

IMPACTS OF CLIMATE CHANGE ON AMPHIBIANS

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Figure 1. Amphibian eggs are more vulnerable to desiccation as they lack a hard shell. Andean glass frog ([Hyalinobatrachium pellucidum](#)) eggs in Río Bigal, Orellana, Ecuador. Photo courtesy of [Anton Sorokin](#).

AMPHIBIANS' VULNERABILITY TO CLIMATE CHANGE

The many dimensions of the **anthropogenic**¹ climate crisis (see **Box 1**) have diverse and often devastating repercussions for Earth's biodiversity (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Thomas et al. 2004; Parmesan 2006; Wake and Vredenburg 2008; Barnosky et al. 2012). Amphibians serve as sensitive indicators for researchers studying these repercussions, since they have several traits that render them particularly vulnerable to changing climatic conditions (Blaustein et al. 2003; Catenazzi 2015).

Physiologically, amphibians can be profoundly affected by minute changes in temperature and moisture due to their **ectothermy**², their unshelled and desiccation-prone eggs (Fig. 1), and their highly water-permeable skin (Duellman and Trueb 1994; Corn 2005; Blaustein et al. 2010; Li et al. 2013).

Behaviorally, amphibians' often have limited **dispersal**³ ability and a tendency towards strong **site fidelity**⁴, which affects their ability to track their climate niche as that niche shifts geographically and hinders their ability to colonize new areas with favorable conditions.

¹ Anthropogenic: caused by humans

² Ectothermy: body temperature regulation through the use of environmental, rather than internal, heat sources.

³ Dispersal: the movement of organisms across the landscape

⁴ Site fidelity: the tendency of an organism to remain in or regularly return to a particular site



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Ecologically, amphibians are tightly dependent on water availability in their habitats, which play critical roles in their reproduction, **biphasic**⁵ lifecycle, activity levels, and migration (Carey and Alexander 2003).

BOX 1.

Environmental features of amphibian habitat directly impacted by the climate crisis

- Air and water temperature
- Hydrological regimes
 - Precipitation
 - Stream flow
 - Size and depth of water bodies
 - Contaminant concentrations in water bodies
 - Amount and duration of winter snowpack
 - Pond **hydroperiod**⁶
 - Soil moisture
 - Fog regimes
- Rate of extreme weather events (e.g. hurricanes, tornados, intense fires)
- Duration of seasons
- Extent and quality of coastal habitat due to sea level rise (e.g. saltwater intrusion into coastal wetlands)
- Frequency, intensity, duration, and regularity of cyclical climatic patterns (e.g. El Niño, La Niña)
- Degree of climatic variability (e.g. fluctuations between extreme heat and cold weather)
- Novel climatic conditions for regions or habitats
- Novel interspecific interactions (e.g. through changing phenology, ranges, or species extinctions)

There is still limited data on how and to what extent the climate crisis is affecting amphibians, due in large part to a lack of long-term monitoring data (Zellmer et al. 2020). Many existing studies of this question take an **inductive**⁷ rather than a **deductive**⁸ approach, so that alternative hypotheses--e.g., that observed changes were driven by land use change or disease--cannot ultimately be rejected (Li et al. 2013). This limitation also means that we often have not yet identified the mechanism by which changing conditions act on amphibians, or have not yet disentangled direct from interactive effects.

Despite these difficulties in studying these questions, we can still state with confidence that the climate crisis is affecting amphibians, and that in many cases it appears to be affecting them profoundly (Fig. 2). Here, I will summarize the current evidence that climate change is impacting amphibians' physiology,

⁵ Biphasic: having two phases. For amphibians, they begin their lives in an aquatic larval stage, and then metamorphose into an adult stage that may be terrestrial, semi-aquatic, or aquatic.

⁶ Hydroperiod: The amount of time that water stays in a particular place before drying

⁷ Inductive: Inductive methodologies infer a probable conclusion based on a body of evidence.

⁸ Deductive: If we instead use deductive methodologies for causal inference, we start with a known general principle, and are using this to estimate parameters for the particular case in question.



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behavior, and demography. To read about ways that the climate crisis impacts amphibians interactively, through [synergisms](#)⁹ with other threats, please navigate to our [Synergisms](#) page.



Figure 2. The upslope movement of cloud layers due to climate change is thought to be the main driver of the endangerment of the bumpy glass frog ([Centrolene heloderma](#)), endemic to a small area just outside of Quito, Ecuador. Photo courtesy of [Anton Sorokin](#).

PHYSIOLOGICAL IMPACTS

Aspects of amphibian physiology being reshaped by the climate crisis include their size, **body condition**¹⁰, and immune functioning. These items will be covered in the following segment. To read about how the climate crisis impacts amphibian **phenology**¹¹, which is often ruled by physiological processes stimulated by environmental cues, continue on to the section entitled “BEHAVIORAL IMPACTS: Phenology”, below.

⁹ Synergism: a situation when multiple interacting factors have an overall impact larger and different than simply their additive impacts.

¹⁰ Body condition: a metric, generally derived from the body size and mass of an individual, which can be used to indicate an amphibian's available energy reserves (Peig and Green 2010; Brodeur et al. 2020).

¹¹ Phenology: the way that living organisms time their life-history events to synchronize with cues in their environment



Body size

Shrinking body size is a common response of species to a warming world (Daufresne et al. 2009; Gardner et al. 2011). Ectotherms, particularly, are expected to shrink rapidly in body size as temperatures rise, since their ability to regulate their body temperature depends on their absorbing or sheltering from environmental heat (Daufresne et al. 2009). As their environment warms, their metabolic rate and hence their energy demands increase. Meanwhile, their capacity to acquire energy—for example, the time they can engage in foraging— may decrease (Feder and Berggen 1992; Sinervo et al. 2011). Declines in average population body size can result. This shrinking can either be due to a decline in individual animals' growth rates or due to selection over generations for a less energetically costly, smaller body size (see **Box 2**). Even if a smaller body size is, energetically speaking, an adaptive response to a warming world, it may entail negative consequences. Body size reductions can make amphibians more vulnerable to desiccation (Heatwole et al. 1969) and depress female **fecundity**¹² (Reading 2007).

So far, there is only limited evidence that climate change is decreasing amphibian body size. The body size of common toads (*Bufo bufo*) decreased over 22 years of monitoring in the UK, associated with a trend of increasingly mild winters. This association was backed up by lab studies demonstrating that depressed body size would be an expected outcome of winters that are too warm for amphibian hibernation (Reading 2007). In another study, the body size of 6 of 15 Appalachian *Plethodon* salamander species studied declined over a period of 55 years, associated with drying and warming trends. Accompanying **biophysical models**¹³ suggested that these relationships could be attributable to increasing metabolic costs while these species' annual duration of activity remained stable (Caruso et al. 2015). Further studies are needed to determine the true effects of smaller body size on fitness, but the link between amphibian fitness and body condition (below) is much clearer.

Body condition

Just as body size may decline if an organism's nutritional demands are not met, so may body condition. Body condition is an important metric as it can serve as a proxy for individual fitness, since a decline in body condition tends to result in reduced fecundity and can even be associated with population declines (Reading 2007). Reading's 2007 long-term monitoring study of common toads, referenced above, also found corresponding declines in their body condition. Meanwhile, a recent study of California newts (*Taricha torosa*) found that the body condition of southern populations, which were exposed to extreme heat events and drought, declined by 20% over eight years. Northern populations are predicted to follow suit in the next 50 years (Fig. 3; Bucciarelli et al. 2020).

¹² Fecundity: The number of viable offspring potentially produced by an organism

¹³ Biophysical models: Complex models using an understanding of both biological and physical processes to gain a more mechanistic understanding of a situation, or to make better predictions of how things will change under different future conditions.



Figure 3. Rough-skinned newts ([Taricha granulosa](#)) shelter from the sun in the cracks of a desiccated cattle pond in Berkeley, California, USA. Photo courtesy of [Anton Sorokin](#)

Immune functioning

There are many ways the climate crisis could impact the complex dynamics between amphibians and their pathogens and parasites (Blaustein et al. 2010). For a more complete discussion of the synergisms between climate change and amphibian disease, please visit our [Synergisms page](#). However, one very direct way that climate change is reshaping amphibian disease dynamics is by modulating their immune functioning, increasing their susceptibility to infection.

As ectotherms, amphibians' immune systems can ramp up with warming temperatures or be suppressed by cooling temperatures (Cone and Marchalonis 1972; Green (Donnelly) and Cohen 1977; Wright and Cooper 1981; Cooper et al. 1992; Maniero and Carey 1997; Matutte et al. 2000). These temperature-regulated changes to the immune system could leave amphibians susceptible to emerging pathogens (Maniero and Carey 1997; Carey et al. 1999; Rojas et al. 2005; Kilpatrick et al. 2010). For instance, our climate crisis is amplifying the strength of the 'Greenland block' effect (Gramling 2015), an existing climatic pattern causing longer and colder winters in North America. Among many impacts on amphibians, these more extreme winter storms force tadpoles to metamorphose more quickly, such that immune defenses that already tend to be compromised in juvenile frogs are still less effective at defending them from disease (Rollins-Smith et al. 1988; Holden et al. 2015).

Increased variability in climatic conditions is, in and of itself, capable of suppressing amphibian immune function and increasing the risk of disease outbreaks (Rohr and Raffel 2010; Raffel et al. 2013). For



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instance, the lag time required for amphibians to adjust their immune activity in response to short- or long-term temperature fluctuations could leave them vulnerable to infection or else result in their investing more energy than is optimal on immune activity (Raffel et al. 2006). Furthermore, the energetic cost of multiple bouts of upregulation and downregulation itself may take a significant toll on amphibians (Blaustein et al. 2010).

Changes to precipitation, as much as changes to temperature, can influence immune functioning of amphibians by causing them stress or promoting phenological changes. As an example, larval Wood frogs (*Rana sylvatica*) in a simulated pond-desiccation experiment were forced to metamorphose more quickly, compromising the immune functioning of the resulting juveniles (Gervasi and Foufopoulos 2008).

BEHAVIORAL IMPACTS

Thermoregulatory behaviors

Amphibians and reptiles deploy a variety of **thermoregulatory behaviors**¹⁴, which they can use to buffer the impact of climate change. For example, they can move between available **microclimates**¹⁵ to keep their body temperature within an optimal range (Kearney et al. 2009), and particularly to avoid temperatures that are costly or lethal to them (Sinervo et al. 2011; Huey et al. 2012; Sunday et al. 2014). However, these behaviors are not without costs. Avoidance behaviors limit animals' opportunities to forage, search for mates, and grow, or relegate them to suboptimal habitats (Sinervo et al. 2011).

Phenology

Phenology refers to the way that living organisms time their life-history events to synchronize with cues in their environment. Organisms like amphibians, with complex life histories, rely on environmental cues (Corn and Muths 2002; Carey and Alexander 2003; Corn 2003) to initiate many developmental or periodic transitions throughout their lives. These cues might come in the form of a threshold temperature, the first seasonal rainfall, or the timing of snowmelt. It is unsurprising, then, that the best-documented responses of amphibians to the climate crisis are changes in phenology of their hibernation, **metamorphosis**¹⁶, and their breeding.

A well-documented trend in amphibians is earlier breeding events. This response is not uniform across species or even necessarily across the range of a single species (Fig 4; Beebee 1995; Blaustein et al. 2001; Gibbs and Breisch 2001; Chadwick et al. 2006; Todd et al. 2011). Still, on average amphibian breeding events have shifted earlier at twice the rate that birds, trees, and butterflies have done so

¹⁴ Thermoregulatory behaviors: a behavior exhibited for the purposes of controlling body temperature. For example, a tadpole might move between shallower and deeper water depending on the temperature of these zones throughout the day.

¹⁵ Microclimates: fine scale variation in climatic parameters, like temperature or moisture, across complex environments. For example, a frog might seek a cooler and moister microclimate by sheltering under a rock when the larger environment is on average hotter and drier.

¹⁶ Metamorphosis: transitional period from the larval to adult form

(Parmesan 2007). We do not yet understand whether these phenological changes are driven by **molecular evolution**¹⁷ or **plasticity**¹⁸ (**Box 2**). Although the rapidity of these changes suggest that they arise from plasticity—the ability to change a trait, in this case breeding, without genetic change—controlled experiments have not yet been conducted to answer this question (Urban et al. 2013).



Figure 4. A male spring peeper (*Pseudacris crucifer*) calling for a mate at the beginning of the spring breeding season in the Southeastern USA. Spring peepers are an example of a species whose breeding phenology has shifted earlier in the calendar year as the climate warms, but this is not true for all populations across their range. Photo courtesy of [Anton Sorokin](#)

As we might expect, there is more evidence for amphibians' phenological response to climate change in temperate than in tropical regions. One important behavior ruled by seasonality is **brumation**, a life history trait of most temperate amphibians, in which they spend part of the year escaping extreme hot or cold temperatures by sheltering in hibernacula. Slight shifts in temperature or moisture may induce a brumating amphibian to emerge, at which point they typically migrate to water bodies for breeding (Fig. 5). By altering the cues that stimulate emersion from hibernacula, climate change may cause amphibians to awake from torpor and initiate migration and breeding when environmental conditions are still inhospitable or unstable. On average, temperate amphibians are breeding earlier and earlier in the calendar year as average temperatures increase (Blaustein et al. 2001; Gibbs and Breisch 2001; Benard 2015). For those species that are shifting their phenology, there can be negative biological consequences. For example, amphibians breeding too early in the season are sometimes more

¹⁷ Molecular evolution: genetic sequence change across generations.

¹⁸ Plasticity: The ability of an organism to change a trait in response to the conditions it experiences, without the need for underlying genetic sequence change.



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vulnerable to floods, resulting from rapid snowmelt, and additionally are subject to more early season freezes, which later in the calendar year would be less common (Burrowes 2009; Williams et al. 2015).

While there are plentiful studies documenting phenological shifts in temperate species, the long-term datasets required for such documentation are simply not yet available for tropical regions (Whitfield et al. 2016). From these regions, environmental cues like the earlier onset of spring or earlier seasonal rainfall are not the general rule. Rather, the broadly relevant change is that evaporative rates are increasing as temperatures increase, shortening the hydroperiods of ponds and wetland habitats. In many regions, these shortened “wet seasons” force larval amphibians to speed their developmental rate if they are to emerge in time and survive (Donnelly and Crump 1998).

This transitional period from the larval to adult form, or metamorphosis, is a point in amphibian life history when we might expect them to be particularly vulnerable to novel or changing environmental stressors (Lowe et al. 2021). The transition between body forms can be costly, both sapping much of their available energy while simultaneously mismatching them temporarily to both their larval and their adult habitats (An 1978; Crump 1984). External cues guide the timing, rate, extent of morphological change undertaken, survivorship, and eventual body condition of juvenile amphibians (An 1978; Tejedo et al. 2010; Lowe et al. 2021). We already have evidence that the climate crisis is reshaping these equations (Benard 2015), and with further study, many more examples will doubtlessly come to light. For instance, amphibians are able to remain mobile during their metamorphosis, so a strategy of many aquatic larval amphibians is to move between shallower and deeper water to avoid temperature extremes, feed, and escape predators (Holomuzki 1986). However, with the more extreme and strongly fluctuating temperatures induced by climate change, shallower zones are becoming more abiotically inhospitable to larval amphibians (Finlay et al. 2001). These abiotic changes decrease their ability to move between shallower and deeper zones, increasing their exposure to predators, and thus potentially increasing their mortality rates (Lowe et al. 2021).

BOX 2.

Are amphibians' adaptive responses to the climate crisis attributable to molecular evolution (i.e., selection) or to plasticity?

The ability of amphibians to rapidly adapt to changing environmental conditions would help populations and, indeed species, to persist and survive the climate crisis (Hoffmann and Sgró 2011). Such '**evolutionary rescue**' could occur through two major modes: molecular evolution, in which selection drives genetic change over time, or plasticity, in which an organism changes in response to environmental cues without undergoing genetic change.

Currently, most of the evidence for rapid molecular evolution in amphibians is derived from **common garden experiments**¹⁸ or studies along spatial gradients, rather than demonstrating rapid evolution in

¹⁹ Common garden experiments: An experiment in which organisms sourced from different locations are raised in a common environment in order to piece apart the contributions of genetics and environment to the traits they exhibit.



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a single amphibian population over time (Urban et al. 2013). Such studies are useful for guiding predictions of how amphibians may adapt to climate change but do not provide direct evidence for if or how that genetic adaptation will occur (Kawecki and Ebert 2004; Merila and Hendry 2014).

Meanwhile, there is clear evidence for plasticity's contribution to amphibians' rapid response to contemporary climate change. Plastic changes in physiology or behavior can definitely buffer amphibian populations against some aspects of climate change, and the degree of plasticity a species exhibits can itself be a trait under selection (Lind and Johansson 2007). Still, we must remember that not all traits can change plastically, and that the extent of trait change plasticity may be insufficient (Urban et al. 2013).

It can be encouraging to reflect on the sometimes extreme adaptive change amphibians have undergone across their evolutionary history to keep pace with a sometimes radically-changing environment, like the fluctuations in body size of the Natterjack toad ([*Bufo calamita*](#)) tracking repeated glacial cycles across the Pleistocene (Martinez-Monzon et al. 2018). Still, it is difficult to predict whether amphibian adaptation will be able to keep pace with the accelerating rates of current change (Gienapp et al. 2008; Meester et al. 2018). The rate at which their **climatic niche**²⁰ will need to evolve in order to persist vastly outstrips the challenges they have met in the past (Bush et al. 2004; Quintero and Wiens 2013). Further, the many dimensions of this climatic change (see Box 1) are accompanied by many other components of anthropogenic environmental change (e.g. land use change, contamination, and introduced species; Botero et al. 2015). There is already some evidence that, when the pace of environmental change is too rapid, amphibian populations may be unable to adapt rapidly enough and instead decline (Arietta and Skelly 2021).

²⁰ Climatic niche: the set of climatic conditions to which an organism is adapted



Figure 5. An Eastern spadefoot ([Scaphiopus holbrookii](#)) emerges from brumation in North Carolina, USA, triggered by a heavy rain event, to forage and look for a mate.

DEMOGRAPHIC IMPACTS

Climate change can impact the **demographics**²¹ of wild amphibians by causing changes to their distributional range, to population **connectivity**²², and to their overall population abundance and persistence.

Range shifts

Climate-driven range changes occur when species shift their geographic distribution by latitude or by elevation in order to track their climatic niche (Parmesan 2006). These range shifts can entail expansion into new habitat, contraction from regions that become inhospitable, or a combination of both expansion and contraction along a 'leading' and 'trailing' edge. Although there is still almost no documentation of contemporary climate-driven latitudinal range shifts in amphibians, the evidence that amphibians are undergoing elevational range shifts is beginning to mount (Li et al. 2013).

²¹ Demographics: attributes describing the dynamics of a population, such as birth rate, death rate, immigration, emigration, or fecundity.

²² Connectivity: the degree to which gene flow-- or genetic exchange-- can occur between populations on a landscape.



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We generally expect that wildlife will shift upslope as the climate warms in order to seek cooler conditions. However, the directionality of elevational range shifts are frequently more **heterogeneous**²³ than that (Tingley et al. 2012; Rapacciuolo et al. 2014), which is also true of amphibians. Contemporary elevational range shifts of amphibians have been documented in many places throughout the world, including the Ecuadorian Andes (Bustamante et al. 2005), South Africa (Botts et al. 2015), Appalachian Mountains of the United States (Moskwick 2014), the Peruvian Andes (Fig 6; Seimon et al. 2007; Steigerwald et al. 2021), and the Iberian peninsula (Bosch et al. 2018; Enriquez-Urzelai et al. 2019). In most cases it can be difficult to disentangle range changes that may be driven by pervasive habitat degradation and loss, but in Madagascar and Indonesia elevational range shifts were documented in stably protected areas that have not been transformed by land use change (Raxworthy et al. 2008; Kusrini et al. 2017).

The poor documentation of latitudinal shifts—sometimes recording only weak shifts, and sometimes no shifting at all (Hickling et al. 2006; Enriquez-Urzelai et al. 2019)—may relate to the greater challenges they present. The velocity at which climatic niches are moving along the latitudinal gradient greatly outpaces their velocity along the elevational gradient, such that amphibians have to travel much further towards the poles than towards mountain peaks if they are to track their climatic niche (Enriquez-Urzelai et al. 2019). Amphibians generally have relatively low dispersal ability and frequently some degree of **philopatry**²⁴ (Marsh and Trenham 2001). This means that vast distances are a challenging barrier, particularly when they include ecological barriers that may be impermeable to amphibians like seas, mountains, or powerful rivers.

²³ Heterogeneous: not being uniform but rather mixed or varied. In this case, wildlife may shift upslope with climate change, but other species will shift downslope, remain stable, or possibly expand or contract in both directions.

²⁴ Philopatry: natal site fidelity (defined above). When an organism tends to stay at or regularly return to the site of its birth.



Figure 6. The marsupial frog ([Gastrotheca marsupiatu](#)) is one amphibian species that may have expanded its upslope range in response to climate change in the Peruvian Andes (Steigerwald et al. 2021). Photo courtesy of [Anton Sorokin](#).

Population declines and **extirpation**²⁵

As the climate continues to change, more than a third of animal species could contract to less than half their current distributional range, with amphibians being disproportionately represented among these species (Warren et al. 2013; Scholes et al. 2014). In these areas of range contraction, what we are seeing is warming trends extirpating species from what used to be viable habitat for them (Parmesan 1996; Parmesan et al. 1999; Pounds et al. 1999). In fact, one in six species is predicted to go extinct within the century following a business-as-usual carbon emissions scenario (Urban 2015).

Discussions about whether climate change were already driving amphibian declines launched in earnest in the early 1990s. Baffled herpetologists were watching amphibian populations blink out in well-protected habitat, where the usual major menace of habitat loss could not be blamed (Blaustein and Wake 1991; Wake 1991; Pounds and Crump 1994; Lips 1998; Lips et al. 2006). Our climate crisis may be responsible for driving these declines through direct or indirect mechanisms (Donnelly and Crump 1998; Pounds et al. 1999; Alexander and Eischeid 2001; Catenazzi 2015). Here, we'll process through some of

²⁵ Extirpation: Local extinction, when a species disappears from a region.



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the major direct mechanisms through which the climate crisis is endangering amphibians: reductions in water availability, more extreme weather events, and warming trends. However, interactions between climate change and other simultaneous threats to amphibians may be hugely important in driving our global amphibian biodiversity crisis. In particular, the way that climate change may be provoking amphibian disease outbreaks has gathered much attention and study. To learn about the direct impact of the climate crisis on amphibian immune functioning read “PHYSIOLOGICAL IMPACTS: Immune functioning”, above. To read more about how the climate crisis impacts amphibians interactively, through **synergisms**²⁶ with other threats, navigate to our [Synergisms](#) page.

Given the intimate connections between amphibians and water throughout their life history, it is no surprise that changes to water availability in their habitat may be the strongest climate-linked driver of amphibian declines (Araújo et al. 2006). In so many places across the world, the dry season is becoming drier and longer, and local amphibians have declined precipitously or disappeared entirely (Weygoldt 1989; Stewart 1995; Pounds et al. 1999; Daszak et al. 2005). Severe and unprecedented droughts have dried amphibian breeding ponds entirely, desiccated their wetland habitat, reduced their fecundity, and increased their mortality, resulting in massive amphibian population crashes (Figure 7; Corn and Fogleman 1984; Ingram 1990; Pounds and Crump 1994; Laurance 1996; Taylor et al. 2006; McMenamin et al. 2008; Cayuela et al. 2016; Weinbach et al. 2018; Kissel et al. 2019). There are also more subtle ways in which reduced water availability may be choking out amphibians. For species that brumate under snowpack, less snowfall means less insulation against the extreme cold of their environment, reducing survivorship across the winter (Muths et al. 2020). Studies have also found a link between changing mist regimes, driven by rising sea surface temperatures, and amphibian population crashes and extinctions (Pounds and Crump 1994; Pounds et al. 1999). As a final intriguing example, exposure to desiccation may make larval amphibians less responsive to chemical alarm signals, increasing their predation risk (Rohr and Madison 2003).

²⁶ Synergism: a situation when multiple interacting factors have an overall impact larger and different than simply their additive impacts.



Figure 7. The grim sight of rough-skinned newt ([Taricha granulosa](#)) corpses, first desiccated by the extreme drought and now covered by the first rains of the winter in Contra Costa County, CA, USA. Photo courtesy of [Anton Sorokin](#).

The increased frequency and intensity of other extreme weather events provoked by the climate crisis (Timmermann et al. 1999; Alexander et al. 2006) is also expected to exacerbate amphibian declines. Powerful floods, hurricanes, and frosts have already been linked to amphibian declines across entire regions (Heyer et al. 1988; Woolbright 1997; Corn 2000; Lowe 2012). Meanwhile, profound changes to cyclical weather events like El Niño and La Niña, which shape weather at a global scale (Timmermann et al. 1999), mean that these events may now strike amphibian populations before they have had time to recover from the last cycle (Carey and Alexander 2003).

Among extreme weather events potentially impacting amphibians are more and increasingly severe heat waves (Weinbach et al. 2018), but overall increases in average temperatures have also been associated with several amphibian population declines (Heyer et al. 1988; Alan Pounds et al. 2006; Alford et al. 2007). There are a number of possible ways in which warmer temperatures can drive declines. For instance, in regions where amphibians normally brumate during the winter, warmer winters may result in lower body condition, fecundity, and survivorship among females (Reading 2007). Temperature may also affect the sex ratio of amphibians, skewing the number of males and females born in a season due to anomalous incubation temperatures²⁷ (Eggert 2004; Nakamura 2009). Different temperature tolerances between amphibians and other species in their community can also mean that changing environmental temperatures will impact their ecological interactions with predators, prey, or

²⁷ Within the normal temperature ranges experienced by amphibians, temperature does not impact sex determination. However, when temperatures fluctuate outside of the normal range experienced by a species, these extreme temperatures can skew sex ratios of developing amphibians-- even to the point of complete masculinization or feminization. Generally (though there are exceptions), extreme high temperatures result in larvae developing testicles while extreme low temperatures result in ovaries.



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parasites. For instance, when tadpoles have a narrower thermal tolerance than their predators, it can increase their predation risk as temperatures rise, or as water temperature rises during periods of pond desiccation (de Mira-Mendes et al. 2019; Pintanel et al. 2021).

A final example of a mechanism implicating rising temperatures in amphibian declines comes from a 35-year monitoring project of leaf-litter herpetofaunal communities in Costa Rica. Warmer temperatures and fewer annual days without precipitation (although the overall amount of precipitation did not increase) resulted in faster decomposition rates and less standing leaf litter. Ruling out several competing hypotheses, the authors implicated this reduction in standing leaf litter over time in the steep amphibian community declines they observed (Wake 2007; Whitfield et al. 2007).

BOX 3.

What was our Climate Change perspective ten years ago? See our archived version of this page:

https://amphibiaweb.org/declines/climatechange_2006.html

LITERATURE CITED

- Alexander, M. A., and J. K. Eischeid. 2001. Climate variability in regions of amphibian declines. *Conserv. Biol.* 15:930–942.
- Alexander, L. V., X. Zhang, T. C. Peterson, J. Caesar, B. Gleason, A. M. G. Klein Tank, M. Haylock, D. Collins, B. Trewin, F. Rahimzadeh, A. Tagipour, K. Rupa Kumar, J. Revadekar, G. Griffiths, L. Vincent, D. B. Stephenson, J. Burn, E. Aguilar, M. Brunet, M. Taylor, M. New, P. Zhai, M. Rusticucci, and J. L. Vazquez-Aguirre. 2006. Global observed changes in daily climate extremes of temperature and precipitation.
- Alford, R., K. Bradfield, and S. Richards. 2007. Global warming and amphibian losses. *Nature* 447:E3–E4.
- An, S. 1978. Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): social behavior as a possible defense. 59:1014–1022.
- Araújo, M. B., W. Thuiller, and R. G. Pearson. 2006. Climate warming and the decline of amphibians and reptiles in Europe. *J. Biogeogr.* 33:1712–1728.
- Arietta, Z.A., and D.K. Skelly. 2021. Rapid microgeographic evolution in response to climate change. *Evolution*. doi: <https://doi.org/10.1111/evo.14350>
- Barnosky, A. D., E. A. Hadly, J. Bascompte, E. L. Berlow, J. H. Brown, M. Fortelius, W. M. Getz, J. Harte, A. Hastings, P. A. Marquet, N. D. Martinez, A. Mooers, P. Roopnarine, G. Vermeij, J. W. Williams, R. Gillespie, J. Kitzes, C. Marshall, N. Matzke, D. P. Mindell, E. Revilla, and A. B. Smith. 2012. Approaching a state shift in Earth’s biosphere. *Nature* 486:52–58. Nature Publishing Group.
- Beebee, T. J. C. 1995. Amphibian breeding and climate. *Nature* 374:219–220.



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- Benard, M. F. 2015. Warmer winters reduce frog fecundity and shift breeding phenology, which consequently alters larval development and metamorphic timing. *Glob. Chang. Biol.* 21:1058–1065.
- Blaustein, A. R., L. K. Belden, D. H. Olson, D. M. Green, T. L. Root, and J. M. Kiesecker. 2001. Amphibian Breeding and Climate Change. 15:1804–1809.
- Blaustein, A. R., A. C. Hatch, L. K. Belden, E. Scheessele, and J. M. Kiesecker. 2003. Global change: challenges facing amphibians. Pp. 187–198 in R. D. Semlitsch, ed. *Amphibian conservation*. Smithsonian Institution, Washington, D.C.
- Blaustein, A. R., S. C. Walls, B. A. Bancroft, J. J. Lawler, C. L. Searle, and S. S. Gervasi. 2010. Direct and indirect effects of climate change on amphibian populations. *Diversity* 2:281–313.
- Blaustein, A. R., and D. B. Wake. 1990. Declining amphibian populations: a global phenomenon? *Trends Ecol. Evol.* 7:203–204.
- Bosch, J., S. Fernández-Beaskoetxea, T. W. J. Garner, and L. M. Carrascal. 2018. Long-term monitoring of an amphibian community after a climate change- and infectious disease-driven species extirpation. *Glob. Chang. Biol.* 24:2622–2632.
- Botero, C. A., F. J. Weissing, J. Wright, and D. R. Rubenstein. 2015. Evolutionary tipping points in the capacity to adapt to environmental change. *Proc. Natl. Acad. Sci. U. S. A.* 112:184–189.
- Botts, E. A., B. F. N. Erasmus, and G. J. Alexander. 2015. Observed range dynamics of South African amphibians under conditions of global change. *Austral Ecol.* 40:309–317.
- Bucciarelli, G. M., M. A. Clark, K. S. Delaney, S. P. D. Riley, H. B. Shaffer, R. N. Fisher, R. L. Honeycutt, and L. B. Kats. 2020. Amphibian responses in the aftermath of extreme climate events. 1–7.
- Burrowes, P. A. 2009. Climate change and amphibians. Pp. 3268–3287 in H. H. and J. W. Wilkinson, ed. *Amphibian Biology*. Surrey Beatty and Sons Publishers, Australia.
- Bush, M. B., M. R. Silman, and D. H. Urrego. 2004. 48,000 Years of Climate and Forest Change in a Biodiversity Hot Spot. *Science* (80-). 303:827–829.
- Bustamante, M. R., S. R. Ron, and L. A. Coloma. 2005. Cambios en la Diversidad en Siete Comunidades de Anuros en los Andes de Ecuador. *Biotropica* 37:180–189.
- Carey, C., and M. A. Alexander. 2003. Climate Change and Amphibian Declines : Is There a Link? *Divers. Distrib.* 9:111–121.
- Carey, C., N. Cohen, and L. Rollins-Smith. 1999. Amphibian declines: An immunological perspective. *Dev. Comp. Immunol.* 23:459–472.
- Caruso, N. M., M. W. Sears, D. C. Adams, and K. R. Lips. 2015. Widespread rapid reductions in body size of adult salamanders in response to climate change. *Glob. Chang. Biol.* 20:1751–1759.
- Catenazzi, A., 2015. State of the world's amphibians. *Annual Review of Environment and Resources*, 40:91–119.
- Cayuela, H., D. Arsovski, E. Bonnaire, R. Duguet, P. Joly, and A. Besnard. 2016. The impact of severe drought on survival, fecundity, and population persistence in an endangered amphibian. *Ecosphere* 7:1–12.
- Chadwick, E. A., F. M. Slater, and S. J. Ormerod. 2006. Inter- and intraspecific differences in climatically mediated phenological change in coexisting *Triturus* species. *Glob. Chang. Biol.* 12:1069–1078.
- Cone, R. E., and J. J. Marchalonis. 1972. Cellular and humoral aspects of the influence of environmental temperature on the immune response of poikilothermic vertebrates. *J. Immunol.* 108:952–957.
- Cooper, E. L., R. K. Wright, A. E. Klempau, and C. T. Smith. 1992. Hibernation alters the frog's immune system. *Cryobiology* 29:616–631.



Amphibian Conservation: Climate Change

- Corn, P. S. 2000. Amphibian declines: review of some current hypotheses. Pp. 663–696 in D. W. Sparling, C. A. Bishop, and G. Linder, eds. *Ecotoxicology of amphibians and reptiles*. Society of Environmental Toxicology and Chemistry, Pensacola, Florida.
- Corn, P. S. 2005. Climate change and amphibians. *Anim. Biodivers. Conserv.* 281:59–67.
- Corn, P. S. 2003. Linked references are available on JSTOR for this article : Amphibian Breeding and Climate Change : Importance of Snow in the Mountains. 17:622–625.
- Corn, P. S., and J. C. Fogleman. 1984. Extinction of Montane Populations of the Northern Leopard Frog (*Rana pipiens*) in Colorado Author (s): Paul Stephen Corn and James C. Fogleman Published by : Society for the Study of Amphibians and Reptiles Stable URL : <https://www.jstor.org/stable/15.18:147–152>.
- Corn, P. S., and E. Muths. 2002. Variable breeding phenology affects the exposure of amphibian embryos to ultraviolet radiation. *Ecology* 83:2958–2963.
- Crump, M. L. . 1984. Ontogenetic Changes in Vulnerability to Predation in Tadpoles of *Hyla pseudopuma*. *Herpetologica* 40:265–271.
- Daszak, P., D. E. Scott, A. M. Kilpatrick, C. Faggioni, J. W. Gibbons, and D. Porter. 2005. Amphibian population declines at Savannah River Site are linked to climate, not chytridiomycosis. *Ecology* 86:3232–3237.
- Daufresne, M., K. Lengfellner, and U. Sommer. 2009. Global warming benefits the small in aquatic ecosystems. *Proc. Natl. Acad. Sci. U. S. A.* 106:12788–12793.
- Donnelly, M. A., and M. L. Crump. 1998. Potential Effects of Climate Change on Two Neotropical Amphibian Assemblages. Pp. 401–421 in A. Markham, ed. *Potential Impacts of Climate Change on Tropical Forest Ecosystems*. Kluwer Academic Publishers, Washington, DC.
- Duellman, W. E., and L. Trueb. 1994. *Biology of Amphibians*. The Johns Hopkins University Press, Baltimore.
- Eggert, C.. 2004. Sex determination: the amphibian models. *Reprod. Nutr. Dev.* 44(6):539–549.
- Enriquez-Urzelai, U., N. Bernardo, G. Moreno-Rueda, A. Montori, and G. Llorente. 2019. Are amphibians tracking their climatic niches in response to climate warming? A test with Iberian amphibians. *Clim. Change* 154:289–301. *Climatic Change*.
- Feder, M. E., and W. W. Berggen. 1992. *Environmental physiology of the Amphibia*. University of Chicago Press, Chicago.
- Finlay, K. P., H. Cyr, and B. J. Shuter. 2001. Spatial and temporal variability in water temperatures in the littoral zone of a multibasin lake. *Can. J. Fish. Aquat. Sci.* 58:609–619.
- Gardner, J. L., A. Peters, M. R. Kearney, L. Joseph, and R. Heinsohn. 2011. Declining body size: A third universal response to warming? *Trends Ecol. Evol.* 26:285–291.
- Gervasi, S. S., and J. Foufopoulos. 2008. Costs of plasticity: Responses to desiccation decrease post-metamorphic immune function in a pond-breeding amphibian. *Funct. Ecol.* 22:100–108.
- Gibbs, J. P., and A. R. Breisch. 2001. Climate Warming and Calling Phenology of Frogs near Ithaca , New York , 1900 – 1999. 15:1175–1178.
- Gienapp, P., C. Teplitsky, J. S. Alho, J. A. Mills, and J. Merila. 2008. Climate change and evolution : disentangling environmental and genetic responses. *Mol. Ecol.* 17:167–178.
- Gramling, C. 2015. Arctic impact. *Science* (80-.). 347:818–821.
- Green (Donnelly), N., and N. Cohen. 1977. Effect of temperature on serum complement levels in the leopard frog, *Rana pipiens*. *Dev. Comp. Immunol.* 1:59–64.
- Heatwole, H., F. Torres, S. Blasini De Austin, and A. Heatwole. 1969. Studies on anuran water balance-I. Dynamics of evaporative water loss by the coquí, *eleutherodactylus portoricensis*. *Comp. Biochem. Physiol.* 28:245–269.



Amphibian Conservation: Climate Change

- Heyer, W. R., A. S. Rand, C. A. G. da Cruz, and O. L. Peixoto. 1988. Decimations, Extinctions, and Colonizations of Frog Populations in Southeast Brazil and Their Evolutionary Implications. *Biotropica* 20:230.
- Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Glob. Chang. Biol.* 12:450–455.
- Hoffmann, A. A., and C. M. Sgró. 2011. Climate change and evolutionary adaptation. *Nature* 470:479–485.
- Holden, W. M., S. M. Hanlon, D. C. Woodhams, T. M. Chappell, H. L. Wells, S. M. Glisson, V. J. McKenzie, R. Knight, M. J. Parris, and L. A. Rollins-Smith. 2015. Skin bacteria provide early protection for newly metamorphosed southern leopard frogs (*Rana sphenoccephala*) against the frog-killing fungus, *Batrachochytrium dendrobatidis*. *Biol. Conserv.* 187:91–102. Elsevier Ltd.
- Holomuzki, J. R. 1986. Predator avoidance and diel patterns of microhabitat use by larval tiger salamanders. *Ecology* 67:737–748.
- Huey, R. B., M. R. Kearney, A. Krockenberger, J. A. M. Holtum, M. Jess, and S. E. Williams. 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philos. Trans. R. Soc. B Biol. Sci.* 367:1665–1679.
- Ingram, G. J. 1990. The history of the disappearing frogs. *Wildl. Aust.* 27:6–7.
- Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. *Ecol. Lett.* 7:1225–1241.
- Kearney, M., R. Shine, and W. P. Porter. 2009. The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proc. Natl. Acad. Sci. U. S. A.* 106:3835–3840.
- Kilpatrick, A. M., C. J. Briggs, and P. Daszak. 2010. The ecology and impact of chytridiomycosis: an emerging disease of amphibians. *Trends Ecol. Evol.* 25:109–118.
- Kissel, A. M., W. J. Palen, M. E. Ryan, and M. J. Adams. 2019. Compounding effects of climate change reduce population viability of a montane amphibian. *Ecol. Appl.* 29:1–12.
- Kusrini, M. D., M. I. Lubis, W. Endarwin, M. Yazid, B. Darmawan, A. U. Ul-Hasanah, N. Sholihat, A. Tajalli, V. Lestari, H. Utama, D. M. Nasir, D. Ardiansyah, and R. Rachmadi. 2017. Elevation range shift after 40 years: The amphibians of Mount Gede Pangrango National Park revisited. *Biol. Conserv.* 206:75–84. Elsevier Ltd.
- Laurance, W. F. 1996. Catastrophic declines of Australian rainforest frogs: Is unusual weather responsible? *Biol. Conserv.* 77:203–212.
- Li, Y., J. M. Cohen, and J. R. Rohr. 2013. Review and synthesis of the effects of climate change on amphibians. *Integr. Zool.* 8:145–161.
- Lind, M. I., and F. Johansson. 2007. The degree of adaptive phenotypic plasticity is correlated with the spatial environmental heterogeneity experienced by island populations of *Rana temporaria*. *J. Evol. Biol.* 20:1288–1297.
- Lips, K. R. 1998. Decline of a Tropical Montane Amphibian Fauna. *Conserv. Biol.* 12:106–117.
- Lips, K. R., F. Brem, R. Brenes, J. D. Reeve, R. A. Alford, J. Voyles, C. Carey, L. Livo, A. P. Pessier, and J. P. Collins. 2006. Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. *Proc. Natl. Acad. Sci.* 103:3165–3170.
- Lowe, W. H. 2012. Climate change is linked to long-term decline in a stream salamander. *Biol. Conserv.* 145:48–53. Elsevier Ltd.
- Lowe, W. H., T. E. Martin, D. K. Skelly, and H. A. Woods. 2021. Metamorphosis in an Era of Increasing Climate Variability. *Trends Ecol. Evol.* 36:360–375. Elsevier Ltd.
- Maniero, G. D., and C. Carey. 1997. Changes in selected aspects of immune function in the leopard frog, *Ranapiens*, associated with exposure to cold. *J. Comp. Physiol. B* 167:256–263.



Amphibian Conservation: Climate Change

- Marsh, D. M., and P. C. Trenham. 2001. Metapopulation Dynamics and Amphibian Conservation. *Conserv. Biol.* 15:40–49.
- Martinez-Monzon, A., J. F. Bisbal-Chinesta, and H.-A. Blain. 2018. El Cuaternario ibérico como escenario para el estudio de anfibios y reptiles. *Ecosistemas* 27:87–95.
- Matutte, B., K. B. Storey, F. C. Knoop, and J. M. Conlon. 2000. Induction of synthesis of an antimicrobial peptide in the skin of the freeze-tolerant frog, *Rana sylvatica*, in response to environmental stimuli. *FEBS Lett.* 483:135–138.
- McMenamin, S. K., E. A. Hadly, and C. K. Wright. 2008. Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. *Proc. Natl. Acad. Sci. U. S. A.* 105:16988–16993.
- Meester, L. De, R. Stoks, and K. I. Brans. 2018. Genetic adaptation as a biological buffer against climate change: Potential and limitations. *Integr. Zool.* 13:372–391.
- Merila, J., and A. P. Hendry. 2014. Climate change, adaptatio , and phenotypic plasticity : the problem and the evidence. *Evol. Appl.* 7:1–14.
- Moskwick, M. 2014. Recent elevational range expansions in plethodontid salamanders (Amphibia: Plethodontidae) in the southern appalachian mountains. *J. Biogeogr.* 41:1957–1966.
- Muths, E., B. R. Hossack, E. H. Campbell Grant, D. S. Pilliod, and B. A. Mosher. 2020. Effects of snowpack, temperature, and disease on demography in a wild population of amphibians. *Herpetologica* 76:132–143.
- Nakamura, M. 2009. Sex determination in amphibians. *Semin. Cell Dev. Biol.* 20:271–282.
- Parmesan, C. 1996. Climate and species' range. *Nature* 382:765–766.
- Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. *Annu. Rev. Ecol. Evol. Syst.* 37:637–669.
- Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Glob. Chang. Biol.* 13:1860–1872.
- Parmesan, C., N. Ryrholm, C. Stefanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W. J. Tennent, J. a Thomas, and M. Warren. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399:579–583.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37.
- Pounds, A. J., M. R. Bustamante, L. A. Coloma, J. A. Consuegra, M. P. L. Fogden, P. N. Foster, E. La Marca, K. L. Masters, A. Merino-Viteri, R. Puschendorf, S. R. Ron, G. A. Sánchez-Azofeifa, C. J. Still, and B. E. Young. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439:161–167.
- Pounds, J. A., and M. L. Crump. 1994. Declines and Climate Amphibian The Case Disturbance : Toad and the of the Golden Frog Harlequin. *Soc. Conserv. Biol.* 8:72–85.
- Pounds, J. A., M. P. L. Fogden, and J. H. Campbell. 1999. Biological response to climate change on a tropical mountain. 398:611–615.
- Quintero, I., and J. J. Wiens. 2013. Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. *Ecol. Lett.* 16:1095–1103.
- Raffel, T. R., J. R. Rohr, J. M. Kiesecker, and P. J. Hudson. 2006. Negative effects of changing temperature on amphibian immunity under field conditions. *Funct. Ecol.* 20:819–828.
- Raffel, T. R., J. M. Romansic, N. T. Halstead, T. A. McMahon, M. D. Venesky, and J. R. Rohr. 2013. Disease and thermal acclimation in a more variable and unpredictable climate. *Nat. Clim. Chang.* 3:146–151. Nature Publishing Group.



Amphibian Conservation: Climate Change

- Rapacciuolo, G., S. P. Maher, A. C. Schneider, T. T. Hammond, M. D. Jabis, R. E. Walsh, K. J. Iknayan, G. K. Walden, M. F. Oldfather, D. D. Ackerly, and S. R. Beissinger. 2014. Beyond a warming fingerprint: Individualistic biogeographic responses to heterogeneous climate change in California. *Glob. Chang. Biol.* 20:2841–2855.
- Raxworthy, C. J., R. G. Pearson, N. Rabibisoa, A. M. Rakotondrazafy, J. B. Ramanamanjato, A. P. Raselimanana, S. Wu, R. A. Nussbaum, and D. A. Stone. 2008. Extinction vulnerability of tropical montane endemism from warming and upslope displacement: A preliminary appraisal for the highest massif in Madagascar. *Glob. Chang. Biol.* 14:1703–1720.
- Reading, C. J. 2007. Linking global warming to amphibian declines through its effects on female body condition and survivorship. *Oecologia* 151:125–131.
- Rohr, J. R., and D. M. Madison. 2003. Dryness increases predation risk in efts: support for an amphibian decline hypothesis.
- Rohr, J. R., and T. R. Raffel. 2010. Linking global climate and temperature variability to widespread amphibian declines putatively caused by disease. *Proc. Natl. Acad. Sci.* 107:8269–8274.
- Rojas, S., K. Richards, J. K. Jancovich, and E. W. Davidson. 2005. Influence of temperature on Ranavirus infection in larval salamanders *Ambystoma tigrinum*. *Dis. Aquat. Organ.* 63:95–100.
- Rollins-Smith, L. A., S. C. V. Parsons, and N. Cohen. 1988. Effects of thyroxine-driven precocious metamorphosis on maturation of adult-type allograft rejection responses in early thyroidectomized frogs. *Differentiation* 37:180–185.
- Root, T. L., A. Pounds, and C. Rica. 2003. Fingerprints of global warming on wild animals and plants. , doi: 10.1038/nature01333.
- Scholes, R., J. Settele, R. Betts, S. Bunn, P. Leadley, D. Nepstad, J. Overpeck, M. A. Taboada, C. Allen, W. Anderegg, and C. Bellard. 2014. *Terrestrial and Inland Water Systems*. Cambridge University Press.
- Seimon, T. A., A. Seimon, P. Daszak, S. R. P. Halloy, L. M. Schloegel, C. A. Aguilar, P. Sowell, A. D. Hyatt, B. Konecky, and J. E. Simmons. 2007. Upward range extension of Andean anurans and chytridiomycosis to extreme elevations in response to tropical deglaciation. *Glob. Chang. Biol.* 13:288–299.
- Sinervo, B., D. B. Miles, N. Martínez-Méndez, R. Lara-Resendiz, and F. R. Méndez-De La Cruz. 2011. Response to comment on “Erosion of lizard diversity by climate change and altered thermal niches.” *Science* (80-.). 332.
- Steigerwald, E., A. Sorokin, F. P. Condori, Y. J. Guevara, G. Crispin, and J. C. Chaparro. 2021. Elevational range extension of the marsupial frog, *Gastrotheca marsupiata* (Dumétil & Bibron, 1841) (Anura, Hemiphractidae), from southern Peru. *Check List* 17:145–150.
- Stewart, M. M. 1995. Climate Driven Population Fluctuations in Rain Forest Frogs. *J. Herpetol.* 29:437–446.
- Sunday, J. M., A. E. Bates, M. R. Kearney, R. K. Colwell, N. K. Dulvy, J. T. Longino, and R. B. Huey. 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc. Natl. Acad. Sci.* 111:5610–5615.
- Taylor, B. E., D. E. Scott, and J. W. Gibbons. 2006. Catastrophic reproductive failure, terrestrial survival, and persistence of the marbled salamander. *Conserv. Biol.* 20:792–801.
- Tejedo, M., F. Marangoni, C. Pertoldi, A. Richter-Boix, A. Laurila, G. Orizaola, A. G. Nicieza, D. Álvarez, and I. Gomez-Mestre. 2010. Contrasting effects of environmental factors during larval stage on morphological plasticity in post-metamorphic frogs. *Clim. Res.* 43:31–39.
- Thomas, C. D., C. D. Thomas, A. Cameron, A. Cameron, R. E. Green, R. E. Green, M. Bakkenes, M. Bakkenes, L. J. Beaumont, L. J. Beaumont, Y. C. Collingham, Y. C. Collingham, B. F. N. Erasmus, B. F. N. Erasmus, M. F. De Siqueira, M. F. De Siqueira, A. Grainger, A. Grainger, L. Hannah, L.



Amphibian Conservation: Climate Change

- Hannah, L. Hughes, L. Hughes, B. Huntley, B. Huntley, A. S. Van Jaarsveld, A. S. Van Jaarsveld, G. F. Midgley, G. F. Midgley, L. Miles, L. Miles, M. a Ortega-Huerta, M. a Ortega-Huerta, a T. Peterson, a T. Peterson, O. L. Phillips, O. L. Phillips, S. E. Williams, and S. E. Williams. 2004. Extinction risk from climate change. *Nature* 427:145–8.
- Timmermann, A., J. Oberhuber, A. Bacher, M. Esch, M. Latif, and E. Roeckner. 1999. Increased El Nino frequency in a climate model forced by future greenhouse warming. *Nature* 398:694–697.
- Tingley, M. W., M. S. Koo, C. Moritz, A. C. Rush, and S. R. Beissinger. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Glob. Chang. Biol.* 18:3279–3290.
- Todd, B. D., D. E. Scott, J. H. K. Pechmann, and J. Whitfield Gibbons. 2011. Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. *Proc. R. Soc. B Biol. Sci.* 278:2191–2197.
- Urban, M. C. 2015. Accelerating extinction risk from climate change. 148:148–162.
- Urban, M. C., J. L. Richardson, and N. A. Freidenfelds. 2013. Plasticity and genetic adaptation mediate amphibian and reptile responses to climate change. *Evol. Appl.* 7:88–103.
- Wake, D. B. 1991. Declining amphibian populations. *Science* 253:860.
- Wake, D. B. 2007. Climate change implicated in amphibian and lizard declines. *Proc. Natl. Acad. Sci. U. S. A.* 104:8201–8202.
- Wake, D. B., and V. T. Vredenburg. 2008. Are we in the midst of the sixth mass extinction ? A view from the world of amphibians. 105.
- Walther, G. R., E. Post, P. Convey, a Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Warren, R., J. Vanderwal, J. Price, J. A. Welbergen, I. Atkinson, J. Ramirez-Villegas, T. J. Osborn, A. Jarvis, L. P. Shoo, S. E. Williams, and J. Lowe. 2013. Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. *Nat. Clim. Chang.* 3:678–682. Nature Publishing Group.
- Weinbach, A., H. Cayuela, O. Grolet, A. Besnard, and P. Joly. 2018. Resilience to climate variation in a spatially structured amphibian population. *Sci. Rep.* 8:1–9. Springer US.
- Weygoldt, P. 1989. Changes in the Composition of Mountain Stream Frog Communities in the Atlantic Mountains of Brazil: Frogs as Indicators of Environmental Deteriorations? *Stud. Neotrop. Fauna Environ.* 24:249–255.
- Whitfield, S. M., K. E. Bell, T. Philippi, M. Sasa, F. Bolanos, G. Chaves, J. M. Savage, and M. A. Donnelly. 2007. Amphibian and reptile declines over 35 years at La Selva, Costa Rica. *Proc. Natl. Acad. Sci.* 104:8352–8356.
- Whitfield, S. M., K. R. Lips, and M. A. Donnelly. 2016. Amphibian Decline and Conservation in Central America. *Copeia* 104:351–379.
- Williams, C. M., H. A. L. Henry, and B. J. Sinclair. 2015. Cold truths: How winter drives responses of terrestrial organisms to climate change. *Biol. Rev.* 90:214–235.
- Woolbright, L. L. 1997. Local Extinctions of Anuran Amphibians in the Luquillo Experimental Forest of Northeastern Puerto Rico. *J. Herpetol.* 31:572–576.
- Wright, R. K., and E. L. Cooper. 1981. Temperature effects on ectotherm immune responses. *Dev. Comp. Immunol.* 5:117–122.
- Zellmer, A., J. Amanda, and S. Tatum. 2020. Clearing up the Crystal Ball : Understanding Uncertainty in Future Climate Suitability Projections for Amphibians. *Herpetologica* 76:108–120.