Threats

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Bolitoglossa mombachoensis lives in the cloud forest on the uppermost elevations of Volcán Mombacho in Nicaragua. It is listed as Vulnerable, but this status may worsen as climate change and deforestation of lowland forests are predicted to reduce humidity in the cloud forest. © Sean Michael Rovito

Chapter 3

Climate change

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Abstract

Amphibian ecology and distribution are strongly correlated with climate. Regional patterns of amphibian biodiversity are intimately linked to temperature, evapotranspiration rate, and clines in humidity. While amphibians are and will continue to be adversely affected by recent and projected changes in climate, research suggests that adaptation may happen more slowly than the expected rate of environmental shifts. Here, we review conservation-relevant aspects of both realised and potential impacts of climate change, and outline options for amphibian conservation planning and management. Recent advances in our understanding of climate change impacts on amphibians have primarily stemmed from ecological modelling and direct assessment of climatic tolerances and dispersal capacities through physiological assays, landscape genetics, and dispersal tracking. Anthropogenic climate change has already altered amphibian assemblages and their impacts on ecosystem functioning and services. Because of known and hypothesised ecological tolerances, many amphibians might have reached or exceeded most limits in their ability to adapt to or tolerate further climate change, however the uncertainties are substantial. Implementation of conservation planning and action can help to forestall severe impacts of environmental shifts. Scientific research and science-based decision-making and policy development have already lagged; the current pace of conservation planning and action may not allow for effective identification of threats and mitigation. An increased response rate could help to avert further loss of amphibian biodiversity and decay of ecosystem services. The lack of basic field research in natural habitats continues to be an underlying challenge. We suggest priority areas of research to include the development of biologically realistic predictive models of amphibian response to climate change, field verification of model estimates and key parameters, population monitoring across multiple sites and taxa, and a combination of efforts within and across ecosystems to understand how impacts of climate change can be better mitigated.

Introduction

Anthropogenic climate change is affecting biodiversity, globally (Parmesan & Yohe, 2003; Rosenzweig et al., 2008; Scheffers et al., 2016; Walther et al., 2002) – with a particularly strong impact on amphibians (IPCC, 2014; Li, Cohen & Rohr, 2013; *also see* Figure 3.1). Although these animals have adapted to and survived past changes to the Earth's climate (Fey et al., 2015), the contemporary rate of climate change is higher than those previously witnessed over evolutionary scales, with most amphibians in the "slow" ecological response rate category (Williams, Ordonez & Svenning, 2021). All aspects of climate change – air and sea surface temperatures, solar radiation, UV, humidity, cloud cover, precipitation, extreme weather event frequency, and sea level rise – can affect amphibian biodiversity (*see* Figure 3.2). Many amphibian populations are also under additional stress due to other drivers, such as disease and habitat loss, which amplify when acting in synergy (Alton & Franklin, 2017; Cordier et al., 2020; Velasco et al., 2021). Here, we identify key impacts of climate change on amphibians, possible biological response-to-climate-change scenarios, research gaps, and potential management strategies and policy considerations for conservation actions. We offer this review in the context of the larger ACAP 2024, offering a pluralistic overview of extinction drivers and real-world solutions.

Status update

Observed impacts of climate change on amphibians

- #### Observed population declines and changes in distribution

   Despite very limited long-term data and ongoing surveys on amphibian populations, we have documented declines and potential increasing synergies of extinction drivers. Cahill et al. (2013) evaluated local population extirpations with climate change or weather variation and found just two studies on amphibians. Since then,

however, numerous studies have demonstrated similar population extirpations and range losses due to climate change. For example, in *Lithobates yavapaiensis* severe drought drove high mortality and population extirpation (Zylstra et al., 2019), *Pseudophryne pengilleyi* lost 42% of its breeding sites following drought (Scheele et al., 2012), and *Ambystoma talpoideum* populations were extirpated following drought and flooding (Walls, Barichivich & Brown, 2013). Species' Red List assessments which specifically reference climate change include 107 CR (Critically Endangered), 105 EN (Endangered), 35 VU (Vulnerable), and 19 NT (Near Threatened) assessed species, with drought, habitat shifts and alteration, storms, and flooding as the top three specific climate change threats (IUCN, 2020).

- #### Observed extinctions

   Of the 37 amphibian species classified by The IUCN Red List of Threatened Species™ (Red List) as Extinct or Extinct in the Wild, six implicate climate change as a causal threat, often through synergies with disease and habitat loss, but also more directly as a result of extreme weather, such as flooding and drought (https://www.iucnredlist.org). This allows us to contextualise contemporary amphibian extinctions due to climate change relative to the group's background extinction rate. Although efforts to quantify extinction rates among amphibians are complicated by the limited fossil record (particularly in the tropics), imprecise knowledge of the species richness, unknown life history traits of some clades, and imperfect detection, data from a single amphibian fossil assemblage suggested a background extinction rate of 5.2% per million years (Alroy, 2015). Estimates of contemporary extinction also vary: although IUCN reports 37 species as Extinct (EX) or Extinct in the Wild (EW) (IUCN, 2020), other estimates suggest at least 200 species of frogs alone have gone extinct in recent decades (Alroy, 2015), and contemporary extinction rates that

a)

b)
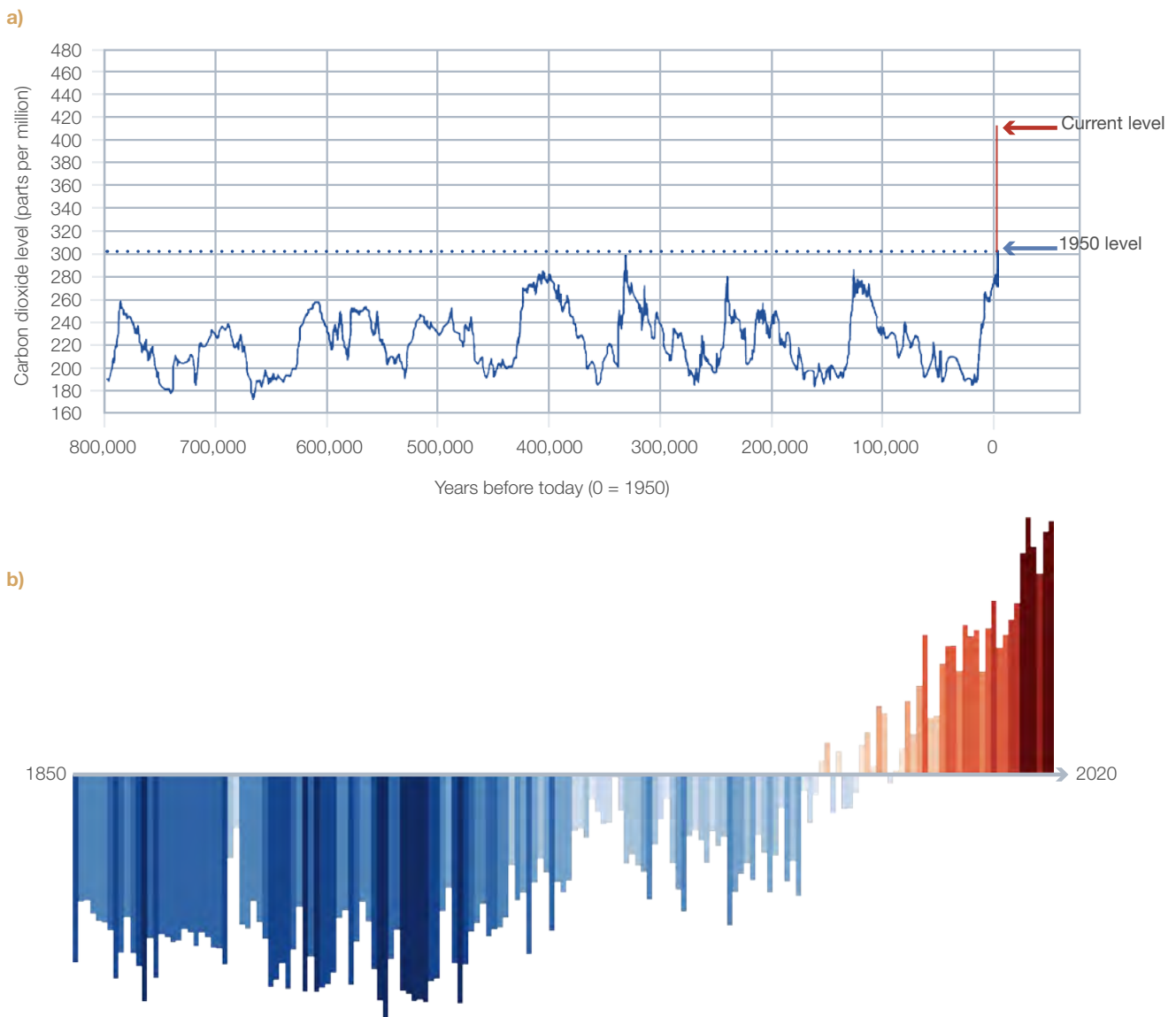
Figure 3.1: Trends in **a)** atmospheric carbon dioxide and **b)** global temperature. **a)** Atmospheric carbon dioxide has not been above the blue dotted line during the past 800,000 years. Source: NASA (https://climate.nasa.gov/climate_resources/24/graphic-the-relentless-rise-of-carbon-dioxide/), and **b)** Global temperatures have increased by over 1.2°C since 1850. Source: Warming Stripes - Ed Hawkins, University of Reading (https://showyourstripes.info/).

are 211 times greater than background extinction rates (McCallum, 2007; Millennium Ecosystem Assessment, 2005).

Updating estimates from Barnosky et al. (2011) to reflect current Red List assessments of recognised extinctions and current species richness (https://amphibiaweb.org/ and https://www.iucnredlist.org), we estimate an amphibian extinction rate of 9 extinctions per 1000 species per 1000 years (or million species-years) over the past 500 years.

Estimating extinction at the same time scale, but limiting it to those species for which climate change has been implicated as a threat (currently 6 species categorized as Extinct or Extinct in the Wild), results in 1.5 extinctions per million species-years. This estimate jumps to 80 extinctions per million species-years due to climate change-related threats if we assume an extinction debt, that without human intervention, assumes species currently categorised as Vulnerable or Endangered will ultimately become Extinct.

Figure 3.2: Theoretical framework of direct and indirect drivers of extinction threat and decline risk to amphibians posed by climate change. Source: Developed by David Bickford, Guinevere Wogan and Soledad Delgado Oyarzún

● **Observed changes in phenotype and phenology**

As ectotherms, amphibians are among the few taxa likely to respond strongly to changing climate (Buckley, Hurlbert & Jetz, 2012). Determining the ability and extent that a species can undergo phenotypic adaptations or respond to phenological shifts because of climate change are among the key ongoing research questions (Radchuk et al., 2019). The recent focus on amphibian phenotypic responses provides nascent insights into expected trends with a warming climate, although more studies are needed to support or refute these hypotheses. One prediction is that amphibians will respond to warming climate by reducing body size (Sheridan & Bickford, 2011). Reductions in body size may affect reproductive output and demography (Hernández-Pacheco et al., 2021). Studies have detected signatures in support of this prediction in several species of amphibians such as the *Plethodon* salamanders (Caruso et al., 2014); worsening body condition in the California newt *Taricha torosa* (Bucciarelli et al., 2020), and the common toad *Bufo bufo* along with a confounding decrease in reproductive output (Reading, 2007).

However, the predicted phenotypic response has not been recorded in all species analysed, such as North American wood frog (*Lithobates sylvaticus*) and a mole salamander (*Ambystoma maculatum*) (Kirk, Galatowitsch & Wissinger, 2019; Sheridan et al., 2018). In contrast, the reverse trend has been observed in some species with body size increase in response to climate change, as observed over four decades in *Hynobius tokyoensis* (Okamiya, Hayase & Kusano, 2021). A second prediction is that within colour polymorphic species, some morphs may have advantageous functional associations related to climatic conditions, although there is debate about the directionality of change (lighter or darker; Delhey et al., 2020; Tian & Benton, 2020). This has been extensively studied in the eastern red-backed salamander (*Plethodon cinereus*), with studies of both the spatial and temporal distribution of morph frequencies (Evans et al., 2018; Gibbs & Karraker, 2006); the effects of temperature on morph frequencies (Evans, Urban & Jockusch, 2020); and the physiological differences between morphs (Moreno, 1989). Although the idea that morph frequencies can be used as bioindicators of climate change has come under scrutiny (Evans et al., 2018; Moore & Ouellet, 2015).

One of the most widely documented trends among amphibians is a pronounced shift to early breeding.

On average, amphibian breeding phenology is advancing by 6.09 ± 1.65 d per decade with a range between 17.5 d delay to 41.9 d advance (Ge et al., 2015; Ovaskainen et al., 2013; Prodon et al., 2017; While & Uller, 2014). Many traits, both species-specific (e.g. reliance on temperature cues for timing of breeding, ability to track resources to be exploited) and more generalized characteristics relating to life history (e.g. body size, clutch size, number of clutches, early vs. late and/or explosive breeding, life span, etc.) influence phenological responses (While & Uller, 2014). In correspondence, frog species are also calling earlier in the year (Walpole et al., 2012). Moreover, climate change has an impact on vocalisation, which is a critical signal for mate choice. For example, adult males of *Eleutherodactylus coqui,* have responded to increasing temperatures over a 23-year period by vocalising at higher frequencies and for shorter durations across an elevation gradient (Narins & Meenderink, 2014).

The ability of amphibians to compensate for phenological alterations varies and is species-specific. For example, development is disrupted in tadpoles of *Rana arvalis* when present in colder temperatures with scarce food resources (Burraco, Laurila & Orizaola, 2021). Warming temperatures can also alter predator-prey dynamics, as observed when

Box 3.1: Sea level rise and salinity

Freshwater systems are vital for amphibians with biphasic life cycles (i.e. those that occupy both aquatic and terrestrial habitats at different stages of their life cycle) and permanently aquatic species. Numerous species of amphibians may be found in coastal freshwater wetlands, which are becoming increasingly vulnerable to tropical cyclonic storms (hurricanes) and associated storm surge and coastal flooding (Walls et al., 2019). Globally, coastal wetlands are expected to be among the most severely impacted by climate change because of increased flooding and secondary salinisation from sea level rise along with increased frequency and intensity of coastal storms (Albecker & McCoy, 2017). Both the frequency and intensity of the strongest North Atlantic tropical cyclones have increased since the 1970s (Bhatia et al., 2019; Hartmann et al., 2013). Moreover, using the IPCC RCP8.5 baseline scenario of greenhouse gas emissions, Kirezci et al. (2020) projected that, by 2100, an increase of 48% (compared to present day) of global land area will be vulnerable to episodic coastal flooding from a 1 in 100-year return period event. Thus, any climate change-driven alterations to the frequency and intensity of storm events could amplify future coastal flooding due to sea level rise, posing an unprecedented challenge for conservation and management of amphibians in coastal ecosystems (Kirezci et al., 2020; Walls et al., 2019).

larger predatory *Ambystoma macrodactylum* larvae (benefiting from an earlier hatching and longer period of development) can significantly reduce survival rates of their smaller prey *Pseudacris regilla* if they do not undergo a similar phenological shift (Jara et al., 2019). It remains to be seen if both predator and prey can develop behavioural responses to the changing climatic conditions. Overall, our understanding of the phenological responses to climate change among amphibians is increasing and points to shifts in most species studied. However, existing studies are strikingly skewed toward the northern hemisphere (Cohen, Lajeunesse & Rohr, 2018).

- **Movement ecology and migration of amphibians**

Movement is a fundamental yet poorly understood component of amphibian biology. The extent and ability of an organism to move within and across habitats affect gene flow, metapopulation dynamics, population viability, and species distributions, all of which also affect vulnerability to changing climate (Pittman, Osbourn & Semlitsch, 2014). Amphibians move based on interactions between individuals or species, resource availability such as breeding ponds, and as a response to changes in the physical environment (Joly, 2019). Although there are numerous studies predicting the response of amphibian populations to changing climate, they are not yet validated because we know very little about dispersal abilities of amphibians and our insights into the fine-scale movement mechanisms are limited (Pittman et al., 2014). Dispersal estimates that do exist for amphibians generally come from individual mark-recapture studies, telemetry studies or genetic estimates, and recent work shows that dispersal estimates from mark-recapture and genetic analyses are remarkably congruent (Wang & Shaffer, 2017). Telemetry studies, in particular, may be able to shed light on environmental cues that lead amphibians to disperse. For example, Henrique and Grant (2019) found that movement among *Leptodactylus latrans* was positively correlated with darker phases of the moon,

higher temperatures, and increased precipitation, suggesting that there are both behavioural and environmental cues at work. Earlier studies using genetic data have shown a positive association of both dispersal distance and vagility with body size in several species of anurans and salamanders (Hillman et al., 2014). In recent years, there has been an increasing emphasis on understanding movement behaviour and there has been much progress since a unifying framework for studying movement was proposed (Joly, 2019; Nathan et al., 2008). Models that include dispersal have been widely used in other organisms, but are only recently being applied to amphibians (e.g. Penner & Rödel, 2019).

Movement ecology research of amphibians allows potential to infer patterns and understand underlying processes of population dynamics and gene flow. It also provides insights into the adaptive significance of behaviours, and identifies physiological constraints of an organism in relation to fine-scale environmental variation. Future climate change research will benefit from technological advancements such as the miniaturization of GPS tags (Cagnacci et al., 2010), harmonic direction finding (Pašukonis et al., 2014), passive infrared transponders (Cucherousset et al., 2008), and increasing accessibility of genome-wide sequencing techniques (McCartney-Melstad, Gidiş & Shaffer, 2018). However, it may be impossible to use most of the tools except genomic techniques for studying the movement ecology of fossorial amphibians such as caecilians.

- **Amphibian responses to climate change – evidence of climate-tracking**

Many of the studies of amphibian movement in regard to climate change have focused on mechanisms that enable tracking both in situ (through adaptation) and across space (through dispersal). Empirical research has characterised the thermal traits of many species, including tolerance to heat and cold, thermal breadth, and safety thermal margin (Brattstrom, 1968;

Catenazzi, Lehr & Vredenburg, 2014; Christian et al., 1988; Mokhatla, Measey & Smit, 2019; Navas, 1997; 2003; Nowakowski et al., 2018; von May et al., 2017). Niche divergence in physiological traits is both common and evolutionary labile (Nowakowski et al., 2018; von May et al., 2017), while thermal traits vary across sympatric species (von May et al., 2019), across parts of a species' range (Mittan & Zamudio, 2019), and even over an individual's lifetime, as plasticity and both short- and long-term acclimation are common (Gunderson & Stillman, 2015; Riddell et al., 2018; Tejedo et al., 2010; Urban, Zarnetske & Skelly, 2013; Valladares et al., 2014). However, acclimation to warm temperatures in one life stage (e.g. larvae) does not imply that other life stages (metamorphic, juvenile, adults) will retain increased tolerance to higher temperatures (Enriquez-Urzelai et al., 2019). Other relevant physiological information available for amphibians include water loss, water uptake, ability to find water, type of development, and larval habitat (Cruz-Piedrahita, Navas & Crawford, 2018; Madelaire et al., 2020; Nowakowski et al., 2018; Riddell & Sears, 2015; Scheffers et al., 2013; Sunday et al., 2014). Although less studied, it has been proposed that water balance may be a more critical process determining local adaptation and persistence relative to thermal tolerance (Cruz-Piedrahita et al., 2018).

Amphibian species can also track climate change by shifting along elevational and altitudinal climate gradients to remain within a suitable microhabitat. The degree that a species needs to disperse to remain in the same climatic niche depends on the velocity of climate change, reflecting the spatial gradient in climate (steep clines up mountains, shallow clines along latitude), and speed of local climate change (Loarie et al., 2009). Efficient climate tracking is expected for species that can disperse well, not only across natural landscapes but also in patchy and disturbed landscapes (Chen et al., 2011). For amphibians, dispersal varies by orders of magnitude with some species moving only metres and others moving kilometres (Semlitsch, 2008; Sinsch, 2014). Synergies with other processes known to impact survival – e.g.

biotic interactions, disease dynamics (chytridiomycosis), and land use change (fire regimes) – are also known to interact with tracking (Moskwik, 2014; Seimon et al., 2017).

Local-scale inventories, resurveys, and monitoring, tied to measurements of environmental change on the ground, provide the best evidence of spatial climate tracking in amphibians. Resurveys in the Tsaratanana Massif, in Africa, detected significant changes in the altitudinal range of seven out of 19 species within a period of 10 years of documented warming (Raxworthy et al., 2008). In North America, increasing air temperatures have been statistically correlated with upslope movement of a hybrid zone in *Plethodon* salamanders (Walls, 2009).

Insights from modelling

Developing effective conservation strategies is important as more species become more vulnerable to extinction and population declines from climate change (Foden et al., 2019). Understanding the range of impacts and mechanisms that amphibians face both physiologically and ecologically (*see* species interactions below), is a critical step to preventing extinctions, although there is increasing urgency to mitigate loss since the effects of climate change are already impacting amphibian species at a global scale. Our understanding of future changes to amphibian distributions and extinction risk has been informed by a variety of different types of models. These include vulnerability assessments that incorporate correlative, specific trait-based, mechanistic, and combined models. These models can be used both to predict future responses to climate change scenarios as well as to develop mitigation strategies to prevent losses.

- **Modelling: Vulnerability assessments**

It is important to select appropriate climate change vulnerability assessment (CCVA) approaches for quantifying vulnerability and there have been four basic ways to do it to date: trait-based, correlative,

mechanistic, and combined approaches. One considerable caveat in these endeavours is that we lack species-specific data for most taxa, and the best available data are often inadequate to do a comprehensive assessment (Urban et al., 2016). Unreliable or even misleading results can make conservation situations worse (e.g. Kroll, Runge & MacCracken, 2009). Since the best available data are usually insufficient, Williams et al. (2008) suggest relying on closely related species' relevant traits. For amphibians, there are a few important traits regarding species' vulnerability to climate change: mountaintop distribution, direct development (Nowakowski et al., 2018; Scheffers et al.,

2013; von May et al., 2019), and lowland or coastal distribution are traits that m to incur extreme vulnerability to amphibians but there is high variability across amphibian species' vulnerability. Since amphibians have physiological responses that are relatively easy to identify (e.g. to hydroperiod, available moisture and relative humidity, seasonality, etc.), many have small geographic ranges, and many populations are declining, there are important considerations for CCVAs that are unique to each species and/or geographic assemblage. For example, species-level estimates of tolerances to heat and cold are essential for inferring species' vulnerability to climate change (Nowakowski et al.,

Table 3.1: Abundant datasets enable scientists to monitor and model the potential impacts of climate change on amphibian distribution

Example	Description	Source
Environmental data		
WorldClim 2	High resolution interpolated monthly temperature and precipitation	Fick & Hijmans, 2017
Climatologies at High Resolution for the Earth's Land Surface Areas (CHELSA)	High resolution interpolated monthly temperature and precipitation	Karger et al., 2017
Global surface water	High resolution data on water bodies	Pekel et al., 2016
Gridden temperature and precipitation climate extremes indices (GHCNDEX)	Gridded data on climate extremes (e.g. temperature and precipitation)	Donat et al., 2013
Microclimate data		
NicheMapR	R package; integrates terrain and atmospheric forcing data; generates hourly time-series of microclimatic conditions, above and below ground	Kearney et al., 2020
MICROCLIMA	R package; estimates microclimatic details from global data with high accuracy	Maclean, 2020
Species distribution data		
Global Biodiversity Information Facility (GBIF)	International network and data infrastructure; open access to occurrence data of all types of life on Earth	www.gbif.net
FrogID	National citizen science project; aids amphibian monitoring in Australia	https://www.frogid.net.au
iNaturalist	Citizen science-led database of species identity and locality records	https://www.inaturalist.org

2018; Sunday et al., 2014), as are obtaining accurate measures or estimates of physiological traits and microclimates (Storlie et al., 2014).

Models of species' ranges under future climatic conditions are powerful tools to predict where the impact of climate change on amphibians may be greatest. Current models are supported by a large number of global climate, microhabitat, and species occurrence data (Table 3.1). Two primary approaches, correlative and mechanistic, have been used to forecast geographic ranges under future climates. Correlative models of species distributions infer species-specific environmental suitability based on climatic descriptions of known occupancy (with voucher specimens and/or observations; Nix, 1986; Phillips, Anderson & Schapire, 2006; Venables & Dichmont, 2004) and often forecast pervasive distribution shifts in response to anthropogenic climate change (Milanovich et al., 2010; Urban et al., 2016). Correlative models are relatively simple to fit with presence-only data, applicable across spatial scales, and perform well across a relatively short time window (e.g. < 20 breeding seasons). They also provide useful insights and testable hypotheses about demographic, range size, and species richness trends, especially for data-limited species, as is the case for most species, and especially those in hyper-diverse regions like the tropics (Box 3.2). Moreover, correlative models that have been projected into the past, particularly back to the Pleistocene and Holocene, have been successfully validated with genetic data describing past amphibian population trends (Amaro et al., 2012; Carnaval et al., 2009), as well as patterns of endemism (Carnaval et al., 2014).

However, correlative models are neither completely nor perfectly explanatory. Since they are based on environmental suitability inferred from species occurrence and usually neglect other mechanisms, such as species interactions, correlative models may fail to describe species' fundamental niches (Godsoe & Harmon, 2012; Higgins et al., 2020). Additionally, correlative models of species distributions projected onto future climates depend on the degree to which dispersal is parameterized. Since many amphibians

are poor dispersers, limiting the future range of a species to a subset of the regions that it currently occupies may be biologically realistic. Studies that assume no dispersal typically predict larger range contractions than those in which dispersal is explicitly included (Lawler et al., 2010; Zellmer, Slezak & Katz, 2020). The lack of estimates of direct dispersal capacity for most amphibian species limits application of correlative modelling results.

Mechanistic models include key biological processes that enhance predictive accuracy for climate change responses (Gilman et al., 2010; Hoffmann & Sgró, 2011; Urban et al., 2016)—namely physiology, demography, dispersal, species interactions, evolution, and other responses to environmental variation (Urban et al., 2016). Despite requiring significantly more data, they likely approximate the fundamental niche of a species more closely than correlative models and may be more informative about causal factors affecting geographic range changes. The most commonly used mechanistic models for amphibians, biophysical models, predict areas where species can maintain a positive energy balance and incorporate physiological parameters (such as metabolic rate, thermal maxima, and behavioural limitations to foraging time) with environmental data (e.g. relative humidity, soil moisture, and ground-level temperature) to predict the timing and efficiency of foraging, and energy assimilation and expenditure (Kearney & Porter, 2004; Peterman & Gade, 2017; Riddell et al., 2018). Mechanistic models also allow both behavioural and physiological plasticity, such as avoidance of extreme temperatures and meta-bolic rate acclimation to increasing temperatures, which can have dramatic effects on prediction of future ranges for amphibians relative to correlative models (Lyons & Kozak, 2020; Riddell et al., 2018). Despite these advantages, mechanistic models remain underutilised, often because of a dearth of necessary data, even for the best-studied species (see Urban et al., 2016). Furthermore, while some parameter values may need to be estimated fromz incomplete data, small changes in parameter values can have major effects on model results (Peterman & Gade, 2017).

**Box 3.2**: Gaps in our knowledge on effects of climate-change on amphibians

In this box, we use data from a recent systematic review (literature from 2005–2015: Winter et al., 2016) on climate change in amphibians (and reptiles) to illustrate trends for the global, taxonomic, and distribution of research on climate change.

In this global dataset, there was a clear bias towards North American and European amphibians, a trend seen in amphibian studies more generally (da Silva et al., 2020), with a positive bias on studies on salamanders (Box Figure 3.1a). Studies are of only a single species or no studies at all came from Africa, Asia, and Australia despite their high amphibian biodiversity (Zellmer et al., 2020). South America was relatively well covered with studies covering many taxa in Argentina, Brazil, and Colombia (Box Figure 3.2). Efforts to model amphibian range shifts under future climates are geographically heterogeneous, with most studies in the United States, South America (primarily Brazil), and Europe. The taxa studied are indicative of regions where research was conducted.
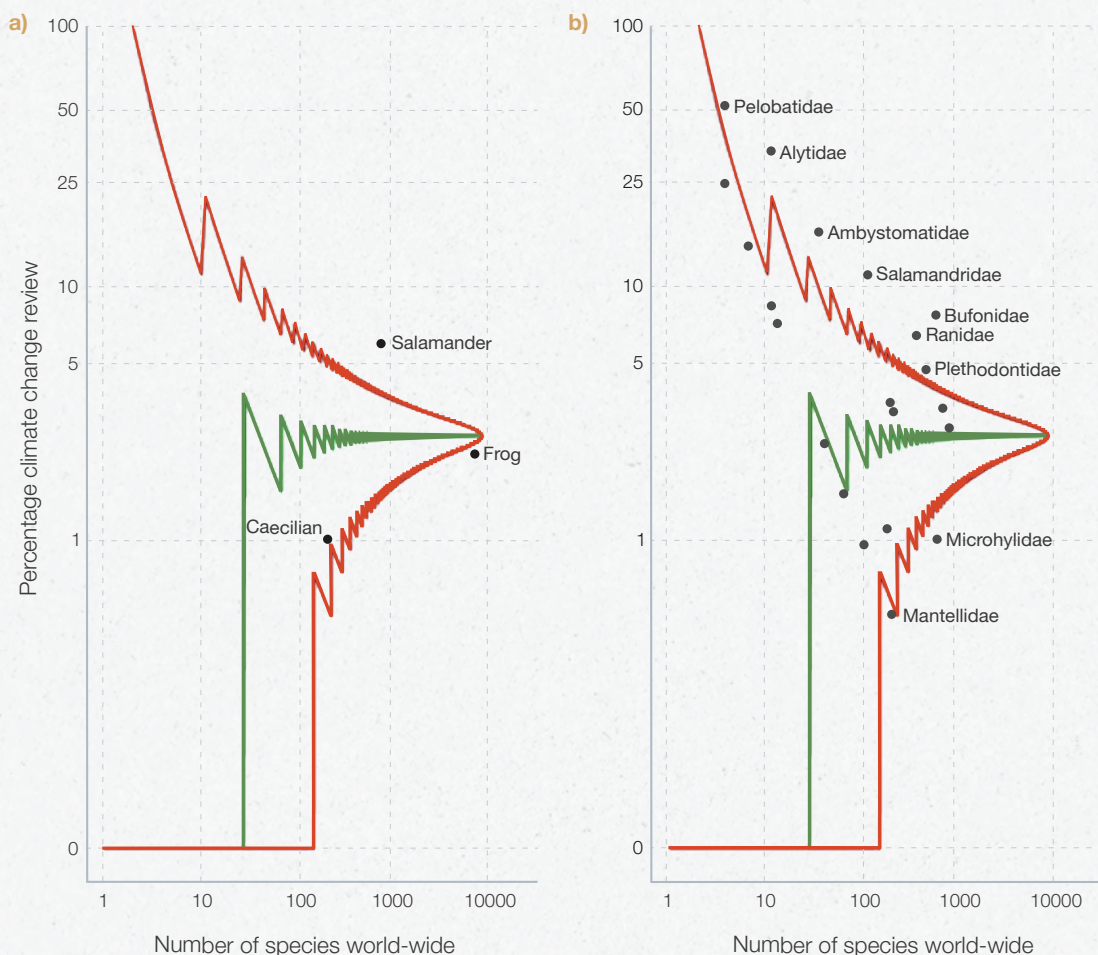
Box Figure 3.1: The taxonomic bias in data on amphibian climate change studies reflects the geographic distribution of species investigated. In this figure the taxonomic groups are placed with reference to their size (number of species on a log scale x-axis) and the proportion in the review (% in climate change review - y-axis). The brown and green lines represent parity and 95% confidence intervals, respectively, and are jagged due to the log scale of the x-axis. **a)** Only two studies included caecilians (below the green line of parity but not outside the lower 95% confidence interval, brown line). Studies on salamanders were significantly overrepresented (above the brown 95% confidence line interval), while those on anurans were underrepresented (below the brown 95% confidence interval) in the dataset. Salamanders are particularly well represented in the dataset including ambystomatids, salamandrids, and plethodontids. **b)** Of the frogs studied, boreal families such as ranids, bufonids, pelobatids and alytids were all overrepresented, while the more tropical mantellids and microhylids were underrepresented. Source: Data from Winter et al., 2006.

Fewer number of studies — Larger number of studies
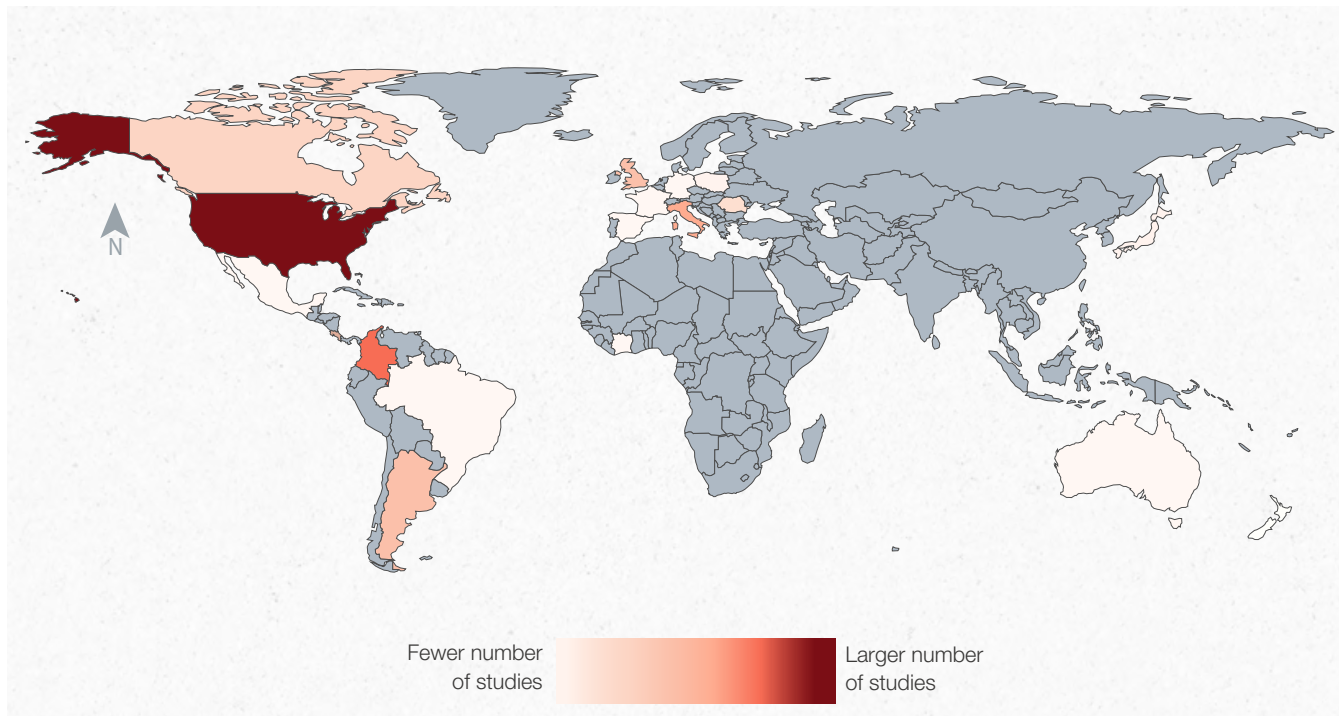
Box Figure 3.2: Data from Winter et al. (2016) on 193 species from 24 families of amphibians representing all three orders of amphibians that demonstrate a distinct geographic bias in the literature on amphibians and climate change. Darker colour indicates a greater number of studies. Note that the criteria for including literature in this review were relatively stringent (*see* Winter et al., 2016), and there may be more studies from other areas of the globe that were excluded or have been published since 2016. Source: Winter et al. (2016).
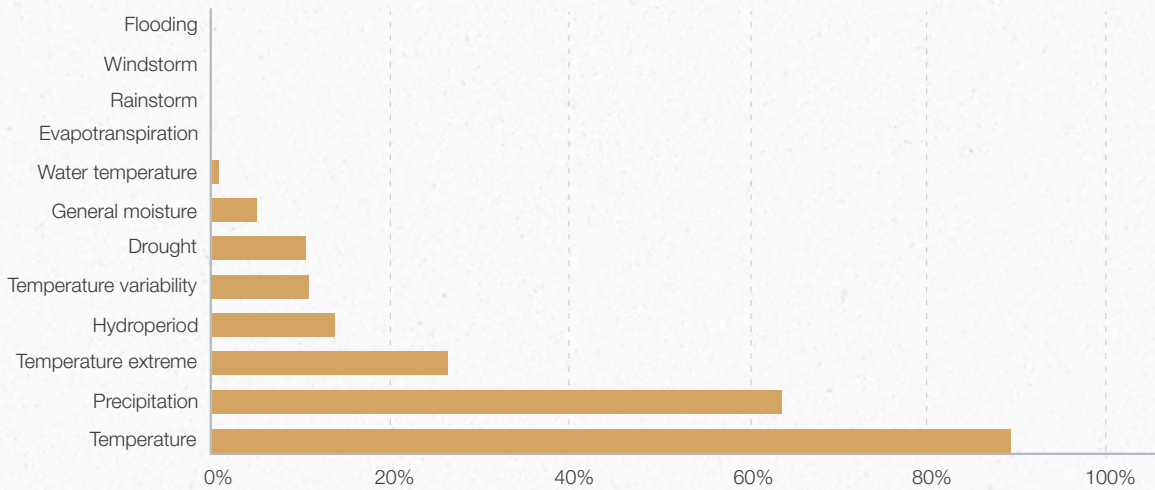
Most studies reviewed by Winter et al (2016) use both temperature and precipitation (Box Figure 3.3.a), variables known to correlate with species richness in amphibians (Pyron & Wiens, 2013), and expected to alter under most climate change scenarios (Sodhi et al., 2008). However, studies that include extreme events such as storms, droughts and fires (*see* Box 3.3) are largely absent, despite the fact that these effects may be major drivers of extinction (Foden et al., 2019). Very few studies examine key environmental variables such as habitat requirements for amphibians, prey items, and soil and leaf litter characteristics (Box Figure 3.3b), and only a small subset examine human impact variables such as habitat fragmentation or presence of invasive species (Box Figure 3.3c). Taken together, this suggests that future studies of climate change and amphibians will need to rely on newer methods, more data, and better-quality datasets that include microhabitat data in order to be useful for providing needed insights for conserving amphibian biodiversity.

Why do we need data on tropical species?

The tropics hold the vast majority of extant amphibian species richness, yet data from these areas are most scant (Box Figure 3.2). It has been argued that these species are most vulnerable to the proximate effects of climate change (Foden et al., 2019). Tropical species often live close to their upper thermal tolerance limit and show narrow thermal performance breadths (Navas, Gomes & Carvalho, 2008), which makes them particularly vulnerable to climate change. Underlying physiological mechanisms allowing some amphibians to cope with variation in temperature remain unclear, yet genetic studies suggest many mechanisms may be involved (Yang et al., 2016). To understand how animals cope with variation in temperature and hydric stress, we need a combination of physiological studies with those that investigate underlying genetic mechanisms.

However, to predict future impacts of global change we also need species distribution models that use the biology of these understudied animals (Foden et al., 2019). Future models will require the use of physiological data to build mechanistic species distribution models, and transcriptomic data to provide a powerful tool to predict future impacts of climate change on all amphibians. This in turn relies on scientific capacity growing and being supported by these countries in order to facilitate data collection.

a) Climatic

b) Environmental
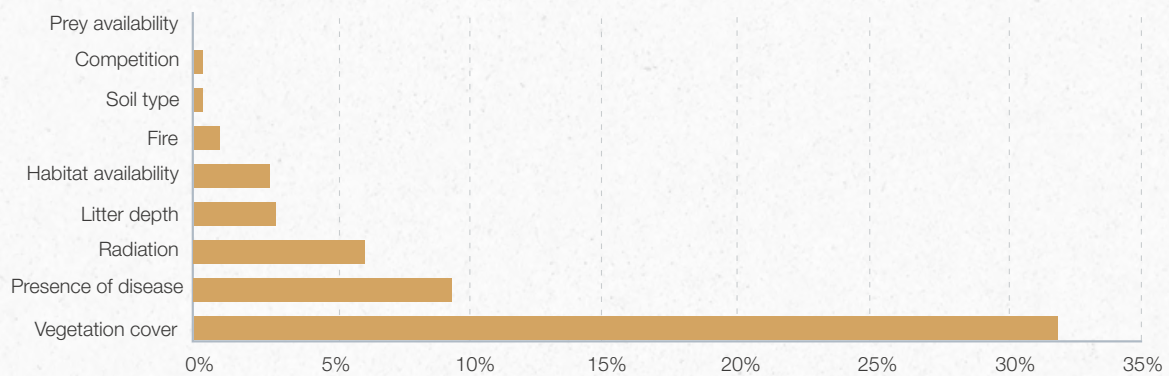
c) Anthropogenic

Box Figure 3.3: **a)** Climatic, **b)** Environmental, and **c)** Anthropogenic variables used in studies reviewed by Winter et al (2016). Presence of the term was used to calculate percentage from 325 entries. Source: Winter et al (2016).

● **Modelling amphibian extinction risk from climate change**

Amphibians are sensitive to climate change owing to their physiological vulnerability to temperature, humidity, and precipitation, high sensitivity to desiccation due to their highly vascularized skin (*see*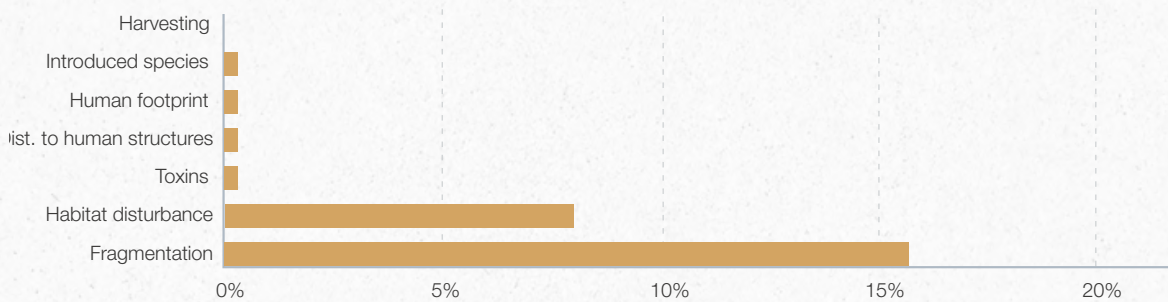 vulnerabilities section), low dispersal (*see* movement ecology section), susceptibility to climate mediated factors such as disease outbreaks, and potential interactions with existing threats from habitat degradation, invasive species, and high levels of endemicity (Alford, Bradfield & Richards, 2007; Blaustein et al., 2001; Corn, 2005; Gibbons et al., 2000; Gunderson & Stillman, 2015; McMenamin, Hadly & Wright, 2008; Pounds et al., 2006; Reading, 2007; Wake, 2007). Although high relative vulnerability claims are frequently made, our ability to generalise is limited and uncertainty of

how these trends are geographically and taxonomically distributed still remains high in the absence of validated model predictions.

● **Predicted risks**

We aggregated data for amphibians and calculated the predicted relationship between warmer global temperatures and amphibian declines (Figure 3.3). Based on multi-species models, amphibian extinction risk is expected to increase rapidly with temperature (slope = 0.69, N = 42, 95% Cis: 0.58, 0.73), and this rate is higher (~50% risk) than predictions for other taxonomic groups. Other syntheses based on expert opinion (Foden et al., 2013) and species-area approaches (Thomas et al., 2004) predict that climate change threatens 12–60% of amphibians with extinction.
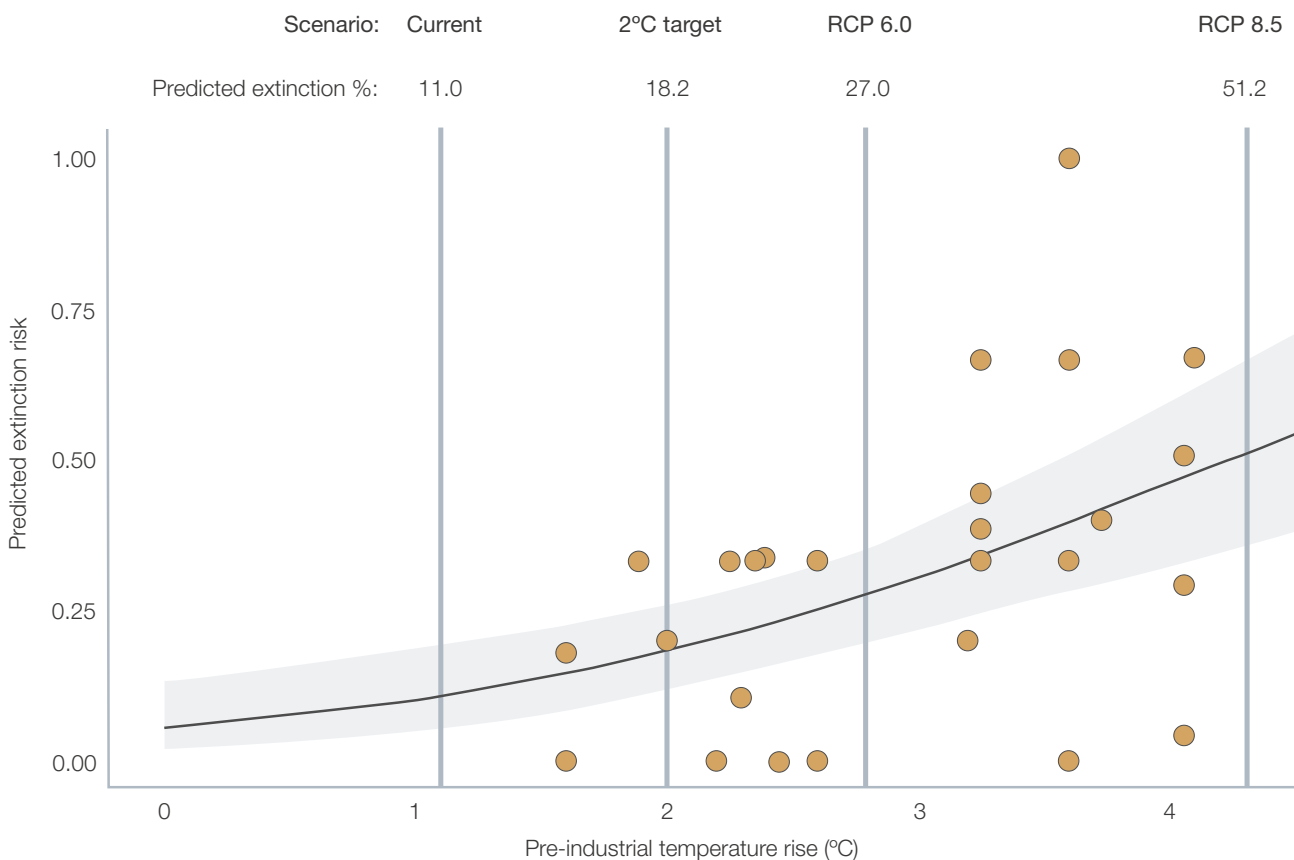
Figure 3.3: Predicted global amphibian extinction risk based on pre-industrial temperature rise from 42 multi-species predictions of amphibian extinction risk from climate change. Estimated relationship transformed from logit and plotted with 95% confidence intervals (grey ribbon). Details of analysis in Urban (2015). Extinction risks are for four climate scenarios: current post-industrial temperature rise of 0.8 C, the policy target of 2 C, and Representative Concentration Pathways (RCPs) 6.0 and 8.5. Source: Urban (2015).

Genetic adaptation of amphibians to climate change

Although not unique to amphibians, we know little about how amphibians might respond to climate change through genetic adaptation (Merilä & Hendry, 2014; Urban et al., 2016; Urban, Richardson & Freidenfelds, 2014). Few predictions account for potential resilience through adaptation, with only one of 131 studies addressing potential adaptive change (Urban et al., 2016). Genetic variation can allow populations to adapt to climate change and thereby persist despite a changing climate (Carroll, Fredrickson & Lacy, 2014; Hoffmann & Sgró, 2011). Local adaptation is especially important for poor dispersers, like most amphibians that cannot track shifting climates (Urban et al., 2012).

It is also important to note that many species are comprised of hundreds or thousands of semi-independent populations (González-Suárez & Revilla, 2013; Hughes, Daily & Ehrlich, 1997; Jetz, Ashton & La Sorte, 2009), each potentially adapted to local conditions including climate (Rehfeldt et al., 2002). These divergent populations might respond differently to climate change in distinct ways depending on the match between their traits and changing local conditions (Pelini et al., 2010). For poor dispersers, adaptive population differentiation can slow or preclude range shifts because all populations are perturbed from local optima (Pelini et al., 2010). For good dispersers, locally adapted populations can track changing climates across space through genotypic sorting (Urban et al., 2012) as opposed to evolution based on in situ standing genetic variation.

A review of genetic responses to climate variation uncovered 11 amphibian studies (Urban et al., 2014). Ten of the 11 studies documented genetic variation for at least one of the traits related to climate variation. Sixty-five percent of traits demonstrated significant genetic variation and 48% of the traits demonstrated significant genotype-by-environment interactions (Urban et al., 2014). For instance, frogs adapted to different thermal regimes

in space (Freidenburg & Skelly, 2004; Orizaola, Quintela & Laurila, 2010; Skelly & Freidenburg, 2000), and salamanders adapted different colour morphs over time (Gibbs & Karraker, 2006). Most studies focused on phenological changes in breeding and life history traits such as growth, development, and survival rates. However, most evidence comes from space-for-time substitutions, suggesting that genetic variation exists across heterogeneous landscapes that could contribute to climate resilience. However, we know much less about local genetic variation that allows responses in situ. Moreover, most studies are from North America and Europe so we know even less about the potential for adaptation in the tropics, where the greatest amphibian biodiversity occurs.

● **Genomics & evolvability**

The large genomes of amphibians and limitations in funding have hindered efforts to generate genome assemblies for all but a handful of species. Advances in sequencing technologies have already started to remove this barrier, with completion of the first chromosome-level assemblies for salamanders (*Ambystoma mexicanum*; Nowoshilow et al., 2018) and caecilians (*Rhinatrema bivittatum*; Rhie et al., 2021). In addition to the early genomes for *Xenopus tropicalis* (Hellsten et al., 2010) and *X. laevis* (Session et al., 2016), chromosomal-level assemblies now also exist for several non-model frog species that encompass greater taxonomic and geographic variation (*see* Chapter 13). These genomic resources will be essential to identify genes that underlie critical climate-related traits. To date, few studies have pinpointed genes involved in amphibian climate change tolerance. As a rare example, Saito et al. (2019) demonstrated that neuronal heat sensor genes in *Xenopus* from warmer climates diverged from those species inhabiting cooler climates. A second example comes from a transcriptomics study of the montane salamander *Plethodon metcalfi* to identify genes involved in desiccation (Riddell et al., 2019). A third study used time-series from
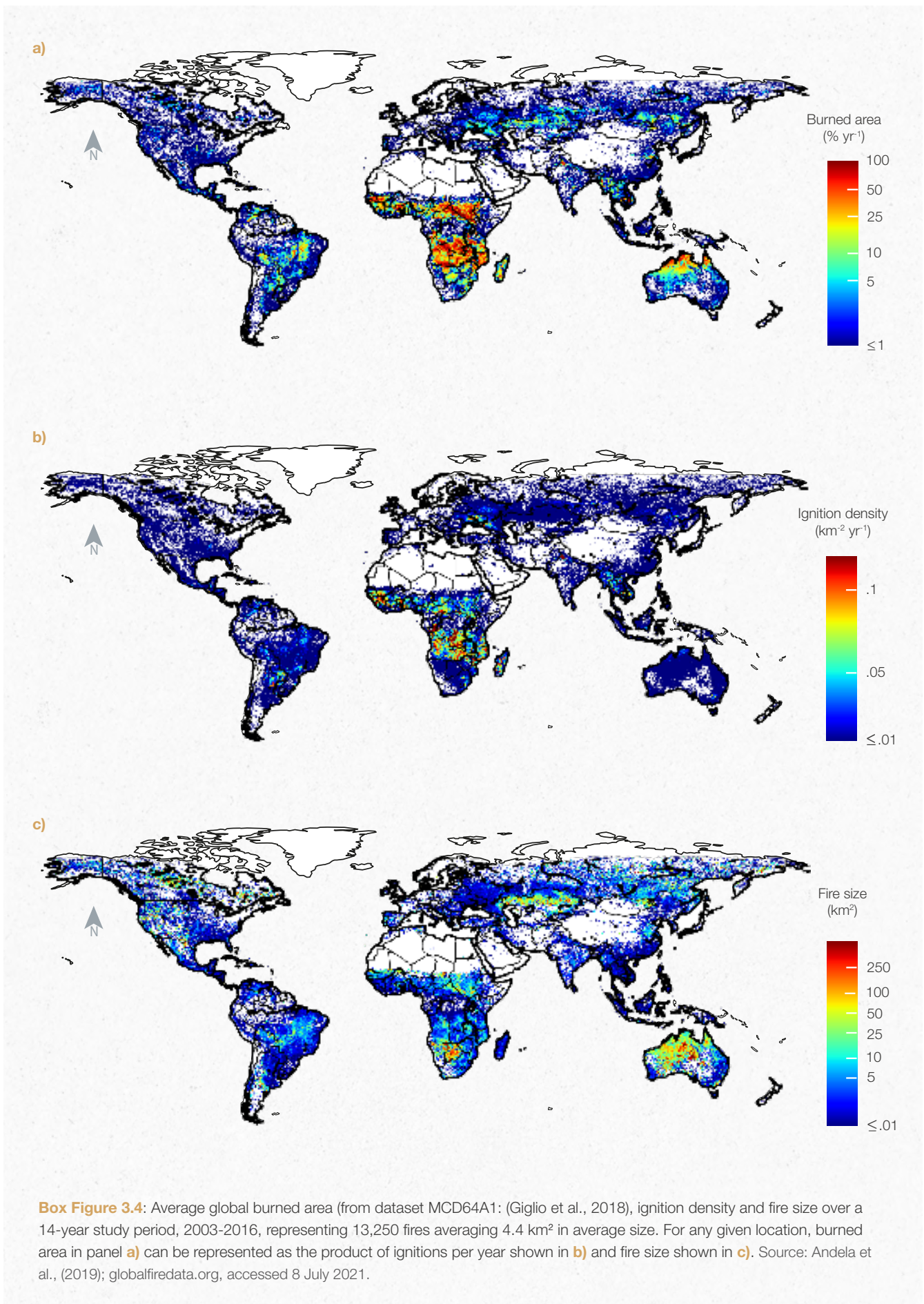
Box 3.3: Amphibians and fire

In many ways fire has set the most dramatic direct challenges to society that hinge on climate change and society's ability to become a part of natural systems and not apart from them (Stromberg, 1997). The size, frequency, and severity of fires are anticipated to increase under climate change (Dale et al., 2001). In particular, extreme fire-weather conditions including drought and hot-dry-windy air conditions coupled with human factors such as fire suppression activities of past decades (e.g. McDonald, Srock & Charney, 2018; Moritz et al., 2014; Srock et al., 2018; Turner & Romme, 1994) and increasing human-mediated fire starts are triggering widespread fires—a worldwide signature is evident (Box Figure 3.4). However, there is an overall lack of knowledge of the response of amphibians to fire (Driscoll et al., 2010), hindering our ability to assess fire risk and make informed management decisions. Research could help advance understanding of the impact of fires on amphibians, particularly in areas such as Australia, North America, and the Amazon basin, given the more frequent and more severe fires predicted as a consequence of global climate change (Moritz et al., 2012; Williams et al., 2008).

In North and South America, amphibian response to fire and fire effects to broader ecosystems are emerging. Pilliod et al. (2003) reviewed data from 15 studies of prescribed and wildfires in North America, finding: **1)** spatial and temporal variability of fire effects on amphibians reflecting their life history, habitat associations, species range extent, and time-since-burning; **2)** direct mortality effects as well as indirect effects on microclimate, aquatic habitat sedimentation and altered hydroperiod, nutrient pulses, and microhabitat changes to duff, litter, and down wood; and **3)** a need for long-term data. Hossack and Pilliod (2011) reviewed seven studies with pre- and post-fire data and seven retrospective studies. They found that studies of plethodontid salamanders and southwestern-USA stream-breeding amphibian species reported negative fire effects on populations, individuals, or critical habitat attributes. Cousins et al. (2019) reported high amphibian productivity in high-elevation pond-meadow complexes within areas with past wildfires in Oregon, supporting the apparent resilience of these amphibians to fire disturbance that may help bolster broader ecosystem recovery through food web interactions.

Although monitoring efforts in tropical regions of the Americas also give the impression that fires may be reasonably well tolerated by local amphibian communities (Drummond, Moura & Pires, 2018; Warren-Thomas et al., 2013), this likely reflects the composition of the communities sampled to date, and the environmental filters that they have encountered. For instance, inventories in bamboo and *terra firme* forests in the Peruvian Amazon (Madre de Dios) detected generally lower (but not statistically significant changes in) amphibian diversity and abundance following anthropogenic fires associated with a severe drought in 2005 (Warren-Thomas et al., 2013). However, all species then recorded were known to be resistant to habitat alterations, and the inventory included no primary forest specialist species; as such, the sampling area may have been located in a transition zone already occupied by fire-resistant species. Similarly, in South American rupestrian grasslands known to be regularly subjected to wildfires, Drummond et al. (2018) found no statistically supported reduction in amphibian diversity following burning. The authors largely attributed these results to the timing of the fire (the dry season, when most riparian amphibians are hidden in rock outcrops, burrows or termite mounds), but noted that the single species known to be a direct developer and to utilise grasses as shelter was that with lower observation records and decreased abundance following burning. With increased attention recently turning to the burning of large tracks of rainforests in the Amazon region (Bullock et al., 2020), it remains to be seen whether more significant changes will be detected in the composition and abundance of the many direct developers and wet forest-dependent species known to occupy this domain.

Box Figure 3.4: Average global burned area (from dataset MCD64A1: (Giglio et al., 2018), ignition density and fire size over a 14-year study period, 2003-2016, representing 13,250 fires averaging 4.4 km² in average size. For any given location, burned area in panel **a)** can be represented as the product of ignitions per year shown in **b)** and fire size shown in **c)**. Source: Andela et al., (2019); globalfiredata.org, accessed 8 July 2021.

Australia

Australia's 2019/2020 fire season brought the interaction of climate change and fires to the forefront in the country, with more than 17 million hectares of forest burnt in Australia (Boer, de Dios & Bradstock, 2020; Noble, 2020). While a natural part of many ecosystems in Australia, fires of this extent are not typical (Boer et al., 2020), and a large proportion of wetter habitats, which historically burn infrequently, also burnt. The handful of studies on the impact of fire on Australian frogs have indicated overall resilience to fires (Bamford, 1992; Driscoll & Roberts, 1997; Lowe, Castley & Hero, 2013; Potvin et al., 2017; Westgate, Driscoll & Lindenmayer, 2012; Westgate et al., 2018), and short-term postfire persistence of many frog species across the fire was revealed via citizen science (Rowley et al., 2020), but the long-term impact of the summer 2019/2020 fires on Australian frogs remains unknown. Particular concern is held for species with small geographic ranges, especially rainforest-dependent species.

Mitigations to reduce fire effects

In the USA Southwest, the effects of human-mediated disturbances in fire-prone areas that could affect amphibian habitat conditions could be reduced by: **1)** reducing livestock grazing on native plants and near aquatic ecosystems that may result in altered fire-related processes and functions; **2)** preventing human-transmission of invasive species, especially non-native plants that alter fire regimes; and **3)** actively reducing fuel loads in areas subject to wildfire (Jones, Halama & Lovich, 2016). These are all interacting factors as dry conditions and lightning strikes are predicted to increase with climate change in many areas. In the Northwest USA, management recommendations to address fuel treatments in forests to safeguard against wildfire risk were developed for known sites of the Siskiyou Mountains salamander, a species of concern (Clayton et al., 2009). Due to elevated concerns for human communities-at-risk of wildfire within the salamander's range, alternative measures were developed to address salamander persistence to better inform management decisions when trade-offs between people and biota are used to inform decisions. In many ways, these actions suggest a cultural reset of societal norms to integrate people into natural systems designed for mutual coexistence. Although a suite of approaches can be derived for multiple threats, a downscaled species-specific, geography-specific, and threat-combination specific approach is likely most effective to address the contexts of known local-to-regional issues, while simultaneously addressing human socioeconomics of the system.

a broadly distributed species to hone in on a set of candidate loci involved in thermal adaptation (Cayuela et al., 2022).

Identification of a full suite of these genes would allow assessment of genetic variation within populations and across species ranges and could serve as a potential baseline estimate of adaptive capacity. Furthermore, transcriptomics (e.g. Riddell et al., 2019; Yang, Qi & Fu, 2016) and epigenetics (Wogan et al., 2020) may provide new insights into plasticity that could also be quantified

within populations and across species' ranges in conjunction with adaptive capacity.

● Landscape genetics

As a discipline, landscape genetics is a recently emerged field, but there has been a proliferation of studies focused on amphibians due to their overall low vagility and their thermophysiological require-ments that link them to the environments where they exist. With respect to climate change, these

studies suggest environmental conditions that facilitate or impede dispersal (e.g. environmental resistance; Wang, Savage & Shaffer, 2009), quantify fine-grained spatial genetic variation (Savage, Fremier & Shaffer, 2010), and gene flow (Homola, Loftin & Kinnison, 2019; Sánchez-Monteset al., 2018). Furthermore, these same approaches could specifically be used to evaluate climate corridors by highlighting least-cost dispersal pathways (Epps et al., 2007). Taken a step further, landscape genomics can be used to identify genotype-environmental associations and make predictions about the spatial distribution of adaptive alleles (Manel et al., 2018). There have recently been several amphibian landscape genomics studies that evaluate various genotype-environment associations, for example, local adaptation across a drying landscape in the Australian frog *Pseudophryne guentheri* (Cummins et al., 2019), and lowland-highland adaptation across elevational transects in the Andes (*Boana platanura*; Medina et al., 2021), highland adaptation of genes coding for metabolism in the Tibetan plateau (*Bufo gargarizans*; Yang et al., 2016), as well as adaptations along latitudinal gradients (*Rana arvalis*; Rödin-Mörch et al., 2019).

Ecological interactions - species interactions

In addition to direct physiological effects, interspecific interactions frequently determine climate responses (e.g. Davis et al., 1998; Park, 1954). In cases where mechanisms of climate-induced declines and extinctions are understood, most involve indirect impacts via species interactions rather than direct physiological impacts (Cahill et al., 2013). Climate change can modulate the strength or even alter the direction of species interactions (Van Der Putten, Macel & Visser, 2010; Visseret al., 1998), including elevational range expansions and contractions (Raxworthy et al., 2008). Divergent abilities to track climate changes through range expansion can create no-analogue communities composed of species with no history of co-occurrence or coevolution (Urban et al., 2012). Interactive effects often stem from stronger negative species interactions (e.g. novel or stronger predation risk or disease), fewer resources,

interspecific competition, or loss of mutualists (Gilman et al., 2010).

For amphibians, climate change has likely contributed to declines by exacerbating disease, suggested by the case of the golden toad (*Incilius periglenes*). The golden toad declined in concert with climate-mediated changes to dry-season mist frequency and increased exposure to pathogens (Pounds et al., 2006; Pounds, Fogden & Campbell, 1999; Pounds & Crump, 1994). Variation in breeding phenology (Beebee, 1995; Gibbs & Breisch, 2001) could also lead to changes in interaction strength, as responses can differ relative to photo- and hydro-period and weather cues. For instance, if *Hyla cinerea* tadpoles develop late, they suffer greater predation from growing dragonfly nymphs (Rasmussen & Rudolf, 2016). In some cases, overwintering amphibians are expected to gain an advantage as winters become milder, supporting top amphibian predators (Herstoff & Urban, 2014). On the other hand, climate-mediated desiccation also increased behaviours that boost predation risk in red spotted newts (Rohr & Madison, 2003).

Differential changes in phenology can also alter competition among species, for example, by synchronising otherwise asynchronous competitors or causing one species to breed earlier and become a superior competitor. Interactions with other stressors -e.g. invasives and climate change - increased drying limits in *Rana sierrae* recruitment in small ponds while fish introductions limit their recruitment in larger lakes (Lacan, Matthews & Feldman, 2008; M. Urban *pers. comm.*). Additionally, warming can cause outbreaks of pathogens and parasites such as outbreaks of parasitic copepods on *Rana boylii* and trematodes that cause malformations in developing frogs (Kupferberg et al., 2009).

Evidence of management

- **Evidence of positive results for amphibian conservation with climate change**

  Conservation actions for climate change focus on habitat management and rescue measures for

at-risk populations. Provision of breeding, foraging, or dispersal habitat conditions can be an effective adaptive management approach for climate change (Sutton et al., 2015). As mitigations are costly, Mims et al. (2018) offered an approach for regional species prioritisation that merged species rarity with climate sensitivity.
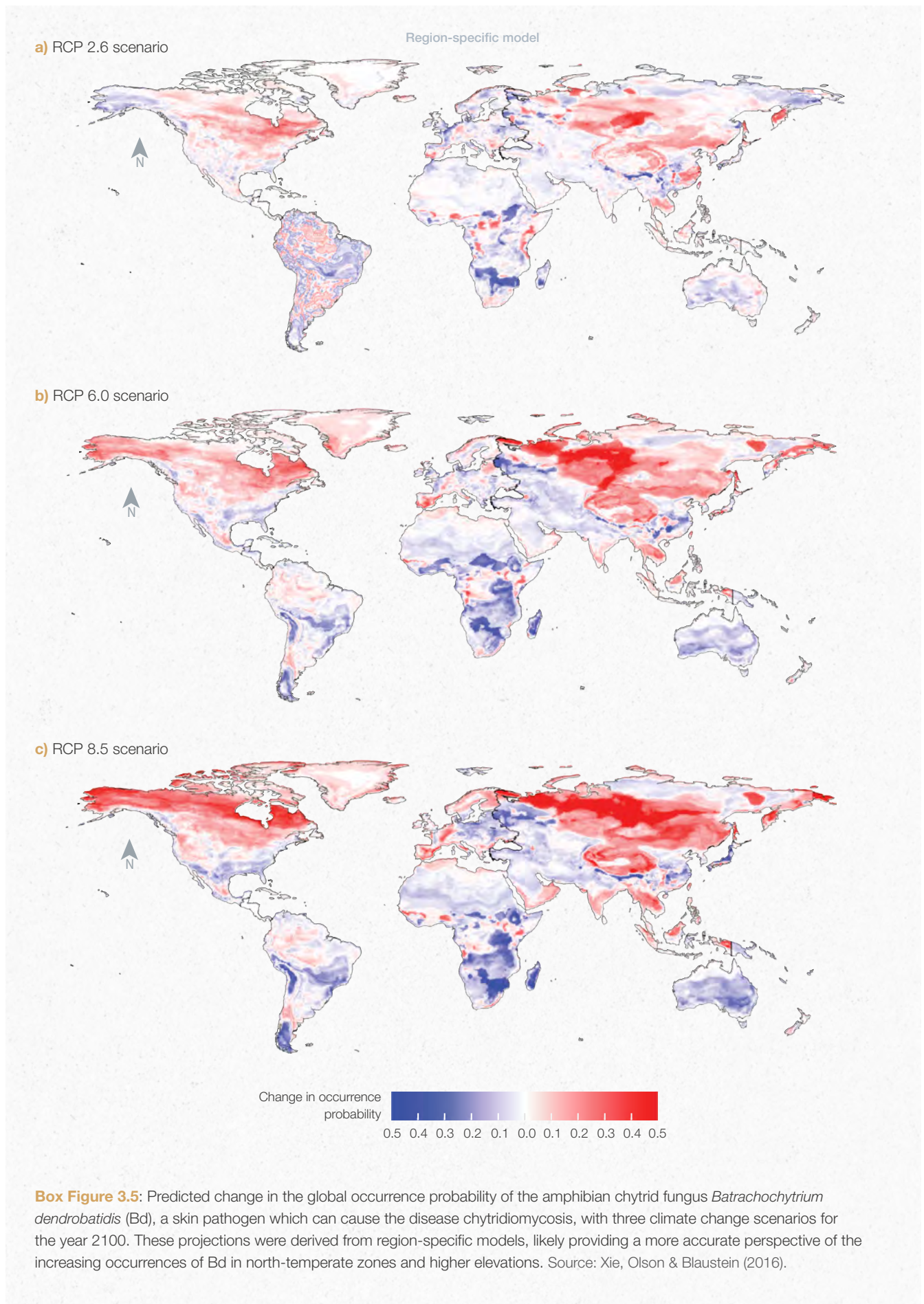
At local scales, Shoo, Olson, and Hero (2011) provided examples of installation of microclimate and microhabitat refuges for amphibians, addressing: **1)** riparian zones including their microclimate regimes (Olson et al., 2007; Olson, Coble & Homyack, 2020; Olson et al., 2014; Olson & Burton, 2014); **2)** microclimate refugia including downed wood (e.g. Kluber, Olson & Puettmann, 2008, 2009; Rittenhouse et al., 2008), leaf litter, and bromeliads (Donnelly, 1989; see also Stynoski, 2009); and **3)** artificial wetting of terrestrial habitat by irrigation sprayers (Australia: Mitchell, 2001), an approach with additional applications (Central America: Pounds et al., 1999; Papua New Guinea: Bickford, 2005; Tanzania: Krajick, 2006). Smith, Meredith & Sutherland (2018) reported 28 studies that created ponds and found that relative to amphibian use they were 80% effective (with 80% certainty) and 0% harm. Pond creation may be especially applicable to threatened species (Cushman & Pearl, 2007; Kupferberg, 1996; Shoo et al., 2011). Mathwin et al. (2020) reviewed efficacy of manipulating water for amphibian conservation and found 17 examples of successful

applications, with extension of hydroperiods to match larval requirements and off-season drying to control predators showing encouraging results. Biebighauser (2015) provided procedures for wetland creation and restoration (~6,000 designs created) that have been implemented across North America (~2,500 wetland projects supervised), with applications in urban and agricultural landscapes including schools (~250 wetlands), mined lands (~400 wetlands), and forests, including measures to forestall invasive predators (Biebighauser, 2007; Gamble & Mitsch, 2009; Hartel et al., 2007; Korfel et al., 2010; Maret, Snyder & Collins, 2006). Similarly, Petranka et al. (2007) reported advantages of creating wetlands along a hydrologic continuum to reduce mortality from several risk factors including drought, pathogens, and pred- ators on early life stages.

At landscape scales, the creation and retention of pond networks can address broader species sustainability functions by providing breeding, foraging, and dispersal habitats among populations (Fog, 1997; Piha et al., 2007). For example, in managed forests, retention of tree islands and downed wood near riparian reserves may provide stepping-stone function that enhances habitat connectivity (Olson & Burnett, 2013; Olson & Kluber, 2014). Likewise, landscape genetic work supports frog dispersal along trajectories with downed wood and retained understory (Spear, Crisafulli & Storfer, 2012). Furthermore, forest

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Box 3.4: Synergies: disease ecology

Synergies between climate change and infectious diseases have received a great deal of attention in recent years. In particular, several hypotheses have been proposed relating the emergence of the amphibian disease chytridiomycosis caused by fungi of the genus *Batrachochytrium* (primarily *B. dendrobatidis, Bd*), to climate change. Pounds et al. (2006) proposed the chytrid thermal optimum hypothesis, which posits that increased cloud cover led to a convergence between daytime and night-time temperatures leading to increased growth of *Bd* and amphibian declines in Monteverde, Costa Rica. They also proposed that climate change was increasing the number of dry days and decreasing mist frequency with detrimental consequences to amphibians. Subsequent analyses found no statistical support for the chytrid thermal optimum hypothesis (Rohr & Raffel, 2010; Rohr et al., 2008). An isotopic tree ring study showed no long-term drying trend at Monteverde but did reveal that major declines in the 1980s corresponded to a

a) RCP 2.6 scenario

Region-specific model

b) RCP 6.0 scenario

c) RCP 8.5 scenario

Change in occurrence
probability

0.5 0.4 0.3 0.2 0.1 0.0 0.1 0.2 0.3 0.4 0.5

Box Figure 3.5: Predicted change in the global occurrence probability of the amphibian chytrid fungus *Batrachochytrium dendrobatidis* (Bd), a skin pathogen which can cause the disease chytridiomycosis, with three climate change scenarios for the year 2100. These projections were derived from region-specific models, likely providing a more accurate perspective of the increasing occurrences of Bd in north-temperate zones and higher elevations. Source: Xie, Olson & Blaustein (2016).

particularly dry interval caused by a strong El Niño event. Analyses of temporally detrended data to account for epidemic *Bd* spread also support a role for extreme climatic conditions and increased climate variability caused by El Niño in amphibian declines in Latin America (Rohr & Raffel, 2010). Because climate change is predicted to increase climate variability (Thornton et al. 2014) as well as the strength and frequency of extreme El Niño events (Wang et al., 2019), these results suggest the impact of chytridiomycosis outbreaks on amphibian populations could increase because of climate change (*see* Box Figure 3.5).

Climate change could increase the impact of *Bd* on amphibian populations through milder winter conditions in temperate montane regions. Decreased snowpack in Wyoming (Muths et al., 2020) and earlier thaw date in the Pyrenees (Clare et al., 2016) have been associated with decreased survival with *Bd* and increased prevalence of *Bd,* respectively, and chytridiomycosis outbreaks in central Spain have been linked to milder winter conditions that allow for increased growth of *Bd* (Bosch et al., 2007). Beyond favouring conditions for growth of *Bd,* climate change may affect the interaction between host and parasites or pathogens. The thermal mismatch hypothesis (Cohen et al., 2018, 2017) proposes that while both parasites and hosts should have a performance optimum that matches local conditions, parasites typically have broader thermal tolerances than hosts and that cool-adapted hosts typically have a right-skewed performance curve while warm-adapted hosts typically have a left-skewed curve. Climate change could shift local conditions away from the host performance optimum and, because parasites have a broader performance curve, increase the performance advantage of parasite over host. Climate warming could thus promote increased *Bd* growth and outbreaks in cool-adapted species, a result that has been supported by both lab experiments and a meta-analysis of *Bd* outbreaks (Cohen et al., 2017). These results suggest that the effect of climate warming on *Bd* outbreaks may depend on host physiology, allowing predictions of which species may be most impacted by future outbreaks of *Bd* or other amphibian diseases.

cover is a predictor of connectivity for headwater salamanders (Emel et al., 2019). However, despite limited evidence for amphibian corridors retaining connectivity (Smith & Sutherland, 2014), one study found that corridors retained eight of 13 frogs for as long as 20 years (Becker et al., 2007). At more regional to continental scales, creating corridors that align with the direction of climate changes might allow species to more easily track their climate niche.

Other approaches for species facing extinction from climate change include relocation, reintro-duction, translocation, headstarting, captive rescue colonies, and bio-banking (https://parcplace.org/species/relocation-reintroduction/; chapters in Walls & O'Donnell, 2024). Headstarting and reloca-tions might be both easier and more cost-effective (Griffiths & Pavajeau, 2008). Three reviews found most (65%) amphibian translocations resulted in established breeding populations (Smith &

Sutherland, 2014). Germano and Bishop (2009) identified guidelines to reduce failures.

• **Red List categories & climate change**

An important research finding has been that areas with many species of high sensitivity and low adaptive capacity differ from areas where species are actually exposed to the brunt of climate change (Foden et al., 2013). Indeed, where exposure-based assessments of vulnerability to climate change are done exclusively, we can obtain misleading results that hamper conservation efforts. Some amphibian species (11–15%) are already threatened with extinction (on the Red List) and highly vulnerable to climate change. These species have been identified as a priority for conservation actions (Foden et al., 2013) regardless of their climate change sensitivity. In other words, conservation efforts need not compete unnecessarily, allowing management

actions for amphibians at high risk of extinction, despite many uncertainties of their exposure to climate change.

Gaps: Research & knowledge

- **Baseline data:** We have incomplete knowledge of the diversity and distribution of amphibians. As of May 27, 2021, there are 8,340 species of described amphibians, and in the past 10 years between 100–200 new species have been described each year (https://amphibiaweb.org/). The ranges of many species are poorly known or known only from type localities and population trends and threats are unknown for 1,184 Data Deficient species out of 7,212 assessed species (https://www.iucnredlist.org, see Howard & Bickford, 2014), which means over a quarter of amphibian species (2,312 species) are not assessed or lack sufficient basic data for assessment.

- **Natural history:** Basic life history data are still lacking for many amphibian species. Efforts to compile life history traits for species into an accessible database for the scientific community is essential for addressing climate change vulnerabilities. Databases that address some of these aspects (https://amphibiaweb.org/, https://www.iucnredlist.org, and https://amphibiansoftheworld.amnh.org) primarily address geography and taxonomy, but compiled species-specific trait databases are largely lacking, although the AmphiBIO database has started to fill this void (Oliveira et al., 2017). Fundamental research provides important data to inform amphibians' conservation action plans.

- **Amphibian physiology:** Although amphibian thermophysiology has been reasonably well-described, the group lags significantly behind other ectotherms, particularly lizards (Sinervo et al., 2010), in terms of large-scale applications of mechanistic modelling. Basic information on physiological responses to humidity shifts, demography, dispersal, and microhabitat use are lacking for most species,

preventing more comprehensive mechanistic models from being built (Urban et al., 2016). How to reconcile the time and resources required for mechanistic models and parameter collection remains a challenge, especially if the scientific community aims to generate accurate global-level assessments of potential changes in species distribution. Given that mechanistic models are data-hungry, and that correlative models may lack biological realism or process-based insights, investments in hybrid or mechanistically-informed correlative species distribution models may be worth pursuing. Monitoring networks are needed to validate models and facilitate resurveys, and may be linked to Earth Observation efforts (GEO BON, 2015; Pereira et al., 2013).

- **Models - scenario development:** As most species distribution forecasts developed nowadays focus on the impact of climate alone, the need exists for the inclusion of other change scenarios. The addition of land-use models, expected biological invasions, and synergies that may arise from future climate shifts may be particularly insightful.
  It would also be extremely helpful to do some ground-truthing and validation of models generated from the early 2000s forecast to 2020 (e.g. Milanovich et al., 2010) to understand how well the predictions and real situations match, and to quantify error and bias.

- **Phenotypic responses:** Phenotypic responses to climate change among amphibians are under-studied, and additional studies measuring this are needed across taxonomic groups encompassing a wider range of geographic regions. This work either requires a space for time substitution (Wogan & Wang, 2018), or a time series from long term field sites and monitoring, or from dedicated resampling projects aligned with historical museum samples (Holmes et al., 2016; Moritz et al., 2008).

- **Phenology:** Under climate change, shifting phenologies may alter interactions among species, for example Rollins and Benard (2020)

demonstrated that different experimental combinations measuring body size and phenological shift in metamorphosis between two larval frogs led to divergent body mass outcomes at their terrestrial phase. There are, however, few empirical studies that have documented how shifting phenologies and novel interactions will affect individual species and restructure amphibian communities in the face of climate change.

- **Dispersal:** We know little about amphibian dispersal. Dispersal syndromes and distances are known for only a handful of amphibians, yet these data are critical for understanding how well species will be able to track climate. We need these data from a wide taxonomic range of species encompassing lowlands, mountains, tropics, and temperate regions.

- **Species interactions:** We still know little about how amphibians fit into local food webs and the strength of their interactions with other species. We often do not know what species they eat or a full list of their predators. Knowledge gaps also exist for parasites and pathogens, which often interact with climate change in their impacts. Because many climate-induced declines in amphibians occur not through direct physiological impacts (Cahill et al., 2013), but rather indirectly through changes in species interactions, understanding biotic relationships could be important for accurately predicting climate change responses (Gilman et al., 2010).

- **Adaptation:** Perhaps the largest gap is how much amphibian populations facing a new or even novel climates might be able to adapt and persist in place. To understand adaptability will require an understanding of what specific traits will be under selection in future climates (not just directly from climate, but indirect traits like dispersal or biotic interactions) and measuring genetic variation using experiments or tracking relatives. Ultimately, understanding the genes underlying these responses using genomic approaches could provide direct insights into the possibility and rate of adaptation.

Gaps: Conservation & management

» A proactive management framework can help to reduce risk of future catastrophic storm impacts on vulnerable populations of amphibians in hurricane-prone regions (Sterrett et al., 2019; Walls et al., 2019). Proactive (as opposed to reactive) conservation, in general, is geographically biased and opportunities exist to strengthen this approach in many parts of the world (Ryan, Palen, Adams, & Rochefort, 2014; Walls, 2018).

» Strengthen and diversify stakeholder involvement in both conservation planning and action (Bickford et al., 2012; Hartel et al., 2020; Walls, 2018)

» Encourage development and use of conservation tools (e.g. non-invasive stress hormone assays, genomic assessments) that may help natural resource managers and conservation biologists identify at-risk populations relatively quickly, especially when potential threats are not readily apparent (Rollins-Smith, 2017; Walls, 2018).

» Develop better models of species' reactions to climate change with defined and measurable biological mechanisms. Predictions from climate models, for example, need empirical tests to provide conservation managers with workable approaches to multiple impacts from climate change (Enriquez-Urzelai et al., 2019; Walls & Gabor, 2019).

» Use more studies of behaviour, physiology, genetics and perhaps other disciplines that can have broad utility for understanding amphibian responses to climate change to inform strategies for amphibian conservation and management (Walls & Gabor, 2019).

» Long-term monitoring studies can help researchers to understand how climate change-driven stress ultimately affects individual fitness, population resilience, relative abundances, and range shifts. Additionally, multiple measures of physiological health can provide a more holistic assessment of how climate change-related factors

impact individuals (Walls & Gabor, 2019; Winter et al., 2016).

» Like species of conservation concern, non-threatened species, and especially those with data deficiency, also undergo localised population declines and losses due to climate change. Yet, common or obscure species typically are not the beneficiaries of conservation interventions. Proactively implementing conservation of common species could lead to early detection of climate change-driven issues before endangerment occurs (Walls & Gabor, 2019).

» Develop catastrophe response, rescue, and re-introduction plans. In the face of increasingly extreme weather events predicted as a result of climate change, rescuing amphibians from the wild may be a necessary conservation management action for some species. These rescues may be short-term – holding individuals for weeks to months until the threat to the species or population in the wild is reduced – or may involve the establishment of ex situ populations and reintroductions over longer time frames. Perhaps the first such instance of amphibian rescue in response to an extreme weather event related to climate change occurred in early 2020, when extreme drought conditions initiated the rescue of booroolong frogs (*Litoria booroolongensis*) from a population in northern New South Wales, Australia (https://www.environment.nsw.gov.au/news/saving-the-booroolong-frog-no-croaking-matter).

» Explore assisted migrations and managed relocation **for the most vulnerable species and geographic areas**. Most amphibians are dispersal-limited, making them one of the most climate change vulnerable groups of organisms (Foden et al., 2013). One management practice that has been suggested for dispersal-limited taxa is managed relocations, whereby populations, species, or genotypes are established in climatically suitable regions that exist outside of the natural/historical range of the species for the purpose of maintaining biological diversity or ecosystem functions (Hoegh-Guldberg et al., 2008; Richardson et al., 2009).

Many ethical, legal, and ecological dilemmas arise from this practice (Schwartz et al., 2012), among them is the potential for unintended and unpredictable consequences (Ricciardi & Simberloff, 2009). Despite these caveats, there have been efforts to more generally establish frameworks for assessing which species possess traits that might make them candidates for managed relocation, and which ecosystems and communities might benefit most from managed relocations (Gallagher et al., 2015). Sax, Early & Bellemare (2013) further suggest approaches for estimating tolerance niches as a means to identify climatically suitable potential sites for the establishment of new populations, and for assessing which species require different management interventions (in situ conservation versus managed relocations versus ex situ rescue). With regard to amphibians, managed relocation has mostly been viewed as a potential management response to disease mitigation, which advocates translocating populations to climate refugia that are unfavourable for disease, preferably within or near their natural ranges (Scheele et al., 2014). To our knowledge, there are no instances where managed relocations have been implemented for amphibians to ameliorate the impacts of climate change, and large-scale implementation of assessment frameworks to identify which amphibian species, ecosystems, and communities might benefit from this intervention is lacking. Early and Sax (2011) estimated climate paths for 15 species of amphibians in the Western United States and found that a combination of dispersal and population persistence during short periods of unfavourable climate were needed for amphibians to successfully shift ranges in response to climate change; for those species for which climate paths could not be successfully identified, managed relocations were suggested as a possible intervention.

Discussion

Progress has been made on many aspects of how climate change is already changing and will continue to affect amphibian biodiversity. However, much work remains to better plan for and take actions against

Box 3.5: Synergies: habitat alteration/degradation

Because amphibians are dependent on water or soil moisture, drought can have major negative effects on amphibian survival and reproduction (reviewed in Walls et al., 2013). Examples of drought effects on amphibians include extirpation of terrestrial species (e.g. from decreased soil moisture for lungless salamanders; Jaeger, 1980; reduction in number and water level of breeding pools for Australian frogs; Scheele et al., 2012), and changes in regional hydrology resulting in pond desiccation and population declines (e.g. frogs and salamanders in Yellowstone National Park; McMenamin et al., 2008). Increased evapotranspiration from wetlands and decreased hydrological input as a result of changes in precipitation could cause desiccation of amphibian breeding sites, causing reproductive failure of the species that use them.

Urbanisation, agricultural development, and intensive use of rangelands for livestock grazing are main drivers of habitat loss and degradation (Cameron, Marty & Holland, 2014). The impact of habitat degradation on aquatic breeding amphibians can be exacerbated by climate change and the importance of small water bodies for amphibians is often neglected (e.g. Crnobrnja-Isailović et al., 2022). The increase in frequency of droughts in some regions (e.g. California) has been linked to anthropogenic warming (Diffenbaugh, Swain & Touma, 2015) and threatens species that rely on seasonal wetlands. For example, wetland habitat could be converted to grassland as a result of decreased hydroperiod resulting from climate change, eliminating both habitat and breeding sites for amphibians (Blaustein et al., 2010). Yet, the effects of wetland warming and drying on amphibians may be difficult to predict and not necessarily synergistic or even additive, in part because amphibians may be able to compensate by decreasing metamorphosis time or increasing growth rate in response to higher resource availability (O'Regan, Palen & Anderson, 2014). Although with limited effectiveness, modified and created ponds have been shown to mitigate the impact of extreme drought and habitat loss on pond-breeding amphibians (Baumberger et al., 2020; Pechmann et al., 2001).

the negative effects of climate change. Advances in modelling and data mining, in particular, have enabled a new wave of research on theoretical trajectories and specification of taxa that are expected to be impacted negatively by changes in climate. Further work could help to close gaps in mitigation and restoration research, response to extreme events (e.g., fires), and protected area design and management.
In addition, we clarify that conservation actions rely on thoughtful planning and are informed by data from active and long-term fieldwork.

Challenges and prospects; we need more field data

Abundant metadata analyses and modelling studies are devoted to the topic of climate tracking, yet the number of carefully collected empirical datasets

available for parameterisation is still small and not representative of sites where amphibian species richness or abundance is highest. Moreover, while resurveys may be able to report changes in the altitudinal range of amphibians across multiple regions of the world (e.g. Bickford et al., 2010; Bustamante, Ron & Coloma, 2005), the lack of information on corresponding environmental shifts on the ground precludes statistical tests of associations. An increase in the number and quality of in situ observations can revolutionise our understanding of climate tracking in amphibians, and considerably change predictions in the face of future global change. However, there are several impediments to this, including varying approaches to climate change and biodiversity conservation between nations. This is often compounded by lack of training or infrastructure to conduct climate change research. Finally, in several countries, existing legal frameworks make field

research increasingly challenging and newer legislations may have unintentionally limited international collaborations by making the collection and sharing of genetic material difficult (Prathapan et al., 2018; Rochmyaningsih, 2019).

A potential long-term solution to these challenges could involve separating non-commercial and commercial research; having clear guidelines that enable research on amphibians and nurture international collaborations and skill transfer. The challenges could also be overcome especially in regions outside protected areas by engaging citizens via citizen science programmes and setting up long term monitoring databases (e.g. FrogID, available from https://www.frogid.net.au; iNaturalist, available from https://www.inaturalist.org; Frog watch India, available from https://indiabiodiversity.org; HerpMapper, available from https://www.herpmapper.org/), allowing comparative studies across time and space, and a rapid understanding of biodiversity across large scales after catastrophic events such as fire (e.g. Rowley, Callaghan & Cornwell, 2020).

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Charred forest in Bilpin, New South Wales, Australia, after the extensive bushfires in 2019-20. © Jodi Rowley

Crossodactylodes itambe is a micro-endemic bromeliad-dwelling frog from Brazil, restricted to a single mountain in the Atlantic Forest. Already classified as Critically Endangered due to ongoing habitat degradation from human activity, climate change poses a likely future threat; changes in precipitation and humidity, alongside higher average temperatures, are projected to degrade the high-elevation outcrops on which this species occurs. This species will likely be forced to shift its range to a higher elevation, where dispersal may be hampered by low quality, or lack of suitable habitat. © Michel Becheleni