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Do projections from bioclimatic envelope models and climate change metrics match?

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ABSTRACT

Aim Bioclimatic envelope models are widely used to describe changes in climatically suitable areas for species under future climate scenarios. Climate change metrics are applied independently of species data to characterize the spatio-temporal dynamics of climate, and have also been used as indicators of the exposure of species to climate change. Here, we investigate whether these two approaches provide qualitatively similar indications about where biodiversity is potentially most exposed to climate change.

Location Sub-Saharan Africa.

Methods We compared a range of climate change metrics for sub-Saharan Africa with ensembles of bioclimatic envelope models for 2723 species of amphibians, snakes, mammals and birds. For each taxonomic group, we performed three comparisons between the two approaches: (1) is projected change in local climatic suitability (models) greater in grid cells with larger temporal differences in local climate (metrics); (2) are projected losses or gains of climatically suitable areas (models) greater for species in grid cells with climates that are projected to be less or more available in the future, respectively (metrics); and (3) are projected shifts in the position of climatically suitable areas (models) greater for species in grid cells with climates projected to move farther in space (metrics)?

Results The changes in climatic suitability projected by the bioclimatic envelope models covaried with the climatic changes measured with the metrics. Agreement between the two approaches was found for all taxonomic groups, although it was stronger for species with a narrower climatic envelope breadth.

Main conclusions For sub-Saharan African vertebrates, projected patterns of exposure to climate change given by climate change metrics alone were qualitatively comparable to bioclimatic model projections of changes in areas of suitable climate for species. Assessments based on climate change metrics can thus be useful for making first-cut inferences about the potential effects of climate change on regions with poorly known biodiversity.

Keywords

Africa, bioclimatic envelope model, climate anomalies, climate change, ecological niche model, exposure, vertebrate.

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INTRODUCTION

Earth's climate is known to have varied over millennia, with recent decades witnessing rapid changes (Mann *et al.*, 1998) that are set to continue (IPCC, 2013). As temperature and precipitation regimes change, not only is the climate at any given locality altered, but climatic conditions are also redistributed at broader

spatial scales. Such spatio-temporal dynamics of climate have been suggested to influence biodiversity by causing local population declines (Foden *et al.*, 2007; Allen *et al.*, 2010) and, eventually, translating into changes in the area or position of species' ranges (Nogués-Bravo *et al.*, 2010; Chen *et al.*, 2011). Although applied independently of species data, measured changes in climate parameters over time (hereafter 'climate change

metrics'; Garcia *et al.*, 2014b) have helped to explain the role of past climatic changes in shaping biodiversity patterns (e.g. Araújo *et al.*, 2008; Hortal *et al.*, 2011). If close correspondence exists between climate and biodiversity, it follows that climate change metrics might help to forecast the extent to which species inhabiting particular areas are likely to become exposed to future climatic changes (exposure *sensu* Dawson *et al.*, 2011). Indeed, climate change metrics have been used to assess the potential threats and opportunities that species might face under future climates (e.g. Ohlemüller *et al.*, 2006; Williams *et al.*, 2007; Loarie *et al.*, 2009; Ackerly *et al.*, 2010) as well as the conservation measures that might be required (e.g. Watson *et al.*, 2013). By measuring multiple climatic changes that represent different challenges for species (Garcia *et al.*, 2014), such metrics could be seen as an alternative to the commonly used bioclimatic envelope models (Guisan & Zimmermann, 2000; Peterson *et al.*, 2011) in situations where data on species distributions are absent or incomplete. However, it remains unclear whether the two approaches provide qualitatively similar assessments of the exposure of biodiversity to climate change.

The impacts of climate change on species depend on the degree to which individuals and populations across species ranges are exposed to changes in relevant aspects of climate, their intrinsic sensitivity to these changes (Williams *et al.*, 2008) and, ultimately, also on biotic interactions (Post, 2013) and synergies with other extrinsic threats (Brook *et al.*, 2008). Bioclimatic envelope models and climate change metrics can support spatial analyses of the exposure of species and regions, respectively, to climate change (for review see Garcia *et al.*, 2014b). Bioclimatic envelope modelling has been extensively used in climate change risk assessments for biodiversity at global (e.g. Thomas *et al.*, 2004; Hof *et al.*, 2011) and regional (e.g. Thuiller *et al.*, 2006; Araújo *et al.*, 2011) scales. Assuming that species are at equilibrium with climate (a working assumption rather than a theoretical or empirical expectation; see for discussion Araújo & Peterson, 2012), these models use statistical associations between observed species occurrences and climate parameters to define the envelope of climatically suitable areas for species across a given region. Based on the assumption that such envelopes are conserved across time, future climate suitability for species is then assessed across space depending on how similar the projected climates are to those that define the envelope. The bioclimatic envelope modelling approach can thus provide statistical assessments of the exposure of individual species to climate change by quantifying expected losses, gains or fragmentation of climatically suitable areas, as well as shifts required to track suitable climates (Midgley *et al.*, 2003; Garcia *et al.*, 2014a; Heikkinen *et al.*, 2009).

In turn, climate change metrics quantify the level of exposure of geographical areas to climatic changes, allowing for inferences to be drawn about the potential implications of these changes for the biodiversity inhabiting such areas. Changes at any given locality and changes in the distribution of climates across broader regions can both be measured (Fig. 1; for a review of existing metrics see Garcia *et al.*, 2014b).

Different metrics depict distinct dimensions of climate change, from local changes in average or extreme climates (Katz *et al.*, 2005; Williams *et al.*, 2007) to regional changes in the availability or position of particular climate conditions (Ohlemüller *et al.*, 2006; Ackerly *et al.*, 2010). Each of these dimensions of change is expected to impose distinct threats and opportunities for species (Garcia *et al.*, 2014b). At the local level (e.g. the grid cell), changes in average or extreme climatic conditions can be used as a proxy for the threat of local demographic changes. At the regional level (e.g. a set of grid cells), decreases or increases in the available area of analogous climatic conditions provide indications of the degree of threat of loss or opportunity for gains of areas that are climatically suitable for species across a given region, whereas shifts in the location of climatic conditions can indicate the need for geographical shifts of species ranges.

Climate change metrics have the potential to add useful information to traditional bioclimatic envelope models (Ohlemüller, 2011), and may be the only alternative when species identities or their locations are poorly known or not known at all (Garcia *et al.*, 2014b). Yet to ensure the appropriate use of climate change metrics as an alternative tool for drawing inferences about the exposure of species to climate change, it is crucial to critically examine their outputs. The results provided by metrics can be compared with species spatio-temporal turnover data (mostly unavailable, but see, e.g., Araújo *et al.*, 2005; Tingley *et al.*, 2009) or, in their absence, with the results of other modelling approaches (as done for bioclimatic envelope models and mechanistic models; e.g., Kearney *et al.*, 2010).

Here, we provide the first comparison between the projections provided by climate change metrics and by bioclimatic envelope models, for over 2000 species of sub-Saharan African amphibians, snakes, mammals and birds. If both approaches highlight the geographical areas of greatest threat or opportunity for species, we predict that: (1) projected changes in climatic suitability from bioclimatic envelope models, at the grid cell level, will be greater where differences in local climate as projected by the metrics are also greater; (2) projected losses or gains of areas that are climatically suitable for species across the region, according to bioclimatic envelope models, are larger where climate change metrics project shrinking or expanding climates, respectively; and (3) projected shifts in the position of areas that are climatically suitable for species across regions, according to bioclimatic envelope models, are greater where climates are projected by the metrics to move farther. We test these predictions individually for each taxonomic group. As climate change metrics are applied independently of species data, we assess the influence of the breadth of species bioclimatic envelopes on the level of agreement between the two approaches.

MATERIALS AND METHODS

Bioclimatic envelope models

We used published baseline (1961–90) and late-century (2081–2100) projections of climatically suitable areas for sub-Saharan African species of birds (1506), mammals (623), amphibians

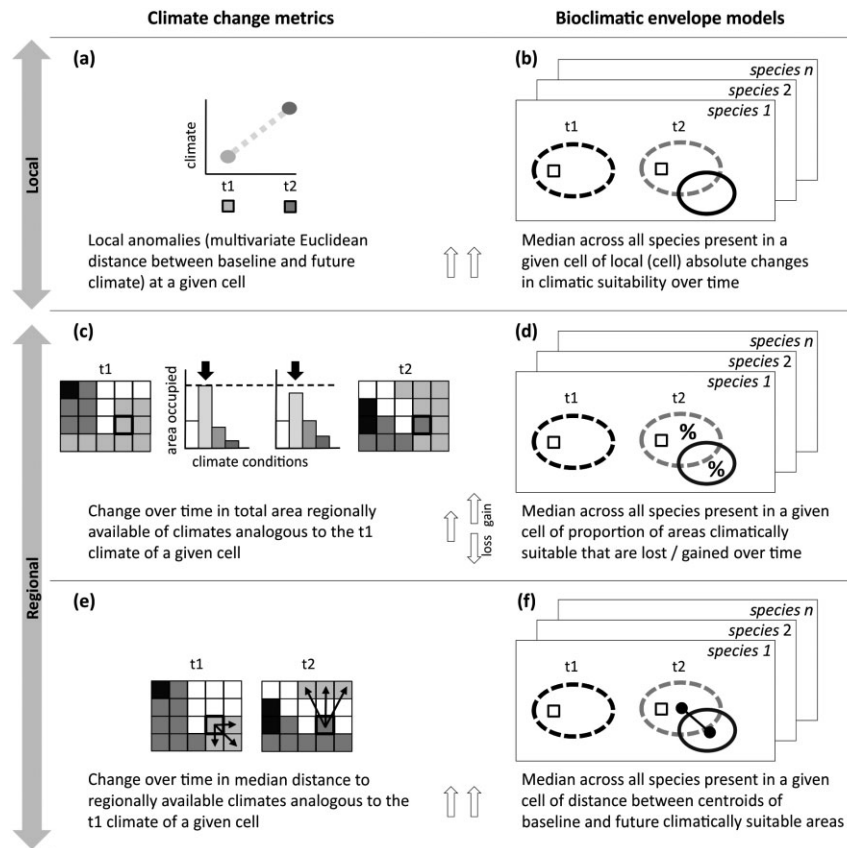


Figure 1 Bioclimatic envelope models versus climate change metrics. The different temporal changes in climatically suitable areas for species, derived from bioclimatic envelope models for sub-Saharan African amphibians, snakes, mammals and birds (b, d, f), were each compared with relevant metrics projecting future climate change in sub-Saharan Africa (a, c, e). For a given locality (cell with thick outline in the schematic representation), local climate change metrics refer to changes occurring over time at that locality, and regional metrics refer to changes in the distribution of the climate conditions of that locality across broader regions. For example, the climate conditions in the selected cell in t1 change to a darker shade in t2 (local change, a), whereas the total area available across the region with the cell's climate condition in t1 decreases from nine cells in t1 to eight cells in t2, and moves farther in space (regional changes, parts c and e respectively). Based on bioclimatic envelope models for a given species in t1 (dashed line) and projections for t2 (solid line), local changes in suitability at any given cell refer to the absolute difference in suitability for the species in that cell over time; the median differences for all species occurring in that cell were then computed (b). In turn, regional changes in suitability for a given species refer to the proportion of the t1 area of climatic suitability that is lost or gained in t2 (d), or the distance between the centroids of the climatically suitable areas at t1 and t2 (f); the median area proportions or distances across all species present at a given cell were then computed (d and f, respectively). The arrows in the middle of each panel indicate whether the two approaches are expected to be positively or negatively related (arrows pointing in similar or opposite directions).

(284) and snakes (310), at 1° resolution (c. 111 km × 111 km at the equator) (Garcia *et al.*, 2012). The models were built with three climatic variables: mean temperatures of both the warmest and coldest months, and annual precipitation. Baseline data for these variables were from the Climatic Research Unit (New *et al.*, 2002) and future projections were from a multi-model ensemble of nine general circulation models (GCMs; Meehl *et al.*, 2007; Tabor & Williams, 2010) under the A1B emissions scenario (see Table S1 in Supporting Information for the list of GCMs and Garcia *et al.* (2012) for detailed methods). The models were calibrated using 75% of the species occurrence data, and evaluated on the remaining 25% using true skill statistics (TSS; Allouche *et al.*, 2006; see model evaluation in Fig. S1). The projections used in our study reflected the consen-

sus among seven modelling techniques (the median projection; see a list of all techniques in Fig. S1), and assumed unlimited dispersal of species.

Based on the areas of climatic suitability for species projected for the baseline and future periods, we computed four types of changes: local changes in climatic suitability, and losses, gains and shifts of areas of climatic suitability for species. For each species, local (cell-based) change in suitability was computed as the absolute value of the difference between the baseline and future probabilities of climatic suitability of any given cell, to account for both potential improvement and deterioration in suitability. Calculation of the remaining types of changes was based on the model projections in binary form, converted from probabilities based on a threshold maximizing TSS. Losses or

gains of climatically suitable areas were quantified for each species as the proportion of the baseline areas projected to be lost or gained in the future across sub-Saharan Africa. Shifts in the position of climatically suitable areas were measured for each species by the great-circle distance between the centroids of baseline and future areas.

Climate change metrics

We used the selected climate variables to compute three climate change metrics: local anomalies, regional changes in area of baseline-analogous climates and regional changes in distance to baseline-analogous climates. These three metrics were selected because they are the ones most closely associated with the concepts underpinning bioclimatic envelope models. Firstly, whether a given locality is projected by the models to remain suitable or to become unsuitable for a species depends on the degree of local change in climate relative to the bioclimatic envelope breadth and position for that species. Local anomalies provide a measure of change in local climate, which is, however, independent of species climate envelopes. Secondly, model projections of changes in the size or position of areas that are climatically suitable for a given species are contingent on the regional availability and location of the climatic conditions characterizing the envelope. Changes in area of, and distance to, analogous climates provide a measure of regional climate availability, albeit independently of the range of different suitable climates for a given species.

Differences in local climate, or local anomalies, were estimated by first scaling the variables from zero to one, and then computing, for each cell, the multivariate Euclidean distance between baseline and future climates. Metrics of regional change relied on the definition of analogous climates: when can two cells be considered to have similar climates? Following Ohlemüller *et al.* (2006), we considered climatic conditions to be analogous across space and time if they differed by less than pre-defined thresholds. To define the optimal thresholds for each climate variable, we tested a sequence of 20 thresholds spanning from half of the mean historical inter-annual variability (1961–90) across sub-Saharan Africa to 10 times that value (Ackerly *et al.*, 2010). For each threshold, we derived a classification of all cells across the study area, whereby cells that differed by less than the set thresholds for all variables were assigned the same class. To select the threshold yielding the optimal classification, we compared the 20 classifications obtained with the Köppen–Geiger climatic classification (Peel *et al.*, 2007) using two approaches. With the ANOSIM test (Clarke & Warwick, 1994), we assessed with 999 permutations whether our classes of cells differed more between Köppen–Geiger classes than within the same Köppen–Geiger class. With the TSS test (Allouche *et al.*, 2006) we assessed the accuracy of our classification to discriminate between Köppen–Geiger classes. For each Köppen–Geiger class, we computed the probability that the climatic differences between cells in that class and cells in different classes were greater than the set thresholds (true negative fraction) and the probability that the differences

between cells within the same Köppen–Geiger class were smaller than the set thresholds (true positive fraction). We then computed the median TSS across all Köppen–Geiger classes. For regional metric calculations, we used the threshold maximizing the ANOSIM and TSS statistics simultaneously.

Using the optimal threshold, we identified, for a given cell, all other cells across sub-Saharan Africa with climates analogous to that cell's climate in the baseline period. We repeated this procedure for the future period (searching throughout the study area for future climates that are analogous to that cell's baseline climate), and calculated the temporal change in area with analogous climates. Positive values indicated expanding climates, negative values indicated shrinking climates and zero reflected no change. We also calculated the change in distance to baseline-analogous climatic conditions. For each cell, we computed the median of the great-circle distances to all cells with analogous climates, in both baseline and future periods, and retained the change over time. Negative values indicated that similar climates were projected to move closer, whereas positive values indicated they were projected to move farther.

Comparison of bioclimatic envelope models and climate change metrics

For each taxonomic group, we assessed whether the changes in climatic suitability projected by the bioclimatic envelope models covaried with the dimensions of climate change measured with the metrics (Fig. 1). First, local (cell) changes in climatic suitability for species were compared with local climate anomalies. Using the median absolute changes in climatic suitability across species in each cell, we asked whether this median was greater in grid cells exposed to large climate anomalies than in grid cells exposed to small anomalies. The median value of anomalies across sub-Saharan Africa was used to differentiate large from small anomalies.

Second, changes in climatically suitable areas for species in each taxonomic group were compared with regional changes in climate. For each cell, we computed the median projected loss of climatically suitable areas across species occurring in that cell. We then asked whether the median projected losses in cells with shrinking climates was greater than the same median loss in expanding climates. We repeated the analysis for projected median gains of climate space, with the expectation that gains would be greater in cells with expanding climates. Finally, we asked whether the median projected shift in position of climatically suitable areas was greater in cells with climates projected by the metrics to move farther apart than in cells with climates projected to move closer.

For each comparative analysis, we used Wilcoxon signed-rank tests to assess the statistical difference between the two groups of grid cells exposed to different degrees of climate change. To assess the magnitude and direction of the differences, we also measured effect size. We used Cliff's delta (Cliff, 1993), a nonparametric alternative measure of effect size that is robust to violations of the normality assumption. Cliff's delta estimates the probability that a value selected from one of the groups

being compared is greater than a value selected from the other group, minus the reverse probability. It varies from -1 to $+1$, with zero indicating complete overlap between the distributions of the two groups and values farther from zero reflecting smaller overlap. The sign of the delta estimate reflects which group dominates. In our tests, positive values indicated dominance according to expectations (see Fig. 1), whereas negative values indicated dominance contrary to expectations.

Sensitivity analysis to differences in species envelope properties

As climate change metrics are applied independently of species data, we investigated whether the comparisons performed were affected by the properties of species bioclimatic envelopes. We first assessed species envelope breadth using the outlying mean index analysis (OMI; Dolédec *et al.*, 2000). The OMI analysis identifies the ordination axes that optimize the separation between species occurrences, and quantifies the envelope position and breadth for each species along those axes. Envelope breadth is quantified as the dispersion of environmental conditions occupied by species, with larger dispersion values indicating wider breadth. We then defined two groups of species across the four taxonomic groups with bioclimatic envelope breadth above and below the median breadth, and repeated the comparative tests between models and metrics for each group individually. We expected the correspondence between the two approaches to be greater, i.e., larger, positive, effect sizes measured with Cliff's delta, for species with narrower climatic breadth. Species endemic to more restricted ranges of climatic conditions are likely to depend more strongly on tracking climates (Williams *et al.*, 2007; Ohlemüller *et al.*, 2008) than species with more generalist climate preferences.

RESULTS

Climate change metrics revealed that tropical areas of Africa were the most exposed to large local (cell) anomalies in mean temperatures of the coldest and warmest months and in annual precipitation (Fig. 2a). In turn, bioclimatic envelope models forecast larger absolute changes in local climatic suitability for species in tropical areas extending into West Africa as well as the Ethiopian Highlands (Fig. S2). For all four taxonomic groups, projections by bioclimatic envelope models and climate change metrics were consistent with our expectations that changes in local (cell) climatic suitability for species were greater where climate anomalies were also greater [Fig. 2b; Wilcoxon signed rank-test, P -values < 0.05 ; Cliff's delta (confidence interval), 0.45 (0.40–0.49) for birds, 0.49 (0.44–0.53) for mammals, 0.44 (0.39–0.48) for snakes and 0.45 (0.41–0.50) for amphibians]. The same qualitative conclusion held when the comparison was done separately for positive and negative changes in local suitability (Fig. S3).

For regional metric calculations we used the values of three times the inter-annual variability of each climatic parameter across sub-Saharan Africa as thresholds to define analogous climates (Fig. S4). Regional metrics showed a decrease in area

available for most conditions across the study region, with the exception of a narrow strip from West Africa to the Ethiopian Highlands where the prevailing climatic conditions were projected to expand in an area over sub-Saharan Africa (Fig. 2c). These expanding climatic conditions were characterized by high temperatures of the coldest and warmest months across the study area (Fig. S5a, b). The projections from the bioclimatic envelope models built for the four taxonomic groups showed greater losses than gains of climatic suitability between the baseline and future periods (Fig. S2). Median losses of climatically suitable areas across species were greater in southern Africa and the eastern African mountains. By contrast, species in West Africa and the Sahel were projected, on average, to gain higher percentages of their baseline climatically suitable areas and undergo larger displacements of such areas.

For all taxonomic groups, the median percentages of climatically suitable area lost were higher for species occurring in shrinking climates than for species occurring in expanding climates [Fig. 2d; Wilcoxon signed rank-test, P -values < 0.05 ; Cliff's delta (confidence interval), 0.49 (0.41–0.57) for birds, 0.45 (0.37–0.53) for mammals, 0.41 (0.33–0.48) for snakes and 0.45 (0.38–0.51) for amphibians]. By contrast, median percentages of suitable climate area gained, according to the bioclimatic envelope models, were higher for species in areas of expanding climates [Fig. 2e; Wilcoxon signed rank-test, P -values < 0.05 ; Cliff's delta (confidence interval), 0.27 (0.21–0.33) for birds, 0.39 (0.32–0.45) for mammals, 0.47 (0.41–0.53) for snakes and 0.55 (0.48–0.62) for amphibians].

Regional metrics of change in the position of climates generally revealed a tendency for increased distances between similar climatic conditions (Fig. 2f). By contrast, for the montane areas of Ethiopia, eastern African and South Africa the distances to similarly colder conditions were projected to decrease (Fig. S5c, d), which could be a consequence of the disappearance of such conditions in distant cells. In these montane areas, the median distances that the models projected the climatically suitable areas to shift were significantly smaller than the median distances in the remaining areas [Fig. 2g; Wilcoxon signed rank-test, P -values < 0.05 ; Cliff's delta (confidence interval), 0.26 (0.19–0.33) for birds, 0.26 (0.18–0.33) for mammals, 0.35 (0.28–0.42) for snakes and 0.35 (0.28–0.41) for amphibians].

The correspondence between the two approaches investigated here for assessing exposure to climate change was stronger for the species across the four taxa with more specialized climatic envelopes (Fig. 3). For all comparative tests involving local and regional metrics, Cliff's delta values were higher (positive) for the group of species with wider climatic breadth.

DISCUSSION

A critical first step towards understanding the potential consequences of 21st-century climates for biodiversity is to assess the exposure of species or areas to future climatic changes. Bioclimatic envelope models are well suited for assessing the potential exposure of species to climatic changes (Dawson *et al.*, 2011; Moritz & Agudo, 2013), whereas climate change metrics

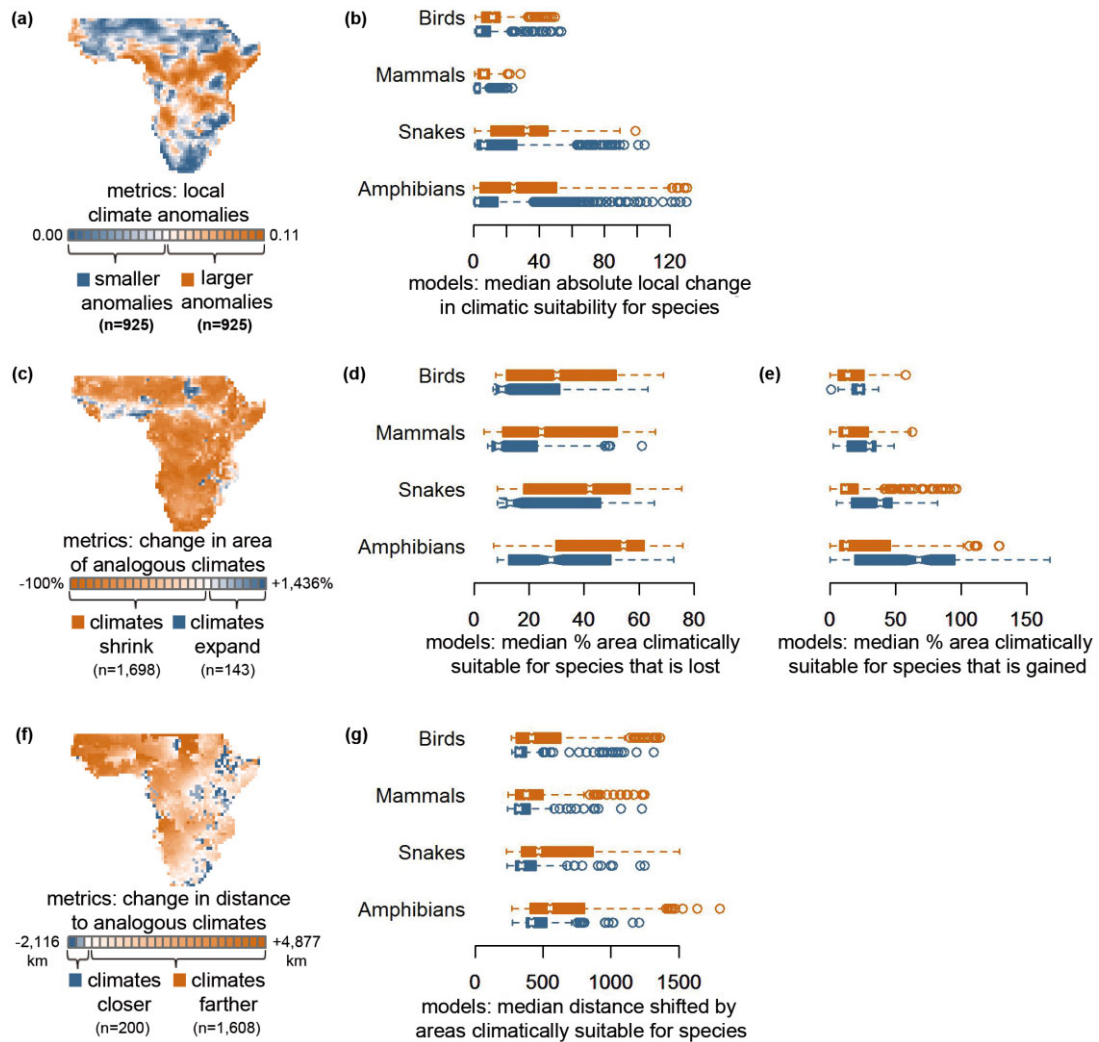


Figure 2 Comparison of projected changes in climatic suitability for species between areas exposed to different levels of climate change. Temporal changes in climatic suitability for sub-Saharan African amphibians ($n = 284$), snakes ($n = 310$), mammals ($n = 623$) and birds ($n = 1506$), from bioclimatic envelope models, were compared between groups of 1° grid cells with different levels of climate change as measured with climate change metrics (see Fig. 1 for details on the comparisons performed). For metric-based local climatic changes, or local anomalies, occurring at each locality over time (grid cell level, a), grid cells were grouped into small changes (below the median across all cells) and large changes (above the median). The model-based median absolute changes in local (cell) climatic suitability across all species present in each cell were then compared between areas of small (for each taxonomic group, bottom bars) and large (top bars) metric-based local climatic changes (b). Metric-based projected changes over time in the available area of climates analogous to a given cell's climate (c) were grouped into shrinking (area decreases) or expanding (area increases) climates. The proportion of areas climatically suitable for each species that was projected by the bioclimatic envelope models to be lost (d) or gained (e) was then averaged across all species present in each cell, and compared between areas of expanding (bottom bars) and shrinking (top bars) climates. Metric-based projected changes in distance to climates analogous to a given cell's climate (f) were grouped into areas where analogous climates were projected to move farther away and closer in the future. The distance shifted by each species' climatically suitable areas over time, according to the models, was then averaged across all species present in each cell and compared between areas with climates moving farther away (top bars) and closer (bottom bars) (g). The maps were drawn using quantile classification.

can help to quantify the potential exposure of geographical areas and assess the implications for species occurring in those areas (Ohlemüller, 2011; Garcia *et al.*, 2014b). In our study, bioclimatic envelope models for sub-Saharan African vertebrates qualitatively matched climate change metrics (Fig. 2). That is, grid cells with greater climate anomalies, as described by the metrics, had greater changes in climate suitability for species,

as projected by the models. In turn, larger changes in the area or position of analogous climates were indicative of larger changes in the size or position, respectively, of climatically suitable areas for species as projected by the models.

Congruence between projections of bioclimatic envelope models and climate change metrics is consistent with the view that metrics are useful for assessing the exposure of biodiversity

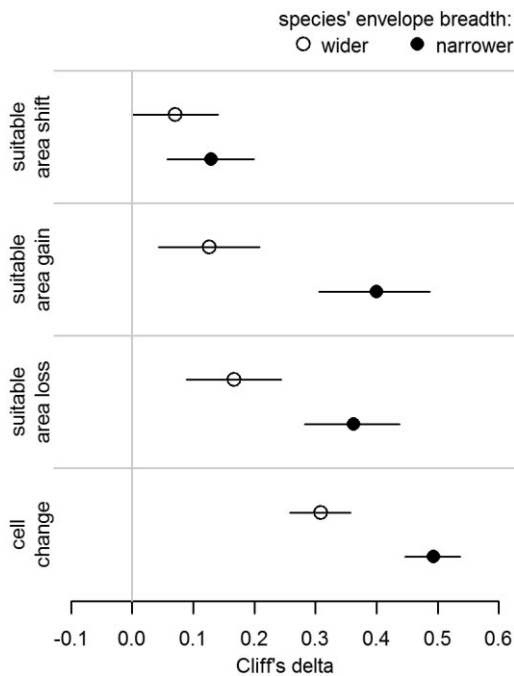


Figure 3 Comparison between bioclimatic envelope models and climate change metrics for groups of species with different climatic breadth. For sub-Saharan African vertebrates ($n = 2723$), changes in areas of climatic suitability for species, projected by bioclimatic models, were compared between areas exposed to different levels of climate change, as measured by climate change metrics. The effect size estimations using Cliff's delta are shown here for the comparative tests performed for two groups of species individually: species with wider and narrower climatic breadth (open and closed circles, respectively). For each species group, median absolute changes in local (cell) climatic suitability for species were compared between areas of large and small local anomalies; median projected losses and gains of climatically suitable areas across species were compared between areas of shrinking and expanding climates; and median projected shifts of climatically suitable areas were compared between areas with climates moving farther versus closer. Lines to the left and right of the circles indicate the lower and upper confidence intervals of the calculated Cliff's delta.

to climatic changes. Interpreting metric outputs as indicators of climatic threats and opportunities for species requires some of the same working assumptions that underpin bioclimatic envelope models. It needs to be assumed that the selected climate variables and their spatial and temporal scales are relevant for species, and that the region of study contains the full range of suitable conditions for species (Peterson *et al.*, 2011; Anderson, 2013). Here, the same spatial resolution, climate variables and dispersal assumptions used in the bioclimatic models (Garcia *et al.*, 2012) were applied in our calculation of the metrics to ensure comparability of results. The ecological interpretation of the outputs of each approach, and the results of our comparison between the two approaches, might, however, be sensitive to these choices. Firstly, our 1° grid overlooks the microclimatic drivers of species distributions. Only finer-scale resolutions would ensure that the models capture the

microclimatic drivers of species distributions and that the metrics account for the spatial heterogeneity of climate.

Secondly, the choice of climatic variables can affect the comparison of the two approaches, particularly when there is divergence between the variables with highest importance in the models and those showing the greatest relative change over time in the (multivariate) metrics. Although the variables used have previously been shown to explain the distributions of vertebrates in sub-Saharan Africa (e.g. Thuiller *et al.*, 2006; Botts *et al.*, 2013; Beale *et al.*, 2013), small sets of variables might only explain coarse differences in climate and in climatic suitability for species across space, whereas larger sets can capture finer differences across space. A larger set could include variables deemed biologically relevant for African vertebrates, such as precipitation seasonality and the ratio of actual to potential evapotranspiration (e.g. Huntley *et al.*, 2006; Botts *et al.*, 2012), but potentially at the expense of increased risk of over-fitting for species with insufficient records (Fielding & Bell, 1997) and thus a reduced ability of models to transfer to future climates (Peterson *et al.*, 2011). The choice of variables would also be likely to differ across the four taxonomic groups.

Thirdly, the four taxonomic groups are differently sensitive to our full dispersal assumption considered in both the models and the metrics. Dispersal limits for different species or groups of species could be accounted for in the models by restricting projected gains of climatically suitable areas within such limits, and in the metrics by restricting the search of analogous climates to a radius around each cell defined by the same limits.

At the same time, the reliance of climate change metrics on climate data alone, independently of information on the biogeography of species ranges, limits their interpretation in two ways. First, climate change metrics disregard any information about the bioclimatic envelopes of individual species. In a given cell, the same changes in climate can result in lost (or gained) climatic suitability for a species with a narrow climatic envelope, while they may enable another species with more generalist climatic preferences to remain within (or outside) its bioclimatic envelope. Likewise, reduced availability of given climatic conditions across a region poses a greater threat to species that depend exclusively on such conditions than to species that inhabit a broader variety of climatic conditions. These differences may explain why we found a better match between models and metrics for species with narrower bioclimatic envelopes (Fig. 3), although alternative explanations may rest on the poorer model performance that is typical for species with wide geographical (and likely climatic) ranges (Stockwell & Peterson, 2002; Segurado & Araújo, 2004; see Fig. S6). By the same token, lower levels of agreement might exist for species that are highly dependent on non-climatic factors, or whose modelled distributions are determined primarily by a subset of the variables used. Our results show that models and metrics match for assemblages of species at coarse resolutions, but the level of agreement between the two approaches may differ for individual species depending on their characteristics.

Second, in disregarding information about the geographical ranges of species, climate change metrics are blind to associated

measures of species richness or complementarity. That is, they identify areas where climate-induced threats are expected to be greatest, irrespective of the conservation importance of those areas (e.g. Watson *et al.*, 2013). One possible way of including such information is to overlay climate change metric outputs with layers of species richness (e.g. Ohlemüller *et al.*, 2008) or protected areas (e.g. Loarie *et al.*, 2009; Gillson *et al.*, 2013), or to restrict the computation of metrics to areas of conservation importance (e.g. Beaumont *et al.*, 2010; Wiens *et al.*, 2010). By contrast, bioclimatic envelope models add precision to priority setting in that they also consider the numbers or the irreplaceability of affected species (e.g. Williams *et al.*, 2005; Kujala *et al.*, 2013; Alagador *et al.*, 2014).

Importantly, climate change metrics can be applied when and where limited knowledge of biodiversity exists, thereby broadening the scope of exposure assessments to species that are known, poorly known or even unknown. Familiar applications of bioclimatic envelope models exclude species with small sample sizes due to the statistical limitations of the models (e.g. Stockwell & Peterson, 2002). Most assessments of the effects of climate change relying on such models are thus biased against narrow-ranging species. Such bias is particularly acute in the tropics (Feeley & Silman, 2011), and has potential consequences for conservation priority setting under climate change (Platts *et al.*, 2014). Climate change metrics can be applied by examining the patterns of change according to multiple metrics, and identifying the most important dimensions of change. The potential implications for biodiversity can then be assessed by relying on the association between different metrics and different threats and opportunities for species, based on both empirical evidence and ecological theory (Garcia *et al.*, 2014b).

Appreciating the full array of dimensions of climate change captured by available metrics can also help to make assessments of the impact of climate change more complete. In this study, we considered the three climate change metrics that are most closely associated with the bioclimatic envelope models used, capturing local changes in average climates and regional changes in the area and position of analogous climates. However, other metrics such as local changes in climate extremes or variability, the timing of specific climate events and the velocity at which climates are displaced over the local topography could be equally important (for a critical review see Garcia *et al.*, 2014b). Another example is that of local anomalies standardized by inter-annual variability, highlighting the importance of local changes in areas of low historical variability such as the tropics (Williams *et al.*, 2007). These and other dimensions of change can be integrated into bioclimatic envelope models (e.g. Zimmermann *et al.*, 2009; Altwegg *et al.*, 2012) or complement model-based assessments. Undoubtedly, the field of climate change ecology can only advance with the integration of multiple approaches and tools.

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REFERENCES

- Ackerly, D.D., Loarie, S.R., Cornwell, W.K., Weiss, S.B., Hamilton, H., Branciforte, R. & Kraft, N.J.B. (2010) The geography of climate change: implications for conservation biogeography. *Diversity and Distributions*, **16**, 476–487.
- Alagador, D., Cerdeira, J.O. & Araújo, M.B. (2014) Shifting protected areas: scheduling spatial priorities under climate change. *Journal of Applied Ecology*, **51**, 703–713.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., (Ted), Gonzalez, P., Fensham, R., Zhangm, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **210**, 660–684.
- Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, **43**, 1223–1232.
- Altwegg, R., Broms, K., Erni, B., Barnard, P., Midgley, G.F. & Underhill, L.G. (2012) Novel methods reveal shifts in migration phenology of barn swallows in South Africa. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 1485–1490.
- Anderson, R.P. (2013) A framework for using niche models to estimate impacts of climate change on species distributions. *Annals of the New York Academy of Sciences*, **1297**, 8–28.
- Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*, **93**, 1527–1539.
- Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005) Validation of species–climate impact models under climate change. *Global Change Biology*, **11**, 1504–1513.
- Araújo, M.B., Nogués-Bravo, D., Diniz-Filho, J.A.F., Haywood, A.M., Valdes, P.J. & Rahbek, C. (2008) Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, **31**, 8–15.
- Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D. & Thuiller, W. (2011) Climate change threatens European conservation areas. *Ecology Letters*, **14**, 484–492.
- Beale, C.M., Baker, N.E., Brewer, M.J. & Lennon, J.J. (2013) Protected area networks and savannah bird biodiversity in the face of climate change and land degradation. *Ecology Letters*, **16**, 1061–1068.

- Beaumont, L.J., Pitman, A., Perkins, S., Zimmermann, N.E. & Yoccoz, N.G. (2010) Impacts of climate change on the world's most exceptional ecoregions. *Proceedings of the National Academy of Sciences USA*, **108**, 2306–2311.
- Botts, E.A., Erasmus, B.F.N. & Alexander, G.J. (2013) Small range size and narrow niche breadth predict range contractions in South African frogs. *Global Ecology and Biogeography*, **22**, 567–576.
- Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology and Evolution*, **23**, 453–460.
- Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.
- Clarke, K.R. & Warwick, R.M. (1994) Similarity-based testing for community pattern: the two-way layout with no replication. *Marine Biology*, **118**, 167–176.
- Cliff, N. (1993) Dominance statistics – ordinal analyses to answer ordinal questions. *Psychological Bulletin*, **114**, 494–509.
- Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C. & Mace, G.M. (2011) Beyond predictions: biodiversity conservation in a changing climate. *Science*, **332**, 53–58.
- Dolédec, S., Chesse, D. & Gimaret-Carpentier, C. (2000) Niche separation in community analysis: a new method. *Ecology*, **81**, 2914–2927.
- Feeley, K.J. & Silman, M.R. (2011) The data void in modeling current and future distributions of tropical species. *Global Change Biology*, **17**, 626–630.
- Fielding, A. & Bell, J. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.
- Foden, W., Midgley, G.F., Hughes, G., Bond, W.J., Thuiller, W., Hoffman, M.T., Kalembe, P., Underhill, L.G., Rebelo, A. & Hannah, L. (2007) A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags. *Diversity and Distributions*, **13**, 645–653.
- Garcia, R.A., Burgess, N.D., Cabeza, M., Rahbek, C. & Araújo, M.B. (2012) Exploring consensus in 21st century projections of climatically suitable areas for African vertebrates. *Global Change Biology*, **18**, 1253–1269.
- Garcia, R.A., Araújo, M.B., Burgess, N.D., Foden, W.B., Gutsche, A., Rahbek, C. & Cabeza, M. (2014a) Matching species traits to projected threats and opportunities from climate change. *Journal of Biogeography*, **41**, 724–735.
- Garcia, R.A., Cabeza, M., Rahbek, C. & Araújo, M.B. (2014b) Multiple dimensions of climate change and their implications for biodiversity. *Science*, **244**, 1247579.
- Gillson, L., Dawson, T.P., Jack, S. & McGeoch, M.A. (2013) Accommodating climate change contingencies in conservation strategy. *Trends in Ecology and Evolution*, **28**, 135–142.
- Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Heikkinen, R.K., Luoto, M., Leikola, N., Pöyry, J., Settele, J., Kudrna, O., Marmion, M., Fronzek, S. & Thuiller, W. (2009) Assessing the vulnerability of European butterflies to climate change using multiple criteria. *Biodiversity and Conservation*, **19**, 695–723.
- Hof, C., Araújo, M.B., Jetz, W. & Rahbek, C. (2011) Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*, **480**, 516–519.
- Hortal, J., Diniz-Filho, J.A.F., Bini, L.M., Rodríguez, M.Á., Baselga, A., Nogués-Bravo, D., Rangel, T.F., Hawkins, B.A. & Lobo, J.M. (2011) Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecology Letters*, **14**, 741–748.
- Huntley, B., Collingham, Y.C., Green, R.E., Hilton, G.M., Rahbek, C. & Willis, S.G. (2006) Potential impacts of climatic change upon geographical distributions of birds. *Ibis*, **148**, 8–28.
- IPCC (2013) *Summary for policymakers. Climate change 2013: the physical science basis. Contribution of Working Group I to the fifth assessment report of the Intergovernmental Panel on Climate Change* (ed. by T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley). Cambridge University Press, Cambridge and New York.
- Katz, R.W., Brush, G.S. & Parlange, M.B. (2005) Statistics of extremes: modeling ecological disturbances. *Ecology*, **86**, 1124–1134.
- Kearney, M.R., Wintle, B.A. & Porter, W.P. (2010) Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters*, **3**, 203–213.
- Kujala, H., Moilanen, A., Araújo, M.B. & Cabeza, M. (2013) Conservation planning with uncertain climate change projections. *PLoS ONE*, **8**, e53315.
- Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, **462**, 1052–1055.
- Mann, M.E., Bradley, R.S. & Hughes, M.K. (1998) Global-scale temperature patterns and climate forcing over the past six centuries. *Nature*, **392**, 779–787.
- Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J. & Zhao, Z.-C. (2007) Global climate projections. *Climate change 2007: the physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change* (ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller), pp. 747–845. Cambridge University Press, Cambridge and New York.
- Midgley, G.F., Hannah, L., Millar, D., Thuiller, W. & Booth, A. (2003) Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biological Conservation*, **112**, 87–97.
- Moritz, C. & Agudo, R. (2013) The future of species under climate change: resilience or decline? *Science*, **341**, 504–508.
- New, M., Lister, D., Hulme, M. & Makin, I. (2002) A high-resolution data set of surface climate over global land areas. *Climate Research*, **21**, 1–25.

- Nogués-Bravo, D., Ohlemüller, R., Batra, P. & Araújo, M.B. (2010) Climate predictors of late Quaternary extinctions. *Evolution*, **64**, 2442–2449.
- Ohlemüller, R. (2011) Running out of climate space. *Science*, **334**, 613–614.
- Ohlemüller, R., Gritti, E.S., Sykes, M.T. & Thomas, C.D. (2006) Towards European climate risk surfaces: the extent and distribution of analogous and non-analogous climates 1931–2100. *Global Ecology and Biogeography*, **15**, 395–405.
- Ohlemüller, R., Anderson, B.J., Araújo, M.B., Butchart, S.H.M., Kudrna, O., Ridgely, R.S. & Thomas, C.D. (2008) The coincidence of climatic and species rarity: high risk to small-range species from climate change. *Biology Letters*, **4**, 568–572.
- Peel, M.C., Finlayson, B.L. & McMahon, T.A. (2007) Updated world map of the Köppen–Geiger climate classification. *Hydrology and Earth System Sciences*, **11**, 1633–1644.
- Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. & Araújo, M.B. (2011) *Ecological niches and geographic distributions*. Princeton University Press, Princeton, NJ.
- Platts, P.J., Garcia, R.A., Hof, C., Foden, W., Hansen, L.A., Rahbek, C. & Burgess, N.D. (2014) Conservation implications of omitting narrow-ranging taxa from species distribution models, now and in the future. *Diversity and Distributions*, **20**, 1307–1320.
- Post, E. (2013) *Ecology of climate change. The importance of biotic interactions*. Princeton University Press, Princeton, NJ.
- Segurado, P. & Araújo, M.B. (2004) An evaluation of methods for modelling species distributions. *Journal of Biogeography*, **31**, 1555–1568.
- Stockwell, D.R.B. & Peterson, A.T. (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling*, **148**, 1–13.
- Tabor, K. & Williams, J.W. (2010) Globally downscaled climate projections for assessing the conservation impacts of climate change. *Ecological Applications*, **20**, 554–565.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., De Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Thuiller, W., Broennimann, O., Hughes, G., Alkemade, J.R.M., Midgley, G.F. & Corsi, F. (2006) Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Global Change Biology*, **12**, 424–440.
- Tingley, M.W., Monahan, W.B., Beissinger, S.R. & Moritz, C. (2009) Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences USA*, **106**, 19637–19643.
- Watson, J.E.M., Iwamura, T. & Butt, N. (2013) Mapping vulnerability and conservation adaptation strategies under climate change. *Nature Climate Change*, **3**, 989–994.
- Wiens, J.A., Seavy, N.E. & Jongsomjit, D. (2010) Protected areas in climate space: what will the future bring? *Biological Conservation*, **144**, 2119–2125.
- Williams, J.W., Jackson, S.T. & Kutzbach, J.E. (2007) Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences USA*, **104**, 5738–5742.
- Williams, P., Hannah, L., Anelman, S., Midgley, G., Araújo, M., Hughes, G., Manne, L., Martínez-Meyer, E. & Pearson, R. (2005) Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology*, **19**, 1063–1074.
- Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A. & Langham, G. (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology*, **6**, 2621–2626.
- Zimmermann, N.E., Yoccoz, N.G., Edwards, T.C., Meier, E.S., Thuiller, W., Guisan, A., Schmatz, D.R. & Pearman, P.B. (2009) Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences USA*, **106**, 19723–19728.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Table S1 General circulation models in the ensemble used in the study.

Figure S1 Sensitivity and specificity for the bioclimatic envelope models used in the study.

Figure S2 Projected changes in climatic suitability for sub-Saharan African vertebrate species.

Figure S3 Comparison of projected changes in local climatic suitability for species between areas exposed to different levels of local anomalies.

Figure S4 Selection of optimal threshold to define analogous climates.

Figure S5 Climatic characterisation of sites across classes of projected climatic changes.

Figure S6 Comparison between bioclimatic envelope models and climate change metrics for groups of species with different model sensitivity.

BIOSKETCH

Raquel A. Garcia's research focuses on the impacts of climate change on biodiversity. She is interested in using different data and approaches to explore the biogeographical changes that may result from climate change, particularly in Africa, and to understand the mechanisms behind such changes.

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