

Review

# Ecophysiology of Amphibians: Information for Best Mechanistic Models

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**Abstract:** Several amphibian lineages epitomize the faunal biodiversity crises, with numerous reports of population declines and extinctions worldwide. Predicting how such lineages will cope with environmental changes is an urgent challenge for biologists. A promising framework for this involves mechanistic modeling, which integrates organismal ecophysiological features and ecological models as a means to establish causal and consequential relationships of species with their physical environment. Solid frameworks built for other tetrapods (e.g., lizards) have proved successful in this context, but its extension to amphibians requires care. First, the natural history of amphibians is distinct within tetrapods, for it includes a biphasic life cycle that undergoes major habitat transitions and changes in sensitivity to environmental factors. Second, the accumulated data on amphibian ecophysiology is not nearly as expressive, is heavily biased towards adult lifeforms of few non-tropical lineages, and overlook the importance of hydrothermal relationships. Thus, we argue that critical usage and improvement in the available data is essential for enhancing the power of mechanistic modeling from the physiological ecology of amphibians. We highlight the complexity of ecophysiological variables and the need for understanding the natural history of the group under study and indicate directions deemed crucial to attaining steady progress in this field.

**Keywords:** amphibian diversity; complex life cycles; conservation; modeling; physiological ecology; water and temperature

## 1. Introduction

Amphibians are a group of ecological contrasts. They include some of the most successful and resilient invasive species [1], as well as some of the most susceptible lineages to environmental variation. Given the latter cases, amphibians are often regarded as the most threatened vertebrates, with reports of population decline worldwide [2–4]. The causes of declines are manifold, but the primary drivers are loss and fragmentation of habitat. Also, individual effects and synergisms among climate change, pollutants, presence of alien species, and emerging diseases, are also relevant [5–7]. Because of these extremes, the claim of “high amphibian sensitivity”, which is often invoked in conservation-oriented research (e.g., [8]), underestimates the great diversity in resilience to environmental change that characterizes this group. Amphibians also have complex life cycles in which different life stages use

different—even contrasting—habitats and microhabitats, which should add remarkable difficulty in model elaboration [9–11]. In fact, despite the high diversity of the amphibians (e.g., [1,12]), ecological data on resilience and susceptibility to the above threats are limited to relatively few species, life stages, and environments [13]. It is fundamental to ask why lineages of amphibians differ in sensitivity and resilience to environmental change, and what mechanisms (e.g., physiological or demographic) underlie resilience, when present. Also, we must ask how other ecological aspects relate to (lack of) resilience, geographical distribution, and trait variation (e.g., [14–18]). A leading framework to address these questions relies on ecological approaches known as “mechanistic models” because of their aim to link physiology mechanisms to ecological patterns for various contexts, including patterns of distribution.

Overall, mechanistic models rely on traits assumed (by modelers) to be crucial to the ecology of a given lineage, and models are as good as the traits used to feed them. Then, to model, an abstract fundamental niche must be expressed through tangible features reflecting aspects of the physical environment that delimitate distribution or any other critical ecological parameter. But given the diversity in sensitivity and susceptibility that exists among amphibians, one must ask, among others, if (a) same physiological traits apply to most lineages; (b) the best databases available reflect the more informative traits; (c) the traits refer to relevant life stages regarding sensitivity to critical conditions for a given species; and (d) whether more informative traits are yet to be described. However, this is rarely discussed when making general predictions about the amphibian response to environmental changes (e.g., [15–21]). Therefore, the problem of mechanistic modeling in amphibians requires deeper integration between physiology and ecology, enhanced or revised databases, profound knowledge of natural history and behavior, and ecophysiological work. Ecological modeling is nowadays a highly disseminated family of approaches to which these considerations matter in at least three main contexts. First, the performance of mechanistic modeling peaks only under a thorough understanding of physiological attributes that are relevant at ecological scales. Second, these attributes may be missing in existing databases. The mere existence of good databases of particular variables is practical but does not turn these variables into proper attributes. Also, the scale at which the physical environment is described in popular databases may not suit organismal sensing, even when considering modern downscaling approaches (e.g., [22,23]). Likewise, attributes based on informed physiology for given lineages and related to ecology at proper scales are likely to produce the best forecasting approach [24,25]. Furthermore, most anuran and urodele amphibians undergo significant habitat transitions due to life cycles and growth, thus experiencing different physical constraints, and therefore, may undertake ontogenetic changes in sensitivity to environmental change [26]. Finally, the impact of non-acute responses and environment-derived physiological stress is likely fundamental to this problem, but only case-specific studies are available [27,28].

Because of ecological contrast among amphibian lineages, care is needed before generalizing, and proper generalizations become crucial [29]. For instance, a visionary link between environmental change and amphibian physiology dates to the 70s, when Beebee [30] proposed a mechanistic hypothesis to explain the decline of the natterjack toads in Britain based on habitat modification and interaction with a competitor (*Bufo bufo*). Since then, attempts have been made to connect specific types of amphibian sensitivity to environmental alterations, and to expand individual effects to population dynamics [31] or impacts on reproductive potential or survival [32]. However, forecasting approaches proliferate in several ecological contexts even if basic premises are usually poorly tested [33]. Thus we judge that room for improving modeling from the source exists, and such source refers to the model data input. Fundamental issues include identification of basic ecophysiological parameters, a critical reappraisal of commonly used ones, integration of parameters such as those reflecting hydric and thermal balance, and careful analysis of the data supporting the chosen parameters.

Let us illustrate the above premises by coming back to lizards, specifically two successful initiatives of modeling vulnerability to climate change based on physiological ecology [34–36]. The models proposed by Sinervo [34] are based on the interaction between ecology, physiology,

and behavior, which lead to the central concept of “hours of restriction”. This modeling idea roots from an ecophysiological theory for lizards that originated in the 1970s. Such theory had foundations on 30 years of keen ecological data and theory, which in turn were followed by 40 years of relevant data on lizard thermal biology. Thus, the models were generated after roughly 70 years of ecological data. Given this remarkable history of ecological research, and pioneering research on physiology converging to ecology [37,38], an unambiguous link between ecology and physiology was established. However, the history of amphibian physiological ecology was quite different, as we shall discuss next. A general point, though, is that given the differences among the natural history among lineages of ectothermic vertebrates, even tetrapods, the application of a theory developed for lizards to other lineages requires caution and critical thinking. The purpose of this paper is to discuss the bridging between ecophysiological data and modeling of amphibian ecology. Specifically, we focus on the potential of such models to predict amphibian responses to global environmental change.

## 2. Ecophysiological Information in Mechanistic Models of Amphibians

### 2.1. Brief Historical Overlook

Early physiological ecology studies with adult anurans resulted mainly in physiology approaching ecology (more than ecology approaching physiology, as in the lizard studies described above). Although recent studies [39–41] take for granted the principle that thermal and hydric relationships are physiologically inseparable, this principle was developed over time through models and studies dating back to the 1970s. Several important papers preceded the seminal Tracy’s monograph [42], and those papers dealt with crucial topics such as the relationship between thermal (energy) and water (mass) balances, and the implications of such balance for amphibian thermoregulation. However, Tracy’s [42] was perhaps the first, and likely the most influential attempt to integrate biophysics, physiology, and behavior in a formal way that could convey mechanistic explanations in ecology. Studies on water relationships were common in the 1960s and 1970s, but they slowly gave in to studies on thermal relationships, largely influenced by the development of strong models proposed for lizards. One important development that occurred between the 1970s and 2000 was the understanding that not all amphibians were “typical” (close to free water surfaces), that is, some species differed from the patterns detected in the 1970s for ranid frogs (e.g., many studies by C.R. Tracy and H.B. Lillywhite) or for salamanders (studied by J. Spotila). The discovery of great diversity in the cutaneous resistance of anuran species (mostly but not exclusively tree frogs) was remarkable and brought about a new dimension of complexity into the dynamics between water and temperature/energy balance [26,43]. Consequently, from the 2000s onwards water and thermal physiology re-emerged as integrated concepts (e.g., [39–41,44–47]). In this context, cutaneous resistance could be incorporated into a mechanistic model [14], even if highlighting the need of more data, given that evaporative water loss is but one parameter in the complex water balance of amphibians in nature. As a result, our knowledge on the intrinsic association between body temperature regulation and water balance across amphibian lineages, and even across anuran species, is still embryonic and limited in many facets [14,41,47] from tolerances to capacities and preferences (e.g., [25,48–53]).

Given the interplay between water and temperature, modeling based on the thermal tolerances of aquatic larval forms is likely useful in some context but attempts to model the ecology of adult anurans based just on temperature is a limited approach (see also Section 3), at best. Navas et al. [25] highlight the importance of solid theory supported by an empirical database, but that the available database may not lend enough support to theory. In this context, the so-called “incremental data” may become essential data, if scientists conclude that some parameters are crucial and known only for few species and ecological contexts. Also, it is necessary to integrate the best tools available and to acknowledge the pros and cons of alternative approaches. For example, from a biophysical perspective, equations have been formalized that describe thermal, hydric and energetic routes [26,42,54–56]. These efforts transformed the field, even if they necessarily simplify (or disregard) physiological or behavioral

adjustment. From a physiological-ecology standpoint, few parameters have been studied in diverse lineages (e.g., [1]), but even the most comprehensive databases are biased from some viewpoints. Variables that are commonly employed in models for amphibians include thermal tolerance (usually through critical thermal limits) [18], curves of thermal performance [19], operative body temperature (e.g., [57]), and water loss [20,57], and metabolism (e.g., [18,57]). Efforts to incorporate multiple information in models, including energetic, thermal, hydric, and behavioral parameters all together have been rare to date [14,18,57,58]. Nonetheless, although increasing complexity enhances model realism, some issues remain with no apparent answers. Complex models require extensive data, which are available for a few taxa only (e.g., *Plethodon* salamanders in most studies with urodeles). Also, many assumptions remain untested, and more critically, they cannot safely be extrapolated from one to another species, as in the case of activity patterns and the threshold of water loss (e.g., [58]). Furthermore, better model-based forecasting of amphibian vulnerability to extinction or range shifts require in-depth knowledge of both fine spatial and temporal scales of environmental sensing coupled with adequate estimates of organismal thermal sensitivity, through the entire life cycle [9,59]. Modern approaches are capable of downscaling macroclimatic factors into microclimatic dynamics [22,23], but the question remains of whether such models capture the appropriate scale of activity and interaction with the medium that characterizes a particular species.

## 2.2. A Comment on Larvae

What nowadays we call physiological ecology of amphibians is a field that emerged from several convergences. For example, in the 1930 and 1940s, several studies focused on thermal effects on egg development, with Moore's seminal contribution [60,61]. These studies were initially associated with the field of embryology, yet they set a line of thinking later applied to the convergence between physiology and ecology. Modern views focusing on anuran larval forms somehow root from these views, and to the related proposal that thermal adaptation could restrict (or explain) patterns of distribution. Current studies on the physiological ecology of aquatic stages of amphibians focus on thermal ecology and are also based on estimates of upper thermal tolerances in embryos, with many early examples from temperate species [62–65]. Furthermore, despite current efforts, information on the thermal tolerance limits of larvae exist mainly for anurans, and within this order, studies exist mostly for temperate species (see Reference [66]), with some efforts on subtropical and tropical lineages [49,67–71]. Therefore, modeling has relied on a pool of thermal physiology information that is, at best, fragmentary, even when thermal limits may be the most relevant variable. For example, sessile clutches, usually laid in shallow waters, are possibly exposed to freezing and heat stress, thus potentially exposing embryo stages to real acute thermal risk. The risk of acute thermal change likely varies with the type and natural history of embryos or eggs, with potential consequences for population recruitment and species endurance, thus remaining as exciting modeling opportunities.

Following our line of argument, we may think of environments less prone to expose larvae to thermal extremes, for example, shaded tropical climates with complex biotic aquatic communities. In such cases, the thermal sensitivity of locomotion (e.g., speed, stamina, maneuverability or other) may matter as an explanatory variable in several ecological contexts. However, for tadpoles, these variables remain practically unreported [19,72,73]. The available database carries a substantial developmental bias with far more information available for adult stages (see [21,74]).

## 3. Expression of Physiological Attributes at Ecologically-Relevant Scales

### 3.1. Synergic Effects of Water Balance and Body Temperature on Behavioral Performance

Translating environmental conditions into organismal performance is one of the significant challenges when interpreting ecological responses to changes in the environment [75]. Temperature is widely studied given the pervasive effect of temperature on virtually all biological systems [76]. However, it is precisely for this broad range of effects that researchers interested in the ecological

climate change research should focus on parameters linkable to fitness. For example, thermal performance curves (TPCs) contain information on how temperature affects a given behavior or physical parameter [77–79]. Naturally, a dependent variable used in TPCs may be a useful proxy for fitness in some lineages, and irrelevant for others. So, pressing questions for amphibians would involve how relevant is a chosen parameter (e.g., locomotion, as discussed above) to natural history (e.g., [80]). When comparing typical anurans, caecilians, salamanders, and newts, a different aspect of locomotion (e.g., speed, stamina, maneuverability, power, force, among others) may be most relevant. And, as said before, for terrestrial lifeforms, hydrothermal curves (e.g., [44,47,81]) may be far more informative and accurate than thermal curves alone, whereas, for a swimming species that breed in brackish water, including larval stages, temperature and salinity might be more useful.

Because TPCs can change according to hydric state [47], hydrothermal relationships matter for amphibians because of several reasons, some of which already mentioned. Among others, water relations may impose limits on thermoregulation restricting individuals to moist microhabitats, which in turn may limit ranges of opportunity for body temperature regulation [42]. So, despite preferences observed in thermal gradients, thermoregulation in the field needs not to be a main behavioral drive for amphibians, an observation that has been reported for decades [43,82,83] and that is fully compatible with the notion of water balance as a critical factor in the evolutionary history of this group [1,84]. Recent approaches aiming to measure the effects of temperature and hydration level simultaneously may prove crucial for more accurate mechanistic modeling (e.g., [40,42,44,47]). Indeed, studies at broad geographical scale have increasingly emphasized the critical role of the interaction between water and energy in driving macroecological patterns that had been historically reasoned to be a function of temperature only, such as geographical gradients of body size in amphibians [85,86].

### 3.2. Behavioral Site Selection and Hydrothermal Regulation

The neuroethology components of hydrothermal regulation in amphibians have been just scratched [43,82,87]. The behavioral control of body temperature in ectothermic vertebrates, in terms of the patterns of thermoregulation and the many related responses, encompasses a body of literature beyond the scope of this paper (e.g., the precision of thermoregulation, opportunistic thermoregulatory shifts, among others). However, the study of behavioral drives and their neural basis is far more limited, at least in the context here discussed (e.g., [88,89]). We know little about the nature, strength, and dominance of the behavioral drives that different lineages attain in the field. For amphibians, we do not know much about whether preferred temperatures under laboratory conditions emerge in nature, and under which circumstances. We know even less about how these physiological constraints on thermoregulation compete with alternative behavioral inclinations (even antagonistic behaviors). In contrast, the literature is saturated with overgeneralizations for “ectotherms” that assume (even if in between lines) that the behavioral predisposition to thermoregulate is similar among lineages (e.g., analogous in lizards and anuran amphibians). All these issues matter for amphibians because the drivers of thermoregulation in this group are so poorly understood, and may be context-dependent. For instance, the need to thermoregulate may be stochastic or simply different among ectothermic lineages (e.g., [90]). In the case of lizards, the notion of a permanent drive for thermoregulatory activity has been examined and, together with evidence of negative skewness of lizard body temperature towards the cold end [91], available data has led to the conclusion that thermoregulatory responses may emerge stochastically [92]. Because so little is known about amphibian hydrothermal regulation as a neuroethological system, we may call “thermoregulation” behaviors different conducts, such as avoidance of extreme temperature and close behavioral regulation of body temperature. There may be hydric zones favoring thermoregulation (e.g., [93]), wide thermal ranges in which thermoregulation is minimal [94], and other complexities. A same type of modeling based on thermoregulation would hardly be general for amphibians.



### 3.3. Metabolic Links to Thermal and Water Balance, and Behavior

Metabolic requirements may modulate behavior and displays many physiological correlates (e.g., [95]). For example, digestive performance may influence selection for thermal and hydric conditions, and therefore some amphibians may thermoregulate more actively during their less active period [74]. This aspect of natural history poses several questions when modeling thermoregulation (e.g., using same models when thermoregulation is, or is not, at peak during maximum activity). The so-called postprandial thermophilic response, i.e., the selection of higher body temperature during digestion [96], remains unmeasured in several taxa, so that we do not know about the ecological impact of such behavior, and how it may be affected by environmental change. This response and other correlates of energetics need to be better explored as possible constraints on amphibian behavior, yet they will not be independent of water and temperature [97]. From a different energetic perspective, dormancy and metabolic depression play an essential role under seasonal or even diel variation [48]. However, entering at awakening from a given period of inactivity and aphagia during hibernation or estivation is not just a matter of energetics [95]. Metabolic tradeoffs permeate the range of body and ambient temperatures and, in aquatic forms, the physical state of water (frozen or hyperosmotic) [1]. These interactions in turn, relate to dehydration tolerance and resistance, tolerance to oxygen fluctuations, and several other factors that may constitute ecological bottlenecks. Therefore, in seasonal species, the main limiting factor may not be the thermal physiology during the most active part of the year, but unexplored aspects of estivation or hibernation (e.g., [48]).

### 3.4. Environmental Thermal and Hydric Tolerances

The assessment of physiological thermal tolerances across taxa and environments as correlates of ecological constraints have been of broad interest to researchers over the past decade [38,98–100]. When discussing amphibians, however, some generalizations may complicate interpretations. On the one hand, it is typical for amphibians that upper thermal limits are close to death whereas lower thermal limits are just close to inactivity. Because death is not the same as an impaired activity, these parameters do not have the same ecological implication and do not bear a similar relationship with the abstraction of the fundamental niche. These considerations matter for mechanistic modeling, as it is backed by the very concept of Hutchinson's fundamental niche [101], which is based on constraints imposed by abiotic factors [102]. So, whereas thermal limits may be relevant parameters for modeling amphibians, the uncritical use of these two parameters in mechanistic models may be problematic. If modeling were supposedly based on limits to survival, the thermal ranges to be used would require a different assessment of lower critical temperatures. This action, in turn, would lead to substantially broader thermal niches. Instead, if modeling was based on impaired behavior, the thermal range would be comparably narrower. Relying on a mixed approach, considering near death values at the upper range and impaired behavior at the coldest end could substantially alter inferences of distribution, range shifts and vulnerability to climate changes at ecologically relevant scales.

Some other issues to keep in mind are that critical temperatures, as well as other physiological parameters, may vary with season [103,104] or, more generally, may be prone to adjustment [105,106]. For instance, developmental fitness traits of amphibians are dependent on thermal variability, so that predictability of animal performance is compromised under fluctuating conditions [107]. Also, the implications of exposure to subcritical temperatures are virtually unknown [25]. Exposition to near-critical limits or to frost may not be uncommon in subtropical and high-elevation tropical amphibians [108,109], warning for a potential impact on amphibian during extreme—even short-term—conditions. Finally, the relationships between critical temperatures and TPC's deserves some discussion. If the curves are to reflect fitness, enhancing information on their limits may affect the evaluation of performance under scenarios of environmental change. For example, anurans typical from high altitudes in Paramos ecosystem in Colombia display high thermal tolerance to cold; and critical thermal minimum (CT<sub>min</sub>) is likely a crucial parameter in this ecological context [109]. In contrast, maximum critical temperatures may not be evolutionarily selected in this environment (or

not to the same extent). The opposite may be the case when considering anurans from the semi-arid Caatingas of Brazil, in which the upper thermal tolerances (CT<sub>max</sub>) are likely critical [110], but no reason exists to attribute lower thermal limits to adaptive evolution. A similar pattern holds for tadpoles in tropical rainforest, which adjust their upper thermal tolerances to microenvironmental variation in peak maximum temperatures, but no correspondence between lower thermal tolerance (CT<sub>min</sub>) and environmental coldest temperature exists [69].

Back to the issues related to hydrothermal balance, the inherent trade-offs between temperature and water may alter responses and tolerances, thus modifying the thresholds for activity limits. For example, the threat of desiccation may be more limiting than of overheating for some amphibian species and contexts [111] and, in this scenario, individual tolerance related to water budget deserves much more investigation. Hydration levels, related behavioral cues and voluntary tolerance of dehydration may vary with habitat use, even within closely related species in the same family or genus [1,105]. Moreover, hydration levels may alter water loss and gain because dehydration decreases the speed of further desiccation and enhances water uptake [111]. In aquatic stages water economy is irrelevant, but the water-land transition during metamorphosis climax does expose unusually tiny organisms to atmospheric evaporative conditions, resulting in enhanced risk of dehydration and evaporative cooling of metamorphs [66].

Still, regarding the link between water and temperature, dehydration tolerance has been argued to be a preadaptation for freeze tolerance in amphibians, so that it could also carry qualitative information on temperature tolerance [112]. Furthermore, dehydration tolerance implies stress on the cardiovascular system (e.g., hyperosmolality, hypovolemia or hyperviscosity), a topic difficult to explore in further detail given limited data on cardiovascular capacity among amphibians. These complex relationships highlight the importance of additional physiological traits interfering on both thermal and hydric tolerance limits. Therefore, hydoregulation and its relation to thermal issues appear definitively to be a relevant avenue that more studies should focus in the future, especially in contexts of modeling predictions based on ecophysiological responses to environmental/climate changes.

### 3.5. Accommodating Plasticity, Ontogenetic Variation, and Population-Level Process

Earlier stages of amphibian development display plasticity in traits like thermal tolerances—believed to affects fitness (e.g., [113]), but also in larval developmental rates and size at metamorphosis [114], metabolic rates [115], acclimation scope in thermal tolerance limits [116]. To this plasticity adds up the pool of potential adaptive (evolutionary) responses to changing conditions [117,118]. Existing models often assume stationary reactions of physiological traits under changing condition, but recent models underscore that rapid evolution of reaction norm through phenotypic plasticity are plausible (e.g., [119]). Incorporating evolutionary potential should increase model complexity, but attempts have been made for other groups [120,121], and progressively they should provide a much-detailed picture of the species' potential (or lack of) to adjust to the changing climate.

In species with complex life histories such as amphibians, selection due to climate change can act simultaneously on multiple traits in ways that differ through the life cycle. Furthermore, owing to the diversity of combinations of ontogenetic pattern, reproduction sites, larval microhabitat, and environmental conditions throughout metamorphosis, certain particular stages must be more sensitive to environmental stress, and thus more critical for modeling purposes [107]. If earlier life stages are more sensitive to environmental stress than adult forms, then recruitment is affected, thus impacting the population dynamics and resilience to environmental change [11], consequently altering the predictions of models compared to those based on adult parameters.

The question of how an individual behavior scales up into population-level processes has a value on its own and is still largely overlooked. However, population dynamics are constrained by a great variety of processes that act on population size and growth, which ultimately determine its distribution,

persistence and adaptive potential. These processes include local distribution, behavior, dispersal patterns, interactions, and genetic structure, which make modeling virtually impossible to tackle in a unified framework [122]. Therefore, the inexorable uncertainty involved in ecological processes need to be accommodated when constructing mechanistic models. Modeling the responses of organisms to climatic variation at the population level, which is ultimately the critical level of interest when addressing species, should likely require the integration of probabilistic reasoning in the modeling workflow (e.g., [122,123]).

#### 4. Conclusions and Prospects

A much-needed association between ecophysiology, biophysical ecology, ecology, and climatology has been emerging as a venue to address the response of species to ongoing environmental change [24]. This integration has been primarily developed in the context of mechanistic models of species distribution and endurance to changing conditions, which should provide insights on the multidimensional nature of species response to surrounding environment at multiple environmental contexts and by incorporating different biological attributes of species [101,124]. Because this is a developing process, care is necessary when employing concepts and data to address potential responses of species to environmental changes. Here, we point out some caveats and directions we deem crucial for a steady increment in this field that is consequential for conservation. These directions are aimed explicitly for amphibians, and include (i) increasing information on hydrothermal regulation and developing new parameters, if necessary; (ii) considering trade-offs between hydrothermal and metabolic requirements and their implications across contrasting environments and life histories; (iii) enhance the quality and complexity of mechanistic models by careful selection of parameters; (iv) provide a comprehensive amphibian hydrothermal sensitivity through the entire life cycle; (v) incorporate the notion of a non-static physiology that is prone to adjustment; (vi) enhance research on the consequences of exposure to sub-lethal limits at individual and population levels; and (vii) accommodate some degree of stochasticity within the models to improve the connection between impacts at individual and population levels.

We also stress that, given the diversity of amphibians, it is urgent to overcome existing shortfall of ecophysiological data and to make a stronger effort to care for the standardization of or—at least—enhanced consistency in protocols of data collection, as to improve the quality of collective, yet independent, initiatives. Finally, we urge for the accommodation of within-species variability and acclimation, which ultimately should reflect population-level patterns and responses. This step should enhance predictive power and add realism of modeled responses, giving an option to adjustment (and even adaptation) to environmental change.

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