably true for the field of thermal biology, where the majority of studies focus on interspecific variation in thermal traits—even though temperature is considered a significant abiotic factor driving the biology, ecology, and evolution of species and determining why a species lives where it does (Huey and Stevenson 1979; Overgaard et al. 2014; Nowakowski et al. 2018). In ectothermic organisms like amphibians, which rely on environmental conditions and behavior to regulate body temperature, understanding intraspecific variation in thermal traits is crucial for gaining a comprehensive understanding of how global change impacts populations. While depending on environmental temperatures for thermoregulation may be energy efficient, it renders amphibians especially vulnerable to the effects of climate change, including rising temperatures and increased temperature variability (Deutsch et al. 2008; Bodensteiner et al. 2020).

Amphibians exhibit a variety of climate-relevant traits that researchers examine to identify temperatures that optimize or limit performance and can inform on the consequence of changing temperatures to amphibian physiology (Huey and Stevenson 1979; Llewelyn et al. 2016; see Table 1). Thermal tolerances, measured as critical thermal limits, are an indication of the maximum (CT_{max}) and minimum temperature (CT_{min}) an organism can survive within and can be a useful metric to understand distributional changes and extinction risk (Angilletta et al. 2002;

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Table 1 Climate-relevant thermal traits and their ecological relevance.

Thermal trait	Term	Abbreviation	Alternative terms or abbreviations used in literature	Description of term and ecological relevance	Example ref(s). showing how thermal trait can relate to species' distribution forecasting
Thermal tolerance	Critical thermal maximum	CT_{max}	Upper thermal limit (*UTL*)	Maximum temperature an individual can survive within. Can inform on distributional range when examined in correlation with environmental temperatures.	Diamond et al. (2012); Kellermann et al. (2012); Sunday et al. (2019)
	Critical thermal minimum	CT_{min}	Lower thermal limit (*LTL*)	Minimum temperature an individual can survive within. Can inform on distributional range when examined in correlation with environmental temperatures.	Sunday et al. (2019)
	Warming tolerance	*WT*		The temperature range between CT_{max} and current or predicted environmental temperature. Can inform on the amount of warming that can occur before lethal temperatures are reached.	Deutsch et al. (2008); Gerick et al. (2014)
	Acclimation response ratio	*ARR*		The acclimation capacity of a thermal trait, predominantly calculated with thermal tolerances, and informs on the change in thermal tolerance detected with a change in acclimation temperature.	Barria and Bacigalupe (2017); Enriquez-Urzelai et al. (2020); Ruthsatz et al. (2022); Cicchinoet al. (2023a)
Thermal performance	Thermal performance curve	*TPC*		Curve describing performance over a temperature gradient. Performance is ideally measured as a fitness trait, but often an indirect fitness trait is measured as a fitness proxy. Informs on how performance will change spatially and temporally with variable environmental temperatures.	Clusella-Trullas et al. (2011); Ruiz-Aravena et al. (2014)
	Thermal optimum	T_{opt}	T_o	The temperature at which a given trait reaches maximum performance (P_{max}). Informs on the environmental temperature where the trait measured or fitness is at its highest.	Clusella-Trullas et al. (2011)
	Thermal safety margin	*TSM*		The temperature range between T_{opt} and the current or predicted environmental temperature. Informs on the amount of warming that can happen until a decrease in performance or fitness is seen (small TSM's means a slight increase in environmental temperature will decrease performance, large TSM's mean the species has more buffer from warming). It should be noted that some studies calculate this as T_{opt} - T_e.	Deutsch et al. (2008); Huey et al. 2009; Gerick et al. (2014); Sunday et al. (2014)

Table 1 Continued

Thermal trait	Term	Abbreviation	Alternative terms or abbreviations used in literature	Description of term and ecological relevance	Example ref(s). showing how thermal trait can relate to species' distribution forecasting
	Operative temperature	T_e	Often used as a proxy to body temperature (T_B)	The temperature(s) that an individual experiences within their natural environment. Can inform on the actual temperature's species will need in their environment when microhabitats are considered (and not solely based on average air temperature).	Camacho et al. (2015)
	Optimal temperature range	B_{80}	T_{br}, P_{br}, P_{80}	The range of temperatures where performance is above 80% of the maximum performance. This range of optimal temperatures may be used in place of T_{opt}.	
Thermal preference	Temperature preference	T_{pref}	T_p	The environmental temperature an individual will select to reside in. Informs on the thermoregulatory behavior of species in the wild.	Ruiz-Aravena et al. (2014)
	Temperature selection	T_{sel}		A term to describe the temperature range an individual will reside in that is non-preferential but chosen due to experimental design (for example, an individual may choose to reside on one side of a thermal gradient to avoid extreme temperatures on the other side of the gradient, but this may not reflect a true preference). May inform on the thermoregulatory behavior of species in the wild when considering experimental methodology.	Navas et al. (2021); Delgado-Suazo and Burrowes (2022)
	Temperature preference range	T_{set}	$T_{set(80)}$	A range of environmental temperatures an individual will select to reside in. Informs on the thermoregulatory behavior of species in the wild.	

Climate-relevant thermal traits that researchers use to examine species' thermal niches, common abbreviations found throughout the literature, descriptions of terms and their ecological relevance, and examples of studies showing how thermal traits can inform on species responses to climate change.

Kellermann et al. 2012; Khaliq et al. 2023). Thermal performance is measured by quantifying a relevant trait across temperatures and creating a thermal performance curve (TPC), and identifies at what temperature(s) fitness (or indirect fitness) is optimal (T_{opt}) (see Sinclair et al. 2016 for further discussion). Temperature preference (T_{pref}) or temperature selection (T_{sel}; Navas et al. 2021), which allow ectotherms to control body temperature by moving to suitable microclimates, is often quantified to examine thermoregulatory behavior and can inform on how behavior will affect vulnerability to climate change. Temperature preference can aid or buffer natural selection because it modulates how often individuals are exposed to raw environmental conditions, and hence selective pressures (Bogert 1949; Muñoz and Bodensteiner 2019). While broad trait

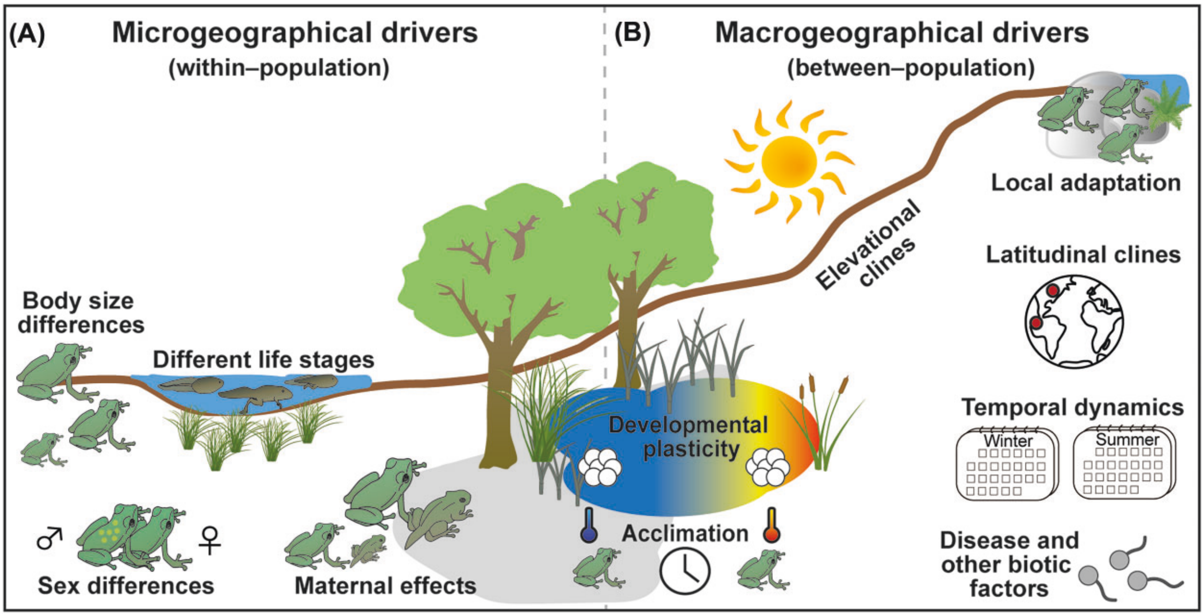

Fig. 1 Micro- and macrogeographical drivers of intraspecific thermal trait variation in amphibians. Intraspecific variation in thermal traits can be found at (**A**) small, microgeographical scales (within-population) and across (**B**) large, macrogeographical scales (between populations) and may be caused by multiple drivers. For example, differences in body size, life stage, and sex can all contribute to variation found within a single population. Phenotypic plasticity produced from acclimation, developmental plasticity, or maternal effects may be important contributors to both within and between population variation. Adaptation to local environmental conditions, including differences driven by elevational and latitudinal clines, are important spatial drivers when considering macrogeographical patterns—as are large-scale temporal dynamics, including seasonal effects, and disease, which may play an important role in intraspecific thermal trait variation. Credits: Frog and tree symbols: Tracey Saxby, Integration and Application Network (ian.umces.edu/media-library); White cattail: Jane Hawkey, Integration and Application Network (ian.umces.edu/media-library); Grasses: Dylan Taillie, Integration and Application Network (ian.umces.edu/media-library).

comparisons are often conducted between species (e.g., Hoffmann et al. 2013; May et al. 2019; Bennet et al. 2021; Pottier et al. 2022; DuBose et al. 2024; Pottier et al. 2024; Ruthsatz et al. 2024), ignoring variation within a species may result in inaccurate predictions of climate change impacts.

Intraspecific variation is often discussed in terms of macrogeographical patterns, such as latitudinal or elevational gradients that drive temperature variation to which local populations are exposed (Phillips et al. 2016). These large-scale spatial and temporal dynamics (e.g., seasonal variation) may cause between-population differences in thermal traits (Fig. 1). Yet, thermal conditions found in and across microhabitats at a smaller, local scale may also drive intraspecific thermal trait variation within a population (Fig. 1). Microgeographical spatial and temporal thermal effects have been shown to result in adaptive differences in thermal performance within a single population (Blanckenhorn 1991; Kawecki and Ebert 2004; Blanquart et al. 2013; Richter-Boix et al. 2015), but receive little attention compared to large-scale patterns (Phillips et al. 2016). Here, we aim to highlight the drivers of micro- and macrogeographical intraspecific thermal trait variation in amphibians. We examine the drivers of intraspecific variation in thermal tolerance, thermal performance, and temperature preference because these traits can provide key information on how temperature may restrict an amphibian's current and predicted distribution, informing on species vulnerability, evolutionary trajectories, and resilience under future climate change scenarios (e.g., Sunday et al. 2011, 2019; Claunch et al. 2023; also see Table 1 for information on other climate-relevant metrics). Second, we make recommendations for future work in this area. Ultimately, our goal is to demonstrate why it is important for researchers to holistically consider intraspecific variation to determine the resilience of amphibians to global change.

Methods

We surveyed the literature by searching Google Scholar with the following keywords: "intraspecific variation" or "within-species variation" AND "amphibian" AND either "thermal biology," "thermal preference," "temperature preference," "thermal performance," or "thermal tolerance." For a more comprehensive review of references on ontogeny, please see Bodensteiner et al. (2020) that may contain additional literature on developmental plasticity. For macrogeographical drivers (i.e., local adaptation, elevational clines, latitudinal studies, temporal dynamics, and range-edge dynamics), we only included studies where it was apparent that thermal traits from more than one population of a given species were examined. This means that some studies may have focused on interspecific variation but in doing so, had included two populations of a single-species, and thus, the study was included here. Please note that this was not intended to be a comprehensive review, but to highlight the importance of considering intraspecific thermal trait variation in amphibians.

Microgeographic sources of intraspecific variation

Intraspecific variation within a population or across a small geographical area is important when considering that this is the scale relevant to gene flow and dispersal in amphibians. Although a common assumption is that high rates of gene flow in small areas will prevent local adaptation, fine-scale patterns in thermal environments are important for generating phenotypic variation for selection to act upon (see Richardson et al. 2014 for review and discussion on microgeographical adaptation).

Of the relatively few studies that examine thermal trait variation at fine spatial scales, work has focused on intraspecific variation in critical thermal limits and temperature preference in adult herpetofauna (e.g., Muñoz et al. 2014; Bestion et al. 2015; Gilbert and Miles 2017; Goodwin et al. 2019; Herrando-Pérez et al. 2019; Rivera-Ordonez et al. 2019; von May et al. 2019; Percino-Daniel et al. 2021; Ohmer et al. 2023) (see Supplementary Table S1 for studies on amphibians). However, physiological differences between life stages and sexes, varying body sizes, or due to phenotypic plasticity can drive phenotypic differences that can contribute to resilience to changing conditions.

Ontogeny

Thermal physiology can vary across life stages and sexes, and there are often strong patterns associated with body size, although the mechanisms driving these relationships are still debated (Bodensteiner et al. 2020; Verberk et al. 2021; Gunderson 2024). When considering ontogeny, ectothermic organisms may experience "critical windows" of heightened likelihood to phenotypic change that can drive intraspecific variation, including susceptibility to thermal stress during development (Mueller 2018). This may be the result of aerobic demands at different life stages due to morphological and/or physiological reorganization (Pörtner 2002; Leiva et al. 2019; Ruthsatz et al. 2024), and/or adaptation to different thermal environments individuals are exposed to (as in the transition from aquatic tadpole to terrestrial juvenile, e.g., thermal adaptation hypothesis; Huey et al. 1999). For example, in Ruthsatz et al. (2022), the authors found that late-stage larvae had higher thermal tolerances than early stage larvae (CT_{max} increased 48%, from ∼25°C to ∼37°C), but this declined slightly as amphibians reached metamorphic climax. This agrees with other work that has found that individuals near metamorphic climax have lower CT_{max} than preceding larval stages (Agudelo-Cantero and Navas 2019; for a review see Bodensteiner et al. 2020), and this period is the most energetically expensive in terms of oxygen consumption (Padilla et al. 2024). Furthermore, sessile eggs are unable to thermoregulate, and larvae confined to more thermally homogeneous aquatic environments may have fewer opportunities to do so, making them more vulnerable to changing conditions (Turriago et al. 2015). Interestingly, a recent meta-analysis found that CT_{max} in amphibians significantly differs between pre- and post-metamorphic life stages, with pre-metamorphic life stages often exhibiting a higher CT_{max} (e.g., Ruthsatz et al. 2024). This may be because it is advantageous for egg and aquatic larvae stages to exhibit higher thermal tolerances because they experience limited mobility and often have a smaller body size relative to adults (Ruthsatz et al. 2024).

Sex differences

There may also be sex differences in thermal traits, in which males and females have divergent thermal optima, preferences, and/or critical temperatures. Both growth and development rates at different temperatures (Lambert et al. 2018), as well as the capacity of larvae to plastically respond to changing conditions (Brannelly et al. 2019), can vary between the sexes. A recent meta-analysis of sex differences in thermal acclimation capacity of ectotherms found only marginally greater heat and cold tolerance plasticity in females than males, which may be driven by sexual size dimorphism, but the overall pattern was weak (Pottier et al. 2021).

There is growing evidence that reproductive traits may covary with thermal physiology due to the reciprocal relationship between thermal ecology and mating system dynamics (Leith et al. 2022). For example, Rogers et al. (2007) found that male striped marsh frogs (*Limnodynastes peronii*) had greater acclimation capacity in metabolic enzymes in muscles associated with calling and amplexus than females, which may be linked to reproductive success. Conversely, other studies have found no sex differences in thermal traits in amphibians (Davies et al. 2015; Bókony et al. 2024). If sex differences in thermal traits exist, this may make one sex more vulnerable to heat stress than the other, which could impact reproductive success and the viability of future

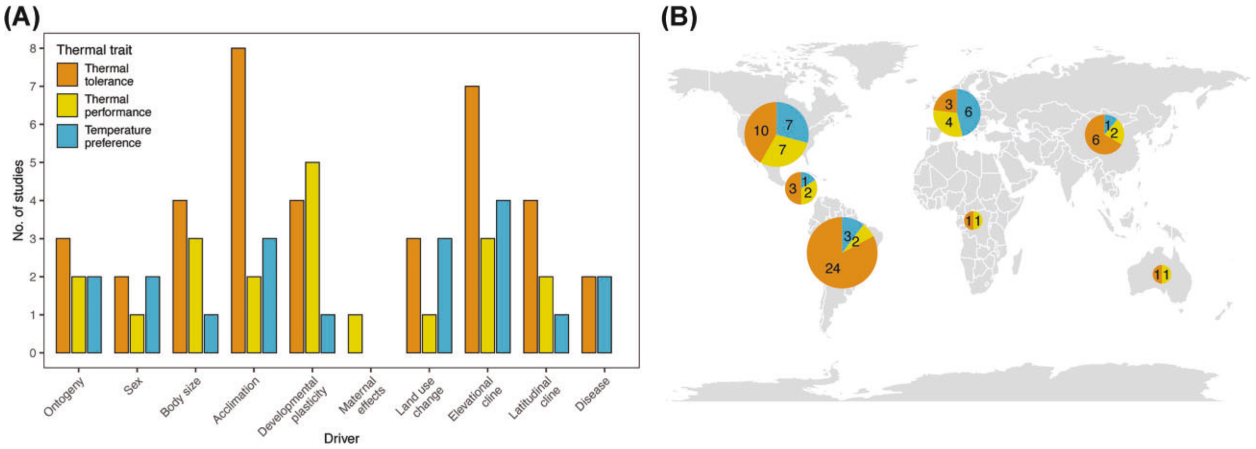

Fig. 2 Studies that examine intraspecific thermal trait variation in amphibians for micro- and macrogeographical drivers. (**A**) The number of studies since the year 2000 that examine within-species variation in thermal tolerance, thermal performance, and temperature preference for each driver discussed here. If a study examined more than one driver and/or thermal trait, it was included as an occurrence in each. (B) Global map showing where studies on intraspecific thermal trait variation have been performed since the year 2000. The location represents where the study species originates and was collected. The size of the pie chart correlates to the number of studies conducted on individual species in each geographic area, with the number of studies for each thermal trait also shown. This is species-level data and includes studies multiple times if they examined a thermal trait on multiple species in that geographical area. Studies included in these figures are found in Supplementary Table S1.

populations (Leith et al. 2022). In a recent meta-analysis in invertebrates, sexual dimorphism in phenotypic plasticity of thermal traits was widespread, but there was a lack of clear systematic patterns (with the exception of female-biased plasticity in cold resistance; Hangartner et al. 2022). Overall, there is a paucity of studies on sex differences in thermal physiology in amphibians (see Pottier et al. 2021; see Fig. 2A), and we encourage future work in this area.

Body size

Body size is intricately linked with thermal physiology in wet-skinned ectotherms such as amphibians, which may be due to physiological constraints governing the relationship between surface area and body mass and corresponding impacts on both heating and water loss rates (Tracy 1976), or life-history optimization (White and Marshall 2023). Body size can be a strong driver of intra- and interspecific differences in critical thermal limits and thermal performance (von May et al. 2019; Ruthsatz et al. 2022; Vidal et al. 2024). This may be the result of inherent physiological differences in oxygen consumption and metabolism between large and small organisms (i.e., physiological differences), or that larger organisms warm or cool at a slower rate than smaller organisms, which can impact measured critical temperatures (i.e., physical differences; Gunderson 2024). Typically, within species, larger individuals demonstrate lower thermal tolerances, but experimental methods can confound large-scale trends, with smaller individuals often being more sensitive to the duration of thermal assays that are used to measure tolerances (Peralta-Maraver and Rezende 2021). However, in amphibians, the opposite trend has also been found, in which larger individuals exhibit higher thermal limits, both within (Barria and Bacigalupe 2017) and across species (von May et al. 2019). Furthermore, thermally sensitive traits like metabolic rate typically scale hypoallometrically with body size (White and Marshall 2023), and this metabolic scaling can be difficult to disentangle from body size effects given that the rate of physiological processes increases with temperature, which can impact development and growth rate.

Temperature also directly affects body size, and there is mounting evidence of organisms decreasing in size in response to climate warming (Sheridan and Bickford 2011; Verberk et al. 2021). In ectotherms, this may be a result of the temperature-size rule (TSR), in which organisms develop quicker and at smaller sizes under warmer conditions (Atkinson 1994), but the physiological and evolutionary mechanisms driving this rule are still debated (Verberk et al. 2021). Indeed, there are examples of population-level reductions in average body size in response to a warming climate in amphibians (Reading 2007; Caruso et al. 2014; Gunderson 2024), but this pattern may also be precipitation-dependent, given the importance of water for amphibian life history and physiology (Sheridan et al. 2022). When considering that morphological traits generally have higher heritabilities (i.e., the potential for a trait to be passed on between generations and hence, the greater response to selection) than behavioral, physiological, or fitness traits (Fisher 1930; Mousseau and Roff 1987), intraspecific variation in body size and its correlation to thermal tolerance has potential to contribute to long-term population resilience to climate change.

While most work has focused on thermal limits, there are comparatively fewer studies that have investigated how ontogeny, sex differences, and body size impact other thermal traits. For example, previous work has found that thermal preference increases with developmental stage in multiple amphibian species, peaking before or near metamorphic climax and then declining rapidly (Floyd 1984; Dupré and Petranka 1985; Wollmuth et al. 1987; Wollmuth and Crawshaw 1988). Similar results were found in newts, with late-stage larvae selecting higher temperatures than early stage larvae (Smolinsk´y and Gvoždík 2009). In addition, body size can impact thermal preference, in which larger amphibians select higher temperatures (Ohmer et al. 2023; Kirsch et al. 2021; Percino-Daniel et al. 2021), or thermoregulate more precisely (Mitchell and Bergmann 2015). Finally, there are only a few studies that we are aware of that have investigated sex differences in thermoregulatory behavior. In newts, gravid females thermoregulate more accurately, but this did not impact egg size (Toufarová and Gvoždík 2016), while male midwife toads carrying eggs prefer higher temperatures than males not carrying eggs (Lange et al. 2022). Overall, ontogeny, sex differences, and body size variation can all lead to widespread intraspecific variation in thermal physiological traits, which may impact a population's responses to changing conditions.

Phenotypic plasticity

Phenotypic plasticity may enable species with complex life cycles, like amphibians, to survive under fluctuating environments (Pottier et al. 2022; Ruthsatz et al. 2022). For example, plasticity in thermal tolerance—where an individual's thermal history can alter thermal limits—has been suggested as a strategy to mitigate the effects of extreme heat events (Ruthsatz et al. 2022; Rohr et al. 2018). Yet, it may be insufficient to buffer organisms from the effects of climate change on its own (Gunderson and Stillman 2015; Morley et al. 2019; Pottier et al. 2024).

Whether variation driven by plasticity is examined across a micro- or macrogeographical scale, we contend that it is important to consider the timescale of thermal history. An individual may exhibit a thermal phenotype that has the potential to fluctuate over a short time frame and is reversible (i.e., acclimation), is affected by their developmental environment and is generally non-reversible (i.e., developmental plasticity), or is determined by their parents and grandparents and is a transgenerational effect (i.e., maternal effects). Whether short- and/or long-term thermal history is considered will determine the process behind plasticity and, hence, the potential for the plastic trait to adapt and contribute to long-term species resilience (Bodensteiner et al. 2020). Here, we discuss phenotypic plasticity at fine spatial scales but want to emphasize that plasticity (particularly acclimation; see the temporal dynamics section) can also drive intraspecific variation more broadly and these processes are ultimately occurring across all spatial and temporal scales.

Acclimation on the microgeographic scale

Reversible acclimation in response to temperature changes is common in ectothermic organisms, including amphibians (Gunderson and Stillman 2015; Seebacher et al. 2015). Acclimation can buffer organisms from temperature variability on a short timescale, and greater plasticity in thermal traits may be adaptive under a changing climate. Acclimation responses in amphibians have been demonstrated for many traits, including critical thermal limits (Fan et al. 2021; Carilo Filho et al. 2022), thermal preferences (Hadamová and Gvoždík 2011; but see Fan et al. 2021 for example of no effect on thermal preference), and the thermal sensitivity of water loss rates (Riddell et al. 2018), locomotor performance (Padilla et al. 2019), and metabolism (Gomes et al. 2004; Rogers et al. 2007; Messerman and Leal 2020). In addition, plasticity in thermal traits can vary both between and within species (for a review and meta-analysis, see Seebacher et al. 2015). Acclimation to one stressor may also impact resistance to another; amphibians acclimated to high salinity environments have shown a decreased CT_{max}, indicating a possible trade-off between tolerance of high temperatures and tolerance of stressful environments (Chuang et al. 2022). This bears significance when assessing the impact of anthropogenic pollutants, like road salts and heavy metals, on amphibians as global average air temperatures continue to increase.

One measure of plasticity, the acclimation response ratio (ARR), has been used extensively to compare thermal plasticity between species (Gunderson and Stillman 2015; Seebacher et al. 2015; Morley et al. 2019), but should be considered a useful measure for understanding the level of intraspecific variation in thermal plasticity as well (Barria and Bacigalupe 2017; Enriquez-Urzelai et al. 2020; Ruthsatz et al. 2022). For example, a study on the European common frog found that late-stage larvae exhibited a higher acclimation capacity in

CT_{max} than early stage larvae (ARR of CT_{max} increased almost two-fold, from 0.333 to 0.635; Ruthsatz et al. 2022).

Developmental plasticity

The thermal environment experienced during development can impact the thermal traits of amphibians during subsequent life stages. In amphibians, there is evidence that plasticity in response to temperature during development can lead to shifts in critical temperatures (Mueller et al. 2019; Pottier et al. 2022; Ruthsatz et al. 2022; Ohmer et al. 2023; but see Enriquez-Urzelai et al. 2019), thermal preferences (Ohmer et al. 2023), and the thermal-sensitivity of performance at later life stages (Drakulić et al. 2016; Ohmer et al. 2023). Developmental plasticity in response to a changing larval environment can result in better fitness in the resulting metamorphic environment (Beaman et al. 2016). Thus, elevated levels of plasticity may be adaptive, particularly if that environment changes rapidly (e.g., along an elevational gradient), or may be maladaptive, depending on whether early life environments are predictive of later-life environments (Beaman et al. 2016; Zhang et al. 2023). In a recent meta-analysis across ectotherms, the evidence for strong effects of the developmental environment on critical temperatures in subsequent life stages was weak (Pottier et al. 2022). However, we need additional studies that investigate long-term impacts (beyond the recently hatched/metamorphosed), as well as additional thermal trait metrics (e.g., thermal preference; see Fig. 2A).

Maternal effects

Maternal effects reflect a type of phenotypic plasticity determined by ancestors—where the offspring's phenotype is determined by the phenotype and environment experienced by the parent (or grandparent; Falconer and Mackay 1996). The effects of transgenerational plasticity on thermal physiology in amphibians have seldom been examined, and there remain large gaps in this research area (Fig. 2A).

What studies have found is that the thermal history of parents can have a significant effect on offspring fitness. For example, in the fire-bellied toad (*Bombina orientalis*), mothers that experienced greater environmental temperature variability reduced maternal investment that decreased offspring fitness and thermal performance of sprint speed (Kaplan and Phillips 2006). In reptiles, the thermal environment the mother experienced during pregnancy significantly shifted temperature preferences by $\pm$ 1°C (Paranjpe et al. 2013) and reduced anti-predatory behavior (Lorioux et al. 2013). Even the pregnancy stage at which various thermal environments are experienced (e.g., early or late embryonic growth, etc.) can differentially affect offspring behavior—with offspring exhibiting less exploratory behavior when their mother was exposed to cold conditions during early development compared to late development (Lorioux et al. 2013). Interestingly, thermal maternal effects may even influence the resilience of offspring to disease. In *Daphnia*, research has shown that mothers that experience warmer temperatures produce offspring more resistant to infection and this was consistent across two populations (Garbutt et al. 2014).

The little research that has been conducted in amphibians, and the corresponding research in other ectotherms, points to evidence that maternal effects can have a significant influence on progeny thermal phenotypes. Crucially, transgenerational plasticity can introduce diversity in thermal traits within a population and offer an alternative inheritance mechanism for selection to act upon (Pfennig and Martin 2009). Thus, this type of plasticity may notably facilitate rapid adaptive evolution because maternal effects can be conferred between generations (Agrawal et al. 1999; Plaistow et al. 2006; Allen et al. 2008). When thinking about resilience to climate change and other global stressors (like disease), understanding the role of transgenerational plasticity in determining intraspecific thermal trait variation is fundamental, and yet remains a largely unexplored topic in amphibians (Fig. 2A).

Macrogeographic sources of intraspecific variation

Within-species thermal biology historically received attention at the macrogeographical scale in insect and reptile species and focused on critical thermal limits (see Chown 2001; Hoffmann et al. 2003; and Angilletta 2009 for reviews). Yet, studies examining if large-scale spatial variation can lead to differences between amphibian populations have become more common (for example, see Pottier et al. 2022 and DuBose et al. 2024 for published databases on amphibian thermal limits; Supplementary Table S1).

Local adaptation

Local adaptation occurs if contemporary selective pressures are strong enough to overcome the rate of gene flow and results in individuals with higher fitness in the local environment when compared to individuals from other populations (Richardson et al. 2014). Preliminary work in amphibians has indicated that local adaptation in thermal traits may exist. For example, a study on temperature preference in wood frog tadpoles (*Rana sylvatica*) found evidence for counter-gradient variation, where tadpoles from cooler environments (closed canopy pools) preferred warmer temperatures (Freidenburg and Skelly 2004). Conversely, a study on two tropical species found that tadpoles from populations that experienced warmer environments preferred hotter temperatures and exhibited a higher CT_{max} (Sanabria et al. 2021). Land-use changes may also drive intraspecific thermal trait variation in amphibians (see Nowakowski et al. 2018 for work on how habitat modification drives *inter*specific variation in CT_{max} in amphibians). For example, populations in converted open-forest habitats exhibited a higher thermal tolerance (CT_{max} that was 1.8°C higher; Frishkoff et al. 2015), thermal performance of jumping speed (T_{opt} that was 2.3°C higher; Frishkoff et al. 2015), and temperature preference (T_{pref} that was 2.0°C higher; Rivera-Ordonez et al. 2019) than those in closed forests. Yet, this is not always consistent across thermal traits—Rivera-Ordonez et al. (2019) also found that a shift in thermal preference did not indicate a correlated shift in thermal tolerance.

Importantly, while the studies discussed here and in the sections below use methods that suggest that local adaptation most likely occurred (for example, Freidenburg and Skelly 2004 collected eggs from different ponds and reared in a common environment to remove acclimation and developmental plasticity effects), we were not able to find studies on intraspecific thermal trait variation in amphibians that clearly tested whether differences were due to local adaptation or plasticity. Although we realize the difficulty of such studies for relatively long-lived organisms like amphibians, for local adaptation to be confirmed across populations, reciprocal transplant studies (an experiment where individuals from two or more environments are swapped and fitness is measured to assess relative fitness of each population in their local versus foreign environment) or common garden experiments with maternal effects removed (an experiment where amphibians would be collected from the wild, reared in a common environment for at least two generations to remove transgenerational effects, and then thermal traits are measured) must be performed. Additionally, it would be an oversight to not highlight that researchers should also consider the growing field of bioinformatics as a tool to detect genomic changes linked to local environments (Meek et al. 2023). However, genomic differences detected between populations may be due to non-adaptive or neutral evolution, and we urge that genetic techniques should be combined with experimental approaches to conclude if local adaptation has occurred. Hence, we contend that reciprocal transplant or common garden studies investigating intraspecific thermal adaptation in amphibians should be a research priority. This research would help to disentangle the relative contributions of evolutionary change and plasticity on thermal trait variation, ultimately enhancing our understanding of the mechanisms that can contribute to resilience under global change.

Elevational and latitudinal clines

Macrogeographical variation in environmental temperature can be caused by climate patterns that change with elevation or latitudinal gradients. Much of the current work at this scale tends to focus on investigating if tropical or temperate species exhibit greater thermal breadth (i.e., the temperature range they can survive within). This literature often references Janzen's hypothesis, which posits that temperate species that experience greater seasonal fluctuations should have broader thermal tolerances than tropical species that are exposed to less environmental variability (Janzen 1967). Although initially proposed to explain differences in thermal breadth between species, Janzen's hypothesis has been extended to examine intraspecific variation along elevational clines in tropical amphibians that exhibit broad distributional ranges (i.e., Pintanel et al. 2019; Bovo et al. 2023). Importantly, tropical species may exhibit similar, if not more, intraspecific thermal trait variation than temperate species because spatial complexity in tropical ecosystems may be more multifaceted than temporal variation of temperate climates (Janzen 1967; Llewelyn et al. 2016).

Elevational cline studies in amphibians have largely focused on intraspecific variation in thermal tolerances and thermal breadth, calculated as the range between CT_{max} and CT_{min} (e.g., Delgado-Suazo and Burrowes 2022; Bovo et al. 2023; Cicchino et al. 2023a; Cicchino et al. 2023b; reviewed in Carilo Filho et al. 2022). General trends are consistent with Brett's heat-invariant hypothesis (Brett 1956), which posits that CT_{max} should be more conserved than CT_{min} over elevation and across thermal environments (e.g., Pintanel et al. 2019; Bovo et al. 2023). For example, research on five tropical frog species in Brazil and five tropical frog species in Ecuador found that CT_{max} was more conserved than CT_{min} along an elevational gradient (Pintanel et al. 2019; Bovo et al. 2023; Páez-Vacas and Funk 2024). Yet, evidence also exists for the opposite pattern (where CT_{max} is more variable across elevational clines; e.g., Percino-Daniel et al. 2021; Delgado-Suazo and Burrowes 2022). Research on two different tropical frogs found that CT_{min} was more conserved (Percino-Daniel et al. 2021; Delgado-Suazo and Burrowes 2022), as did a study on tadpoles of two temperate frog species (Cicchino et al. 2023b). Potentially because variation in thermal tolerances seems to be context-dependent and species-specific (as do plastic changes on CT_{max} at different elevations; see Cicchino et al. 2023a), most of the research on intraspecific variation in thermal breadth is not able to conclude if environmental patterns associated with elevation directionally alter thermal breadth. The studies that are available on variation within species provide important data when examining the multitude of hypotheses on thermal tolerance variability across elevation (i.e., Janzen's hypothesis and the climate variability hypothesis, Brett's heat-invariant hypothesis, the cold-variability hypothesis; see Pintanel et al. 2019 and Bovo et al. 2023 for descriptions and context).

Recent literature has also explored if elevational changes can drive intraspecific variation in temperature preference and thermal performance (Enriquez-Urzelai et al. 2018; Trochet et al. 2018; Percino-Daniel et al. 2021; Delgado-Suazo and Burrowes 2022). Counter-gradient variation in temperature preferences (when individuals from cooler environments prefer warmer temperatures compared to individuals originating from warmer environments) was found in tropical frogs (Percino-Daniel et al. 2021; Delgado-Suazo and Burrowes 2022), and in one of the few studies on intraspecific thermal trait variation in a salamander species (Trochet et al. 2018). Overall trends suggest that maximum thermal performance (such as jumping distance or locomotor performance) may show a slight increase with elevation (Navas 1996; Enriquez-Urzelai et al. 2018; Delgado-Suazo and Burrowes 2022). However, the optimal temperature (T_{opt}) for thermal performance appears to be commonly conserved along elevational gradients (e.g., locomotor performance; Navas 1996; Enriquez-Urzelai et al. 2018; and jumping performance; Delgado-Suazo and Burrowes 2022).

Latitudinal studies on intraspecific thermal trait variation are less common in amphibians (Fig. 2A), but also suggest species-specific results. Opposite patterns were found for CT_{max} in temperate (Kim et al. 2022) and tropical frog species (Sanabria et al. 2014; Barria and Bacigalupe 2017). Thermal preference, CT_{min}, and T_{opt} have been shown to increase in populations located at warmer latitudes (T_{opt}: Wilson 2001, T_{pref} and CT_{min}: Barria and Bacigalupe 2017), and while there is some evidence that tropical species demonstrate lower levels of thermal trait plasticity than temperate species (Feder 1978; Feder 1982; Ghalambor et al. 2006), there is also evidence indicating a lack of variation in thermal trait plasticity across latitudinal clines (e.g., Gunderson and Stillman 2015; Riquelme et al. 2016; Simon et al. 2015; Morley et al. 2019).

Temporal dynamics

Disentangling temporal patterns across large-scale elevational and latitudinal clines is difficult and remains relatively unexplored in thermal biology (Giacometti et al. 2024). This is particularly true when examining seasonality as a driver of intraspecific variation in amphibians. Seasonality may be more intense at higher elevations and latitudes, and this may drive variation in climate-relevant traits across this scale. High elevations and latitudes result in shorter seasonal activity windows (i.e., the annual timeframe a species is active for reproduction and growth; Dahl et al. 2012; Mikolajewski et al. 2015; Giacometti et al. 2024). Individuals may optimize physiology and behavior within their seasonal activity window to increase foraging and reproduction, potentially resulting in higher-risk behaviors with fitness trade-offs (Giacometti et al. 2024). Such phenological shifts are commonly documented in amphibians (Todd et al. 2011), and changes have exhibited a strength two to four times greater than responses in other taxonomic groups (Parmesan 2006; Parmesan 2007; Urban et al. 2014). This seasonality may exert strong plastic responses and selective pressures on populations, resulting in adaptation in thermal performance and temperature preference (Enriquez-Urzelai et al. 2018). Additionally, in amphibians that experience multiple seasons across their lives, thermal traits may vary annually when considering plasticity effects and may contribute to long-term resilience differentially depending on seasonal selective pressures. Investigating this will be crucial for enhancing our comprehension of how amphibians will respond to climate change (Giacometti et al. 2024), and these temporal changes need to be considered when predicting species resilience.

Range-edge dynamics

Individuals that reside at the edge of a species range—or when thinking at a microgeographical scale, at the edge of a population—may experience different environmental conditions and constraints than those found at the center of a species range. Although individual fitness is generally thought to be lower at range edges (Kawecki 2008), environmental conditions that drive variation in thermal traits at margins can be just as advantageous, if not more (Granado-Yela et al. 2013; Valladares et al. 2014). Thus, intraspecific variation formed in peripheral populations can contribute to resilience to climate change, particularly if conditions increase plasticity in thermal traits or contribute to directional selection in thermal traits that is favorable under fluctuating conditions and rising temperatures (Rehm et al. 2015). For example, peripheral populations located at lower elevations may experience greater environmental heterogeneity and warmer conditions than those at higher elevations, generating higher within-species thermal tolerances (as found in some amphibian populations: Percino-Daniel et al. 2021; Delgado-Suazo and Burrowes 2022; Cicchino et al. 2023b).

Indeed, marginal populations can play an important role in species persistence under climate change by harboring advantageous phenotypic plasticity (Chevin and Lande 2011) and thermal alleles, and may indicate at what range-edge (trailing versus leading edge) future distributional changes and/or adaptation may occur (Valladares et al. 2014). Differences in thermal preferences between individuals at trailing and leading edges can also be an indicator of dispersal responses to global change. For example, a study in reptiles found that individuals that preferred cooler temperatures dispersed further in warming climates than those that preferred warmer temperatures (most likely to "chase" their optimal environment; Bestion et al. 2015). Hence, recording thermal trait variation at range edges (and at peripheral populations) in amphibians and incorporating these into spatial distribution and mechanistic niche models can inform on how populations may track future climate change.

Considering other abiotic and biotic drivers

It would be unreasonable to ignore the influence that abiotic factors other than temperature can have on driving intraspecific thermal trait variation in amphibians. For example, as wet-skinned organisms, variation in water availability and changes to relative humidity across spatial and temporal scales will influence local phenotypes (Greenberg and Palen 2021; Delgado-Suazo and Burrowes 2022). Additionally, recent studies have found that anthropogenic impacts can be detrimental to intraspecific variation (Stockwell et al. 2003; Miraldo et al. 2016). For example, habitat degradation and landscape connectivity can influence available microhabitats and affect gene flow that may alter thermal traits (Nowakowski et al. 2018). Artificial selection and human-induced regional extinctions can cause declines in genetic diversity (Des Roches et al. 2018). Humans also tend to change environments in ways that make them more uniform, which may lead to strong directional selection that depletes phenotypic and genetic variation.

Biotic factors will most certainly play a role in shaping the thermal biology of populations. Population dynamics, community composition that affect species interactions and food availability, invasive species, and factors like disease can all potentially drive variation in thermal traits. Notably, introduction of invasive species may deplete intraspecific variation simply by affecting population dynamics and potentially reducing abundance. Importantly, because disease is a significant threat to amphibians (Luedtke et al. 2023), we discuss its implications on intraspecific thermal trait variation below.

Disease

In addition to generating population-specific patterns, species-specific thermal biology may moderate the susceptibility of organisms to other global change stressors, like pathogenic infections (Deutsch et al. 2008; Kearney et al. 2009; Rohr and Raffel 2010; Huey et al. 2012; Navas et al. 2013; Sunday et al. 2014; Nowakowski et al. 2018). In amphibians, the fungal pathogen *Batrachochytrium dendrobatidis* (Bd) has caused hundreds of population declines and extinctions worldwide (Skerratt et al. 2007; Scheele et al. 2019), and as both host and pathogen are ectothermic, temperature is a key factor driving susceptibility to disease (Woodhams et al. 2008; Sauer et al. 2020; Cohen et al. 2017). While Bd grows optimally between 15 and 25°C (Piotrowski et al. 2004), there is increasing evidence that Bd can more readily overcome host defenses at cooler temperatures. There are patterns of amphibians declining and pathogen prevalence increasing at the cold end of species distributions, at higher elevations, and at closed canopy sites (Muths et al. 2008; Becker et al. 2012; Sonn et al. 2019; for a review see Haver et al. 2022), and many documented cases of seasonal infection prevalence, with infections peaking during winter/cooler months (Kriger and Hero 2007; Phillot et al. 2013; Wilber et al. 2022). In addition, realistic heat pulses (Greenspan et al. 2017b), access to warm refugia (Waddle et al. 2024), and reduced canopy cover (Roznik et al. 2015) can increase amphibian survival with Bd, but this may only be the case in warm-adapted species.

Just as pressing, and what has received little attention thus far, is understanding the impact of disease on intraspecific variation in climate-relevant thermal traits. Recent work has found that infection can change thermoregulatory behavior (Sherman 2008; Barrile et al. 2021) and restrict thermal tolerances in amphibians (Greenspan et al. 2017a; Siddons and Searle 2021)—potentially increasing risk of diseased populations to climate change by reducing the host's ability to withstand thermal stress. Furthermore, amphibians that prefer warmer temperatures harbor lower Bd infection loads, which can reduce their risk of chytridiomycosis (Sauer et al. 2018). These changes may also result in different evolutionary trajectories of populations impacted by disease if environmental pressures drive selection on disease-determined phenotypical changes to thermal traits.

In some amphibian species, conservation efforts are underway to protect both naive populations and those that are persisting with Bd infections. These populations may also represent the greatest chance of resilience to climate change if they harbor increased thermal tolerances and greater intraspecific thermal trait variation, and particularly if captive breeding programs reintroduce genetically diverse individuals with "hardy" thermal genotypes. Even with these endeavors, it is critical that we better understand population-level effects of disease on thermal biology and, conversely, how intraspecific variation in thermal traits may impact disease resilience. We encourage researchers to consider the importance of elucidating how different genotypes and/or pathogen strains interact with various populations of a given species. Until we can further clarify how disease and thermal biology interact with population-specific traits, we cannot fully comprehend the extent of how disease and climate change will interact and affect species resilience in a changing world.

Expanding intraspecific thermal trait studies to assess resilience

Amphibians are considered one of the most threatened vertebrate groups (Luedtke et al. 2023) and understanding the factors underlying intraspecific thermal trait variation in amphibians and their role in enhancing species resilience to climate change is paramount for the conservation of these vulnerable taxa. By better understanding the drivers behind variation and collectively including them in predictions, we can more accurately plan and implement conservation measures. For example, examining local adaptation across elevational and latitudinal clines can help to isolate regional targets of selection that can help researchers identify the potential of a species to establish in new environments (Campbell-Staton et al. 2018), as well as the potential for evolution in the trait of interest.

A useful method to assess amphibian performance over space and time under different climate scenarios is mechanistic niche modeling (Kearney and Porter 2009; Briscoe et al. 2022; Riddell et al. 2023). We contend that researchers should use these models to include intraspecific thermal trait variation (since they are parameterized using physiological traits) across micro- and macrogeographical scales to assess resilience under global change. For example, incorporating acclimation responses into mechanistic niche models results in more optimistic predictions of amphibian performance under climate change (Riddell et al. 2018; Sinervo et al. 2024). We highlight the following specific areas as topics for future work to contribute to this goal:

- Future investigations should examine the potential implications of sex on amphibian thermal physiology and how it affects sex-biased mortality and population viability.
- Researchers interested in developmental plasticity should prioritize investigating the long-term impacts (beyond the recently hatched/metamorphosed life stage) of different developmental environments on thermal trait expression.
- Future work should focus on identifying how transgenerational plasticity affects progeny thermal phenotypes.
- When considering evolutionary potential and rescue as a means of resilience in amphibians, investigations into thermal trait heritability need to be conducted. Importantly, researchers should also consider how fluctuating environments across micro- and macrogeographical scales change heritability of thermal traits because heritability can be influenced by non-genetic environmental factors that make comparisons across populations, environments, and thermal traits invalid (Houle 1992).
- Reciprocal transplant or common garden studies investigating local adaptation in thermal traits should be a research priority and can help to clarify the respective roles of evolutionary change and plasticity on intraspecific thermal trait variation.
- While plasticity and evolutionary potential have been increasingly incorporated into niche models (Valladares et al. 2014; Duputié et al. 2015; Riddell et al. 2018; Riddell et al. 2023; Sinervo et al. 2024), there is a need to better understand and include the effects of seasonality and range-edge dynamics on within-species thermal trait variation in predictive models.
- Researchers should consider the importance of the interaction between a population and a particular genotype or strain of pathogen to fully comprehend how disease may impact intraspecific thermal trait variation and, subsequently, include the variability of these effects into resilience predictions.
- Lastly, we recognize that it is often unfeasible or impractical to measure all sources of intraspecific thermal trait variation for one species. While striving to gather such data remains a priority, in cases where it is unattainable, we contend that researchers should consider using data imputation to estimate thermal traits based on known relationships (for example, see Pottier et al. 2024) rather than omitting multivariate sources of intraspecific thermal trait variation.

Conclusion

Environmental temperatures fluctuate both spatially and temporally, and discerning patterns within a species amidst these changes is crucial for predicting distributional changes and evolutionary capabilities of organisms responding to changing climates (Williams et al.

2008; Violle et al. 2012; Richter-Boix et al. 2015). Indeed, intraspecific thermal trait variation may be the key to determining a species' capacity for resilience to climate change (Llewelyn et al. 2016). Here, we aim to highlight the small- and large-scale drivers of intraspecific thermal trait variation in amphibians. In doing so, our goal is to underscore the significance of thoroughly realizing spatial and temporal variations in the thermal biology of a species, and to emphasize the importance of integrating these insights into mechanistic niche or species distribution models for a more comprehensive understanding of species resilience to global change.

Author contributions

J.M.C. and M.E.B.O. conceptualized and wrote the manuscript, J.M.C. created the figures and tables, and both authors approved of the final version.

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Supplementary data

Supplementary Data available at *ICB* online.

Conflict of interest

The authors declare no conflict of interests.

Data availability

No new data were generated or analysed in support of this research.

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