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REVIEW

Review and synthesis of the effects of climate change on amphibians

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Abstract

Considerable progress has been made in understanding the responses of amphibians to climate change, with successful research carried out on climate change-associated shifts in amphibian phenology, elevational distributions and amphibian–parasite interactions. We review and synthesize the literature on this topic, emphasizing acutely lethal, sublethal, indirect and positive effects of climate change on amphibians, and major research gaps. For instance, evidence is lacking on poleward shifts in amphibian distributions and on changes in body sizes and morphologies of amphibians in response to climate change. We have limited information on amphibian thermal tolerances, thermal preferences, dehydration breaths, opportunity costs of water conserving behaviors and actual temperature and moisture ranges amphibians experience. Even when much of this information is available, there remains little evidence that climate change is acutely lethal to amphibians. This suggests that if climate change is contributing to declines, it might be through effects that are not acutely lethal, indirect, or both, but evidence in support of this suggestion is necessary. In fact, evidence that climate change is directly contributing to amphibian declines is weak, partly because researchers have not often ruled out alternative hypotheses, such as chytrid fungus or climate–fungus interactions. Consequently, we recommend that amphibian–climate research shift from primarily inductive, correlational approach as to studies that evaluate alternative hypotheses for declines. This additional rigor will require interdisciplinary collaborations, estimates of costs and benefits of climate change to amphibian fitness and populations, and the integration of correlative field studies, experiments on 'model' amphibian species, and mathematical and functional, physiological models.

Key words: amphibian decline, *Batrachochytrium dendrobatidis*, breeding date, climate-linked epidemic hypothesis, global warming

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INTRODUCTION

The Earth is warming, and this has already had major consequences on biodiversity (Walther *et al.* 2002; Parmesan 2006). A meta-analysis of breeding dates and global warming for 203 species in the northern hemi-

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sphere shows that amphibians have had stronger shifts toward earlier breeding than all other taxonomic/functional groups (Parmesan 2007), advancing more than twice as fast as trees, birds and butterflies. Amphibians have permeable and exposed skin, shell-less eggs, complex life cycles (e.g. tadpoles of anurans need aquatic habitats and adults require terrestrial habitats) and are ectothermic, which renders them vulnerable to both aquatic and terrestrial changes in temperature and precipitation (Duellman & Trueb 1986). Important aspects of amphibian biology, such as growth, development, foraging and timing of hibernation and breeding, are likely to be affected by climate.

Approximately 41% of amphibian species are threatened with extinction (listed in the IUCN Red List as 'vulnerable', 'endangered' or 'critically endangered') (Hoffmann *et al*. 2010), one taxon having a percentage higher than any other vertebrate taxon (Stuart *et al*. 2004; Wake & Vredenburg 2008). In addition, many amphibian declines have occurred very recently. Approximately 7.6% of amphibians (435 species) are defined as 'rapidly declining species', which means they are in a higher IUCN threat category in 2004 than they were in 1980. To make matters worse, the threatened status of amphibians may be underestimated due to data deficiency. For instance, 22.5% of amphibian species (1294 species) are listed as data deficient, compared to only 0.8% of birds (78 species) and 5.3% of mammals (256 species) (Stuart *et al*. 2004).

Although there are many causes of amphibian declines, such as habitat loss, overexploitation, pollution, invasive species and emerging diseases (Stuart *et al*. 2004; Wake & Vredenburg 2008), the influence of global climate change on amphibians has been the subject of an increasing body of research in recent decades. Similarly, our understanding of the biological responses to climate change in general is increasing rapidly. For instance, it was only since 2009 that a third universal response to climate change, shrinking body sizes, was identified (Daufresne *et al*. 2009). Consequently, despite a few past reviews on the responses of amphibians to aspects of global climate change (Carey & Alexander 2003; Corn 2005; Blaustein *et al*. 2010), a new synthesis that identifies current gaps in the literature should help to further advance our understanding of climate change–amphibian interactions. Importantly, a consistent conclusion from previous reviews on this subject was that the evidence directly linking climate change to amphibian declines was tenuous (Carey & Alexander 2003; Corn 2005).

Part of the reason that the evidence directly linking climate change to amphibian declines is weak is that many researchers have taken a confirmatory or inductive approach to addressing the hypothesis rather than a hypothetico-deductive or parameter estimation-based approach. Consequently, important alternative hypothesis for amphibian declines were not considered or ruled out. A prominent alternative hypothesis to climate change-causing declines is the arrival of the amphibian chytrid fungus, *Batrachochytrium dendrobatidis* (*Bd*). Evidence suggests that chytridiomycosis, the disease caused by *Bd*, is a novel, infectious and fatal disease of amphibians in many regions of the globe (Skerrat *et al*. 2007). It is important to consider *Bd* as an alternative hypothesis to any decline because it is considered a well-documented cause of amphibian declines worldwide (Wake & Vredenburg 2008). Since the discovery of the pathogen by Berger *et al*. (1998), knowledge of its biology has increased rapidly. *Bd* infects the keratinized epidermis of metamorphosed amphibians and the tooth rows and jaw sheaths of anuran larvae (Berger *et al*. 1998; Longcore *et al*. 1999). It disrupts cutaneous osmoregulatory functions, leading to electrolyte imbalance and death of susceptible amphibians (Voyles *et al*. 2009). For additional information on *Bd*, we refer readers to Kilpatrick *et al*. (2010) and Fisher *et al*. (2009). Kilpatrick *et al*. (2010) review the emergence of this disease, including the origin of the pathogen, its impacts on host populations and the ecology of its transmission, and Fisher *et al*. (2009) review the molecular, epidemiological and ecological evidence that *Bd* evolved from an endemic ancestral lineage to achieve global prominence via anthropogenically mediated spread.

Here, we review and synthesize the literature on climate change effects on amphibians. We conducted a literature search in Google Scholar using the key words 'global warming' or 'climate change' + 'amphibians' or 'amphibian declines'. We organize this review into 5 sections: (i) direct lethal effects of climate change and climate-induced habitat loss; (ii) direct sublethal effects of climate change; (iii) indirect effects of climate change mediated by biotic factors; (iv) indirect effects of climate change mediated by abiotic factors; and (v) evidence for positive effects of climate change. Rather than simply reviewing the literature, we make an effort to evaluate the conclusions of studies, detect patterns in the literature and identify major knowledge gaps to guide future research.

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DIRECT LETHAL EFFECTS OF CLIMATE CHANGE AND CLIMATE-INDUCED HABITAT LOSS

Several rigorous studies have attributed amphibian declines to spells of warm, dry conditions that either desiccated post-metamorphic amphibians or eliminated aquatic habitat. For instance, D'Amen and Bombi (2009) found an association between warm, dry conditions and amphibian declines in Italy; Sodhi *et al*. (2008) discovered that IUCN Red List species experienced greater seasonal fluctuations in temperature and precipitation than species not on the Red List; and Lowe (2012) suggested that reductions in precipitation were reducing adult recruitment and causing salamander declines in New Hampshire. None of these studies, however, ruled out the arrival of the amphibian chytrid fungus as an explanation for these declines.

Pounds *et al*. (1999) show that the loss of amphibians at Monteverde, Costa Rica was associated with reduced dry-season mist frequency driven by global warming, which was negatively related to sea surface temperatures in the equatorial Pacific. Anchukaitis and Evans (2010) used high-resolution oxygen isotope measurements from trees to reconstruct a century of hydroclimatology in the Monteverde cloud forest of Costa Rica. They found that the inter-annual variability in dry season moisture was driven by El Niño events at the site, with no global warming trend. Consistent with the finding of Pounds *et al*. (1999), the extinction of golden toads in the Monteverde cloud forest coincided with an extremely dry season associated with the 1986–1987 El Niño event. While the patterns in these studies clearly suggest that increased dryness caused amphibian declines, alternative hypotheses, such as the arrival of *Bd*, were not considered. The authors also had only a single spatial location and, thus, the generality of their hypothesis remains unclear.

Analysis of population dynamics of 9 amphibian species at the Savannah River site in South Carolina, USA showed that 4 of 9 species declined significantly between 1978 and 2004 (Daszak *et al*. 2005). The 4 declining species had the longest larval periods and, therefore, the authors attributed the declines to an increase in the frequency of drought at the site, which reduced the length of time that standing water was available for larval development. The authors commendably considered the arrival of *Bd* as an alternative hypothesis to the amphibian declines. Their histological survey of museum specimens revealed that *Bd* was present in 1 of the declining species (*Rana sphenocephala* Cope, 1889), but none of the other 3 species [*Ambystoma talpoideum* (Holbrook, 1838b), *A. tigrinum* (Green, 1825) and *Pseudacris ornate* (Holbrook, 1836)] had museum specimens available or analyzed for *Bd*. Hence, it remains unclear whether the arrival of *Bd* increased due to dryness, or whether both were the cause of these declines.

In Yellowstone National Park, in western USA, recent climate warming and wetland desiccation have been attributed to severe declines in 4 native amphibian species (McMenamin *et al*. 2008). Over the past 6 decades, annual precipitation during the warmest months of the year decreased and temperature increased in the Park. As a result, the number of permanently dry ponds in northern Yellowstone increased 4-fold between 1992 and 2008. Amphibian abundance and species richness in the remaining ponds also declined significantly. This study, however, did not rule out other factors for the declines, such as the effects of disease or the synergy between climate change and disease (Corn 2007); the authors do acknowledge that outbreaks of *Bd* and ranavirus have been documented in all 4 species at Yellowstone (McMenamin *et al*. 2008). Further, several concerns were raised regarding the authors definition of a population, the lack of spatial independence among their replicates, the lack of consistency between the temporal patterns in their data and their conclusions and confounding sampling methods used to detect amphibians with time (Patla *et al*. 2009).

Whitfield *et al*. (2007) revealed that 17 species of amphibians and lizards at La Selva Biological Station, Costa Rica declined in density by 75% from 1970 to 2005. The amphibian chytrid fungus was not detected in 140 individuals collected from 3 amphibian species that declined, suggesting that *Bd* was probably not the reason for the declines. During the period of the study, minimum temperatures increased by ~1 ºC and the number of dry days per year decreased by ~50%. Warmer and wetter conditions are known to reduce leaf litter, a critical microhabitat for both amphibians and reptiles. Consequently, Whitfield *et al*. (2007) attributed the declines to climate-driven reductions in the quantity of standing leaf litter, but leaf litter unfortunately was not actually measured (Wake 2007). Conversely, Raffel *et al*. (2010) found that leaf litter was positively associated with *Bd* prevalence on amphibians. In contrast to all the studies described above that suggested that climate change was associated with amphibian declines, Davidson *et al*. (2002) found no correlation between climatic variables

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and declines of frogs in California, USA and there was little evidence that amphibian declines in USA (Colorado), Central America and Australia were associated with climate change (Alexander & Eischeid 2001; Carey *et al*. 2001).

Because of the concerns with many of the studies that asserted that climate change was directly associated with amphibian declines, we still lack convincing evidence that anthropogenic climate change alone has caused any declines of amphibians, a taxon with many species that have persisted through climatic changes in geological time that have greatly exceeded those observed in the last century. In fact, there are only a few cases, at best, where actual temperatures or moisture levels associated with recent amphibian declines clearly exceeded critical maxima or minima (Carey & Alexander 2003), which are the temperatures or moisture levels that are acutely lethal (see Box 1). Despite this limited evidence for a direct link between declines and warming and/or drying conditions, there are recent studies that offer insights into geographic locations where these climatic phenomena might pose the greatest threat to amphibians. For instance, Duarte *et al*. (2012) quantify the critical thermal maxima of 47 amphibian species located in temperate and subtropical zones. They discovered that the maximum field temperatures of subtropical species were much closer to their critical thermal maxima than were the maximum field temperatures of temperate species. This suggests that subtropical species might be more sensitive to small increases in temperature than are temperate species, consistent with previous work on ectothermic taxa in general (Deutsch *et al*. 2008; Dillon *et al*. 2010). However, global warming is expected to cause a greater increase in temperature in temperate than subtropical zones and, thus, the net effect of this differential warming and differential susceptibility is most important for determining the consequences of climate change and where to target our conservation efforts (Dillon *et al*. 2010; Rohr *et al*. 2011a,c; Box 1).

DIRECT EFFECTS OF CLIMATE CHANGE THAT ARE NOT ACUTELY LETHAL

Given that there is little evidence that climate change has been directly lethal to amphibians, if climate change is causing amphibian declines, it is likely doing so through non-acutely lethal or indirect effects (mediated by other organisms or factors) that eventually lead to their demise. Effects of climate change that are not acutely lethal are manifold and can include reduced foraging, increased desiccation, reduced fecundity, and shifts in phenology and distributions. In fact, there are 3 suggested universal responses of species to global warming: (i) changes in phenology; (ii) shifts in geographic distributions; and (iii) body-size reductions (Daufresne *et al*. 2009). We discuss each of these in turn and then discuss other effects of climate change that are not acutely lethal that could theoretically contribute to population declines.

Breeding phenology

Climate change is likely to alter the timing of seasons and, thus, it is possible that species may alter the timing (i.e. phenology) of their breeding. Many amphibian species aggregate around water bodies or wet microhabitats when they breed and male frogs often call when in breeding condition (Duellman & Trueb 1986). Therefore, the timing of amphibian breeding is easily observed and is, thus, used extensively by researchers in studies of phenology. Our search in Google Scholar revealed 14 long-term studies on the effects of global warming on the timing of amphibian breeding. These studies monitored breeding times over spans of 10–140 years. All the studies were conducted in the temperate zone of the northern hemisphere and at elevations ranging from 85–2040 m.

These studies included a total of 44 populations of 31 species, of which 28 populations showed earlier breeding dates (2–59.5 days), 13 populations showed no change in breeding dates and 3 populations bred later (15.3–76.4 days). Of the 21 species represented by only 1 population, 6 species showed no significant change in breeding dates and 15 species showed a change in breeding dates, with spring-breeding species tending to breed earlier and autumn-breeding species tending to breed later. Of the 10 species represented by multiple populations, the results are generally equivocal, with some species breeding earlier, some not changing their timing of breeding and others breeding later.

Interestingly, all but 1 of the studies on the effects of climate change on the phenology of amphibians are from the USA and Europe. This may be due to several factors, such as more scientific research occurring in the USA and Europe than in many other parts of the world or greater phenological research effort in temperate than tropical regions because of the more pronounced seasonality. It is important that the true cause of the biased geographic distribution of amphibian phenology studies be determined.

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Many of the documented shifts in amphibian phenology might have no impact on populations; alternatively, shifts in phenology could affect fitness and/or populations (Yang & Rudolf 2010). For instance, if amphibians are tempted out of hiding prematurely, they can be vulnerable to winter relapses that may be especially lethal to embryos and larvae that cannot withstand freezes (Gibbs & Breisch 2001; Todd *et al*. 2011). Single freeze events have been observed to wipe out entire populations (Heyer *et al.* 1988). Winter relapses can also slow embryo and larval growth, extending their exposure to UVB radiation, aquatic predators, and any contaminants that might be in freshwater ecosystems (Kiesecker *et al.* 2001; Rohr *et al*. 2011b). Moreover, if amphibians arrive at breeding sites before spring rains, their chances of desiccation might increase (Corn & Muths 2002).

Changes in the phenology of other species could also create disadvantages for species that begin breeding at historic times (Walther *et al.* 2002). For instance, using the example presented by Beebee (2002), earlier arrival of the protracted breeder *Bufo calamita* (Laurenti, 1768) could interfere with tadpoles of the explosive, early breeder *Rana temporaria* Linnaeus, 1758, leading to increased competition or potentially even predation of tadpoles. Walther *et al.* (2002) suggest the same problem but with newts (*Triturus* spp.) as an alternative potential predator. While it has been common to quantify shifts in amphibian breeding phenology associated with climate change, the consequences of these shifts on amphibian fitness or population dynamics have not been well studied and, thus, should be the emphasis of future research (Box 1).

Shifts in ranges

As the Earth warms, animals are predicted to shift their distributions poleward and to higher elevations. Poleward migrations have been observed in fish, insects, birds and mammals (Walther *et al*. 2002), but actual evidence of this phenomenon in herpetofauna is lacking. Bio-climatic envelope models, however, have been developed to predict how amphibians might shift their ranges in response to climate change (Araujo *et al*. 2006; Lawler *et al*. 2010). Araujo *et al*. (2006) suggest that, under the extreme assumption of universal dispersal, most of the 108 herpetofaunal species (42 amphibian species and 66 reptile species) in Europe would expand their distribution northward by 2050. Under the alternative extreme assumption of no dispersal, most species would lose a portion of their range. By assuming more realistic dispersal limitations of amphibians, Lawler *et al*. (2010) suggest that amphibian species in portions of the western hemisphere would experience high species turnover and would have more restricted ranges by 2071. Although we have predictions of the future distribution of amphibians, we have no tests of these predictions, little evidence that amphibians are shifting their ranges poleward, and a limited understanding of the dispersal limitations of amphibians and how land cover data will direct amphibian movements (Box 1).

There is some evidence of shifts in the elevational ranges of amphibian species in response to global warming. For example, between 1967 and 2003, 6 species in the Andes of Ecuador increased their altitudinal ranges in response to warming (Bustamante *et al*. 2005). In the Tsaratanana Massif of northern Madagascar, 3 of 19 amphibian species surveyed showed upslope trends and 1 a downslope trend associated with warming (Raxworthy *et al*. 2008). Forero-Medina *et al*. (2011) consider how land cover composition would affect the elevational shifts of montane amphibians in response to global warming and suggest that species that can get to suitable higher elevation habitats will be more isolated than previously, reducing the stability provided by meta-population structure, and that many species could be funneled to unsuitable habitat. Indeed, Laurance *et al*. (2011) reveal that, relative to endothermic vertebrates, tropical amphibians are upper elevational zone specialists with little room to shift to higher elevations with global warming. Additional research is needed to understand the limitations to dispersal that amphibians face with impending climate change (Early & Sax 2011; Box 1).

Shrinking body sizes

In addition to shifts in phenology and distributions, shrinking body sizes have recently emerged as a third important ecological response to climate change (Gardner *et al*. 2011; Sheridan & Bickford 2011). Several mechanisms are likely at work driving a decrease in body size with increasing temperatures (e.g. derivations of Bergmann's rule), one of which is that increases in temperature can increase metabolic rates, resulting in larger bodies being more energetically costly than smaller ones (Gardner *et al*. 2011; Sheridan & Bickford 2011). Sheridan and Bickford (2011) hypothesize that climate-change driven decreases in atmospheric dissolved O_2 and increases in the variability of precipitation could lead to smaller primary producers that, in turn, might decrease the body sizes of consumers (Fig. 1).

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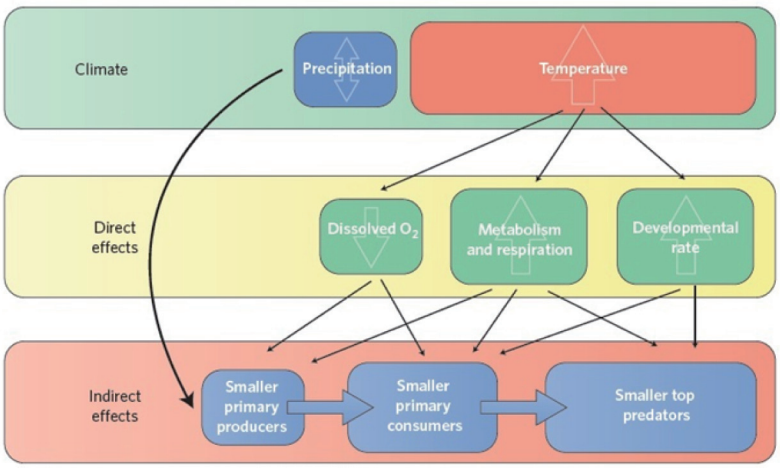

Figure 1 Hypothesized mechanism by which climate change might impact organismal body size (from Sheridan & Bickford 2011).

Evidence for negative correlations between body size and global warming is available for insects, crustaceans, fish, reptiles, birds and mammals (Gardner *et al*. 2011; Sheridan & Bickford 2011). It is hypothesized that ectotherms should be shrinking faster than endotherms because they cannot regulate their temperature like endotherms (Daufresne *et al* 2009). Evidence in amphibians, however, is scant and the evidence that does exist is inconsistent. There is evidence that mild winters are associated with a decrease in the size of the common toad, *Bufo bufo* (Linnaeus, 1758), especially for females, that eventually results in fewer eggs laid annually (Reading 2007). In contrast, cooler, high altitude sites had smaller bullfrogs, on average, than warmer, low altitude sites (Liu *et al*. 2010). In a study from 1963 to 2003, the body length of 2 of 3 Ranid frog species increased rather than decreased as habitat warmed (Tryjanowski *et al*. 2006). Further studies are needed to determine whether the body size or morphology of amphibians is changing with climate change and the potential consequences of any change on individual fitness and population sizes (Box 1). For instance, smaller body sizes might reduce fecundity and should increase the surface area-to-volume ratio of amphibians, potentially increasing the risk of desiccation for a taxon that is already relatively susceptible to dry conditions.

Other effects that are not acutely lethal

In addition to the 3 universal responses to climate change, there are several other sublethal effects of climate change that could affect amphibian fitness and contribute to amphibian declines. For instance, increased temperatures will increase amphibian metabolic rates and caloric needs. If amphibians cannot increase their food intake to meet these greater metabolic demands, growth and body condition could decline, which could increase their risk of desiccation and disease, and reduce fecundity and adult recruitment (Martin *et al*. 2010). Many regions of the globe are expected to become drier with climate change, which could increase the risk of desiccation. In addition, amphibians often exhibit water conserving behaviors when conditions dry, such as increasing their refuge use and burying and decreasing their activity and exposed surface area (Rohr & Madison 2003; Rohr & Palmer 2005). These behaviors, in most cases, preclude foraging and reproductive activities (Rohr & Madison 2003; Rohr & Palmer 2005), which, in turn, could reduce body size and condition, fecundity and recruitment. Indeed, increases in temperature and dryness have already been associated with reduced amphibian fecundity (Reading 2007) and adult recruitment (Lowe 2012).

We have observed substantial amphibian declines despite the fact that most shifts in temperature and moisture have been within the non-critical range (i.e. between the critical thermal or hydration minima and maxima) of amphibians. Although it is plausible, we simply lack studies that demonstrate that climatic shifts within the non-critical range can cause substantial amphibian mortality or amphibian population declines (Carey & Alexander 2003). Reductions in amphibian densities often reduce competition for resources in

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the survivors, and, thus, there can be density-mediated compensation to climate-induced reductions in survival (Vonesh & De La Cruz 2002; Rohr *et al*. 2006). Consequently, even if climate change has fitness consequences for some individuals, it might not cause population declines. We desperately need studies that can add to the weight of evidence that climatic shifts within the non-critical range can cause substantial amphibian mortality and amphibian population declines and that can demonstrate the mechanisms by which these shifts do so (Box 1).

INDIRECT EFFECTS MEDIATED BY BIOTIC FACTORS

Several authors have proposed that climate change might additively or synergistically enhance the threats that biotic factors, such as pathogens, predators and competitors, pose to amphibians. For instance, Pounds and Crump (1987) found that harlequin frogs in Costa Rica aggregate in waterfall spray zones as conditions dried and this increased their risk of predation by frog-biting flies. Similarly, elevated desiccation risk was shown to compromise the anti-predator behaviors of juvenile red spotted newts, *Notophthalmus viridescens* (Rafinesque, 1820) (Rohr & Madison 2003). Furthermore, species differences in phenological shifts in response to climate change or climate-induced expansions of the ranges of invasive species could result in new heterospecific competitive and predatory interactions among amphibians. For example, the predicted expansion of the range of the Cuban tree frog, *Osteopilus sepentrionalis* (Duméril & Bibron, 1841), with global warming could increase competition with adult amphibians or predation on native tadpoles (Rodder & Weinsheimer 2009).

Of the biotic factors that could interact with climate change, pathogens have probably received the most attention. For example, Kiesecker *et al*. (2001) provide evidence that El Niño-driven reductions in water depth increased the exposure of amphibian embryos to UVB, and increased amphibian mortality as a result of water mold, *Saprolegnia ferax* (although it is unclear whether this would have much of an effect on overall population dynamics; see Vonesh & De La Cruz 2002). Reductions in water depth were also shown to concentrate larval amphibians and trematode-infected snails, resulting in significant increases in amphibian trematode infections (Kiesecker & Skelly 2001).

Pounds and Crump (1994) propose the climate-linked epidemic hypothesis for amphibian declines. They hypothesize that amphibian declines are caused by epidemics triggered by particular climatic conditions and/or climate change. This hypothesis has been most frequently applied to *Bd*, probably because it is the one pathogen that seems to be causing amphibian declines globally (Stuart *et al*. 2004; Wake & Vredenburg 2008). This has prompted debates on whether global warming, *Bd*, or the combination of these 2 agents cause amphibian declines (Lips *et al*. 2006; Pounds *et al*. 2006; Alford *et al*. 2007; Bosch *et al*. 2007; Di Rosa *et al*. 2007; Lips *et al*. 2008; Rohr *et al*. 2008; Rohr & Raffel 2010).

Some authors propose the drought-linked chytridiomycosis hypothesis for declines of amphibians. According to this hypothesis, a prolonged or intensified dry season triggers or exacerbates outbreaks of chytridiomycosis (Pounds *et al*. 1999; Burrowes *et al*. 2004; Lampo *et al*. 2006). This hypothesis is based on the assumption that dry conditions can increase amphibian stress levels and, consequently, reduce immunity to *Bd* infections (Lampo *et al*. 2006), and can make amphibians aggregate at high densities at remaining moist microhabitats, which might promote the transmission of *Bd* (Pounds *et al*. 1999; Rohr & Madison 2003; Burrowes *et al*. 2004; Lampo *et al*. 2006). However, to date, evidence supporting the hypothesis has generally been lacking. Kriger (2009) argues that dry conditions are unlikely to benefit *Bd* because *Bd* has waterborne zoospores and cannot survive desiccation (Fisher *et al*. 2009; Kilpatrick *et al*. 2010). Moreover, amphibians live longer with *Bd* infections under dry than wet conditions (Bustamante *et al*. 2010). Furthermore, droughts are often accompanied by higher temperatures that can be unfavorable for the growth of *Bd* (Piotrowski *et al*. 2004). Indeed, amphibians can use warm temperatures to clear themselves of *Bd* (Woodhams *et al*. 2003; Chatfield & Richards-Zawacki 2011; Daskin *et al*. 2011) and there are negative associations between *Bd* abundance on amphibians and the temperature of freshwater ecosystems (Raffel *et al*. 2010; Forest & Schlaepfer 2011).

Pounds *et al*. (2006) propose the chytrid-thermal-optimum hypothesis for amphibian declines. This hypothesis assumes that the outbreaks of chytridomycosis are triggered by a shrinking thermal envelope, in which maximum temperatures decrease and minimum temperatures increase. This would shift temperature towards the optimal range for growth of *Bd*. Pounds *et al*. (2006) analyze the last year in which each of >100 species of harlequin frogs in the genus *Atelopus* were observed, in relation to changes in sea surface and air tempera-

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tures in Latin America. They conclude that temperatures at many highland localities were shifting towards the growth optimum of *Bd* and, thus, facilitated outbreaks of chytridiomycosis and associated amphibian declines. Several subsequent studies support the chytrid-thermal-optimum hypothesis. Bosch *et al*. (2007) found that rising temperatures due to the North Atlantic Oscillation were linked to the occurrence of chytridiomycosis in Peñalara Natural Park, Spain. Di Rosa *et al*. (2007) also find results consistent with the chytrid-thermal-optimum hypothesis, but argue that others factors must also be involved the declines. Two studies suggest that the patterns of amphibian declines in Australia agree with the chytrid-thermal-optimum and climate-linked epidemic hypotheses (Alford *et al*. 2007; Laurance 2008), but that multiple warm periods might be more important in amphibian declines than a single year-long period.

Lips *et al*. (2006) provide convincing evidence that *Bd* was spreading through the environment, showing that *Bd* caused amphibian declines upon its arrival to El Cope, Panama. Lips *et al*. (2008) argue that the introduction and spread of *Bd* was all that was necessary for it to cause declines and particular climatic conditions were unnecessary. By adding variability to the Pounds *et al*. (2006) data, they show that the climatic signal disappeared and conclude that there is no evidence for the climate-linked epidemic spread hypothesis. Both Rohr *et al*. (2008) and Parmesan and Singer (2008) point out that adding enough variability to any dataset will eventually eliminate significant associations and, thus, Lips *et al*. (2008) do not provide any evidence against the climate-linked epidemic spread hypothesis.

Rohr *et al*. (2008) re-analyze the data of Lips *et al*. (2008) and Pounds *et al*. (2006) but exclude assumptions regarding the location, timing and number of *Bd* emergences that were implicit to the Lips *et al*. (2008) study. They detect spatial structure in the timing of *Atelopus* species extinction, but the cause of this structure is not clear. They also detect a strong positive multi-decadal correlation between *Atelopus* species extinctions and mean tropical air temperature the previous year, supporting the patterns of Pounds *et al*. (2006) and subsequent studies (Alford *et al*. 2007; Bosch *et al*. 2007; Di Rosa *et al*. 2007; Laurance 2008) that use the same multi-decadal correlational approach of Pounds *et al*. (2006). However, Rohr *et al*. (2008) reveal that the evidence for mean tropical air temperature causing these amphibian extinctions is tenuous because numerous factors increased over the 3 decades analyzed, many of which were better predictors of these declines than climate change. Moreover, Rohr *et al*. (2008) estimate the annual growth of *Bd* based on temperature-dependent growth in culture and annual mean, maximum and minimum field temperatures. This analysis surprisingly reveals that the estimated amount of temperature-dependent *Bd* growth was a negative rather than positive predictor of amphibian declines, and, thus, Rohr *et al*. (2008) demonstrate that there was little support for the chytrid-thermal-optimum hypothesis.

A follow-up study was conducted by Rohr and Raffel (2010), in which they propose the climate variability hypothesis for amphibian declines associated with disease. Extending the hypothesis of Raffel *et al*. (2006), Rohr and Raffel (2010) postulate that the increased climatic variability and extreme events driven by global climate change would provide a temporary advantage to pathogens in host–pathogen interactions because pathogens are always smaller (fewer cells and processes) and have faster metabolisms than their hosts and, thus, should be able to acclimate more quickly upon a temperature shift. Rohr and Raffel (2010) evaluate this hypothesis using the *Atelopus* decline database, but look at fluctuations around the multidecadal trends to reduce the influence of temporal confounders. These analyses reveal that mean climate variables are not nearly as strong of predictors of these fluctuations in amphibian declines as are variables representing climatic variability, consistent with recent work revealing that diurnal temperature range, a measure of temperature variability, is predictive of *Bd* abundance on frogs in Australia (Murray *et al*. 2011). Indeed, Rohr and Raffel (2010) show that factors reflecting temperature variability are the only proximate climate variables that are entirely consistent with the spatiotemporal patterns of declines known to be caused by *Bd*, and they provide evidence that global El Niño events might be driving *Atelopus* declines via increased regional temperature variability (Fig. 2). These patterns, however, were not apparent unless a pattern consistent with intrinsic spatial spread of *Bd* was controlled for, emphasizing that the primary factor influencing the spread of *Bd* was probably suitable hosts, followed secondarily by suitable climatic conditions. Hence, this paper provides evidence for both spread of *Bd*-related declines and climatic influences on this spread and, thus, offers some of the strongest evidence for both components of the climate-linked-epidemic-spread hypothesis.

To provide an empirical test of the climate-variability hypothesis, Raffel *et al*. (2013) tested whether temperature shifts actually increased *Bd* growth and mortality of frogs. They demonstrated that frogs that experienced a temperature shift, especially a temperature drop, had both more *Bd* and greater mortality than frogs that expe-

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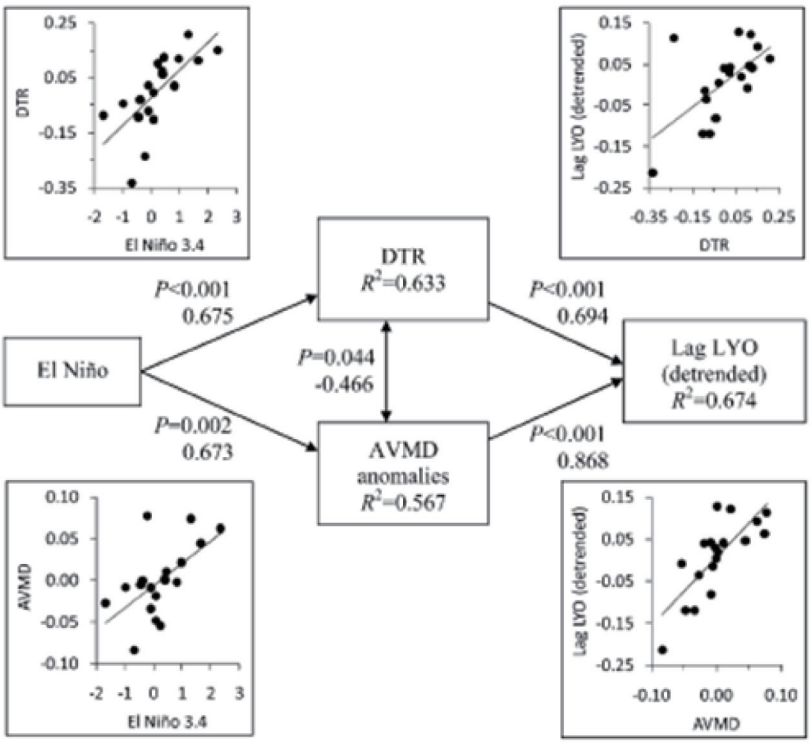

Figure 2 Results of a path analysis testing for relationships among Nino 3.4 (a measure of the strength of an El Niño event), the absolute value of monthly differences in temperature (AVMD), the diurnal temperature range (DTR) and the annual detrended proportion of *Atelopus* species that were observed for the last time (last year observed, LYO). Probability values, standardized coefficients and scatter plots, respectively, are provided next to each path. The scatter plots are based on the residuals from the relationship between AVMD and DTR (from Rohr & Raffel 2010).

rienced a constant temperature, providing a causal link between temperature variability and *Bd*-induced mortality. Raffel *et al*. (2013) also demonstrate that these findings are consistent with a mathematical model on how temperature variability should affect host–parasite interactions. Furthermore, they show that drops in temperature are more predictive of *Atelopus* declines than increases in temperature. This result is consistent with work demonstrating that *Bd* outbreaks generally occur during cool seasons (Retallick *et al*. 2004; Kriger & Hero 2007; Kinney *et al*. 2011) and that drops in temperature trigger the release of *Bd* zoospores (Woodhams *et al*. 2008), reduce the ability of amphibians to mount an antimicrobial skin peptide-based immune response (Ribas *et al*. 2009), and, instead, induce a more pronounced inflammatory reaction that is associated with higher *Bd* burden. Work on the climate variability hypothesis for amphibian declines provides an example of the value of taking a hypothetico-deductive or parameter estimation-based approach to science and linking models, field patterns and experiments to enhance the weight of evidence supporting a hypothesis (Box 1).

Given the growing support for a link between climate and *Bd* growth, authors have emphasized the importance of developing models to predict the future distribution of *Bd* under various climate change scenarios (Rohr *et al*. 2011b). This might help target limited conservation resources and prepare for future threats. Rodder *et al*. (2010) use maximum entropy species distribution models to forecast the future distribution of *Bd* and suggest that anthropogenic climate change might actually reduce both its geographic extent and its impact on amphibian biodiversity (Fig. 3). These models, however, do not explicitly consider temperature variability and their accuracy will depend on the general limitations of species distribution modeling and on how well the amphibian–*Bd* system meets the many assumptions of these correlative models (Rohr *et al*. 2011b).

INDIRECT EFFECTS MEDIATED BY ABIOTIC FACTORS

Climate change might also interact with other abiotic factors to affect amphibians. Hof *et al*. (2011) assess the

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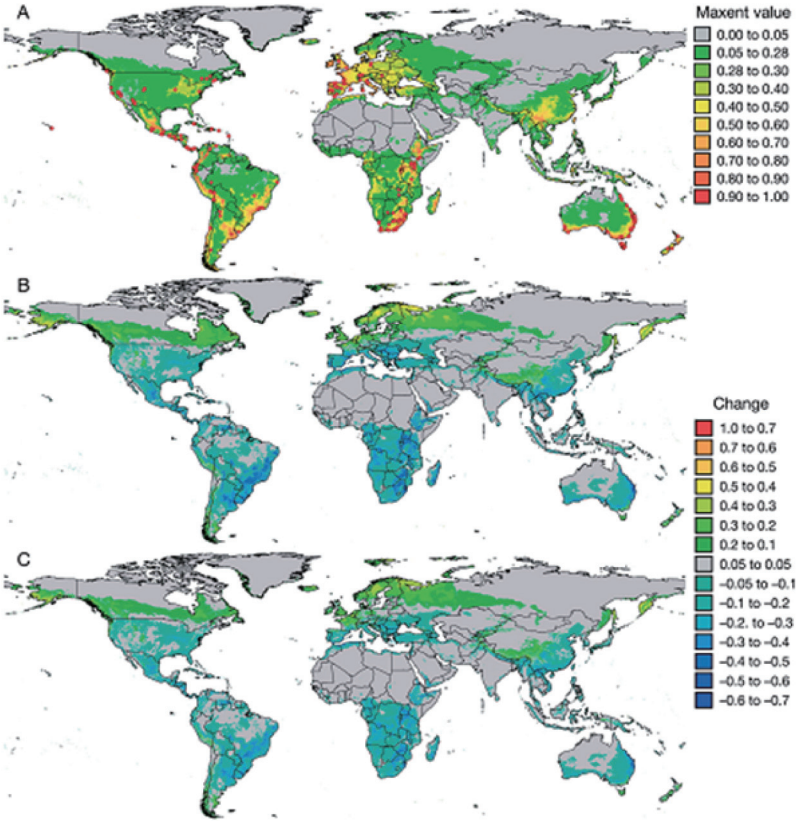

Figure 3 (A) Potential distribution of *Batrachochytrium dendrobatidis* (*Bd*) under current climatic conditions based on a Maxent species distribution model (SDM) and *Bd* presence localities used for SDM building (red dots), with warmer Maxent colour indicating higher suitability to the fungus. (B) Change in the potential distribution of *Bd* under future climatic scenarios (i.e. the year 2080) relative to current conditions based on mean values per grid cell of the A2a family when projected onto the CCCMA, CSIRO and HADCM3 models. (C) Change computed with the mean predictions of the climate change models assuming B2a conditions (from Rodder *et al*. 2010).

spatial distribution and interaction of 3 threats to amphibians: climate change, land-use change and *Bd*. Their models indicate that regions with the highest projected change in land-use and climate coincide, but largely do not overlap with the highest areas of *Bd* suitability. Consequently, they suggest that future habitat loss and climate change are more likely to additively or synergistically interact to affect amphibians than are future habitat loss and *Bd* or climate change and *Bd*. Their models, however, do not explicitly consider temperature variability.

Climate change is also expected to increase the frequency and intensity of fires and other catastrophic natural disasters. Much of the literature on amphibian responses to fire suggests that it has few adverse effects on amphibians (Pilliod *et al*. 2003; Hossack & Corn 2007). However, whether amphibians are capable of withstanding the projected increases in the frequency and intensity of fires remains to be seen (Pilliod *et al*. 2003).

Anthropogenic climate change will also cause sea level rise and more intense hurricanes with greater storm surges. Although most amphibians do not inhabit salt water environments, as sea level rises, there will be salt water intrusion into freshwater environments. Consequently, there will inevitably be a reduction in freshwater habitats for amphibians along coastlines. Indeed, salt water intrusion and damage from several hurricanes was significantly associated with reductions in amphibian abundance and diversity in Louisiana, USA (Schriever *et al*. 2009).

Climate change might also affect levels of UV radiation. The effect of UV on amphibians has been a topic of extensive and controversial research. Given the size of this literature and space limitations, we will not review it here. We encourage interested readers to examine meta-analyses on the effects of UV on aquatic organisms and amphibians by Bancroft *et al*. (2007, 2008) and several arguments against the role of UV in amphibian declines (e.g. Palen *et al*. 2002; Palen & Schindler 2010).

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Pounds and Crump (1994) propose the climate-linked contaminant pulse hypothesis, whereby atmospheric contaminants scavenged by mist and cloud water in montane areas reach critical concentrations when conditions are abnormally warm and dry. Little support for or against this hypothesis exists because of the lack of good information on: (i) the spatiotemporal contaminant concentrations to which amphibians are exposed; (ii) the synergistic actions of various chemicals; and (iii) the physiological responses of amphibians to these exposures (Carey *et al*. 2001). Davidson *et al*. (2001) provide some support for this hypothesis by demonstrating a correlation between upwind pesticide use and the decline of alpine frogs in California, USA, but more recent work suggests that the arrival of *Bd* is a more parsimonious explanation for these declines (Bradford *et al*. 2011). Studies do propose, however, that climate change could exacerbate the effects of pollution in several ways. Recent research suggests that climate change might increase the use of pesticides (Kattwinkel *et al*. 2011), enhance the toxicity of contaminants (Noyes *et al*. 2009), and increase the damage caused by contaminant releases (Rohr *et al*. 2013). In contrast, warmer temperatures will reduce the duration of the aquatic larval period for many amphibians, which should reduce their exposure to contaminants that concentrate and accumulate in freshwater ecosystems (Rohr *et al*. 2011b). Consequently, to determine the net effect of climate change–pollution interactions on amphibians, we must consider both the positive and negative effects of these 2 factors (Rohr *et al*. 2011b; Box 1).

EVIDENCE FOR POSITIVE EFFECTS OF CLIMATE CHANGE

Thus far, we have predominantly emphasized the adverse effects of anthropogenic climate change on amphibians because amphibians are declining, but climate change might also have positive effects on amphibian fitness and populations. Climate has fluctuated throughout the evolutionary history of living organisms, and amphibians have not only survived 4 mass extinctions associated with major climate disturbances (Carey & Alexander 2003; Wake & Vredenburg 2008), but have often thrived following them. A study on the phylogenetic relationship and historic biogeography of Holarctic plethodontids reveals that historic global warming benefited the plethodontid salamanders (Vieites *et al*. 2007). Like angiosperms, arthropods, birds and mammals, the rapid diversification and dispersal of plethodontid salamanders coincided with major global warming events during the late Cretaceous and again during the Paleocene Eocene thermal optimum period. This concurs with the species distribution models of Araujo *et al*. (2006), which suggest that global warming will benefit amphibians more than cooling. Similarly, McCaffery and Maxell (2010) use 9 years of demographical information to show that a warming climate with less severe winters is likely to promote population viability of Columbia spotted frogs, *Rana luteiventris* Thompson, 1913, by increasing winter survival and breeding probability. They suggest that amphibians and other ectotherms inhabiting alpine or boreal habitats, currently at or near their thermal ecological limits, might benefit from milder winters associated with a warming climate if suitable habitats remain intact. Likewise, some models suggest that warming might make *Bd* less problematic (Rodder *et al*. 2010; Hof *et al*. 2011) and empirical work suggests that warming might reduce amphibian exposure to contaminants by accelerating their aquatic larval development (Rohr *et al*. 2011b).

DISCUSSION AND CONCLUSIONS

The progress made in understanding the effects of climate on amphibian fitness and populations is laudable, especially given the fledgling nature of the discipline. However, like any young and burgeoning area of research, there are many unanswered questions and advances to be made. Although climate change-associated shifts in amphibian phenology have been well documented, shifts in the distributions, body sizes and morphologies of amphibians in response to climate change have not been well studied. Cases where actual temperatures or moisture levels have clearly exceeded the critical maxima or minima of extirpated or extinct amphibians are rare. This suggests that if climate change is contributing to declines, then it might be doing so through effects that are indirect, not acutely lethal, or both. Consequently, we need more convincing evidence that climatic shifts within the non-critical range (between the critical maximum and minimum) can cause population declines and evidence that common biotic and/or abiotic factors additively or synergistically interact with climate change to facilitate amphibian losses. If climate change is contributing to declines, we hope it is only doing so through indirect mechanisms because it will be almost impossible for local wildlife managers and practitioners to manage global climate change, but it might be feasible for them to manage more local biotic or abiotic factors that interact with climate to enable declines (Box 1). Never-

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BOX 1 FUTURE RESEARCH DIRECTIONS

Phenology

While it has been common to quantify shifts in amphibian breeding phenology associated with climate change, the consequences of these shifts on amphibian fitness and population dynamics have not been well studied.

Distributional shifts

Although we have predictions of the future distribution of amphibians under various climate change scenarios, we have no tests of these predictions, little evidence that amphibians are shifting their ranges poleward or up in elevation, a limited understanding of the dispersal limitations of amphibians and how land cover data will direct amphibian movements, and very little information on the consequences of any distributional shifts on amphibian fitness and population dynamics.

Body size

Is climate change causing reductions in amphibian body sizes and/or changes in their morphology and, if so, what are the consequences at the level of the individual and population?

Importance of non-acutely lethal effects

There are only a few cases, at best, where actual temperatures or moisture levels have clearly exceeded the critical maxima or minima of extirpated or extinct amphibians. Consequently, we need more convincing evidence that climatic shifts within the non-critical range (between the critical maximum and minimum) can cause substantial amphibian mortality and population declines and that demonstrate the mechanisms by which they do so.

Importance of indirect effects

Various biotic and abiotic factors might additively and synergistically interact with climate change, but the evidence for these interactions is lacking. We need to better understand which factors interact with climate change and the importance of these interactions to declines relative to direct effects of climate change that are acutely lethal or have more chronic effects. If indirect effects of climate change are the cause of many amphibian declines, then locally managing the biotic or abiotic factors that interact with climate change might be a more promising approach to reducing amphibian declines than attempting to manage climate change itself.

Relative importance of components of climate change

Climate change is expected to alter many components of the environment, such as ultraviolet radiation, carbon dioxide levels, and the mean, range and variances of temperature and moisture. Our understanding of the relative importance of these components of climate change on amphibians is limited but is important because it could help target management.

More rigor

Much of the work on the links between amphibian declines and climate change has been correlative and taken an inductive approach. We encourage hypothetico-deductive and parameter estimation approaches that rule out, or evaluate the level of support for, alternative hypotheses to the declines (e.g. arrival of *Bd*, habitat loss, interactions among these 2 factors and climate change). We also encourage linking field studies, models and experiments to increase the weight of evidence for a causal association between climate change and amphibian declines.

Species-specific data and functional models

For most amphibians, thermal tolerance and dehydration breaths and current maximum environmental temperatures and minimum environmental moisture levels are unknown, but are crucial for determining whether climate change is acutely lethal or has substantial sublethal effects. Furthermore, these data are crucial for parameterizing functional models that might be more predictive of the impacts of climate change on amphibian species than correlational-based models (e.g. species distribution models).

Engineering a future for amphibians under climate change

How feasible and effective is it to combat the potential adverse effects of climate change on amphibians by increasing shelters and canopy cover and installing irrigation to maintain water potentials in wetland and upland habitats?

Net effects

Climate change should have both positive and negative effects on amphibians. Furthermore, regions will experience different intensities of climate change and have species with different sensitivities to climate change. Hence, we need to be sure to estimate the net effect of climate change on species.

theless, researchers have suggested testing the feasibility of several local and regional management options to combat adverse effects of climate change on amphibians, such as the installation of irrigation to maintain water potential at breeding sites; the addition of shelters in upland habitats (e.g. logs and cover boards) to reduce desiccation and thermal stress; increasing canopy cover over ponds and upland habitats to reduce temperatures; and ensuring that there are hydrologoically-diverse and connected wetland habitats to support larval development under variable precipitation regimes (Shoo *et al*. 2011; Box 1).

Perhaps the most important recommendation we have is to make an effort to shift from a primarily inductive,

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correlational approach to understanding climate–amphibian interactions to more hypothetico-deductive and parameter estimation approaches that rule out, or evaluate the level of support for, alternative hypotheses to declines. Most effects of climate change on populations will occur in the future, when climate change intensifies, and, thus, cannot yet be observed in the field. In addition, evidence in support of climate change directly contributing to amphibian declines is weak, at least partly because researchers have not often ruled out plausible alternative explanations for the declines, such as the arrival of *Bd* or climate change–*Bd* interactions. Given the many amphibian species that are extinct and, therefore, unavailable to study, this additional and necessary rigor will almost certainly entail using a combination of correlative field studies, experiments on extant 'model' amphibian species, mathematical models and interdisciplinary collaborations to build a weight-of-evidence case for a causal association between climate change and amphibian declines (Box 1).

One approach that might prove useful is the implementation of more functional, physiological-based models coupled with field data on climate. Measurements of amphibian thermal tolerances, thermal preferences, dehydration breaths, opportunity costs of water conserving behaviors and actual temperature and moisture ranges that amphibians experience would be crucial for determining whether climate change is acutely lethal or has substantial sublethal effects. Moreover, these data would be crucial for parameterizing functional, physiological models that might be more predictive of the impacts of climate change on amphibian species than correlational-based models (e.g. species distribution models) (Kearney *et al*. 2008; Kearney & Porter 2009; Buckley *et al*. 2010). Finally, we must remember that climate change will likely have both positive and negative effects on amphibians and that geographic regions will vary in terms of both the severity of and species sensitivities to climate change. Hence, we must make a concerted effort to quantify the net effect of climate change on species in general (Box 1).

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SUPPORTING INFORMATION

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Table S1 Long-term studies on the relationships between breeding dates of amphibians and climate factors

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