Hot and bothered: Using trait-based approaches to assess climate change vulnerability in reptiles

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Hot and bothered: Using trait-based approaches to assess climate change vulnerability in reptiles

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ABSTRACT

One-fifth of the world's reptiles are currently estimated as threatened with extinction, primarily due to the immediate threats of habitat loss and overexploitation. Climate change presents an emerging slow-acting threat. However, few IUCN Red List assessments for reptiles explicitly consider the potential role of climate change as a threat. Thus, climate change vulnerability assessments can complement existing Red List assessments and highlight further, emerging priorities for conservation action.

Here we present the first trait-based global climate change vulnerability assessment for reptiles to estimate the climate change vulnerability of a random representative sample of 1498 species of reptiles. We collected species-specific traits relating to three dimensions of climate change, sensitivity, low adaptability, and exposure, which we combined to assess overall vulnerability.

We found 80.5% of species highly sensitive to climate change, primarily due to habitat specialisation, while 48% had low adaptability and 58% had high exposure. Overall, 22% of species assessed were highly vulnerable to climate change. Hotspots of climate change vulnerability did not always overlap with hotspots of threatened species richness, with most of the vulnerable species found in northwestern South America, southwestern USA, Sri Lanka, the Himalayan Arc, Central Asia and southern India. Most families were found to be significantly more vulnerable to climate change than expected by chance.

Our findings build on previous work on reptile extinction risk to provide an overview of the risk posed to reptiles by climate change. Despite significant data gaps for a number of traits, we recommend that these findings are integrated into reassessments of species' extinction risk, to monitor both immediate and slow-acting threats to reptiles.

1. Introduction

Latest climate data show that the rate of global surface temperature warming since 1950 continues unabated, rising between 0.113 °C and 0.116 °C per decade (Karl et al., 2015). Impacts from climate change are expected to intensify, with global surface temperature increase likely to exceed 4 °C by 2100 if no mitigation measures are put in place (World Bank, 2014), presenting a major emerging threat to biodiversity (Dickinson et al., 2014; Pacifici et al., 2015). Climate change effects on species include changes to species' ranges, both altitudinal (e.g. Menendez et al., 2014) and latitudinal (e.g. Hill et al., 2002), habitat associations (e.g. Menendez and Gutierrez, 2004), life-history phenology (e.g. Pearce-Higgins et al., 2015), disease emergence (e.g. Sarmiento-Ramirez et al., 2014), and increased extinction risk (Carpenter et al., 2008; Dickinson et al., 2014).

Frameworks for assessing species' extinction risk, such as the IUCN Red List of Threatened Species (IUCN, 2015b), have been criticised for insufficiently incorporating emerging and often slow-acting climate change threats (Keith et al., 2014; Thomas et al., 2011). At present, the most commonly identified threats to species on the IUCN Red List are habitat loss, overexploitation and invasive species (IUCN, 2015b), while only 8% of the 67,000 species assessed under the current criteria system (IUCN, 2001) are recorded as threatened by climate change (IUCN, 2015b). The IUCN Red List Criteria effectively account for climate

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change in threatened species (Akcakaya et al., 2014; Pearson et al., 2014), although a number of factors may still prevent the adequate listing of climate change for threatened species: species may be perceived as susceptible to climate change, but may not yet be exposed to significant changes, or vice versa (Foden et al., 2013); assessors may approach climate change threats inconsistently due to uncertainties surrounding current projections of climate change and their effects on species (Keith et al., 2014; Westoby and Burgman, 2006); other threats, acting synergistically with climate change, may be more easily understood and recorded, thus underestimating the importance of climate change (Hof et al., 2011).

To complement existing frameworks, climate change-specific assessments were developed using a number of different approaches (Pacifici et al., 2015). With over a million terrestrial species potentially already 'committed to extinction' by the middle of the century due to climate change (Keith et al., 2014), climate change vulnerability assessments are of utmost importance to effectively quantify climate change threats, inform mitigation and adaptation policy and prevent adverse effects from climate change (Young et al., 2015).

Since considerable uncertainty exists surrounding climate change projections and their effects on species (Tuberville et al., 2015), assessing intrinsic biological traits which predispose species to climate change risk has more recently emerged as an alternative approach; these are collectively known as trait-based approaches. These approaches have been used to complement IUCN Red List extinction risk assessments, providing a supplementary analysis that can be used to inform overall species risk and identify additional conservation priorities (Foden et al., 2013).

Trait-based approaches collate data concerning different 'dimensions' of climate change vulnerability, typically including species' sensitivity, adaptability, and exposure to climate change (Foden et al., 2013; Pacifici et al., 2015; Still et al., 2015). Trait-based assessments often rank species vulnerability within the dataset, as many of the trait value thresholds used are arbitrary (Foden et al., 2013; Pacifici et al., 2015), and are most often expressed as "low" and "high" vulnerability (Carr et al., 2014; Foden et al., 2013). Comparisons between analyses are therefore difficult (Foden et al., 2013; Pacifici et al., 2015). Despite this shortcoming, trait-based approaches are becoming increasingly common in the scientific literature (Young et al., 2015), with recent assessments of a range of taxa including birds and amphibians (e.g.; Carr et al., 2014; Foden et al., 2013; Hagger et al., 2013), mammals (Dickinson et al., 2014), reptiles (e.g.; Carr et al., 2014; Hagger et al., 2013), insects (e.g.; Conti et al., 2014), plants (e.g.; Still et al., 2015), and corals (Foden et al., 2013). Trait-based approaches have been widely adopted by conservation planning agencies as a prioritization technique for climate change-affected species (Dawson et al., 2011; Pacifici et al., 2015; Williams et al., 2008); they can, however, still be constrained by limited data availability, especially for commonly incorporated traits such as dispersal capacity, for which few data exist beyond well-studied species (Foden et al., 2013; Pacifici et al., 2015). Although being referred to as 'trait-based', traits are often derived indirectly from species' ranges (e.g. climatic and environmental factors), rather than being based on species-specific data (e.g. from laboratory experiments on temperature or water requirements) which are generally sparse.

Of the currently 10,272 described reptile species (Uetz and Hošek, 2015), around one in five species is estimated to be threatened with extinction, based on a random sample of 1500 species (Böhm et al., 2013); climate change was only listed as a threat in 9% of threatened terrestrial reptiles compared to 17% of threatened freshwater and marine reptiles. However, the impacts of climate change on reptiles potentially affect all aspects of their life-history (Meiri et al., 2013). Most reptiles have specific microhabitat, temperature and moisture requirements for metabolism and reproduction; they are thus likely to be highly sensitive to climate change (Tuberville et al., 2015). Approximately 85% of reptiles are oviparous (Tinkle and Gibbons, 1977) and may be affected by increasing temperatures during development (Hawkes et al., 2009), potentially skewing the sex ratio for species with temperature-dependent sex determination, reducing hatching success, or shifting breeding season phenology (Hawkes et al., 2009; López-Luna et al., 2015). Other aspects of reptile life-history affected by climate change include altered behaviour patterns such as time spent foraging, basking, or resting (Bickford et al., 2010; Meiri et al., 2013), changes in the use of habitat and resources (Bickford et al., 2010; Scharf et al., 2014), disease (Sarmiento-Ramirez et al., 2014) and altered habitat structure which may also impact prey diversity and abundance (Whitfield et al., 2007).

Here, we use a trait-based approach (Foden et al., 2013; Carr et al., 2014) to estimate climate change vulnerability of a random representative sample of 1498 species of reptiles from 70 families, all of which have been previously assessed as part of the Sampled Red List Index (SRLI) for the IUCN Red List (Böhm et al., 2013). Specifically, we examine data availability for trait-based climate change vulnerability assessments, determine taxonomic and geographic variability of climate change vulnerability, and discuss how climate change vulnerability assessments complement what we have previously learned about conservation priorities from IUCN Red List assessments.

2. Methods

2.1. Species dataset

Our assessment was based on a sample of 1500 reptile species for which IUCN Red List assessments had previously been carried out as part of the Sampled Red List Index project (Böhm et al., 2013); for the current assessment, two species were no longer taxonomically valid, resulting in a final total of 1498 species for assessment. For the IUCN Red List assessment by Böhm et al. (2013), species had been randomly selected from the species list at the start of the assessment (Uetz and Hošek, 2015) following the approach in Baillie et al. (2008). A sample of this size was previously found to produce a broadly representative picture of extinction risk and trends over time (Baillie et al., 2008), and spatial patterns derived from such samples were found to be in broad agreement with spatial patterns derived from comprehensive assessments in both mammals and amphibians (B. Collen, unpublished data). Of the 1498 species in our assessment, 49 were listed as being threatened by climate change on the IUCN Red List (with 20 of these in the threatened categories Vulnerable, Endangered or Critically Endangered). All analyses and spatial data extractions were carried out in R version 3.1.2 (R Core Team, 2014), unless otherwise indicated.

2.2. Climate change vulnerability assessment

We closely followed the approach by Foden et al. (2013) and Carr et al. (2014) which assesses three dimensions of climate change vulnerability: sensitivity, poor adaptability and exposure (Foden et al., 2013; Fig. 1). Here, species which are both sensitive to climate change and have low adaptability are considered 'biologically susceptible' to climate change. Biologically susceptible species which are also highly exposed to climate change are referred to as 'climate change vulnerable' species (represented by the area where the three dimensions overlap; Fig. 1). We selected traits for three trait sets pertaining to sensitivity and two trait sets pertaining to low adaptability, identified as important factors affecting climate change vulnerability of species by Foden et al. (2013) and Carr et al. (2014) during expert workshops: 1. Specialised habitat and/or microhabitat requirements; 2. Narrow environmental tolerances or thresholds likely to be exceeded due to climate change; 3. Dependence on interspecific interactions likely to be disrupted by climate change; 4. Poor dispersal ability; 5. Low capacity to adapt in-situ through genetic micro-evolution. One of the trait groups assessed by Carr et al. (2014), dependence on environmental triggers likely to be disrupted by climate change, was not included in our analysis due to a lack of data for reptiles in the literature. Similarly, few data are available

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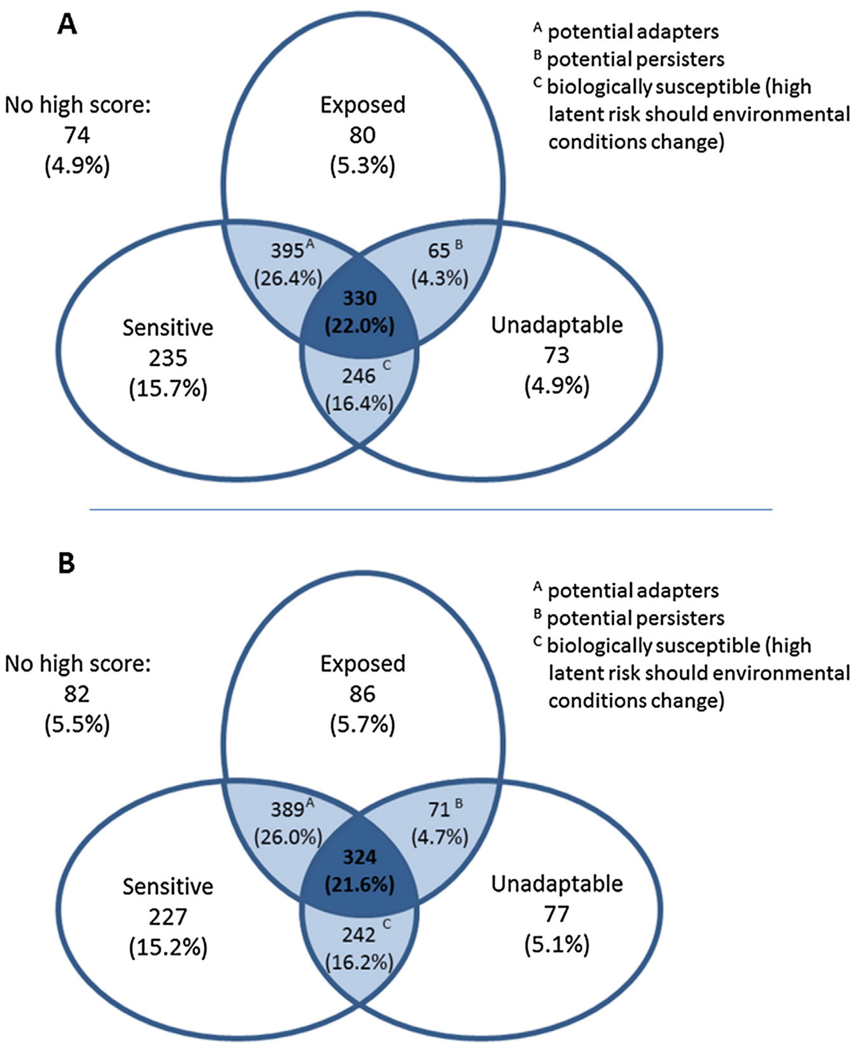

Fig. 1. Climate change vulnerability of species according to the IUCN method (Foden et al., 2013). A: Using the full set of trait variables, species scored as 'high' across all three dimensions (sensitivity, poor adaptability and exposure) were classed as overall highly vulnerable to climate change (N = 330; 22.0%). B: Excluding low data quality traits (microhabitat specialisation (S2), temperature-dependent sex determination (S8) and interspecific dependencies (S10)), 324 species were classed as highly vulnerable to climate change (21.6%). Seventy-four (full assessment, A) and 82 species (low data quality traits excluded, B) were scored as 'low' in all three dimensions. Species will have different monitoring requirements: potential adapters require monitoring of adaptive response to climate change, potential persisters require population monitoring; biologically susceptible species require environmental/climatic monitoring.

in the literature on intrinsic dispersal capacity, which meant that this trait had to be excluded from the analysis. Traits and underlying hypotheses on their effect on climate change vulnerability are summarised in Table 1.

Traits were collected from published and grey literature, and information given in the IUCN Red List of Threatened Species. Environmental tolerances and exposure to climate change were calculated from distribution maps published on the IUCN Red List, using those parts of the distribution where species are recorded as 'extant', 'probably extant', 'native' or 'reintroduced' (Joppa et al., 2015). Distribution maps on the IUCN Red List usually exist in the form of generalised range polygons, thus potentially including large areas of unoccupied, potentially unsuitable areas; this can make calculations of climatic requirements and tolerance from these distribution maps unrepresentative (Foden et al., 2013). To address this, we produced amended distribution maps by excluding areas of unsuitable habitat from our analyses through removing altitudes at which a species did not occur (from published literature) and cross-referencing habitat types listed on the IUCN Red List (IUCN, 2015a) with the spatially explicit Global Land Cover 2000 habitat types. This consists of 23 categories, including natural and human-transformed habitats and water bodies, at 1 × 1 km resolution (http://www.eea.europa.eu/data-and-maps/data/global-land-cover-250m; Table S3). Detailed information on the methods, traits and potential caveats can be found in the Supplementary Materials.

2.3. Sensitivity dimension

Sensitivity traits and thresholds are summarised in Table 1. We defined habitat specialisation as the number of habitat types occupied by a species, according to the IUCN Red List habitat classification (Table S2). Species were classified as microhabitat specialists if they were recorded as exclusively dependent or recorded in any of the following microhabitats in their IUCN Red List assessment: mountain rapids/rivulets, ephemeral pools, bamboo, vines, fallen trees, dead wood, tree hollows, trees bordering water, riverine or gallery forests, ant hills, dunes, open patches in grassland, rocky areas and outcrops, cliffs, caves, and small streams, as well as freshwater- and forest-dependent species.

We classed species as restricted to high-altitude habitat if they only occurred above 1000 m. To assess this, we used data on altitudinal range recorded in IUCN Red List assessments. Any data gaps were supplemented with altitudinal data at 10 arcminute resolution (Hijmans et al., 2005), extracted by overlaying amended species distributions and extracting mean, maximum and minimum altitude for each species.

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Table 1
Species traits for which data were collected, by dimension (sensitivity, poor adaptability, exposure) and trait group (A. Specialised habitat/microhabitat requirements; B. Narrow environmental tolerances or thresholds; C. Dependence on interspecific interactions; D. Poor dispersal ability; E. Poor evolvability), including hypotheses for inclusion in the assessment and thresholds applied. Traits were scored as contributing to high or low vulnerability as shown in the threshold column.

Trait set	Variable	Description	Vulnerability threshold	Hypotheses
Sensitivity				
A	S1. Habitat specialisation	Number of habitats a species occurs in	Low > 1 habitat type High = 1 habitat type	Habitat generalists are more likely to adapt to changing habitat conditions with climate change as they have more habitat options available to them
A	S2. Microhabitat specialisation	Species is dependent on one or more of the identified microhabitats[a]	Low = false High = true	Species which occur in microhabitats affected by climate change will be more affected by climate change overall
A	S3. Restriction to high-altitude habitat	Species is found only at 1000 m above sea level or above	Low = false High = true	Species which occur solely in high-altitude habitat will be more affected by climate change due to consequences of altitudinal range shifts
B	S4. Tolerance of changes to precipitation regimes	Average absolute deviation in precipitation across the species' historical range	Low = highest 75% (>30.97 mm) High = lowest 25% (<30.97 mm)	Species with narrow tolerance to precipitation regimes will be most affected by precipitation changes due to climate change
B	S5. Tolerance of temperature changes	Average absolute deviation in temperature across the species' historical range	Low = highest 75% (>1.28 °C) High = lowest 25% (<1.28 °C)	Species with narrow tolerance to temperature regimes will be most affected by precipitation changes due to climate change
B	S6. Sensitivity to change in fire regime	Species relies upon a specific fire regime (or lack of) across its entire range	Low = false High = true	Fire regimes are likely to change with changing climate, thus directly affecting species dependent on specific regimes
B	S7. Sensitivity to change in flooding regime	Species relies upon a specific flooding regime (or lack of) across its entire range	Low = false High = true	Flooding regimes are likely to change with changing climate, thus directly affecting species dependent on specific regimes
B	S8. Temperature-dependent sex determination	Sex of offspring is known to be dependent on temperature during incubation	Low = false High = true	Species with temperature-dependent sex determination will be more vulnerable to the effects of climate change due to temperature changes affecting population sex ratios
C	S9. Dependence on narrow range of food types	Species diet consists of a low number of species from a single dietary category	Low = false High = true	Species with dietary specialisation are likely to be more affected by changes in prey base due to climate change
C	S10. Interspecific dependencies	Species is dependent upon another to modify or create habitat suitable for itself OR could experience increases in one or more of the following as a result of climate change: Predation, competition, parasitism, disease	Low = false High = true	Species whose population dynamics are dependent on interspecific interactions are likely to be more affected by changes in abundance and distribution of the other species in question
Adaptability				
D	A1. Barriers to dispersal	Species occurs in isolated areas due to the presence of barriers to dispersal (i.e. a species is isolated because it occurs exclusively on mountaintops, small islands and/or polar edges of land masses)	Low = false (no known barriers) High = true	Species which are not isolated due to presence of extrinsic barriers to dispersal are more likely to be able to disperse out of areas experiencing climate change
E	A2. Slow turnover of generations	Generation length (here replaced by longevity as a proxy for generation length)	Low = shortest 75% (<10 years) High = longest 25% (>10 years)	Species with longer generation length/longevity are likely to have slower life histories and lower reproductive frequency/output, hence affecting their ability to produce offspring fast enough to potentially trigger adaptation by genetic variability
E	A3. Reproductive capacity	Reproductive output (mean clutch/litter size × mean no. clutches/litters per year)	Low = highest 75% (>3.8) High = lowest 25% (<3.8)	Species with low reproductive output will be more affected by climate change since they will not produce enough offspring to potentially trigger adaptation by genetic variability
Exposure				
	E1. Exposure to sea level rise	Habitat types are exposed to sea level inundation (i.e. species occurs only in inundation exposed coastal habitats and in no or only one other habitat type)	Low = false High = true	Habitats which are coastal and already exposed to inundation by the sea will become even more affected due to sea level rise; specialists of these habitat types will thus be more affected by climate change
	E2. Changes in mean temperature	Substantial changes in mean temperature occur across the species' range (measured as absolute difference in mean temperatures × 10 across the species' range for all months between 1975–2050)	Low = lowest 75% (<27.25 °C) High = highest 25% (>27.25 °C)	In areas where temperature changes are largest, climatic change exposure is going to be highest and species are more likely to be affected
	E3. Temperature variability change	Substantial changes in temperature variability across the species' range (measured as absolute difference in average absolute deviation in temperature × 10 across the species' range for all months between 1975 to 2050)	Low = lowest 75% (<7.32 °C) High = highest 25% (>7.32 °C)	In areas where temperature changes are largest, climatic change exposure is going to be highest and species are more likely to be affected
	E4. Changes in mean precipitation	Substantial changes in mean precipitation occur across the species' range (measured as absolute ratio of change in mean precipitation across the species' range for all months between 1975–2050)	Low = lowest 75% (<0.55 mm) High = highest 25% (>0.55 mm)	In areas where precipitation changes are largest, climatic change exposure is going to be highest and species are more likely to be affected
	E5. Precipitation variability change	Substantial changes in precipitation variability across the species' range (measured as absolute ratio of change in average absolute deviation in precipitation across the species' range for all months between 1975 to 2050)	Low = lowest 75% (<0.47 mm) High = highest 25% (>0.47 mm)	In areas where precipitation changes are largest, climatic change exposure is going to be highest and species are more likely to be affected

[a] Mountain rapids/rivulets, ephemeral pools, bamboo, vines, fallen trees, dead wood, tree hollows, trees bordering water, riverine or gallery forests, ant hills/termitaria, dunes, open patches in grassland, rocky areas and outcrops, cliffs, and caves; freshwater- or forest-dependent.

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Any data derived from this spatial data process were assumed to be of lower data quality than information from IUCN Red List assessments. We assessed species' tolerance to changes in precipitation and temperature regimes by deriving average absolute deviation (AAD) across amended species distributions from global temperature and precipitation datasets for the period of 1950–2000 at 10 arcminute resolution (Hijmans et al., 2005). AAD represents a variable of dispersion, essentially representing tolerance of variability in temperature and precipitation across space and seasons for each species (Foden et al., 2013). Hence, for a dataset {x1, x2,…, xn}, AAD is defined as

$$\frac{1}{n}\sum_{i=1}^{n}|x_i - m(X)|$$

where each x represents a monthly mean for a cell within a species' amended range (Foden et al., 2013).

Species with the 25% lowest AAD (i.e. lowest environmental tolerance) were classed as being highly sensitive. Similar quartile thresholds were also used for other continuous trait variables; while highly arbitrary, these provide an easy-to-use approach to split a continuous variable into a high/low classification. This approach has also been used in similar assessments (Foden et al., 2013; Carr et al., 2014). For more information, and vulnerability scores based on different thresholds, see the Supplementary Materials.

Information on sensitivity to changes in fire and flooding regimes and interspecific dependencies was taken from IUCN Red List assessments, with species classed as 'high' sensitivity if it was stated they were dependent on either of these factors, or were threatened by flooding/drought or natural system modification resulting from fire and fire suppression. Species for which reliance on temperature-dependent sex determination was stated in the literature were ranked highly sensitive, although overall data quality was considered low for this trait due to a lack of information for the majority of species. Dependence on a narrow range of food types was assessed by collating information on diet from the literature and categorising this information into 18 dietary categories, reflecting reptile dietary habits (see Table S4): leaf matter; fruit; seeds; nectar; a single taxonomic group of arthropod; a range of arthropods; other invertebrates; small mammals ≤ 300 mm SVL; large mammals > 300 mm SVL; adult/sub adult birds; bird eggs/juveniles; adult/juvenile reptiles; reptile eggs; adult amphibians; amphibian larvae; freshwater fish; faeces; and an 'other' category for anything outside of these parameters. For species consuming a wide range of arthropods, or several named arthropod taxa, both the single type of arthropod and range of arthropods boxes were checked to indicate a generalist of arthropod prey. Where data were unavailable, we inferred from close congenerics where possible. Species which were restricted to a single dietary category were classified as being highly sensitive.

2.4. Adaptability dimension

Adaptability traits and thresholds are summarised in Table 1. We assessed a species range as having barriers to dispersal if a species occurred exclusively: on mountaintops; small islands of less than 500 m altitude, thus preventing significant elevational dispersal rather than simple inland movement in response to climate change; and/or within 10 degrees north/south from edges of land masses, here termed polar edges. We created spatial data layers from geographic data in ArcGIS for all three barrier components, using altitudinal data at 10 arcminute resolution (Hijmans et al., 2005). Mountaintop distributions were defined in ArcGIS 10.3 (ESRI) by defining grid cells across a 2 × 2 grid cell extent as either above or below the mean altitudinal value (see Supplementary Materials). Finally, we intersected the resulting data layers with the species distributions. Species solely occurring within polar edges of land masses and/or with their entire distribution confined to small islands and/or entirely occurring within cells of above mean altitude were regarded as experiencing geographic barriers to dispersal.

We used maximum longevity of species as a proxy for slow turnover of generations, since in many cases, generation length has not yet been quantified for species (only 31 species had generation length estimates in the IUCN Red List; see Fig. S5 for correlation between generation length and longevity estimates). We collected longevity data from the literature, including captive and wild records. While in some cases, animals in captivity may live longer due to better access to food and medical treatment, in other cases the specific requirements for survival may be unknown or difficult to fulfil, thus potentially reducing longevity (Mason, 2010). Furthermore, records of captive animals are often based on animals that were still alive at the time of data collection (Scharf et al., 2014), thus potentially underestimating longevity. Where data were lacking, we used allometric equations of body mass and longevity by Scharf et al. (2014) to derive an estimate of longevity. We subsequently classed species as having low adaptive capacity if they were amongst the 25% longest-lived species.

Information on reproductive capacity was collected from the literature (based on clutch/litter size and number of clutches/litters per year; Böhm et al., 2016). Where data was missing, we inferred reproductive output from close congenerics. The 25% of species with lowest reproductive output were classed as having low adaptive capacity.

2.5. Exposure dimension

Exposure measurements and thresholds are summarised in Table 1. We collected data on five traits related to exposure: exposure to sea level rise; changes in mean temperature; temperature variability change; changes in mean precipitation; and precipitation variability change. Exposure to sea level rise was assessed from IUCN Red List habitat data; species occurring exclusively or near-exclusively (i.e. in only one additional habitat type) in any of the following habitats were deemed as having high vulnerability to climate change: mangroves, intertidal salt marshes, coastal freshwater, brackish or saline lakes and lagoons, marine lakes, coastal caves, intertidal shorelines (including rocks, beaches, flats and tide pools), sea cliffs, rocky offshore islands, and coastal sand dunes.

As described in Foden et al. (2013), climate change projections at 10 arcminute resolution (Tabor and Williams, 2010) were based on an ensemble of four General Circulation Models (UKMO HadCM3, MPIM ECHAM5, CSIRO MK3.5 and GFDL CM2.1), and considering three emissions scenarios (B2, A1B and A2) for 1975 (mean 1961–1990), 2050 (mean 2041–2060) and 2090 (mean 2081–2100). The different emission scenarios provide us with a mid-range projection (scenario A1B) for changes from 1975 to 2050 (in main results), as well as upper (scenario A2) and lower (scenario B1) bounds for projections (in Supplementary Materials). We assessed mean change in temperature as the absolute difference in the mean between 1975 and 2050, and mean change in precipitation as a ratio: (absolute [((mean precipitation in 2050) − (mean precipitation in 1975) / mean precipitation in 1975)]). For changes in temperature and precipitation variability, we again estimated AAD between 1975 and 2050.

2.6. Vulnerability assessment

We aimed to collect data for all selected traits. In some cases, we inferred information on diet and reproductive output from congenerics (see Supplementary Materials). Given the diversity of data sources and resulting data quality, we also scored data quality (high, medium, low) for all trait data to evaluate the feasibility and suitability of collating trait data from existing published or open access sources rather than through consultation with experts at workshops (the latter being the approach previously used by Carr et al., 2014). This also allowed us to rerun our assessment removing low quality data traits from the analyses.

Species were considered sensitive, low in adaptability, or exposed to climate change if they scored 'high' for any trait under the respective framework dimension. To examine the effect of individual trait variables on the assessment, and to account for the possibility that species may show behavioural adaptation to reduce vulnerability to climate change, we dropped each trait variable in turn for each dimension and summarised the analysis again for comparison.

Species were considered as 'climate change vulnerable' if they scored 'high' across all three dimensions. Unknowns were treated in two ways: as low vulnerability for all traits, giving an 'optimistic' scenario (results in main manuscript), and as high vulnerability, giving a pessimistic scenario (results in the Supplementary Materials). Analyses presented in the main manuscript use climate change emission scenario A1B for 2050. Additional analyses are presented in the Supplementary Materials. We subsequently compared climate change vulnerability of species with their listing on the IUCN Red List.

2.7. Data analysis

To evaluate whether certain families are significantly more vulnerable to climate change than expected by chance, we tested for significant variation in vulnerability levels across families using a chi-square test, followed by further analyses to determine which families deviated from the expected level of vulnerability. Using binomial tests, we calculated the smallest family size necessary to detect a significant deviation from the observed proportion of climate-change vulnerable species and excluded families represented by an insufficient number of species from subsequent analysis. We generated a null frequency distribution of the number of vulnerable species from 10,000 unconstrained randomizations, by randomly assigning 'high' and 'low' vulnerability to all species, based on their frequency of occurrence in the sample. We then counted the number of observed vulnerable species for each family and compared this with the null frequency distribution. The null hypothesis (climate change vulnerability is taxonomically random) was rejected if this number fell in the 2.5% at either tail.

2.8. Spatial analysis

To examine the spatial distribution of climate change vulnerable species versus the distribution of threatened species on the IUCN Red List within our sample, we overlaid a hexagonal grid onto the stacked species' distributions of climate change vulnerable and IUCN Red List threatened species, and calculated respective species richness for each hexagonal grid cell (approximately 7800 km^2 in size). The grid used was defined on an icosahedron, projected to the sphere using the inverse Icosahedral Snyder Equal Area (ISEA) projection to account for the Earth's spherical nature. To evaluate whether climate change vulnerable and IUCN Red List threatened species patterns overlap, we delineated 10% hotspots for each, defined as the 10% richest grid cells, and overlaid IUCN threatened species hotspots with climate change vulnerability hotspots.

3. Results

3.1. Data availability and quality

Trait data differed widely in their availability. Data gaps were largest for temperature-dependent sex determination (78.8% unknown), microhabitat specialisation (32.0% unknown), reproductive output (16.3% unknown) and longevity (13.2% unknown). For all other traits, percentages of unknown were less than 10% (Table S6). Data quality was considered overall low for microhabitat specialisation and interspecific dependencies (which could not be derived consistently from the IUCN Red List information given) and temperature-dependent sex determination (for which few data were available in the literature). In the following, we ran vulnerability analyses including and excluding these low data quality traits to examine their effects on the assessment.

3.2. Summary of sensitivity dimension

Nearly all species (80.5%) were scored as highly sensitive to climate change, primarily due to habitat specialisation (a trait possessed by 41.5% of species). Overall, 550 species were deemed highly sensitive to climate change because of a single trait triggering high sensitivity (Table S7). Narrow precipitation tolerance and habitat specialisation contributed to most species being deemed highly sensitive (162 and 158 of the 550 species, respectively). Dropping habitat specialisation and precipitation tolerance from the trait list each resulted in 87% of species being retained as highly sensitive, and 70% of species being highly sensitive overall. Removal of microhabitat specialisation, sensitivity to changes in fire regime, sensitivity to changes in flooding regime, temperature-dependent sex determination and interspecific dependencies had virtually no effect on the outcome of the sensitivity dimension, retaining 98–99% of highly sensitive species.

Excluding traits with low data quality (microhabitat specialisation, interspecific dependencies and temperature-dependent sex determination) led to 78.9% of species being listed as highly sensitive to climate change, and excluded only 24 species previously ranked as highly sensitive (of which 17 are Least Concern on the IUCN Red List; Table S5). Only one of these species has a listed threat of climate change on the IUCN Red List (*Eretmochelys imbricata*, listed as Critically Endangered).

3.3. Summary of adaptability dimension

Forty-eight percent of species were found to have poor adaptability. Of these, 610 species were deemed to have low adaptability to climate change because of a single trait triggering the threshold: generation turnover contributed to most species being deemed of low adaptability (278 of the 610 species), with reproductive capacity and barriers to dispersal contributing another 240 and 92 species, respectively. Excluding barriers to dispersal from the assessment had the least impact on the adaptability dimension, retaining 87% of low adaptable species and rendering 41.5% of species overall as having low adaptability. The removal of generation length and reproductive output led to a retention of 61.1% and 66.4% of low adaptable species respectively (29–32% of species deemed to have low adaptability overall).

3.4. Summary of exposure dimension

Fifty-eight percent of species were listed as having high exposure to climate change. Of these, 415 species triggered high exposure because of meeting the threshold values for a single exposure trait only, primarily due to the traits of temperature change and temperature variability change (127 and 134 species respectively; Table S7). Dropping exposure to sea level rise from the assessment had the least impact on the exposure dimension, retaining 98% of highly exposed species and rendering 56.7% of species overall as having high exposure. Removing changes in mean temperature and changes in temperature variability led to a retention of 83.0% and 82.3% of highly exposed species respectively (47–48% of species deemed having high exposure overall).

3.5. Summary of climate change vulnerability in reptiles

Overall, 246 of the 1498 species (16.4%) were deemed biologically susceptible to climate change (combining sensitivity with low adaptability), but were not exposed. Combining all three dimensions, 22.0% of species were listed as highly vulnerable to climate change (Fig. 1A).

Excluding sensitivity traits with low data quality (microhabitat specialisation, interspecific dependencies and temperature-dependent sex determination) still led to 324 species overall listed as climate change vulnerable (Fig. 1B). Another 242 species were biologically susceptible

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Table 2
Climate change vulnerability in a subsample of 1498 reptile species by order, biogeographic realm and habitat system. Results for the full assessment including all traits are shown, and supplemented with results of the assessment excluding low data quality traits where these were different (italics).

	High	Low	N	% vulnerable
Taxon				
Reptiles	330	1,168	1,498	22.1%
	(324	*1,174*		*21.6%)*
Amphisbaenia	2	26	28	7.1%
Crocodylia	3	1	4	75%
	(1	*3*		*25%)*
Sauria	177	688	865	20.5%
	(175	*690*		*20.2%)*
Serpentes	139	416	555	25.0%
	(137	*418*		*24.7%)*
Testudines	9	37	46	19.6%
Realm				
Afrotropical	33	257	290	11.4%
	(32	*258*		*11.0%)*
Australasian	33	188	220	15.0%
	(32	*167*		*14.5%)*
Indomalayan	52	262	314	16.6%
	(50	*264*		*15.9%)*
Nearctic	26	72	98	26.5%
Neotropical	166	361	527	31.5%
	(165	*362*		*31.3%)*
Oceanian	0	8	8	0.00%
Palaearctic	44	111	155	28.4%
	(42	*113*		*27.1%)*
Habitat system				
Terrestrial	322	1,149	1471	21.9%
	(316	*1,155*		*21.5%)*
Freshwater	23	57	80	28.8%
	(21	*59*		*26.3%)*
Marine	8	15	23	34.8%
	(7	*16*		*30.4%)*

to climate change (i.e. had high sensitivity and low adaptability, but were not exposed; Fig. 1B).

3.6. Climate change vulnerable species

Overall, percentages of climate change vulnerable species varied between 7.1% for amphisbaenians to 19.6% for turtles and tortoises, 20.5% for lizards, 25% for snakes and 75% for crocodiles, the latter being based on a very small sample size of $N = 4$ (Table 2). Percentage of climate change vulnerable species was lowest in the Oceanian (0%) and Afrotropical (11.4%) realms and highest in the Neotropical (31.5%), Palearctic (28.4%) and Nearctic (26.5%) realms. In the marine realm, 34.8% of species were highly vulnerable to climate change, compared to 28.8% in freshwater and 21.9% of terrestrial species.

At the family level, and excluding families represented by less than 10 species in our sample, Dactyloidae (53.8%), Sphaerodactylidae (44.7%), Viperidae (41.3%), Elapidae (33.3%), Colubridae (32.1%) and Gymnophthalmidae (30.8%) were the most vulnerable families within the analysis, with Atractaspididae, Calamariidae, Lamprophiidae, Leptotyphlopidae and Pseudoxyrhophiidae containing no vulnerable species. Excluding traits with low quality data retained all these families amongst the most and least vulnerable families. Including all traits, 38 of the 70 families in the analysis were significantly more vulnerable than expected by chance ($\chi^2 = 143.4$, $df = 69$, $p\text{-value} < 0.001$), with one family, the Pseudoxyrhophiidae, significantly less vulnerable than expected by chance (Table S8). Lamprophiidae were also less vulnerable than expected by chance, yet occurred at too small a sample size to reject our null hypothesis. Exclusion of traits with low data quality had no effect on the result. Overall vulnerability was highest in the parts of the Amazon basin and northwestern South America, south-western USA, and parts of Southern Asia (e.g., Sri Lanka, southern Western Ghats and Himalayan Arc; Fig. 2A).

3.7. Comparison of climate change vulnerability assessment with IUCN threatened species status

Of the 1498 species in the assessment, 219 are currently listed as threatened on the IUCN Red List. Of these, only 60 species were found to be both vulnerable to climate change (58 species when excluding low data quality traits) and threatened on the IUCN Red List. Spatially, large areas of high climate change vulnerability, specifically in the Amazon basin, southwestern USA/northwestern Mexico, and Iran, do not have a corresponding high richness of IUCN Red List threatened species (Fig. 2B).

4. Discussion

We present the first trait-based global climate change vulnerability assessment for reptiles, supplementing earlier studies on climate change in lizards (Sinervo et al., 2010). Our analysis shows that reptiles are overall highly sensitive to climate change, but limited overlap of sensitivity with low adaptability and high exposure limits the number of overall climate change vulnerable species. Percentage of highly sensitive species was much larger than in previous global studies on birds (64%) and amphibians (72%) (Foden et al., 2013) and marginally higher than in regional studies on reptiles (West Africa: 77.5%; Carr et al., 2014; Tanzania: 71%; Meng et al., 2015, this issue).

Trait-based approaches allow us to tailor assessments to specific taxa, by including traits and variables relevant to the species group in question. However, this means assessments are not directly comparable between studies or taxa (Foden et al., 2013). Any comparisons with other studies, even in terms of levels of sensitivity to climate change etc. have to be taken with a degree of caution. While we endeavoured to replicate the approach by Carr et al. (2014) and Foden et al. (2013) as much as possible, our study differed in terms of data collection and how assessments were carried out. While Carr et al. (2014) and Foden et al. (2013) greatly relied on workshops and expert input to collate data, we relied heavily on existing data sources, including an extensive database on reptile traits developed for previous studies (Böhm et al., 2016), open-access spatial data and literature sources. While more cost-effective, our approach may be more precautionary than assessments derived through workshops, and may for certain traits result in low data quality (e.g. microhabitat specialisation, interspecific dependencies, and temperature-dependent sex determination). However, excluding traits of low data quality had negligible effects on the overall outcome of the assessment. Furthermore, traits associated with climate change vulnerability overlap with those associated with extinction risk, suggesting that trait-based approaches such as our current analysis and consideration of species-specific traits in IUCN Red List assessments may provide us with robust and informative assessments of species at risk from climate change (Pearson et al., 2014; Stanton et al., 2015).

Our assessment uses a representative sample of 1498 randomly selected species to assess climate change vulnerability. This approach was found to derive a broadly representative picture of extinction risk (Baillie et al., 2008) and its applicability to climate change vulnerability assessment is currently being investigated, specifically in the context of arbitrarily set percentage thresholds for sensitivity, adaptability and exposure traits. Because of the random nature of the sample, percentage thresholds should not affect the outcome of the assessment and should be broadly similar to other global assessments of species groups with similar distribution patterns. For example, our thresholds for tolerance of temperature changes and mean precipitation change were ≤1.28 °C and ≥0.55 mm, respectively, similar to thresholds for these traits in other global assessments (e.g. birds: ≤1.44 °C, ≥0.49 mm; amphibians: ≤1.20 °C, ≥0.59 mm; Foden et al., 2013).

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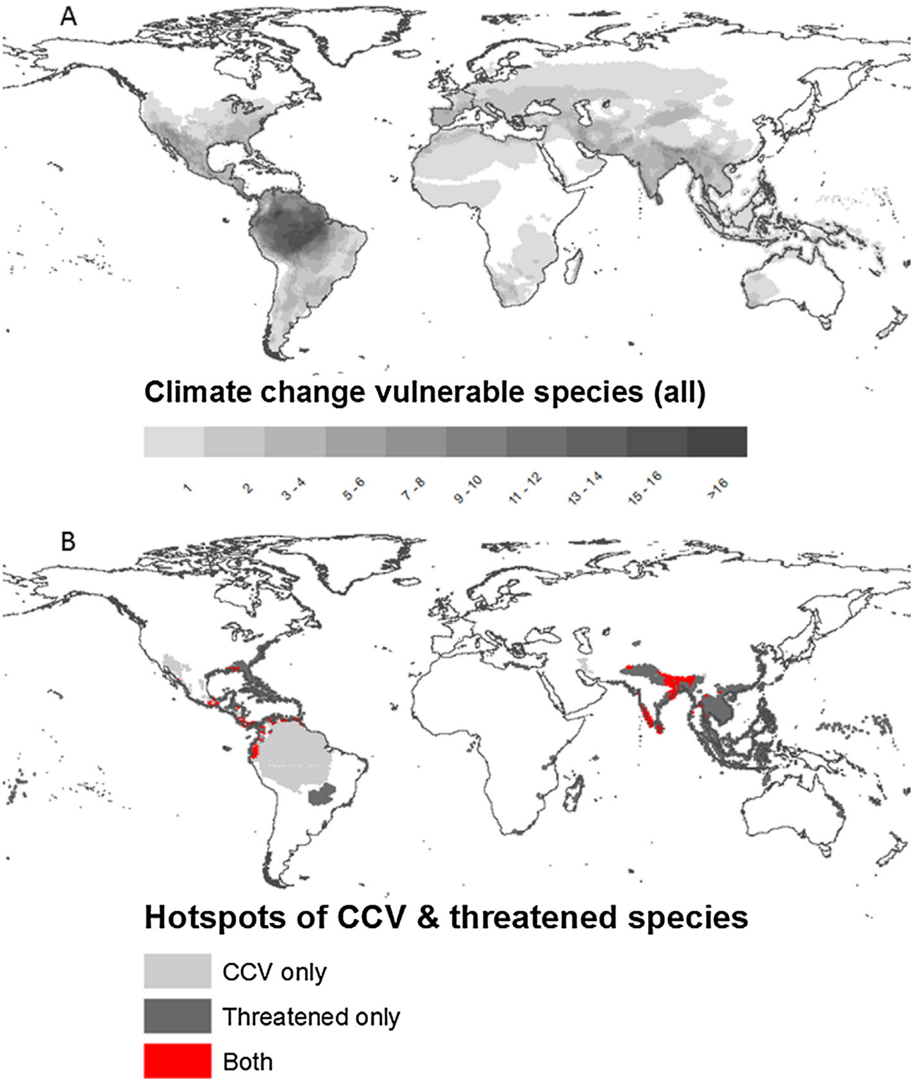

Fig. 2. A. Richness pattern of species that are considered climate change vulnerable (highly sensitive, poorly adaptable and highly exposed). B. overlap (red) of 10% hotspots of climate change vulnerable (CCV) and threatened species on the IUCN Red List; climate change vulnerable species only (light grey), threatened species only (IUCN Red List categories Vulnerable, Endangered and Critically Endangered; dark grey). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.1. Hypotheses, data gaps and quality

Perhaps the biggest challenges for trait-based assessments of climate change vulnerability are the lack of available life-history data (Still et al., 2015) and the fact that climate change may not affect every species in the same way, thus introducing uncertainty in underlying hypotheses about vulnerability traits. In the latter case, for example, temperature increases at high altitudes may not necessarily lead to altitudinal range shifts, as they may instead cause an increase in species survival rates through warmer temperatures. However, to perform effective large-scale regional or global trait-based assessments of species vulnerability requires a framework combining best knowledge about the relationship between traits and vulnerability with a precautionary rather than evidentiary approach.

Considerable data gaps exist in our analysis, especially for traits which are not routinely collected for the purpose of Red List assessments. For example, 16.3% of species lacked data for reproductive output, and for 32% of species we were unable to define microhabitat dependence due to lack of detailed information (probably reflecting, in many cases, lack of information available, especially for highly data deficient species). Additionally, we excluded 'dependence on environmental trigger' as a trait in our analysis due to a near complete lack of data. While our approach relied on data available via published sources, workshops, although costly, may harness more data. For example, only 3% of species had unknown microhabitat dependencies in an assessment of West African reptiles which involved data collation during a workshop (Carr et al., 2014). Many data gaps can be filled by running climate change vulnerability assessments in conjunction with Red List assessments, which would encourage co-ordinated data collection (e.g. through integrated workshops). On the other hand, we used data that were literature-based or open access, which may provide a cost-effective way of assessing species. At the same time, experts could be engaged to ensure data are current and data gaps are filled.

Overall, four sensitivity traits each identified 5% of species or less as highly vulnerable. This could be due to a number of factors such as limited data availability for certain traits (reflecting data deficiency), collinearity of traits, or an indication that some of the traits may simply not relate to climate change vulnerability in a large number of reptiles. Such traits included interspecific dependencies, reliance on a specific fire or flooding regimes, and temperature-dependent sex determination. To obtain broad taxonomic patterns of climate change vulnerability and define spatial priorities at the global level, a trimmed down approach containing fewer traits that contribute extensively to the assessment (for example, habitat specialisation, slow turnover of generations, variables based on climatic data), and which relies on spatial data of climate change threat (e.g. Murray et al., 2014), may be a more time-

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and cost-effective approach. This was also highlighted by the trimmed down approach excluding low data quality traits, which resulted in only a small number of species being removed from the list of climate change vulnerable species. However, climate change can affect species in very specific ways depending on biology and geography, and so the fullest possible complement of traits is required to draw species-level conclusions about conservation management. For example, 25.6% of reptile species in the Albertine Rift were intolerant of changes in a fire regime (Carr et al., 2013), thus highly sensitive to climate change, while in other assessments, including ours, this factor contributed little. In our analysis, inclusion of temperature-dependent sex determination rendered the turtle *Eretmochelys imbricata* highly vulnerable to climate change, while exclusion of this trait led to it having low sensitivity.

It has been argued that climate change velocity may outperform model scenarios in their ability to estimate exposure to climate change, because the velocity of climate change more closely predicts a species' ability to adapt to change or migrate to suitable climate (Hamann et al., 2015). Future analysis on the robustness of climate change vulnerability assessments should compare different methods of estimating exposure, using data directly extracted from climate change scenarios as well as algorithms of climate change velocity. Climate change velocity can also be easily interpreted as one of a number of risk factors putting species at risk of decline and extinction (Hamann et al., 2015), thus potentially helping to improve extinction risk assessments (e.g. for the IUCN Red List) and analyses of the impact of climate change on population decline.

4.2. Consequences for conservation action

Only 3.6% of reptiles in our sample were listed as threatened on the IUCN Red List due to climate change (Böhm et al., 2013), compared to 22% deemed climate change vulnerable in our current assessment. Thirty-eight of the 70 taxonomic families were significantly more vulnerable to climate change than expected by chance, showing that climate change vulnerability cuts across taxon groups. Discrepancy between low vulnerability in the climate change vulnerability assessment and climate change threat on the IUCN Red List was mainly due to a lack of exposure to climate change in the climate change vulnerability assessment, and suggests that assessments of exposure should feature more prominently in IUCN Red List assessments. Furthermore, 62% of the 330 species found to be vulnerable to climate change were not listed in a 'Threatened' or Data Deficient Red List category. These should be given special scrutiny in future reassessments of their Red List status to ensure that their vulnerability is adequately represented within the assessment. In addition, climate change vulnerability assessments can highlight further – and often emerging – priorities for conservation action (Carr et al., 2014; Pacifici et al., 2015). For example, in addition to the 228 species listed as threatened by Böhm et al. (2013), we identify a total of 330 species that likely require attention due to their climate change vulnerability, with limited overlap between the two sets (Fig. 2B). Additional monitoring is required depending on where species fall within the three dimensions of climate change vulnerability (Foden et al., 2013; Fig. 1): potential adapters require monitoring of their adaptive response to climate change (395 species in this study), potential persisters should have their population trends monitored (65 species), while monitoring of the climatic environment is vital for biologically susceptible species (246 species) (Foden et al., 2013).

Increased protection of species through establishment of protected areas may be needed where numbers of potential adapters are high to give these species the best possible chance to adapt to changing climate over time. Given there was little spatial congruence between the main richness hotspots of climate change vulnerable and Red List threatened species, a number of new key areas may require management to minimise climate change effects, at least for reptiles (Fig. 2B).Hotspots of highly vulnerable species were primarily confined to the Amazon basin and southeastern/southwestern USA, while hotspots of threatened species richness are spread across the world's tropical regions (Böhm et al., 2013). Spatial conservation prioritization should take into account both types of hotspots and appropriate conservation actions.

4.3. Conclusions and next steps

Climate change vulnerability assessments are useful in supplementing IUCN Red List assessments by highlighting species which may become highly threatened over time. While labour-intensive, the approach is relatively easily carried out, provided adequate data are available for species-specific traits relating to climate change. To close data gaps, we need to engage in a three-pronged approach by 1) mobilising targeted data collection on traits by collaboration with field herpetologists, including traits excluded here, such a dispersal ability and dependence on environmental triggers, 2) making resulting species trait databases openly available, thus giving transparency to the process, enhancing scrutiny of the data and encouraging input from species experts, and 3) define best practice for collecting missing trait data to reduce uncertainty in assessments (Penone et al., 2014). Similarly, the most current data possible must be utilised to reassess exposure as improved projections become available.

The appropriateness of using a random sample for climate change vulnerability assessments needs to be assessed, akin to the Sampled Red List Index approach (Baillie et al., 2008), to derive broad-scale patterns of climate change vulnerability, and to investigate the relative importance of individual traits to overall vulnerability. For example, incorporating weighting of traits into an assessment could be highly useful, as some traits are likely to respond more intensely to climate change than others (Tuberville et al., 2015). This will also help determine whether less data-intensive and more time-efficient methods may yield broadly similar results for the purpose of global policy planning, rather than making species-specific conservation decisions (for which a full complement of trait data would be needed). This should include consideration of ecosystem or community-level assessments of climate change vulnerability. Current species-specific work is focused on comparing outcomes from different trait-based approaches, and how methods could be further standardised to allow more consistent assessments of climate change vulnerability within and between species.

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Appendix A. Supplementary data

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