A users guide for understanding reptile and amphibian hydroregulation and climate change impacts

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ABSTRACT

Human impacts on ecosystems have intensified water variability for terrestrial life, thus challenging the maintenance of water balance, or hydroregulation. The accelerated development and accessibility of technologies and computational models over the past decade have enabled researchers to predict changes in animal hydroregulation and environmental water with greater spatial and temporal precision. Focusing on reptiles and amphibians, we discuss current methods, limitations and advances for quantifying ecologically relevant metrics of environmental water stressors and organismal responses to both acute and long-term water stress that are applicable for conservation and management. We also highlight approaches that integrate environmental water data with an organism's water balance and physiological, behavioural and life-history traits to predict the limits of species' responses and assess their vulnerability to climate change. Finally, we outline promising future directions and opportunities in hydroregulation studies with a conservation focus, including broader inferences about acclimation responses, linking gene expression to functional changes, and exploring inter- and transgenerational plasticity and adaptive evolution.

Advances in these fields will facilitate more accurate assessments of species' capacities and the limits of hydroregulation in response to a more variable and unpredictable future climate.

Keywords: dehydration, drought, ectotherm, exposure, sensitivity, vulnerability, water balance

MAIN TEXT

The colonisation of land presented substantial physiological and morphological challenges associated with water balance for early terrestrial animals (Gray, 1928; Dial et al., 2015), yet allowed opportunities for novel evolutionary strategies that enabled an explosion of animal diversity on land (Minter et al., 2017). Nevertheless, environmental dryness continues to pose a major challenge for land animals, with biodiversity being highest in humid tropical rainforests and lowest in desert environments (Owen, 1989; Biber et al., 2023; Coelho et al., 2023). Global trends towards aridification can therefore compromise biodiversity, a major conservation concern given accelerated changes in climate and land use, leading to unpredictable changes in water variability and availability (Moustakis et al., 2021; Moss et al., 2024; Zhang et al., 2024). Understanding 1) how environmental water changes over time and space, 2) how animals respond to water variability, and 3) how they differ in resilience and response capacity is necessary to assess vulnerability, and it is a first step in managing extinction risk amid the current global biodiversity crisis. Progress towards these answers has been notable, due to enhanced computational power, novel statistical models, and more temporal and spatially detailed climate data (Brun et al., 2022; Klinges et al., 2024). Additionally, our understanding of hydroregulation strategies across biological levels and species has become more comprehensive (Navas and Carvalho, 2010; Lillywhite, 2017; Rozen-Rechels et al., 2019; Riddell et al., 2021). A key challenge for the management and conservation of species at risk due to climate change is to predictively link ecologically relevant water stressors (exposure risk) with the capacity of animals to maintain water balance (species sensitivity) (**Fig. 1**).

This paper reviews current knowledge on terrestrial water availability for assessing environmental exposure risk, species’ short- and long-term responses to water deficits for evaluating sensitivity, and models predicting vulnerability to environmental drying. We examine key topics and conclude proposing future directions for refining predictions of species' vulnerability in a drying world. Our focus on amphibians and reptiles highlights their role in the aquatic-terrestrial transition and the contrasting hydroregulation strategies that enable them to thrive and reproduce despite dehydration challenges.

1. Environmental exposure risk

1.1 Water availability on land

Water availability can be quantified and interpreted in many ways, and it is heavily influenced by the stochastic nature of the water cycle (Chahine, 1992; Oki and Kanae, 2006) and by the local environment (Kinlaw, 1999; Geiger et al., 2003). Broadly, water enters a terrestrial environment through precipitation, and exits through evapotranspiration and runoff (Oki and Kanae, 2006). The ratio between precipitation and evapotranspiration can be used to calculate the aridity index (Zomer et al., 2022), broadly define climate classifications (Beck et al., 2018), and quantify annual site water balance. In climates with strong seasonal rainfall, precipitation can predict the phenology of breeding events (Gould et al., 2022; Thompson et al., 2022) and the seasonal primary productivity of ecosystems (Lieth, 1973). Once in the environment, water can be stored in the ground, in the air, or accumulated in water bodies (**Table 1**). Water content in the air is typically measured as the pressure of gaseous water, or water vapor pressure (Gates, 1980) which serves as a basis for calculating relative humidity (RH), a common meteorological metric. However, RH is often less relevant for assessing physiological responses in organisms compared to water vapor pressure (Anderson, 1936; Kurta, 2014; Wu, N. C. et al., 2024b). Finally, water vapor pressure and temperature are inherently linked (Campbell and Norman, 2000), and incorporating temperature allows for the calculation of vapor pressure deficit (VPD), a key driver of physiological processes in plants and animals (Adolph, 1932; Novick et al., 2024; Wu, N. C. et al., 2024a). For example, in two environments with the same humidity, that with higher air temperatures will increase VPD (**Fig. 1**).

Water in the soil matter most for species that rely on underground microrefugia (Wu et al., 2015; Giacometti and Tattersall, 2023), or for many amphibians, which obtain water directly from the substrate (Hillman et al., 2009; Comanns et al., 2017). Water fluxes depend on soil properties (Campbell and Norman, 2000), with extreme examples in sand and clay. Wet sands have an open texture and dry quickly, whereas wet clays exhibit high soil moisture tension and dry slowly. In comparison, wet peats dry rapidly and are difficult to rehydrate. However, a valid generalisation is that below-ground climates maintain higher humidity than surface environments, reducing dehydration risk to animals (**Fig. 1**), for example in species that shelter underground (Carvalho et al., 2010), and especially desert dwellers (Woodbury, 1954; Bulova, 2002).

1.2 Quantifying water variability and drought indices

Quantifying spatiotemporal shifts in hydric patterns can be approached in various ways to determine whether an environment is drier than usual. Precipitation and moisture levels, whether in the air or soil, can be measured long-term via weather stations, or short-term using miniature environmental data loggers, with Bramer et al. (2018) and De Frenne et al. (2024) providing examples of commercially available loggers and field deployment considerations. When long-term datasets are available, various hydrological extreme metrics can be calculated (Pisor et al., 2023). For instance, using a monthly rainfall example from Sydney, Australia (**Fig. 2**), one can calculate the duration (D) of high rainfall (above 90th percentile; high likelihood of flooding) and low rainfall events (below 10th percentile; high likelihood of drought), frequency of extreme rainfall events, and measures of intensity (I)—the average of extreme rainfall events—magnitude (M)—the maximum rainfall event—and severity (S)—the cumulative total of extreme rainfall events. Changes in permanent water sources such as lakes, ponds, streams, and rivers can be quantified via drones (Spence and Mengistu, 2016; Woodget et al., 2017), satellites (Nath and Deb, 2010; Zhou et al., 2021), or directly using standard environmental monitoring tools, enabling spatiotemporal quantification of water body dynamics, particularly relevant for species reliant on temporary or permanent aquatic habitats (**Table 1**).

Relevant for policy makers, quantifying environmental drying risk requires simplification of complex metrics and variables. One option is relying on meteorological drought indices reflecting the interplay between the climate variables mentioned in the previous section (**Table 1**). However, theses indexes have no absolute value, meaning that changing indexes relate to species-specific effects that may change among individuals, populations and communities. The simplest drought index is the Standardised Precipitation Index (SPI), which relies only on precipitation data (McKee et al., 1993). Complex counterparts include the Palmer Drought Severity Index (PDSI), which incorporates the hydrological cycle (Palmer, 1965; Wells et al., 2004), and the Normalized Difference Vegetation Index (NDVI), which relies on satellite imaging to quantify vegetation 'greenness' (Rouse Jr et al., 1974). Each index has strengths and weaknesses (Zargar et al., 2011), and all have been used for predicting drought risks, but they are more valuable for long-term appraisals. The utility of drought indices in analysing short-term biological impacts, particularly in animals capable of behavioural and physiological adjustments, remains uncertain. However, integrating drought indices with other environmental processes presents a promising research direction, as shown by a recent assessment proposed by Crausbay et al. (2024), which integrates drought indices with vegetation types, canopy cover, slope, time since fire, and other environmental features, and develops region-specific management actions for decreasing further exposure. These actions include managing environmental water, restoring sites affected by deforestation and urbanisation, and promoting ecosystem persistence under drought conditions (Mathwin et al., 2021). Despite the enormous potential of such analyses, caution is required before implementing actions, especially those related to water supplies to landscapes, which might damage existing habitats or favour the accumulation of predators (Mathwin et al., 2021).

The analytical context discussed here requires moving from quantifying environmental drying risk to calculating case-specific exposure risks to drought. This process is challenging, partially because hydrological variables such as rainfall, evapotranspiration, and soil moisture content exhibit greater uncertainty than temperature trends, due to the stochastic nature of atmospheric processes (Wu, Y. et al., 2024). Nonetheless, the expanding availability of independent hydrological models (**Table 1**) offers a timely opportunity to refine predictions of how reptiles and amphibians will respond to environmental water availability. Once ecologically-relevant water variables are quantified, numerous approaches may integrate them explicitly with biological traits across different levels of organization—from molecules to phenotypes to communities. The interplay between exposure—typically to stressors such as water shortages or drought periods—and biological response is key to understanding structural and functional consequences, providing indicators of sensitivity and vulnerability. The following section discuss sensitivity and vulnerability assessments, with a particular focus on the central theme of this review: hydroregulation.

1.3 Linking Exposure, Sensitivity, and Vulnerability

The vocabulary of ecological climate change research has become complex, with many terms defining interrelated, yet different concepts, including *Sensitivity*, *Vulnerability*, *Risk*, and *Resilience*. These terms have gained prominence across scientific and political discussion, as they are embedded in global agendas on sustainable development, disaster risk reduction, and climate change, and biodiversity loss (Williams et al., 2008; Scholz et al., 2012; Birkmann and McMillan, 2020). While we acknowledge this conceptual variability, our focus is on identifying the most relevant information for predicting future trends and anticipating species declines. To this end, various methodological tools and conceptual frameworks have been employed to assess how organisms and species respond to climate changes. However, quantifying responses is inherently complex, as environmental variability operates across all possible spatial and temporal scales, and science requires operationalisation to specific cases. For instance, both exposure to climate change and species sensitivity to environmental shifts can differ dramatically within reptiles and amphibians. Linking exposure, sensitivity, and vulnerability is a goal benefitted by advances in computational power, more sophisticated statistical models, and large databases, which promote conceptual and disciplinary bridges. For example, connecting environmental changes not only with physiology and behaviour but also with conservation biology and ecosystem ecology (Cooke et al., 2013; Madliger et al., 2018). Methodological approaches have also evolved rapidly, and the most advanced tools explicitly link climate variables with organismal response by considering the underlying physiological and behavioural mechanisms that govern their survival and distribution (see '*4. Assessing vulnerability: integrating exposure and sensitivity*' section).

Porter et al. (1973) and Tracy (1976) developed general microclimate models for quantifying the energy, heat and water budgets of organisms that have been revisited taking into consideration current computing power. Nowadays, it is possible to calculate microclimate at any location, and with fine temporal resolutions (reviewed in Meyer et al., 2023; Kemppinen et al., 2024). Some programs even integrate microclimate (**Table 1**) with the calculated heat and water budgets of organisms (Kearney and Porter, 2020; Kearney and Enriquez-Urzelai, 2023) to estimate tolerance and distribution limits of organisms under real or any simulated climate (Kearney et al., 2018; Cheng et al., 2023). Relative to correlational models (Elith and Leathwick, 2009; Peterson et al., 2011), these developments have added capacity for mechanistic predictions based on physiological limits of vulnerability to climate change (Riddell et al., 2021; Briscoe et al., 2023; Pottier et al., 2025), bringing physiological data into the equation.

2. Species sensitivity risk: short-term impacts

Many acute and long-term responses to environmental drying are parallel to those triggered by other generalised stressors (e.g., temperature, pollutants, food restriction), including altered metabolism, cardiovascular responses, growth, cellular oxidative stress, neuroendocrine pathways, and gene expression. These common biomarkers are well-documented in the literature, both in terms of methodology and interpretation (Bustin et al., 2009; Ribou, 2016; Moretti et al., 2017; Madliger et al., 2018; Lighton, 2019). In this section, we highlight some common responses to drying, with a focus on water-specific responses and minimally invasive methods, outlined in **Table 2**. Most comparative studies compare arid adapted and non-arid adapted species, while experimental studies often involve subjecting animals to restricted water sources or increased environmental dryness.

2.1 Genetic responses

Genetic responses to environmental stress are broad across the literature. Here, we focus on three areas of hydroregulation: (1) the skin barrier, (2) water reabsorption, and (3) cellular repair and immunity (**Fig. 3**). At the site of evaporation, the skin barrier of reptiles is regulated by the epidermal differentiation complex (EDC) gene cluster, which encodes proteins essential for keratinised cells in amniote skin. Among these, corneous beta-proteins (CBPs) genes are crucial for forming the outer layer of the skin, the stratum corneum (Holthaus et al., 2024), while the *Loricrin* gene supports alpha-keratinisation in lizard epidermis (Holthaus and Eckhart, 2024). Under arid conditions, the upregulated expression of CBPs and *Loricrin* increases the thickness and strength of the stratum corneum, enhancing resistance to dehydration. Comparative genomics between the desert tortoise (*Gopherus agassizii*) and the temperate aquatic western painted turtle (*Chrysemys picta bellii*) have identified multiple positively selected genes associated with drought resistance. These genes include *CSTA* and *SDR16C5* (**Fig. 3**), which are involved in keratin formation and lipid-based waterproofing, respectively (Tollis et al., 2017). In contrast, amphibians rely on mucous secretions to minimise water loss, along with other functional roles. For example, *Xenopus laevis* upregulates genes (e.g., *grp94* and *grp75*) related to glucose-regulated protein during dehydration, promoting the synthesis and secretion of protective glycoproteins to reduce water loss while preserving skin moisture (Malik et al., 2023).

Animals adapted to arid conditions exhibit a strong capacity for water reabsorption, enabling them to produce highly concentrated urine while maintaining salt balance. Several genes are essential for cellular water reabsorption, particularly those encoding membrane proteins forming water channels such as aquaporins (AQP). Aquaporin genes, widely present in amphibians and reptiles (**Fig. 3**), and the proteins they encode are crucial for osmoregulation, including transcellular water and solute transport (Suzuki and Tanaka, 2009; Shibata et al., 2014; Chen et al., 2019; Wu et al., 2019). On the other end of osmoregulation, water balance can also be regulated by moving chloride along with sodium or potassium, creating osmotic gradients between cells and their surrounding environment, which drive water reabsorption through osmosis. This process requires ion transport proteins, including those in the Solute Carrier 12 (*Slc12*) family of cation-coupled chloride cotransporters (**Fig. 3**) (Motoshima et al., 2023). The proteins encoded by these genes facilitate sodium reabsorption in renal structures like the distal convoluted tubule and thick ascending limb, generating a hyperosmotic environment that drives water reabsorption via osmosis (Marra et al., 2012).

The kidney is the epitomic organ in water homeostasis, filtering waste while regulating water and ion balance, making it particularly vulnerable to dehydration stress. Thus, impaired kidney function figures among the various forms of stress imposed by chronic water deprivation in amphibians and reptiles. Systems of protection have evolved in lizards and turtles adapted to arid environments, a condition thought to positively select genes associated with kidney repair, such as *DCHS2,* related to cell adhesion, and *CD34*, linked to vascular repair (**Fig. 3**) (Tollis et al., 2017; Araya-Donoso et al., 2022). Another physiological challenge caused by dehydration is disruption of cellular homeostasis, leading to oxidative stress traduced in the accumulation of reactive oxygen species, causing tissue damage (Dupoué et al., 2020c; Ritchie and Friesen, 2022). However, amphibians and reptiles adapted to arid environments activate antioxidant defence mechanisms to mitigate dehydration-induced oxidative stress (Moreira et al., 2020; de Amaral et al., 2024). For instance, numerous antioxidant and detoxification genes are regulated by the transcription factor erythroid 2-related factor 2 (*Nrf2*), a key regulator of oxidative stress responses under elevated reactive oxygen species levels (**Fig. 3**) (Malik and Storey, 2009). With declining genetic sequencing costs and expanding analytical capacity, the coming years hold promise for advancing our understanding of the genetic responses of amphibians and reptiles to hydric stress.

2.2 Neuroendocrine responses

One of the most well-documented effects of pond drying are neuroendocrine responses, which have been extensively studied in amphibians. Water-dependent tadpoles can adjust their developmental rate and, therefore the timing of metamorphosis in response to environmental changes (Newman, 1988; Lai et al., 2002; Benard, 2004; Wu and Kam, 2009; Higginson and Ruxton, 2010; Thompson and Popescu, 2021; Sinai et al., 2022). These environmental cues stimulate the central nervous system, activating the hypothalamo-pituitary-interrenal/adrenal axis to initiate survival mechanisms. During pond drying, the hypothalamus increases the production of a corticotropin-releasing hormone (CRH), stimulating the release of the adrenocorticotropic hormone (ACTH) and thyroid-stimulating hormone (TSH) from the pituitary. This, in turn, activates the thyroid and interrenal glands, elevating thyroid hormones (THs) and corticosterone (CORT) in the bloodstream, which help manage stress, metabolism, and developmental transitions (Kikuyama et al., 1993; Denver, 1997; Kirschman et al., 2017; Ruthsatz et al., 2020). Increased hormone production accelerates metamorphosis, thus shortening the larval period and improving survival as aquatic habitats shrink (Denver, 2013). This hormonal plasticity highlights the resilience of some amphibians, enabling them to cope with environmental fluctuations and complete their life cycle under harsh conditions. Some hormones, such as CORT, are released into surrounding waters through various mechanisms (e.g., secretion and diffusion), and remain stable long enough to be quantified. Therefore, it can be measured non-invasively from water samples, allowing researchers and managers to monitor stress in both laboratory and field settings (Ruthsatz et al., 2023a; Ruthsatz et al., 2023b), However, waterborne and plasma CORT levels may vary across species (Millikin et al., 2019) and depend on environmental contexts (Mausbach et al., 2022).

In terrestrial amphibians and reptiles, acute dehydration triggers fluid balance responses, via mineralocorticoid hormones, including arginine vasopressin, angiotensin, and aldosterone, all of which play key roles in water metabolism, helping organisms retain water and maintain circulatory stability under dehydration stress (McCormick and Bradshaw, 2006; Uchiyama and Konno, 2006; Dantzler and Bradshaw, 2008; Hillman et al., 2009). CORT also contributes to hydroregulation through its mineralocorticoid actions (McCormick and Bradshaw, 2006; Dupoué et al., 2016; Brusch et al., 2020), though it may not consistently correlate with plasma osmolality within a species (Dezetter et al., 2022b). Elevated CORT may mobilise energy reserves via muscle catabolism, reallocating bound water to maintain hydration (Brusch et al., 2018; Dezetter et al., 2021). These hormones also regulate other interrelated processes, including energy metabolism, reproduction, social behaviour, and thermoregulation (Ladyman et al., 2006; Bleu et al., 2013; Carsia et al., 2023; Crino et al., 2024). Therefore, when evaluating hormonal responses to dehydration, researchers should consider these overlapping physiological functions and assess additional traits linked to hydration and water balance.

2.3 Physiological responses

Physiological responses and regulation to acute environmental drying include osmoregulation, cardiovascular function, metabolism, immunity, and the renin-angiotensin-aldosterone system (as mentioned above) are well documented in the literature for amphibians (Feder and Burggren, 1992; Hillman et al., 2009) and reptiles (Pough and Gans, 1982; Dantzler and Bradshaw, 2008; Bradshaw, 2012). Here, we focus on traits commonly measured with conservation relevance, emphasising minimally invasive protocols (**Table 2**). These can be broadly classified into (1) water loss through evaporation, (2) hydration state, and (3) daily water flux.

Evaporative water loss (EWL) is of considerable interest because it responds immediately to low air humidity (Mautz, 1980; Hillman et al., 2009). Evaporation depends on both biophysics (Foley and Spotila, 1978; Campbell and Norman, 2000) and hydration state (Anderson et al., 2017; Senzano and Andrade, 2018; Weaver et al., 2022), but also on physiology, so that the rate of water loss tends to be lower in comparable counterparts from more arid environments, across populations and species (Bentley and Schmidt-Nielsen, 1966; Roberts and Lillywhite, 1983; Cox and Cox, 2015; Salazar and Miles, 2024). EWL mainly occurs through respiratory and cutaneous pathways, with some influence from ocular and cloacal pathways (**Fig. 1**)(Hillman et al., 2009; Pirtle et al., 2019), and the combination of these pathways (total EWL, or TEWL) can be measured simply by the mass loss of the animal (or mass gain of a desiccant) over time, or by respirometry methods (Hillman et al., 2009; Lighton and Halsey, 2011). Physical models (Senzano et al., 2022) or mathematical approaches (Riddell et al., 2017) can be used to quantify EWL, but special consideration of boundary layers is required. These thin layers of fluid (air or water) that form at the interface between an organism's body and its surrounding environment, usually affect heat, water, and gas exchange. Experimentally, respiratory and cutaneous EWL (REWL and CEWL, respectively) can be distinguished by placing a mask with separate airflow for the lungs and skin (Withers, 1977; Senzano and Andrade, 2018) or by using an impervious membrane to isolate body regions (Dmiel, 2001). CEWL can also be measured directly with an evaporimeter in a flux chamber (Lillywhite et al., 2009; Tingley et al., 2012; Oufiero and Van Sant, 2018), a method that has the added benefit of focusing on specific body regions (Weaver et al., 2022; Weaver et al., 2023). For broader comparisons, global databases of EWL for frogs and squamates are available to statistically tease out environmental and phylogenetic drivers of EWL (Cox and Cox, 2015; Le Galliard, J. F. et al., 2021; Wu, N. C. et al., 2024a). However, EWL datasets for other herpetofauna groups, such as Crocodilia, Testudines, Caudata, and Gymnophiona, remain relatively scarce compared to those for frogs and squamates.

Animals in dry environments survive by efficiently storing water, producing metabolic water, mobilising water from tissues, and tolerating low body water content (Cloudsley-Thompson, 1999; Hillman et al., 2009; Lillywhite, 2017). The water content in the body of an animal is expressed as a percentage of whole mass or dry mass and has historically been measured by fully desiccating specimens (Thorson, 1955; Pough et al., 1983; Taigen et al., 1984). Amphibians typically have 77–83% water content by body weight (Hillman et al., 2009), while reptiles range from 63–74% (Thorson, 1968). Shifts in body water allocation may support water balance when facing dehydration, and the nature of such pathways varies across lineages. For example, amphibians can absorb water from their bladders (Sawyer and Schisgall, 1956; Schmuck and Linsenmair, 1997; Suzuki et al., 2015), while snakes and lizards rely on CORT-mediated muscle catabolism to release water originally associated with proteins (bound water), and may obtain water as a byproduct of lipid metabolism (Brusch et al., 2018; Dezetter et al., 2021). Internal water mobilisation can be tracked through changes in blood nutrients, proteins, triglycerides, uric acid, mineralocorticoid hormones, as well as transcriptome and proteome changes in blood and tissue samples (Suzuki et al., 2015; Brusch et al., 2018). Given recently established pathways for muscle catabolism in snakes and lizards, non-invasive methods, such as specimeters, now quantify muscle changes as proxies for water balance in reptiles (Lourdais et al., 2005; Dezetter et al., 2021). In amphibian research, a method to assess hydration states involves measuring the body mass of field-captured individuals, then allowing them to fully rehydrate in a field lab, and recording the subsequent mass. The difference between the initial field mass and the fully hydrated mass indicates the degree of dehydration experienced in their environment. For instance, a study on tropical frog species found that hydration behaviours and voluntary tolerance of dehydration varied with habitat use, even among closely related species within the same family (Tracy et al., 2014). This approach provides insights into species-specific water balance strategies and their adaptability to varying environmental conditions.

Blood biochemistry parameters, such as plasma osmolality and haematocrit, serve as indirect measures of hydration status (**Table 1**) in three dominant contexts, field studies (Capehart et al., 2016; Moeller et al., 2017; Brischoux and Cheron, 2019; Weaver et al., 2024), laboratory experiments (Dupoué et al., 2017; Wu et al., 2017; Dezetter et al., 2022b; Chabaud et al., 2023), and veterinary applications (Perry et al., 2020; Cameron et al., 2024). Plasma osmolality is a direct indicator of hydration, and is best measured using vapor pressure or freezing-point depression osmometers (Nevarez et al., 2012; Wright et al., 2013; Buchmiller et al., 2024), as formulas based on solute concentrations often show poor agreement with direct measurements (Dallwig et al., 2010; Nevarez et al., 2012; Perry et al., 2020). Haematocrit is determined by centrifuging blood in microcapillary tubes, and it is frequently used as a proxy for hydration status, although it responds to multiple influencing factors such as blood oxygen-carrying capacity (Brischoux et al., 2011; Lourdais et al., 2014; Bodensteiner et al., 2021) and does not consistently correlate with plasma osmolality (Dupoue et al., 2015; Dezetter et al., 2021). Therefore, interpreting haematocrit changes as indicators of hydration requires caution, considering additional factors affecting blood viscosity and oxygen transport. Ecologically relevant osmolality measurements should incorporate species-specific normosmotic values, tolerance to variation, temporal dynamics of osmolality shifts, and threshold effects on physiological and behavioural water balance regulation (Dessauer, 1970). Notably, species from xeric environments tolerate greater osmolality fluctuations than those from mesic habitats, underscoring the importance of species-specific considerations in hydration studies (Nagy and Medica, 1986; Brusch and DeNardo, 2017).

Whole-animal water flux, encompassing influx, storage, and efflux (**Fig. 1**), can be quantified using doubly labelled water (DLW), which estimates field metabolic rate and water flux over extended periods (**Table 1**) (Nagy, 1989). DLW has been widely applied to measure daily water flux in reptiles across diverse field conditions (Beaupre, 1996; Christian et al., 1999; Christian et al., 2007; Roe et al., 2008; Harden et al., 2014). For instance, velvet geckos from arid zones exhibit lower water flux rates year-round compared to those in tropical regions, reflecting adaptive water conservation strategies (Christian et al., 1998). The ability to estimate both field metabolic rate and water flux makes DLW a powerful tool for field-based physiological research. However, certain assumptions in DLW-derived metabolic rates can introduce measurement errors (Nagy, 1980). For example, high humidity can overestimate metabolic rates due to excessive water vapor exchange through cutaneous and respiratory surfaces, whereas total water flux aligns more reliably with gravimetric estimates of TEWL (Anderson et al., 2003). Additionally, DLW is unsuitable for species with high water flux, such as semi-aquatic reptiles, because rapid water turnover depletes isotopes too quickly, preventing accurate measurements (Booth, 2002; Jones et al., 2009). The method has limited use for amphibians due to their high water fluxes, but if the primary objective is to assess water turnover, the method could be applied to more terrestrial amphibian species. This would offer valuable insights into the water cost of activity and dispersal under field conditions.

2.4 Behavioural responses

Terrestrial amphibians and reptiles employ diverse behavioural strategies to regulate water balance, which can be broadly classified into (1) water-conserving behaviours, (2) water-seeking behaviours, and (3) moisture-harvesting behaviours. These strategies mitigate EWL, optimise hydration, and enhance survival in desiccating environments. Water-conserving behaviours are those minimising exposure to drying conditions. When avoidance of dehydration is no longer viable, animals may engage in water-seeking behaviours, actively locating and consuming water to restore hydration, or actively collecting and absorbing water from their surroundings. A most universal water-conserving behaviour involves reducing or shifting diel activity and selecting microhabitats that provide moisture, such as burrows, and this type of behaviour have been observed in the field (Daltry et al., 1998; Davis and DeNardo, 2010; Kearney et al., 2018; Moore et al., 2018) and experimentally (Navas et al., 2002; Székely et al., 2018; Rozen-Rechels et al., 2020; Dezetter et al., 2023). Also, water-conserving behaviours relate to body temperatures, which usually enhances rates of water loss (Tracy et al., 2008; Dupoué et al., 2015; Lourdais et al., 2017). Therefore, shifts in thermoregulatory behaviour, including thermal depression, can contribute to water-conserving strategies (Ladyman and Bradshaw, 2003; Anderson and Andrade, 2017; Le Galliard, J.-F. et al., 2021; Camacho et al., 2023). Although the interplay between water and heat budgets complicates the disentangling of hydroregulation and thermoregulation mechanisms (Pintor et al., 2016; Rozen-Rechels et al., 2019), recent modelling approaches considering both joint mechanisms and microclimatic data are improving our understanding of behavioural responses to drying and heating (Kearney et al., 2018; Moore et al., 2018; Encarnación-Luévano et al., 2021). By strictly controlling for temperature, experimental studies have demonstrated hydroregulation behaviours through the active selection of moister microclimate in both wet-skinned amphibians (Mitchell and Bergmann, 2016) and dry-skinned reptiles (Dezetter et al., 2023). This behaviour mitigates the acute effects of desiccating conditions. These findings suggest that both resistance to water loss and hydric performance response curves may influence the timing of behavioural responses to drying in reptiles and amphibians.

Some animals can reduce water loss by modifying body posture and preferring those that reduce the exposed area to the environment (**Table 2**). Placing limbs against the body and using skin folds to cover ventral surfaces against the substrate, as in Anura (Pough et al., 1983) or coiling in Caudata (Cohen, 1952) greatly reduce TEWL (Spotila and Berman, 1976). In addition to postural changes, several species of arboreal frogs use limbs to spread waxy films over their body surfaces during dry seasons or produce cocoons to reduce CEWL (Lillywhite, 2006). By manipulating the hydration state via moisture gradients and assessing postural adjustments, experimental studies can examine the determinants of these behaviours and their benefits for maintaining hydration (Navas et al., 2002; Mitchell and Bergmann, 2016). In reptiles, behaviours such as coiling in snakes or adopting tucked-in postures in lizards may also confer water-saving benefits. However, this aspect has received comparatively limited attention, mostly restricted to studies on egg-brooding behaviour in snakes, where subtle postural shifts can reduce egg surface exposure and limit water loss from the egg clutch (Lourdais et al., 2007; Stahlschmidt et al., 2008; Stahlschmidt and DeNardo, 2010). Finally, the simple closure of eyes can help reduce water loss through the permeable eye membrane in lizards (Pirtle et al., 2019).

When avoiding and restricting drying is no longer possible, reptiles and at least some amphibians will seek water to restore their hydration state (**Table 2**). Experimental systems called "olfactometers" designed by Grubb (1973), and follow-up studies with maze designs, have demonstrated that frogs and lizards can detect and locate free-standing water via olfactory cues (Navas et al., 2002; Madelaire et al., 2020; Ouellet et al., 2020; Lorrain-Soligon et al., 2022; Northrop, 2024). However, generalising is not possible for amphibians. Finding generic water for hydration and finding specific waters for reproduction seem to be independent processes, and both have been identified in some species. For example, telemetric studies show that poison frogs rely on odour cues from stagnant water to find new breeding pools (Serrano-Rojas and Pašukonis, 2021). However, this ability varies across species (Reshetnikov, 1998; Maia, 2014) and may relate to drying tolerance and habitat aridity (Cruz-Piedrahita et al., 2018; Galindo et al., 2024). Particularly, some anuran species rely on structured water search strategies, while others find water by erratic exploration (Maia, 2014). Finally, drinking matters for some species only as others will rely on a specialized, richly vascularized region of the pelvic skin (Willumsen et al., 2007). It has also been reported for snakes subjected to field experimental dehydration or rehydration after capture (Brischoux et al., 2017; Dezetter et al., 2022b) and is triggered by physiological thresholds such as hydration status (Sandfoss and Lillywhite, 2019; Edwards et al., 2021). Quantifying water-seeking behaviour (e.g. time to find water source) should be of consideration for habitat restoration managers when optimising water resources for herpetofauna to persist and flourish in a given habitat (Mathwin et al., 2021).

Moisture and rain-harvesting behaviours are also observed in reptiles (Sherbrooke, 1993; Joel et al., 2017), These behaviours include snakes coiling and flattening their bodies, lizards flattening their bodies, and both lizards and tortoises raising their abdomen and lowering their heads and tails (Repp and Schuett, 2008; Glaudas, 2009; Yenmiş et al., 2024). Similarly, some postural adjustments in amphibians can facilitate moisture and water uptake through the skin, particularly through the pelvic patch (McClanahan Jr and Baldwin, 1969; Bentley and Main, 1972; Hillyard et al., 1998; Word and Hillman, 2005). Overall, water-searching behaviours and related adaptations are critical for understanding species sensitivity and resilience to aridification. For instance, invasive frogs at the forefront of their invasion show distinct water-searching tendencies, with stress differentially affecting this behaviour (Madelaire et al., 2020).

2.5 Life history responses

Water stress can impact life history by influencing (1) growth and the rate of development, (2) body size, and (3) reproduction. Animals can adjust their rate of development under different environmental conditions (see hormonal control under the '*2.3 Neuroendocrine responses*' section). This developmental plasticity can be either adaptive or maladaptive, depending on whether the developmental environment matches the conditions an individual experiences later in life (Monaghan, 2008; Beaman et al., 2016). For the larval stages of amphibians, reduced water availability, such as pond drying, can accelerate larval development, leading to smaller body sizes or incomplete metamorphosis due to resource constraints, crowding, poorer water quality, and increased predation risk (Márquez-García et al., 2010; Gomez-Mestre et al., 2013; Albecker et al., 2023). Some species, however, do not show changes in developmental rate nor exhibit delayed larval development under drying conditions (Richter-Boix et al., 2011), promoting the importance of species-specific responses. It is also clear that developmental plasticity to pond drying can have carry-over effects on post-metamorph individuals and adults. Under pond drying conditions, metamorphs have lower thermal tolerance, are less exploratory and more stressed, and have lower jumping performance and lower immunity (Gervasi and Foufopoulos, 2008; Crespi and Warne, 2013; Charbonnier et al., 2018; Brannelly et al., 2019; Ohmer et al., 2023; Nolan et al., 2025; Wu et al., 2025). Size is particularly important because larger individuals are associated with increased survival rate, performance (Cabrera-Guzmán et al., 2013), and lower risk to disease progression for the same pathogen load (Brannelly et al., 2018; Wu et al., 2018).

Water availability also plays a critical role in the reproductive success of egg-laying reptiles, influencing both egg survival and offspring development. For species that lay eggs on land, eggshell thickness and composition are key determinants of desiccation risk. Flexible-shelled eggs, which lack or have minimal calcareous layers (most squamates and some chelonians), are more porous and susceptible to water loss compared to rigid-shelled eggs with a well-developed calcareous layer (crocodilians, some chelonians, and a few squamates) (Legendre et al., 2022). A meta-analysis showed that substrate moisture had a small but significant effect on hatchling length and mass for reptiles, as well as on sex ratios specifically for chelonians, but not on incubation duration (Bell et al., 2025). However, this meta-analysis did not consider differences in eggshell type due to phylogenetic biases in categorising shell type. Species that nest in arid environments tend to have highly absorbent eggshells and thicker shells, suggesting that species with flexible eggshells may be more vulnerable to environmental drying (D'Alba et al., 2021; Debruyn et al., 2023). At the other extreme, excessive moisture can also be detrimental, leading to reduced oxygen availability in nests, lower hatchling success, and high embryo mortality (Marco and Díaz-Paniagua, 2008; Gatto and Reina, 2022; Warner et al., 2023). These findings underscore that water management in nesting habitats of reptiles is as crucial for egg and juvenile survival as it is for adult life history strategies in response to environmental dryness.

Drying stress during reproduction and early life can impact reproductive output and offspring phenotypes in reptiles (Dupoué et al., 2018; Dupoué et al., 2020b; Dezetter et al., 2021). Successful reproduction requires substantial water investment, particularly during gravidity in oviparous reptiles (Brusch et al., 2019; Dupoué et al., 2020a), and even more so in viviparous species, where pregnant females experience increasing hydration demands as embryos develop in utero (Dupoue et al., 2015; Lourdais et al., 2015; Lourdais et al., 2017). To reduce water loss, gravid females may adjust their behaviour, seeking moister microhabitats (Lourdais et al., 2017). However, under limited water availability, they face a trade-off between self-maintenance and offspring investment, often prioritizing embryonic water allocation at their own physiological expense (Dupoue et al., 2015; Dupoué et al., 2020a; Dezetter et al., 2021). Maternal dehydration can have severe reproductive consequences, including follicular resorption at early stages (Capehart et al., 2016; Zani and Stein, 2018), reduced investment in eggs, and thinner eggshells with altered immune function (Brusch et al., 2019). In later stages, maternal water deprivation increases embryonic mortality (Dezetter et al., 2021), potentially contributing to drought-driven population decline (Madsen et al., 2023). These demographic costs may be exacerbated by fecundity trade-offs, as larger females carrying more embryos experience greater physiological stress (Dupoue et al., 2015; Lourdais et al., 2015; Dezetter et al., 2021). However, the generality of maternal-offspring water trade-offs remains uncertain, as some species, such as *Anolis sagrei*, exhibit no observable effects of maternal dehydration on fecundity, egg size, or egg hydration (Wayne et al., 2025).

3. Species sensitivity risk: long-term impacts

Beyond the immediate effects of drying, animals must also cope with longer periods of desiccation for populations to survive. Understanding the long-term implications of water limitation requires an integrative approach that incorporates adaptation, developmental plasticity, and demographic shifts through experimental and field-based studies. This section explores three key aspects of long-term water deficit impacts: (1) the role of heritability and acclimation in hydroregulation traits, and (2) the influence of water availability on body size evolution.

3.1 Heritability and acclimation of hydroregulation traits

Repeatability and heritability experiments are key to determining whether hydroregulation traits are targets of natural selection. Although often labour-intensive, repeatability measures the consistency of a trait within individuals under similar physiological conditions, whereas heritability assesses its genetic transmission across generations (Wolak et al., 2012). However, our understanding of the repeatability and heritability of hydroregulation traits remains limited. Empirical studies provide some insights into the genetic and phenotypic basis of these traits. For instance, covariance between thermal traits and skin resistance to water loss has been observed in *Plethodon metcalfi* (McTernan and Sears, 2022), significant repeatability of EWL in *Sceloporus consobrinus* (Oufiero and Van Sant, 2018), and the moderate heritability of desiccation tolerance in *Lampropholis* skinks (Martins et al., 2019). While these studies suggest that hydroregulation traits exhibit some degree of plasticity, large-scale assessments of frog populations across natural climatic gradients indicate low variation in EWL rates, suggesting potential constraints on plasticity (Davies et al., 2015; Bovo et al., 2023). These findings emphasize the need for broader geographic and taxonomic coverage (White et al., 2021; Herrando-Pérez et al., 2023) to clarify the magnitude of variation in hydroregulation traits and how they scale over time to shape long-term responses to environmental change.

Acclimation, the ability of organisms to adjust to changing environmental conditions, is another key aspect of survival in fluctuating climates, especially in water-scarce environments. Our understanding of the acclimation potential of hydroregulation traits is limited compared to thermal physiological counterpart traits (Seebacher et al., 2015), although some studies have explored how organisms modify hydroregulation in response to thermal acclimation (Davies et al., 2015). For example, thermal acclimation during development can lead to changes in TEWL that persist until adulthood in snakes (Dezetter et al., 2022a), while the TEWL of lizards decreased in response to warmer temperatures (Vicenzi et al., 2021). Riddell et al. (2019) highlighted that temperature is an important cue for developing a desiccation-resistant phenotype, by regulating water loss through the regression and regeneration of capillary beds in the skin. The growing literature on disentangling the differences in acclimation effects of temperature and drying exposure on hydroregulation provides a promising area for understanding long-term water restrictions or simulated drying to assess the plasticity of these traits across different species (Kobayashi et al., 1983; Kattan and Lillywhite, 1989; Moen et al., 2005; Riddell et al., 2018a; Rozen-Rechels et al., 2020; Weaver et al., 2023).

3.2 Water availability and body size evolution

One notable potential long-term effect of changes in precipitation is altered body size (Gouveia and Correia, 2016; Guo et al., 2019; Pincheira-Donoso et al., 2019). Two contrasting mechanisms have been proposed to explain this relationship: (1) the ‘resource hypothesis’, where higher rainfall boosts primary productivity, supporting larger individuals due to greater food availability

(Rosenzweig, 1968), and the 'water conservation hypothesis', where arid environments favour larger individuals because lower surface-area-to-volume ratios reduce evaporative water loss relative to smaller individuals (Nevo, 1973; Gouveia and Correia, 2016). Evidence from reptile communities supports the resource hypothesis, with some species increasing in size as precipitation rises (Stanley et al., 2020). However, amphibians show a more complex pattern, with body size correlating with higher precipitation in cooler climates but with lower precipitation in warmer regions, possibly indicating a transition from resource-driven to desiccation-resistance-driven selection (Sheridan et al., 2022). Despite these findings, body size responses to climatic water balance remain debated (Servino et al., 2022). In contrast with reptiles, the permeable skin of amphibians makes them particularly vulnerable to desiccation. This key difference may contribute to diverging size trends between reptiles and amphibian communities in response to water availability. To clarify these patterns across sites, long-term body size monitoring in conjunction with environmental data—including analyses of museum specimens with historical climate records—can help elucidate the drivers of body size evolution. Further research is needed to assess long-term changes in skin permeability and their potential correlation with body size variation.

4. Assessing vulnerability: integrating exposure and sensitivity

4.1 Vulnerability indices and organismal traits

A number of vulnerability indices of physiological stress, extinction risk, activity time constraints, habitat suitability, or range shifts have been proposed depending on the question of interest (Deutsch et al., 2008; Kearney and Porter, 2009; Sinervo et al., 2010; Lertzman-Lepofsky et al., 2020; Souza et al., 2023). These indices are projected across space and time and are based on the experimental estimation of fitness-related traits. Some indices relate environmental variables with physiological thresholds (e.g., desiccation tolerance, performance curves; Greenberg and Palen, 2021; Anderson et al., 2023), whereas more complex counterparts are based on biophysical models designed to reflect energy and water exchanges between animals and their microclimatic environments (Kearney et al., 2013; Kearney et al., 2018; Briscoe et al., 2023). Importantly, thermal biology information characterises most indexes (Taylor et al., 2020) despite the high relevance of hydroregulation for water-sensitive groups such as amphibians (Lertzman-Lepofsky et al., 2020; Greenberg and Palen, 2021; Wu, N. C. et al., 2024a).

Models and indexes have been used to predict biological constraints on fitness, using as proxies' development, growth, activity, reproduction, and survival (Sinervo et al., 2010; Kearney et al., 2018). This is because fitness-related traits are key to informing vulnerability to a given source of physiological stress. Yet disagreements exist on whether traits and what traits are good predictors for informing causal links of environmental changes on populations and species (Calosi et al., 2008;

Beissinger and Riddell, 2021). For example, common modelling variables related to hydroregulation include hydration level, rates of water loss, measures of water acquisition (seeking out water sources or specific microhabitats that enhances water uptake or maintenance), and the concentration of body fluids (**Table 2**). Hydroregulation traits are integrated with various functions related to gas exchange, energetics, thermoregulation, and reproduction as previously highlighted in section '*2.1 Species sensitivity risk: short-term impacts*'. Thus, and according to the physiology of the target groups, models exclusively based on hydroregulation may under- or overestimate vulnerability to climate change (Riddell et al., 2018a; Rozen-Rechels et al., 2019). The use of multiple physiological thresholds such as thermal tolerance, reproduction, and growth with hydroregulation through experimental manipulation of environmental stressors or inputting appropriate parameters to mechanistic models will provide more holistic estimations of vulnerability to climate change.

4.2 Challenges in predicting vulnerability

Predicting vulnerability to environmental stressors and how this may scale-up to population or species-level responses remains a key challenge for the conservation of biodiversity (Bovo et al., 2018). Practical limitations include characterising with appropriate data species-specific microclimates, both temporally and spatially (Briscoe et al., 2023). These limitations extend to single-population estimates, and the sometimes-related use of an average value to represent a whole-species. The validity of such approaches is context-specific, but they may not reflect across-population variation in sensitivity to thermal (Herrando-Pérez et al., 2019; Senior et al., 2019; Bovo et al., 2023) and/or drying as well as population plasticity/adaptation to drying condition. The same principle applies to studies using closely related species to represent threatened counterparts (Reemeyer et al., 2024). Mechanistic models that embrace population variability and plasticity in response to environmental drying will allow more explicit predictions of vulnerability across a species range (see 'Future directions'). Validating these predictions is essential, particularly for models that estimate survival, reproduction, and activity, which should be tested against observational data to ensure accuracy. Natural history observations (Greene, 2005), and large-scale longitudinal field and laboratory studies, particularly when there are geographically biased data (White et al., 2021; Herrando-Pérez et al., 2023), can help validate mechanistic models when predicting biological impacts of climate change across a species range or communities (Kearney et al., 2018; Enriquez-Urzelai et al., 2019; Riddell et al., 2019; Briscoe et al., 2023).

5. Future directions

5.1 Linking gene expressions to functional changes in response to environmental drying

Whole genome sequencing is becoming increasingly affordable and accessible for researchers and conservationist (Theissinger et al., 2023; Hogg, 2024). As we previously highlighted, several genes have been identified that are linked to an animal's hydroregulation. Understanding how the expression of these genes translates into functional changes in an animal's water balance is key to uncovering the genetic mechanisms underlying plasticity in response to environmental drying (Somero, 2010). Riddell et al. (2019) identified, in salamanders, over 500 genes in response to acclimation to different temperatures and vapour pressure deficits. Network analysis of these genes revealed suites of gene networks associated with the plasticity of skin resistance and the regulation of skin blood vessel growth. For example, the expression of *hydroperoxide isomerase* (*ALOXE3*), a gene involved in regulating transepidermal water loss, was highlighted. This study underscores an important research direction for identifying which genes are targets of selection when inferring the adaptive potential of species to warming and drying environments. Epigenome-wide association studies represent a promising approach for establishing causal relationships between changes in the epigenome and phenotypic plasticity (Fanter et al., 2022).

5.2 Inter- and transgenerational plasticity in response to environmental drying

Parental environments can shape offspring phenotype via epigenetic mechanisms such as DNA methylation, histone modifications, and non-coding RNAs (Galloway and Etterson, 2007; Beaman et al., 2016; Loughland et al., 2021; Husby, 2022). Intergenerational and transgenerational plasticity, which describe epigenetic inheritance across one or multiple generations, could buffer populations against environmental change, particularly if parental and offspring environments match (Shama and Wegner, 2014; Pettersen et al., 2024). However, despite growing interest in these mechanisms, few studies have explored these processes in amphibians and reptiles. One promising research direction is to experimentally test whether epigenetic modifications induced by water stress persist across generations and whether they enhance desiccation resistance. This could involve controlled desiccation experiments, tracking epigenetic changes and hydroregulation traits across multiple generations (Dupoue et al., 2015; Dupoué et al., 2018), or comparing populations from environments with different hydric regimes to assess whether ancestral exposure to aridity influences offspring water balance. Finally, we identify a critical question remaining unanswered: do hydroregulation strategies have an evolutionary limit? Studies on thermal tolerance suggest that plasticity alone may not be enough to ensure survival under extreme climate shifts (Morgan et al., 2020), but we lack similar insights for hydroregulation. Addressing this could inform conservation strategies, helping predict whether species can adjust to future drying events or if their physiological flexibility has constraints.

5.3 Modelling plasticity and adaptation in response to environmental drying

Animals can remodel their phenotype (physiology, morphology, and behaviour) to maintain optimal performance across a broad range of environments. This plastic response is a well-recognised phenomenon in predicting adaptive responses to climate change (Seebacher et al., 2015; Urban et al., 2016). Models that incorporate plasticity or adaptation tend to better predict a species' extinction risk or range contraction (Riddell et al., 2018b; Kellermann et al., 2020). Therefore, we encourage modelling studies to explicitly incorporate plasticity to provide realistic assessments of vulnerability to climate change (Bush et al., 2016; Gallegos et al., 2024). There is a substantial body of literature on plastic responses to pond drying in tadpoles (Gomez-Mestre et al., 2013; Székely et al., 2017; Delgadillo Méndez et al., 2024; Wu et al., 2025) and responses to soil moisture during embryo development in reptiles (reviewed in Bell et al., 2025). However, in studies of terrestrial drying, many acclimation experiments aimed at quantifying plastic responses have primarily focused on temperature effects on hydroregulation traits. This can confound causal inferences between the effects of temperature and drying (see '*3. Species sensitivity risk: long-term impacts*' section). For instance, the temperature effects on EWL may partially arise from the temperature-dependent nature of the metabolic rate (MR), as MR and the rate of gas exchange are closely linked to respiratory EWL (Woods and Smith, 2010), but see Riddell et al. (2024). It is possible that plasticity to water restrictions may differ from plasticity to temperature changes, potentially altering model predictions of extinction risk. Further studies across a broader range of species are needed to make biologically meaningful statements about the generality of within- and across-generation plasticity to drying, and to improve inferences in modelling vulnerability to future environmental drying scenarios. Finally, models explicitly testing adaptive evolution of traits should be more widespread used (Hansen, 2012; Moen et al., 2022).

5.4 Translating knowledge for managing habitats

Incorporating knowledge on hydroregulation strategies with projected changes in environmental water into land management and conservation planning, particularly at the microhabitat scale, could help mitigate the impacts of habitat modification and climate change on reptiles and amphibians (Nowakowski et al., 2018; Pottier et al., 2025). Complex microhabitats, such as heterogeneous vegetation patches and burrows, provide hydric refuges during droughts, which reptiles and amphibians can exploit through behavioural hydroregulation to avoid desiccation (see '*2.4 Behavioural responses*' section). Conservation efforts should thus prioritise the protection, restoration, or creation of such microhabitats within the range of the focal species to support persistence under increasingly drying conditions (Moore et al., 2018; Weaver et al., 2024). For example, protecting swamps from groundwater loss and surface water contamination has also been recommended for conserving *Eulamprus leuraensis*, an endangered swamp-specialist skink in

Australia (Gorissen et al., 2017). Interventions aimed at extending hydroperiods may protect some amphibians from larval desiccation and enhance population viability by increasing recruitment (Hamer et al., 2016; Mathwin et al., 2021; Mathwin et al., 2023). Likewise, habitat water supplementation through mist irrigation can extend activity time in reptiles and amphibians under arid conditions (Ackley et al., 2015; Mathwin et al., 2021) and support reproduction and dispersal in amphibians (Mitchell, 2001; Channing et al., 2006; Hoffmann and Mitchell, 2022). Providing supplemental hydration, such as drinking water for targeted individuals, could also be an effective conservation strategy for small, range-limited species (Weaver et al., 2024), particularly benefiting gravid or pregnant females by mitigating physiological and reproductive costs during severe droughts (Capehart et al., 2016; Dezetter et al., 2021; Bedard et al., 2025). However, the feasibility of such interventions is questionable (Mathwin et al., 2021; Weaver et al., 2024) and further research is needed to assess the effectiveness, potential negative, and species-specific outcomes of hydrological manipulation and micro-habitat scale management as a conservation tool. To facilitate the global implementation of conservation, informed by recent and emerging hydroregulation research, publications are also needed in more accessible and taxa- and region-specific journals and government reports (Amano and Berdejo-Espinola, 2024; Choi et al., 2024).

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TABLES

Table 1. Environmental water variables and example indices of environmental dryness with definitions and calculations of the variables, their interpretation for reptiles and amphibians, the temporal resolution scale available, and non-exhaustive examples of online global datasets to extract environmental water variables and indices.

Name	Definition and calculation	Interpretation	Resolution	Online database
Environmental water				
Precipitation (P)	Amount of rainfall per unit area (mm or kg m^2).	Less rainfall = less water available for animals to rehydrate.	Hourly to yearly	*CHIRPS*: Global daily rainfall from 1981 to near-present (Funk et al., 2015). *WorldClim 2*: Average yearly precipitation and seasonality from 1970 to 2000 (Fick and Hijmans, 2017). *CHELSA*: Precipitation, and potential evapotranspiration (1981–2010) with future scenarios at three future time periods (2011–2040, 2041–2070, and 2071–2100) under three shared socioeconomic pathways (SSP126, SSP370, SSP585) and across five Earth system models (Brun et al., 2022). *CHELSA-EarthEnv*: Global daily rainfall from 2003 to near-present (Karger et al., 2021). *TerraClim*: Average (1958–2019) global rainfall with future scenarios of +2°C and +4°C (Abatzoglou et al., 2018).
Atmospheric moisture content (RH or e)	Amount of moisture (water vapour) the air holds. Typically expressed as relative humidity (%), absolute humidity (g cm^3), or actual vapour pressure (e_a; kPa)	Less moisture in the air = higher evaporation of water through evaporative surfaces.	Seconds to yearly	*CHELSA*: Near-surface relative humidity (1981–2010) with future scenarios at three future time periods (2011–2040, 2041–2070, and 2071–2100) under three shared socioeconomic pathways (SSP126, SSP370, SSP585) and across five Earth system models (Brun et al., 2022). *TerraClim*: Average (1958–2019) global vapor pressure with future scenarios of +2°C and +4°C (Abatzoglou et al., 2018). *MODIS*: 5-minute interval global water vapour data (https://ladsweb.modaps.eosdis.nasa.gov/missions-and-measurements/science-domain/water-vapor/#modis). *MODIS*: 8-day to annual interval global evapotranspiration data (https://ladsweb.modaps.eosdis.nasa.gov/missions-and-measurements/science-domain/evapotranspiration/).
Soil moisture content (Φ)	Amount of water the soil holds. Expressed as volume (m^3), weight (kg) or water potential (kPa).	Relevant for animals that use burrows to acquire (from the soil/substrate), conserve (no	Seconds to yearly	*NicheMapR*: Above and below-ground microclimate from various sources (Kearney and Porter, 2017). *Microclimc*: Above and below-ground microclimate (Maclean and Klinges, 2021).

		water exchange) and reduce water loss.		
Water surface area	Land area covered by freshwater (%) e.g. lakes, rivers.	Amount of large-bodied freshwater sources for animals to rehydrate and/or breed.	Average over set years.	*HYDROSHEDS*: Global hydrographic products such as catchment boundaries, river networks, and lakes at multiple resolutions and scales (www.hydrosheds.org).
Environmental dryness indices				
Aridity index (AI) or climate moisture index (CMI)	AI = P/PET CMI (mm or kg m^2 month^{-1}) = $P - PET$ The difference (CMI) or ratio (AI) between the average annual precipitation (P) and potential evapotranspiration (PET).	Indicator of the degree of dryness of the climate.	Depending on P and PET resolution, but typically monthly to yearly average.	*CHELSA*: CMI (1981–2010) with future scenarios at three future time periods (2011–2040, 2041–2070, and 2071–2100) under three shared socioeconomic pathways (SSP126, SSP370, SSP585) and across five Earth system models (Brun et al., 2022). *Global-AI_PET_v3*: Global hydro-climatic data averaged (1970–2000) monthly and yearly (Zomer et al., 2022).
Drought index	Standardised index representing meteorological drought based on different formulas: • Palmer Drought Severity Index (PDSI) • Standardised Precipitation Index (SPI) • Normalized Difference Vegetation Index (NDVI)	Indicator of change in environmental dryness relative to 'normal' conditions of the location. The intensity, frequency, and duration of drought events can be calculated from these indices.	Monthly to decades.	*TerraClim*: Average (1958–2019) global PDSI with future scenarios of +2°C and +4°C (Abatzoglou et al., 2018). *Dai_et_al_2004*: global PDSI under three shared socioeconomic pathways: 1870–2002, SSP245, and *SSP585* (Dai et al., 2004). *MODIS*: 16-day and monthly interval global NDVI (https://modis.gsfc.nasa.gov/data/dataprod/mod13.php).
Vapour pressure deficit (VPD)	VPD (kPa) = $e_s - e_a$ The difference between the amount of moisture in the air (e_a) and how much moisture the air can hold when it is saturated at known temperature (e_s).	Determines desiccation risk and relates to the primary productivity of ecosystems (plant growth, food availability).	Depending on e_s and e_a resolution, but typically monthly to yearly average.	*CHELSA*: VPD (1981–2010) with future scenarios at three future time periods (2011–2040, 2041–2070, and 2071–2100) under three shared socioeconomic pathways (SSP126, SSP370, SSP585) and across five Earth system models (Brun et al., 2022). *TerraClim*: Average (1958–2019) global VPD with future scenarios of +2°C and +4°C (Abatzoglou et al., 2018).

Table 2. Example measurements to estimate of an animal's water loss/balance with definitions and calculations, and their interpretation for reptiles and amphibians.

Name	**Definition/calculation**	**Interpretation**
Evaporative water loss	Water loss through evaporative surfaces. Typically expressed as rate of water loss per unit time (g h^{-1}), or resistance to water loss (s cm^{-1}) Measurements of EWL can be whole-body, regional (e.g. ocular, dorsal, ventral, cloacal), exposed cutaneous surface area, or respiratory.	Indicator of the animals' risk of drying to the environment.
Water content	Whole-body mass: The amount of water in the animal. Typically expressed as percentage of whole mass or dry mass (%) in relation to standard (hydrated) body mass. Muscle: The amount of water in a sample of muscle tissue.	How much water is stored and available for the animal to use. Note that fat storage is another source of water through aerobic metabolism.
Blood biochemistry	Osmolality: Biomarker that measures the concentration of dissolved solutes in the blood. Typically expressed as milliosmoles per kilogram or litre of solvent (mosmol kg^{-1}, mosmol l^{-1}). Haematocrit: Proportion of blood volume occupied by red blood cells. Expressed as percentage of blood volume (%).	Indicator of dehydration status.
Water flux	Isotopic analysis of doubly labelled water which traces the movement of water molecules between the organism and environment. Typically expressed as ml kg^{-1} day^{-1}.	Estimate of daily water flux from free-ranging animals. Usually not suitable for semi-aquatic and aquatic species.
Water-seeking or conserving behaviour	Behaviours associated with seeking water (directional movement) and/or saving water (posture to diminish exposed body surface areas, shelter seeking, inactivity).	Indicator of behavioural focus on water balance.

FIGURES

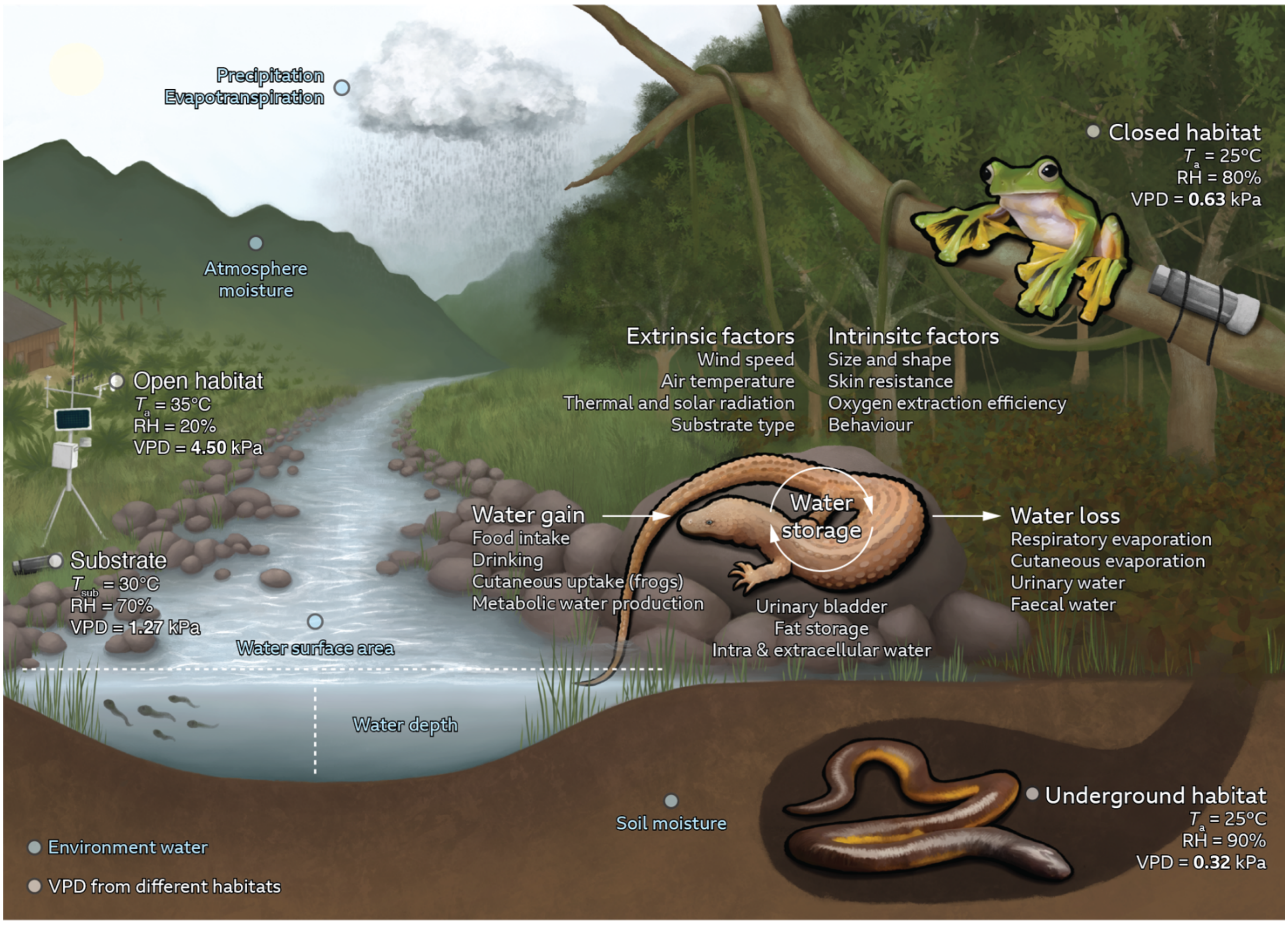

Fig. 1 | Overview of the landscape hydrology and animal hydroregulation. Blue text indicates environmental water that can influence hydroregulation such as precipitation and evapotranspiration, atmospheric and soil moisture content, water bodies (outlined in Table 1), and their interaction with external factors such as wind speed, temperature, thermal radiation, and substrate composition. The landscape includes habitats with different water stressors represented by vapour pressure deficit (VPD in kPa), which is calculated from measured air temperature (°C) and atmospheric moisture content (e.g. relative humidity in %). Hydroregulation includes water gain/loss, water storage and their interaction with extrinsic and intrinsic factors. Representative landscape and animals are based on Borneo's ecosystem. The representative terrestrial lizard is the earless monitor lizard (*Lanthanotus borneensis*), the representative arboreal frog is the Wallace flying frog (*Rhacophorus nigropalmatus*), and the representative subterranean caecilian is the Metang caecilian (*Ichthyophis biangularis*). Illustration by S. Buttimer.

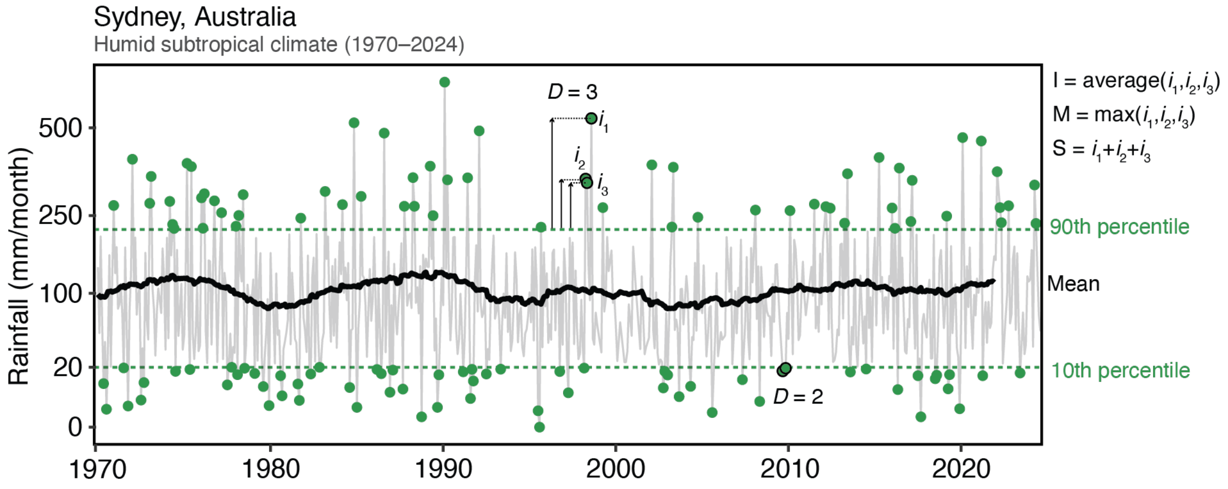

Fig. 2 | Example variation in monthly precipitation in Sydney, Australia from 1970–2024. Monthly precipitation data represented by thin grey lines from the Australian Government Bureau of Meteorology, with the 5-year rolling mean in thick black lines. The 10th and 90th month-specific percentiles represent dry and wet thresholds, respectively. Example durations (*D*) for extremely dry (red points) or wet (blue points) months are shown which is calculated as the number of months consecutive months above the wet and below the dry thresholds. Example calculations of intensity (I), magnitude (M), and severity (S) is also shown for a 3-month wet event (*D* = 3) with a departure of i_1, i_2 and i_3 from the threshold. Frequency can be calculated as the number of times the monthly precipitation is above the wet and below the dry thresholds.

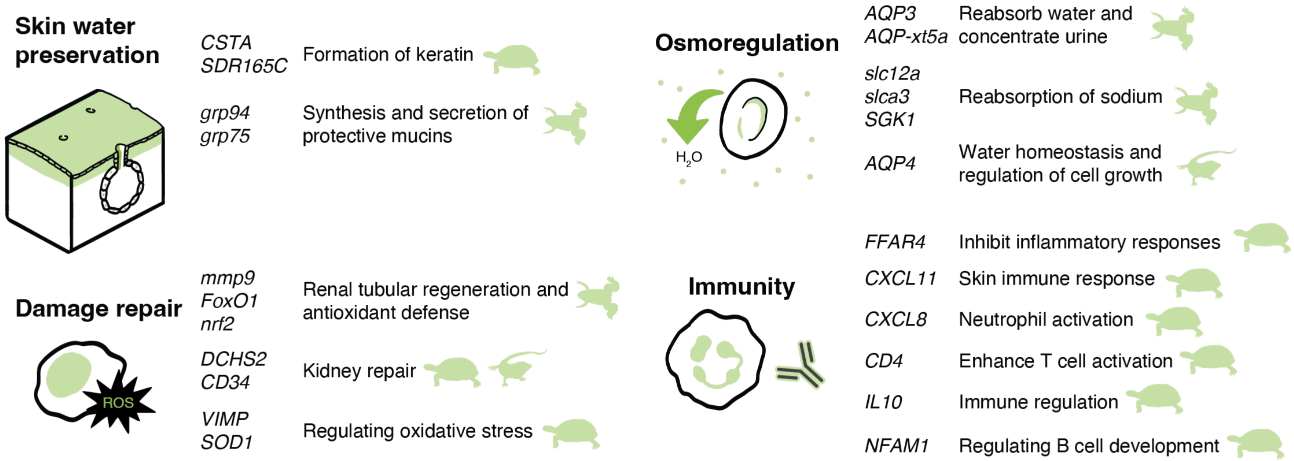

Fig. 3 | Example genes identified in response to water stress. Genes are grouped by the following functions: skin water preservation, osmoregulation, damage repair, and immunity. Specific functions of the genes are described on the right side with the taxon in which the function has been demonstrated.