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Uncertainty in projected impacts of climate change on biodiversity — a focus on African vertebrates

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Abstract. Assessing the future of biodiversity under changing climates is plagued by uncertainty. Drawing on data for sub-Saharan African vertebrates, I focus on some of the major sources of uncertainty surrounding bioclimatic envelope model projections and on possible ways to address them. I examine the uncertainty arising from alternative climate projections and model algorithms and I summarise it through consensus building. To examine ecological uncertainty, I present a framework for teasing apart projected gains, losses, and fragmentation of climatically suitable areas; each of these threats and opportunities can be examined with reference to relevant response-mediating biological traits, such as the species' climatic tolerance, reproductive output, and dispersal ability. A further source of uncertainty in climate change impact assessments based on bioclimatic envelope models is the omission of narrow-ranging species, which are difficult to model. I demonstrate the conservation implications of such omissions, and I investigate how climate change metrics can be used as an alternative tool in assessments. Multiple metrics of change in climate parameters, seen as proxies for the threats and opportunities facing biodiversity, are reviewed and illustrated at the global scale, and compared to bioclimatic models for sub-Saharan African vertebrates.

Keywords. Africa, bioclimatic envelope model, climate change, biological trait, species distribution model, uncertainty, vertebrate.

The uncertain nature of assessments of climate change impacts on species

Population declines, phenological shifts, and species' distributional changes observed in multiple regions prompted the first studies in climate change ecology (Nabout et al. 2012). Together, these studies created a body of evidence suggesting a link between observed changes in nature and climate change (Parmesan and Yohe 2003). Faced with the prospect of increasing rates of climate change during the 21st century, attention in the research community turned to projecting the future impacts on biodiversity (Nabout et al. 2012). Such projections rely on different approaches spanning a continuum from correlative to mechanistic models (Dormann et al. 2012). At the correlative end of the continuum, bioclimatic envelope models (Peterson et al. 2011) use the association between known species' occurrences and climate to characterise the sets of suitable

climatic conditions for species (or the realised subsets thereof). By projecting this characterisation to the future, these models provide estimates of species' exposure to climate change (see e.g., Foden et al. 2013, Dickinson et al. 2014). At the opposite end of the continuum, mechanistic models explicitly include processes such as the species' physiological constraints and plastic acclimation capacity (Kearney and Porter 2009), and the demographic dynamics (Keith et al. 2008) underlying the vulnerability of species to climate change.

As in any other predictive science, projections of climate change impacts on biodiversity contain uncertainty. Uncertainty pervades the entire modelling process (Elith et al. 2002, Wiens et al. 2009, Beale and Lennon 2012), irrespective of the approach used; it stems from decisions regarding the generation of data used in the modelling, the actual modelling and evaluation processes, and the ecological knowledge and theory

Table 1. Some of the major sources of uncertainty in assessments of the impacts of future climate change on biodiversity. Examples are given for three major classes of uncertainty associated with the three components of modelling frameworks as defined by Austin (2002): the data used, the mathematical model, and the underlying ecological knowledge. The list is not meant to be exhaustive, but to capture some of the major sources that are relevant in the context of the work presented here. For each example of uncertainty, the arrows point to the extreme of the correlative ("C", left) to mechanistic ("M", right) model continuum that is most affected.

'Data model' uncertainty:	
decisions about the biological and climatic data used in the modelling	C ↔ M
Error, bias or subjective judgement in species occurrence data	←
Error, bias, or subjective judgement in mechanistic data	→
Omission of species	→
Error in interpolated baseline climate data	↔
Error in future climate projections	↔
Unknown future greenhouse gas emissions	↔
Error in downscaled climate data	↔
'Mathematical model' uncertainty	
decisions about the calibration, evaluation and projection methods	C ↔ M
Choice of algorithm	←
Methods for predictor selection, data partitioning, absence estimation, etc.	↔
Choice of evaluation data and technique	↔
Small numbers of species' occurrence	←
Extrapolation to non-analogue conditions	←
Choice of threshold for deriving binary projections	←
'Ecological model' uncertainty	
decisions about ecological concepts and assumptions underpinning the models	C ↔ M
Missing or inadequate biological components	←
Missing or inadequate climate parameters and dimensions, and response forms	↔
Missing non-climatic factors	↔
Species-climate equilibrium assumption	←
Spatial or temporal scale mismatch/ inadequacy	←
Lack of clarity about the object and output of models	←

used (Table 1). For projections of the effects of climate change on biodiversity to be improved and judiciously used, it is crucial to appreciate and understand their uncertainty.

Whereas the ecological information needed to parameterise mechanistic models is lacking for most known species, climate and species' occurrence data of varying quality have become widely available. As a result, the last decades have seen a surge of studies using bioclimatic envelope models to assess how species might be influenced by

ongoing and future changes in climate (Nabout et al. 2012). However, across this wealth of studies, the uncertainty surrounding model projections is often only partially addressed or even overlooked. In focusing on bioclimatic envelope models, I aim to contribute to a further understanding of the uncertainties underlying assessments of the future of biodiversity under changing climates, and to explore ways to address them (Garcia 2014). My focus is on sub-Saharan African vertebrates, thereby illustrating some of the crucial challenges

for assessments in tropical and sub-tropical areas of high biodiversity and poor biological knowledge. Nevertheless, the methodological advances and over-arching conclusions are more broadly applicable to other geographical regions or taxonomic groups.

Model and climate data uncertainty: quantifying and summarising

Ensembles of models built with alternative assumptions (Araújo and New 2007) offer a way to quantify the uncertainty of model projections. The members of an ensemble are seen as plausible representations of the system under study, and at least partially express the breadth of uncertainty. For over 2,000 species of sub-Saharan African birds, mammals, amphibians, and snakes (Burgess et al. 1998), we build an ensemble of models (Garcia et al. 2012) using seven different algorithms, three multi-model climate projections, and three emissions scenarios. The models use baseline data (New et al. 2002) and projections (Tabor and Williams 2010) at one-degree resolution for three climate predictors: mean temperatures of both warmest and coldest months, and annual precipitation. In our study as in previous studies (e.g., Thuiller 2004, Diniz-Filho et al. 2009), the choice of model algorithm is identified as the major cause of uncertainty. This uncertainty is largest in the Sahel and the Southern Sahara, where future temperatures are expected to fall above the range of the calibration data, and is thus possibly due to model extrapolation (Pearson et al. 2006).

The variation in projections can be summarised by building consensus projections (Araújo and New 2007). The rationale behind consensus is that combining an ensemble of projections, assumed to be independent and representative of the breadth of possible states of the system being forecast, yields lower mean error than any of the individual projections (Bates and Granger 1969, Araújo and New 2007). Building consensus is challenging not only because the required assumptions are difficult to meet, but also because there is still debate on the best way to combine projections (Knutti et al. 2010). We extend previous comparisons of methodologies (e.g., Araújo et al.

2005, Marmion et al. 2009) by exploring a comprehensive suite of five methodologies to build consensus around different model algorithms. Measuring the central tendency among groups of co-varying projections yields the highest accuracy, while avoiding the loss of information about extreme states, which often results from averaging across the entire ensemble. The multi-model climate data mentioned above, which we use to project the models, is the result of the same consensus methodology applied to 17 future climate models. We thereby simplify our input data for the modelling while retaining the variability of the initial ensemble—an advantage that is not trivial in the face of the increasing wealth of climate data available.

Ecological uncertainty: contrasting exposure and vulnerability

Bioclimatic envelope model outputs are not only sensitive to data and methodological decisions, but they also contain ecological uncertainty. While rarely considered, biotic interactions (Araújo and Luoto 2007), the dispersal ability of species (Midgley et al. 2006), and the fundamental climatic tolerances of species (Arribas et al. 2012) have all previously been shown to influence model projections under climate change. When direct incorporation of ecological data in mechanistic models is not viable, bioclimatic envelope model outputs can be contrasted with alternative assumptions about the vulnerability of species. We present an analytical framework to examine projections of changes in climatic suitability with reference to estimates of species' vulnerability to such changes (Garcia et al. 2014a). In contrast to previous studies comparing exposure to vulnerability, we argue that the different extrinsic threats and opportunities arising from the exposure of species to climate change should be examined separately, and matched to specific intrinsic biological traits that are likely to mediate species' responses to each of those threats and opportunities. Losses, fragmentation and gains of areas of climatic suitability impose different constraints on species and have different implications for conservation. Different extrinsic threats are also likely to

interact with specific response-mediating traits (Isaac and Cowlshaw 2004), but the specificity between threats and traits has not been sufficiently addressed in climate change ecology. For example, traits describing plasticity of individuals' phenology, behaviour or physiology may affect the individuals' potential to persist *in situ* under changing climate, whereas traits influencing their capacity to disperse may affect their potential to colonise newly suitable areas or move between fragments of suitable climate.

Using the bioclimatic envelope models built for sub-Saharan African amphibians (Garcia et al. 2012), we spatially overlay projected losses, gains and fragmentation of suitable climate areas with vulnerability classifications derived from available data on characteristics of species or species' ranges that are associated with biological traits or complexes of traits (Foden et al. 2013). For example, for the species with the smallest geographical overlap between areas of baseline and future climate suitability, the gains of climatically suitable areas projected by the models are uncertain due to species' poor dispersal ability. Our results are undoubtedly contingent on the quality of the trait data. The available estimates of dispersal ability, for example, were derived from the characterisation of known distributions of species, rather than from data on empirical movement (e.g., Gamble et al. 2007) or on the set of traits associated with dispersal (Dawson 2014). Although the trait data themselves bring new uncertainties, our results illustrate how interpretation of bioclimatic envelope model projections can alter with consideration of species' vulnerability.

Species data uncertainty: extending assessments to wholesale biodiversity

The uncertainties discussed above apply to projections of the exposure of sub-Saharan African vertebrates to future climate change, but exclude poorly sampled species that could not be modelled due to their small number of occurrence records (Stockwell and Peterson 2002). The bioclimatic envelope models thus cover only 67% of the species in the African vertebrate database and a mere 38% of amphibians. Such bias against nar-

row-ranging species is not unique to the studies presented here, but pervades most modelling exercises under climate change.

Using sub-Saharan African amphibians as a case study, we explore the implications of the bias against poorly sampled species for conservation prioritisation (Platts et al. 2014). Omitted amphibians encompass the vast majority of threatened species, occupy topographically complex areas with cooler, wetter and less seasonal climates, and are exposed to lower climate anomalies in the future. The range size bias is counter to traditional frameworks for identifying priority sites for conservation, which focus precisely on those taxa most likely to be omitted from the modelling. In our study, priorities derived from the subset of omitted species show greater congruence with existing conservation schemes than priorities for modelled species. Under future climate, congruence for omitted species prevails despite the loss of climate space, while priorities for modelled species shift towards those for omitted species.

The above results underscore the importance of complementing models with alternative, more generally applicable tools. One such alternative tool is the use of simple metrics of climate change, which quantify the exposure of geographical areas (rather than species' distributions) to changes in climate parameters. Metrics have previously helped to address a diversity of ecological questions including the potential risks from future climate changes to biodiversity (Williams et al. 2007, Jiménez et al. 2011) and conservation areas (Loarie et al. 2009, Wiens et al. 2011). However, the variety of existing metrics and their ecological implications has hitherto not been fully appreciated. We review climate change metrics and classify them into two groups. The first group comprises local metrics depicting changes at specific localities (grid cell). Examples are climate anomalies (e.g., Williams et al. 2007), changes in the magnitude of extreme climates (e.g., Jiménez et al. 2011) or the timing of climatic events (e.g., Burrows et al. 2011), and the local velocity of climate change (e.g., Loarie et al. 2009). The second group comprises regional metrics characterising

changes in the distribution of climatic conditions over broad geographical areas (collections of grid cells). These metrics can describe temporal changes in the availability of analogous climatic conditions across a region (e.g., Ackerly et al. 2010), as well as changes in the direction to, or distance between, the positions of analogous climatic conditions (e.g., Ohlemüller et al. 2006). Our global analysis highlights the contrasting spatial patterns arising from different metrics applied to end-of-century climate projections. Whereas polar regions face reductions in the global availability of similar climatic conditions, the tropics and hot arid regions are projected to be exposed to average changes beyond historical climatic inter-annual variability, emergence of novel climates, and increased frequency of extreme climates.

To help interpret the diversity of metrics, we propose a conceptual framework for classifying them into common currencies of climatic threat and opportunity for species. The framework is based on principles linking the persistence of populations and species to local and regional climatic suitability, respectively (Jackson and Overpeck 2000), and is built upon published empirical studies. At the local level, decreased climatic suitability can affect the physiology, morphology or behaviour of the organisms in a population (Peñuelas et al. 2013). For example, population declines have been linked to metrics of gradual (Foden et al. 2007) or extreme changes (Allen et al. 2010) in local climate, whereas phenological shifts have been associated with measured changes in the seasonality of climate (Lane et al. 2012). At the regional level, the spatio-temporal dynamics of climate can affect the availability and distribution of climatically suitable areas for species (Jackson and Overpeck 2000). Expansions and contractions of species' ranges over time often match, with time lag, the increases and decreases in the area of given climatic conditions brought about by the Earth's warming and cooling cycles (Nogués-Bravo et al. 2010). At the same time, measured shifts in the position of climatic conditions have been used to explain species' climate tracking in both palaeoecological (Nogués-Bravo et al. 2010) and recent (Parmesan and Yohe 2003) time.

To test the feasibility of the framework proposed for guiding the use of metrics, we compare climate change metrics for sub-Saharan Africa with bioclimatic envelope models built for vertebrates (R. A. Garcia, M. Cabeza, R. Altwegg, and M. B. Araújo unpublished). The agreement found between metrics and models demonstrates that, when carefully implemented and interpreted, metrics can provide first approximations to the same threats and opportunities typically captured by bioclimatic envelope models.

Embracing uncertainty

Unknown future climates, the diversity of model algorithms, species-specific vulnerability to climate change, and the omission of species affect bioclimatic envelope model projections for sub-Saharan African vertebrates (Fig. 1). Other uncertainties exist that are not addressed here (Garcia 2014), such as those associated with the choice of spatial resolution, the choice of predictors, or the sampling bias in species' occurrence data. All these uncertainties impair the successful conservation of biodiversity under changing climates. Despite numerous calls to explicitly address this challenge (Wiens et al. 2009, Beale and Lennon 2012), appropriate treatment of uncertainty has yet to be formalised in impact assessments and conservation adaptation.

While precise projections are unattainable, existing uncertainties should be incorporated in assessments and quantified to the extent possible (Beale and Lennon 2012). Building ensembles of models with alternative assumptions (Garcia et al. 2012) can give a lower bound on the range of uncertainty, whereas the effect of factors not accounted for in the models can be examined a posteriori (Garcia et al. 2014a). If model projections are to inform the adaptive management of climate change impacts on Earth's biodiversity (Garcia and Araújo 2010), they must be as transparent as possible by including a description of their limitations and level of confidence (Fig. 1). Understanding the uncertainty in projections also helps to direct efforts to reduce it where most needed. Increasing the precision and accuracy of bioclimatic envelope models rests partly on im-

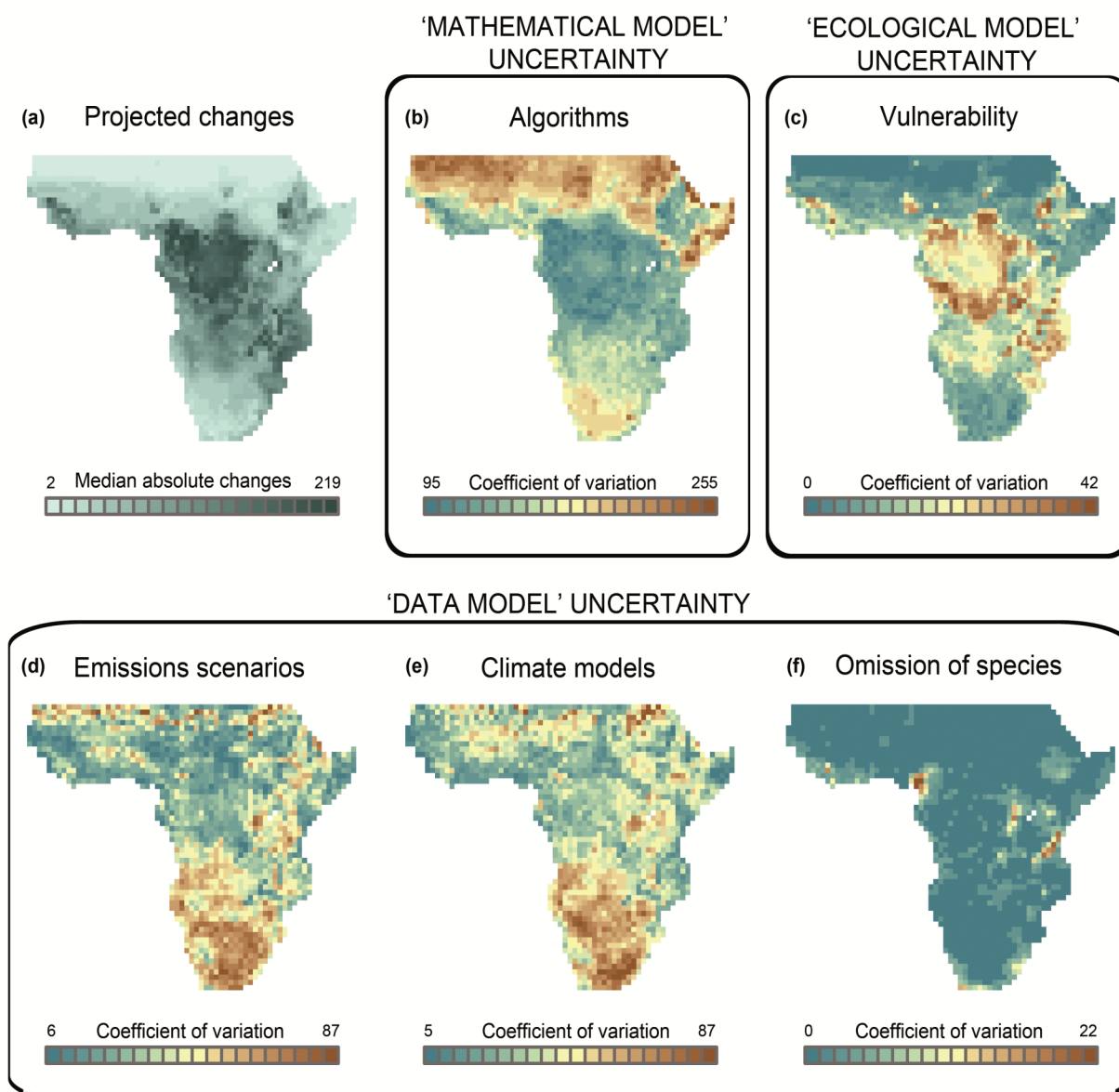


Figure 1. Uncertainties in projections for African amphibians under climate change. Ensembles of bioclimatic envelope models for 263 sub-Saharan African amphibians (Garcia et al. 2012) were used to project changes in the probability of climatic suitability by mid-century. **(a)** Projected median absolute (positive and negative) changes are shown for a multi-model climate projection under emissions scenario A1B, and reflecting the median across seven algorithms. **(b)** The coefficient of variation is shown across projections for alternative algorithms. **(c)** The ecological uncertainty is illustrated by the variation between the raw projections and projections that were modified a posteriori according to estimates of species' dispersal ability and tolerance to climate changes (Garcia et al. 2014a). **(d)** Climate data uncertainty is shown by the variation across three emissions scenarios, and **(e)** three averaged clusters of climate models. **(f)** Data uncertainty arising from the omission of narrow-ranging species is revealed by comparing two hypothetical projections, one assuming loss of climatic suitability for (un-modelled) omitted species and the other assuming continued suitability (Platts et al. 2014).

proving the data on species' occurrences (particularly in tropical regions), and carefully selecting climate predictors, not only in terms of parameters but also dimensions of change (Garcia et al. 2014b).

In an effort to reduce the ecological uncertainty of projections, the field of climate change

ecology is becoming more integrated, harnessing new disciplines and types of data (Dawson et al. 2011) to describe the potential behaviour of the ecological system. Complex models are valuable for guiding species-based conservation, while also advancing ecological theory. Yet, increased realism comes at the expense of applicability to many

species. Mechanistic models have only been empirically tested on few species with available data, and even simple bioclimatic envelope models are not suited to the narrowest-ranging species (Platts et al. 2014). What is more, both correlative and mechanistic models cannot be applied to undescribed species, which are in the vast majority (Mora et al. 2011). While describing the distributions and autecology of species and modelling their responses must remain a priority, gathering data for all species on Earth is impractical. We suggest that investment in models should be accompanied by the development of alternative approaches that circumvent the uncertainty associated with species' data, and that climate change metrics are one candidate approach (Garcia et al. 2014b). Providing conservation planners with useful assessments will certainly require the integration of multiple approaches.

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