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Conservation implications of omitting narrow-ranging taxa from species distribution models, now and in the future

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ABSTRACT

Aim Species distribution modelling (SDM) is commonly used to predict spatial patterns of biodiversity across sets of taxa with sufficient distributional records, while omitting narrow-ranging species due to statistical constraints. We investigate the implications of this dichotomy for conservation priority setting in Africa, now and in the future.

Location Sub-Saharan Africa (excluding islands).

Methods We use multivariate ordination to characterize climatic niches of 733 African amphibians, distinguishing between species eligible for large-scale correlative SDM ($\geq$ 10 records at 1° resolution) and those omitted due to insufficient records. Species distributions are projected under current and future climates using simple niche envelopes. Empirical priorities are derived separately on the eligible and omitted sets and compared with three existing large-scale conservation schemes.

Results Of the 733 amphibian species, 400 have too few records for correlative SDM, including 92% of those threatened with extinction (VU/EN/CR). Omitted species typically occupy topographically complex areas with cooler, wetter and less seasonal climates, which are projected to experience lower rates of climatic change. Priorities derived from omitted species have greater congruence with existing conservation schemes. Under future climate, priorities for eligible species shift towards those for omitted species. Similarly, while omitted species often lose climate space at 1° resolution, persistent populations tend to coincide with existing conservation schemes.

Main conclusions Under current climate, statistical restrictions on SDM systematically downplay important sites for narrow-ranging and threatened species. This issue spans taxonomic groups and is only partially mitigated by modelling at finer scales. Effective biodiversity conservation, now and in the future, relies on our capacity to project geographic determinants of all species, and thus, a wider range of approaches is essential. We conclude, however, that future persistence among narrow- and wide-ranging species alike will be highest within sites already identified for conservation investment and that the focus on these sites ought to be maintained.

Keywords

Africa, amphibians, biodiversity, climate change, conservation priorities, threatened species.

INTRODUCTION

Limited funds for tackling unprecedented rates of biodiversity loss dictate that spatial priorities for conservation must be identified and periodically revised (e.g. Margules & Pressey, 2000; Butchart *et al.*, 2010). In general, biologically rich areas with high irreplaceability, which are also vulnerable to degradation and loss, are given the highest ranks (e.g. Stattersfield *et al.*, 1998; Myers *et al.*, 2000; Wilson *et al.*, 2006). In recent years, the predicted (modelled) impact of climate change on species distributions has become an additional consideration for conservation priority setting (Hannah *et al.*, 2002; Huntley *et al.*, 2006; Dawson *et al.*, 2011).

The collection of biological data is time-consuming and expensive, particularly for rare species (Ahrends *et al.*, 2011). Despite its importance for conservation, such work is chronically underfunded (Balmford & Gaston, 1999; Da Fonseca *et al.*, 2000). In prioritizing sites for conservation, the near-term solution is to project existing distributional data across space and, increasingly, into the future, using environmental correlates (Pressey *et al.*, 2000). Correlative models that predict species distributions under climate change are frequently applied in the scientific literature and are widely cited by conservation planners, who seek to ensure that priorities remain valid under future climates (Williams *et al.*, 2005; Hole *et al.*, 2009; Shoo *et al.*, 2011).

Considerable literature exists on species distribution modelling (SDM), its strengths and limitations (e.g. Wiens *et al.*, 2009; Araújo & Peterson, 2012; Franklin, 2013). For conservation prioritization, perhaps the most fundamental constraint is that, for many SDM methods, only species with adequate numbers of spatially distinct occurrence records can be modelled (Stockwell & Peterson, 2002). In tropical regions, which contain most of the world's biodiversity, species are more often narrow ranging than in temperate zones (Wiens *et al.*, 2006) and even common species' distributions tend to be less well documented (Da Fonseca *et al.*, 2000; Küper *et al.*, 2006; Feeley & Silman, 2011). Consequently, species that have traditionally been used to define conservation priorities are the ones most likely to be omitted from correlative SDM. An important question for conservation planning is whether this omission of narrow-ranging species results in a systematic bias, now or in the future, towards or away from sites prioritized under existing conservation schemes.

We address this question using African amphibians as an exemplar group. Amphibians contain many narrow-ranging and threatened species, but also wide-ranging species more typical of higher latitudes. A further motivation for studying amphibians is the high rates of threat they are predicted to face from climate change, habitat loss and disease, especially in Africa (Sodhi *et al.*, 2008; Hof *et al.*, 2011a; Foden *et al.*, 2013). Comparing species eligible for correlative SDM with those most often omitted due to statistical constraints, we aim to establish whether this dichotomy: (1) restricts SDM to an unrepresentative sample of present-day conditions and/ or exposure to climate change and (2) has potential to undermine or reinforce existing conservation priority schemes, now or in the future. We consider three schemes that have been widely used by international organizations to allocate conservation funds: Conservation International's Hotspots, BirdLife International's Endemic Bird Areas and the World Wildlife Fund's Global 200 set of ecoregions. The extent to which our results generalize across spatial resolutions and taxonomic groups is discussed, and avenues for uniting established conservation prioritization procedures with SDM projections under climate change are identified.

METHODS

Amphibian data

Distributional data were collated for 790 species of amphibian found only on mainland Africa south of the Sahara (Hof *et al.*, 2011a, with database updated to February 2014). The taxonomy of this database was matched to the IUCN list of amphibians for the same region (www.iucnredlist.org, accessed February 2014). The IUCN list includes 747 amphibian species, of which 733 were matched to our database criteria (Table S1 in Supporting Information). The species data are reliable to 1° resolution (111 km at the equator), consistent with most studies of continental-scale biodiversity pattern and prioritization under climate change (e.g. McClean *et al.*, 2005; Huntley *et al.*, 2006; Hole *et al.*, 2009; Garcia *et al.*, 2012).

Each amphibian was allocated to one of two species sets: those that are eligible for correlative SDM at 1° resolution ($N = 333$) and those that are not ($N = 400$), hereafter referred to, respectively, as 'eligible' and 'omitted' amphibians (Fig. 1 and Table S1). We used a ten-record cut-off for the minimum number of records required for SDM. Stricter restrictions have been suggested, such as 50 records in total or ten records per predictor variable in the model (Harrell *et al.*, 1984; Stockwell & Peterson, 2002; Wisz *et al.*, 2008). Depending on the threshold (10–50 records), 33–46% of omitted amphibians would be regarded as 'rare' according to standard definitions in conservation biology (i.e. lower quartile of range sizes within the group; Gaston, 1994). For both species sets, we identified the proportion of species listed as Threatened on The IUCN Red List under different threat categories (Tables S1 and S2).

Climate data

We selected four, weakly collinear (Pearson's $|r| < 0.7$; Dormann *et al.*, 2013), climatic predictor variables, which provide an equal balance between temperature and rainfall and between annual and seasonal conditions: mean annual temperature, annual temperature range, annual rainfall and rainfall seasonality. The latter reflects rainfall contrasts across seasons (R_s) in relation to the total annual rainfall (R_T): $\sum_{s\,=\,1..4} |R_s - R_T/4|/R_T$ (Walsh & Lawler, 1981).
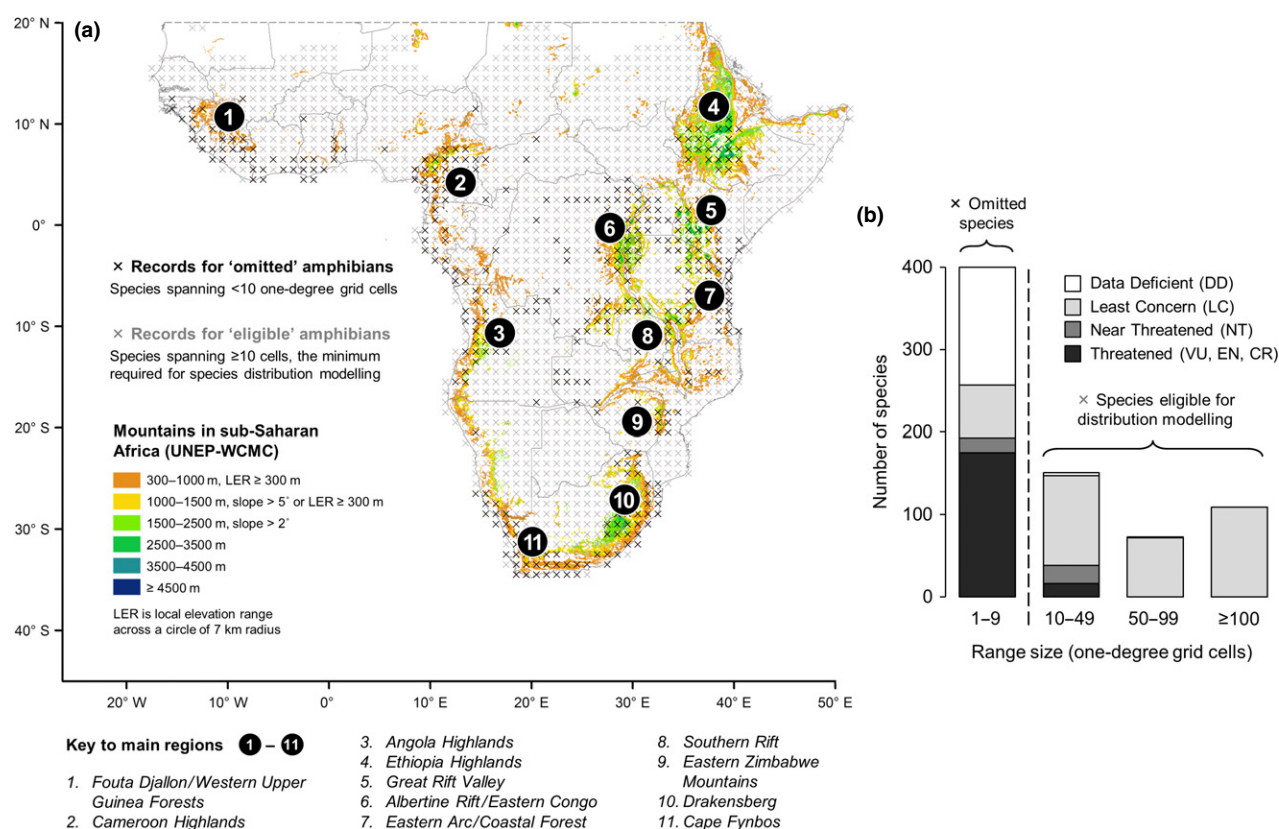
Figure 1 (a) Mountainous areas in mainland Africa south of the Sahara (Kapos *et al.*, 2000), overlaid with the distribution of records for 400 narrow-ranging amphibians (< 10 records at 1° resolution) and 333 more widespread (≥ 10 records) amphibians, the latter being eligible for species distribution modelling, while the former are omitted due to statistical constraints. Stacked bar chart (b) details the number of distinct 1° grid cells known to be occupied by African amphibians, including a breakdown of threat in each range-size category, according to The IUCN Red List (www.iucnredlist.org, accessed February 2014).

Climate grids for the baseline period (1950–2000) were from WorldClim (Hijmans *et al.*, 2005), using mean values to resample from 30″ (1 km) to the 1° resolution of the species data. For future climate (2071–2100), we used a multimodel average over eight CMIP5 GCMs (CanESM2, CNRM-CM5, EC-EARTH, GFDL-ESM2G, HadGEM2-ES, MIROC5, MPI-ESM-LR and NorESM1-M). Each GCM was dynamically downscaled to 0.44° (*c*. 50 km) using the SMHI-RCA4 regional climate model, debiased against WorldClim baselines (Platts *et al.*, 2014) and then resampled to the 1° resolution of the species data. Two representative concentration pathways of the IPCC-AR5 were considered: RCP4.5 and RCP8.5, which here project mean temperature anomalies across sub-Saharan Africa of, respectively, 2.6 °C and 4.5 °C by 2071-2100 relative to the WorldClim baseline.

Niche differences between species

Using multivariate ordination (Outlying Mean Index, OMI; Dolédec *et al.*, 2000), we assessed differences between observed distributions for eligible and omitted species in terms of (1) climatic niche space and (2) projected exposure

to change (future climate anomalies). The OMI identifies ordination axes that optimize separation between species occurrences and quantifies niche position and niche breadth for each species along those axes. Niche position, or marginality, is measured as the deviation of the mean climatic conditions – or future climate anomalies – occupied by a species (its centroid) from the mean conditions/anomalies of the study region (origin of the axes). The larger the deviation, the more marginal the species' niche position is in relation to the study region as a whole. Niche breadth, or tolerance, is quantified as the dispersion of climatic conditions/anomalies occupied by species, with larger dispersion indicating higher tolerance or more variable exposure to change.

Anomalies for temperature variables were computed by subtracting the future from the present values; anomalies for rainfall variables were given by the ratio of future to present values (Fig. S2 in Supporting Information). For each OMI analysis, we performed randomization tests (1000 permutations) to determine whether species' niche positions or exposure to change) differed significantly from random expectations. Calculations were performed in R using the ade4 package (Chessel *et al.*, 2004; R-Core-Team, 2012).

Constructing SDMs without occurrence thresholds

Amphibian distributions were projected in space and time using multidimensional niche envelopes (MDNE). Popular SDM methods, such as maximum entropy and statistical regression, require sufficient occurrence records to parameterise a species' response to, and relative importance of, predictors in a model. The MDNE more simply classifies all conditions within a species' observed climatic range as uniformly viable, and conditions beyond as wholly unsuitable, with all predictors given equal weight (Busby, 1991; Walker & Cocks, 1991). This approach requires no occurrence threshold and so can be applied consistently across the eligible and omitted species sets.

Rather than using mean predictor values at 1° resolution to define the MDNE, we used the lower and upper quartiles of climate conditions within 1° cells, resampled from 30″. This definition reduced the number of type II errors (false negatives) that would otherwise arise from topographic complexity within 1° cells. It also has the advantage of being defined for species having only one record of occurrence, their MDNE being the interquartile range of conditions within the documented 1° cell.

MDNE projections could not be validated directly: by definition, there can be no errors of omission against the 1° training data, while specificity is unknown. We could, however, gauge comparability of MDNE projections for eligible species with those obtained from MAXENT (ver. 3.3.3e; Phillips & Dudik, 2008), using the latter as test data to validate the MDNE results. MAXENT was chosen for its widespread application and favourable performance in comparative studies (e.g. Hernandez *et al.*, 2006). Ten replicates were performed for each eligible species, withholding distinct tenths of the presence data for testing. The final prediction for a given pixel was the mean value over this tenfold cross-validation. Continuous occurrence probabilities were dichotomized into presence–absence maps by maximizing the sum of sensitivity and specificity (Liu *et al.*, 2013).

Future predictions were constrained under a no-dispersal scenario, which is justified by the coarse resolution of the grid (Bateman *et al.*, 2013). Climate change velocities at 1° resolution will likely outpace dispersal capabilities for most African amphibians: to traverse a single pixel, the leading edge of a population would need to migrate 1 km/y, subject to continuous corridors for dispersal and a steady change in climate. Yet, temporal climatic variability and, for all but the most generalist of species, habitat fragmentation are likely to curtail future rates and patterns of range shift relative to the past (Early & Sax, 2011; Hof *et al.*, 2011b; Bennie *et al.*, 2013; Pyron & Wiens, 2013).

Conservation priorities

Grouping predicted distributions by species set (eligible or omitted) and time period (present or future), we derived empirical priority metrics for spatial comparison with three large-scale conservation priority schemes: Biodiversity Hotspots (Conservation International; Mittermeier *et al.*, 2004), Endemic Bird Areas (BirdLife International; Stattersfield *et al.*, 1998) and the Global 200 set of ecoregions (World Wildlife Fund US; Olson & Dinerstein, 1998).

Empirical metrics were chosen to complement these schemes, without confounding the intended comparison between projections based on narrow- versus wide-ranging species (e.g. by explicit inclusion of data on vulnerability and habitat; Margules & Pressey, 2000; Williams *et al.*, 2005; Moilanen *et al.*, 2009). The metrics were: (1) the 100 grid cells with the highest species richness; (2) the 100 grid cells with the highest range-size rarity, defined as the sum of inverse range sizes of all species in a grid cell; and (3) minimum sets of grid cells that represent all species at least once (greedy complementarity). To identify minimum sets, we began with a full set of non-empty cells and reduced it, one cell at a time, until no further reduction was possible without excluding one or more species. The procedure was randomized and repeated 1000 times. The final priority metric was the union over all optimal solutions. Congruence with existing schemes was defined by the number (richness and rarity) or percentage (minimum sets) of empirically prioritized cells that fell within existing schemes.

RESULTS

Degree of (non-climatic) threat

Of the 733 amphibian species, 191 are designated Threatened on The IUCN Red List: 57 (8%) are vulnerable, 96 (13%) are endangered, 37 (5%) are critically endangered, and one was extinct in the wild (*Nectophrynoidesasperginis*, now reintroduced to original locality). Of the remainder, 40 (5%) are designated near threatened and 354 (48%) least concern, while 148 (20%) are data deficient. Because restricted range is one of the criteria for Red Listing species, the degree of threat is highly skewed towards taxa with fewer occurrence records at the 1° model resolution (Fig. 1b). Only 16 of the 191 threatened amphibian species are eligible for correlative SDM, whereas the remaining 175 threatened species, including nearly all of those in the highest threat categories (endangered and critically endangered), are too narrow ranging to model (Tables S1 and S2).

Niche differences between species

Omitted amphibians have been recorded predominantly in tropical highlands (regions 1–9 in Fig. 1a), in grid cells with significantly higher proportions of mountain area (as per Fig. 1a, Wilcoxon signed-rank one-sided, $P < 0.05$) compared with eligible species. Further hotspots for omitted species include the Cape Fynbos and Drakensberg of South Africa (regions 10–11). By contrast, at least one eligible amphibian has been recorded in the majority of grid cells across sub-Saharan mainland Africa (Fig. 1a).

Current conditions

The first two ordination axes of the OMI analysis explained 94% of niche separation between species, with the first axis capturing rainfall gradients and temperature range and the second loaded mainly with mean temperature (Table S3). Eligible and omitted species were found to be significantly different in both their marginality and tolerance (Fig. 2c; Wilcoxon signed-rank one-sided, $P < 0.05$). Whereas eligible species are more ubiquitous on the study area, omitted species occupy climatic conditions that deviate from the average conditions for mainland Africa south of the Sahara (Fig. 2a–b). These marginal environments are characterized by higher annual rainfall with lower seasonality (axis 1) and by cooler temperatures (axis 2). Omitted species also have climatic niches that are narrower than those of eligible species. These patterns hold when the analysis is restricted to species with statistically significant values of marginality (Fig. S1a).

Exposure to change

The OMI analysis on climate anomalies also revealed contrasting patterns between eligible and omitted species (Fig. 2e-i). Under both emission pathways, niche differentiation was explained by anomalies in mean annual temperature and, to a lesser extent, annual temperature range and annual rainfall (axis 1). Axis 2 captured precipitation gradients but with lower loadings. Together, the two axes explained 76–78% of the total variance in species' exposure to climate change, depending on
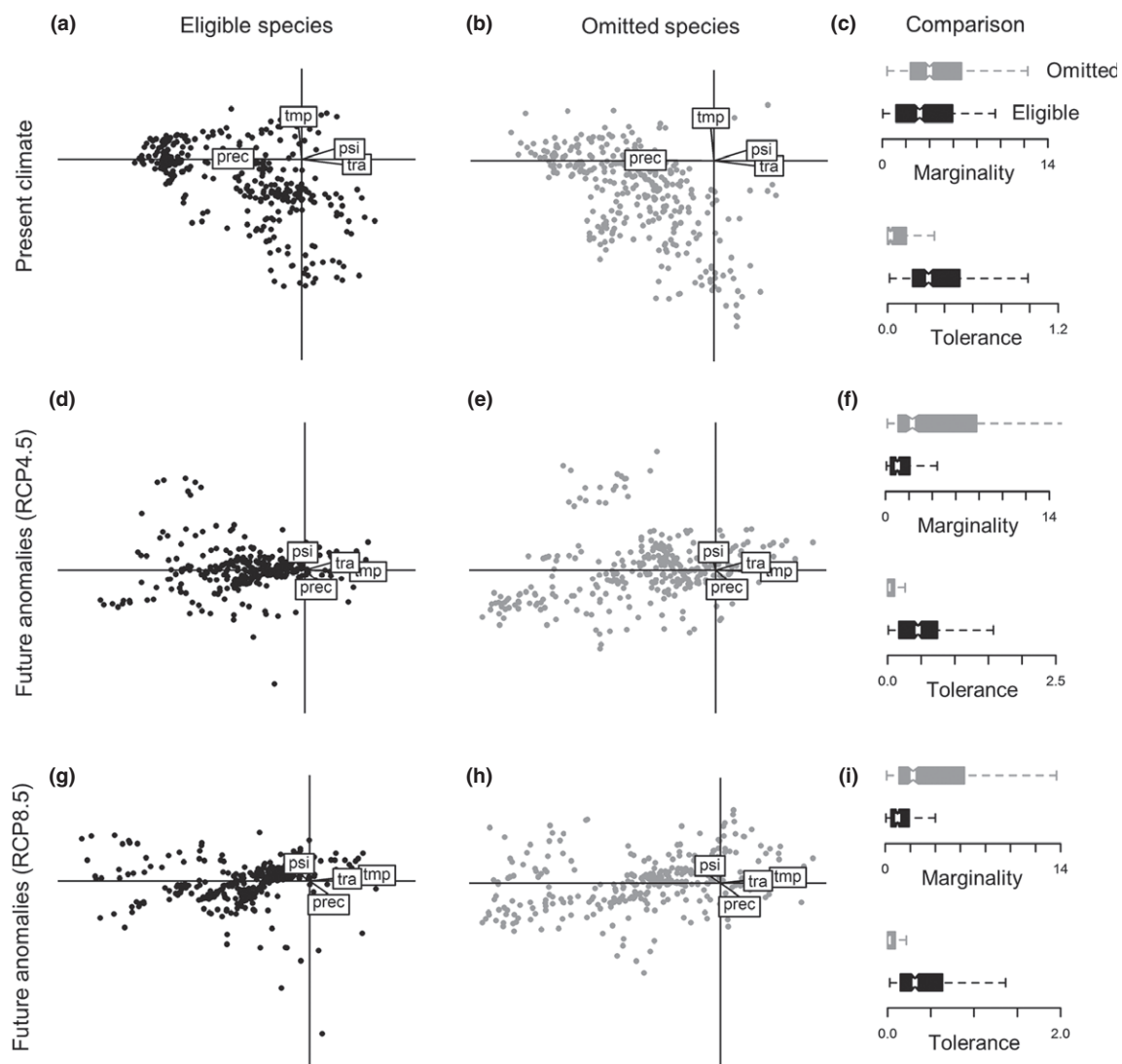
Figure 2 Niche differences between species that are eligible for SDM and the omitted species set. Scatterplots show species centroids in environmental space, represented by the first two ordination axes of the Outlying Mean Index, for present climate (a–b) and for climate anomalies under emission pathways RCP4.5 (d–e) and RCP8.5 (g-h). Boxplots (c, f, i) compare marginality and tolerance for both sets of species. Whiskers extend up to 1.5 times the interquartile range from each box. As indicated by non-overlapping notches, omitted species are significantly more marginal and less tolerant than eligible species (Wilcoxon signed-rank, $P < 0.05$; Fig. S1).

the emission pathway (Table S3). Omitted species were found to be significantly more marginal and less tolerant than eligible species (Fig. 2f,i; Wilcoxon signed-rank one-sided, $P < 0.05$), occupying areas projected to be less exposed to warming (Fig. 2d–e and 2g–h). The same patterns hold when the comparison on both OMI axes is restricted to species with significant marginality (Fig. S1b–c).

Conservation priorities

Model performance

The predictive performance of MAXENT models for eligible species was good, with median cross-validated AUC of 0.95 (interquartile range, IQR: [0.91, 0.97]). At the presence–absence threshold, the median sensitivity was 0.94 [0.91, 0.96] and specificity was 0.91 [0.88, 0.94]. The degree to which MAXENT extrapolated beyond the parameter range of training data was minimal, except for novel high temperatures in the Sahelian zone (Fig. S2). The most important predictor was annual rainfall (median contribution: 36%, IQR: [20, 50]), followed by mean annual temperature (26%, [6, 42]), annual temperature range (23%, [6, 35]) and rainfall seasonality (15%, [5, 19]; Fig. S3).

Using MAXENT predictions as test data, MDNE maps for eligible species had median sensitivity of 0.92 (IQR: [0.78, 0.99]) and median specificity of 0.91 [0.79, 0.97]. For species richness and range-size rarity, MDNE and MAXENT results were highly correlated (Spearman's $\rho = 0.90$ and $\rho = 0.87$; Fig. S4).

Priority metrics for eligible versus omitted species

Under present climate, around a third of priority cells identified by the species richness and range-size rarity metrics were common to both the eligible and omitted species sets (Table 1). Discrepancies were highest in the Ethiopian Highlands, Great Rift Valley, Eastern Arc Mountains and Coastal Forests of East Africa, and in the Cape Fynbos and Drakensberg of South Africa (Fig. 3a–b), which were all largely absent from eligible species' priorities. In the future, priorities for eligible and omitted species converged under both metrics, increasing to 70–81 cells (of a possible 100) for species richness, depending on the emission pathway, and to 55–72 cells for range-size rarity (Table 1).

The current agreement between the minimum set metric for eligible (62 cells) and omitted (195 cells) species was low

(9 cells in common; Table 1). In particular, the Fouta Djallon/Western Upper Guinea Forests, Angola Highlands, Ethiopian Highlands, Eastern Zimbabwe Mountains, Eastern Arc and Coastal Forests were under-represented by the eligible species set (Fig. 3c). In the future, the size of minimum sets reduced for omitted species, due to many narrow-ranging amphibians losing all suitable climate space at the 1° resolution (Fig. 4). Agreement between eligible and omitted species reduced slightly under RCP4.5, but doubled to 18 cells under RCP8.5 (Table 1).

### Comparison with existing conservation schemes

Congruence between empirical priority metrics and existing schemes was generally higher on the omitted species set than on the eligible species set, although this varied depending on the region and metric considered (Fig. 4). For omitted amphibians, 39–70 (richness) and 32–74 (range-size rarity) of prioritized cells coincided with existing schemes, compared with eligible species congruence of 13–50 and 14–46 cells, respectively. Congruence according to minimum sets was more similar for omitted versus eligible species (44–64% vs. 32–71%), suggesting that this metric may be more robust to the omission of narrow-ranging species from priority assessments (Figs. 3 & 4). For both species sets, the degree of congruence with the Global 200 was often higher than with Biodiversity Hotspots, which was higher than with Endemic Bird Areas, due to differences in overall coverage between these schemes (Fig. 4d) and endemism.

Projecting empirical metrics under future climate, congruence with existing schemes reduced in western Africa while generally increasing in eastern and southern Africa. Overall, priorities for eligible species were projected to shift towards existing schemes, due to greater climatic stability at these

Table 1 Number of grid cells common to spatial priority metrics for eligible and omitted amphibians, now and in the future. Eligible species can be modelled using popular methodologies for species distribution modelling (≥ 10 records), while omitted species cannot. Congruence increases in the future, especially under IPCC-AR5 emission pathway RCP8.5

Priority metric	Present (1950–2000)	RCP4.5 (2071–2100)	RCP8.5 (2071–2100)
Species richness	35	70	81
Range-size rarity	33	55	72
Minimum sets	9	6	18

Figure 3 Conservation priorities derived empirically from data on amphibian distributions, separately for species typically omitted from SDM (< 10 records) and those that are eligible (≥ 10 records). Spatial distributions were projected using multidimensional niche envelopes. Future climate was simulated by a regional climate model (eight driving GCMs) under two representative concentration pathways of IPCC-AR5. For species richness (a) and range-size rarity (b), the top 100 scoring cells are selected as priority sites. Minimum sets (c) identify the smallest possible subsets of cells that represent all species at least once; where the solution is not unique, the union across solutions is mapped. Ellipses highlight key sites under-represented on the eligible species set. For a key to regions, see Fig. 1a.
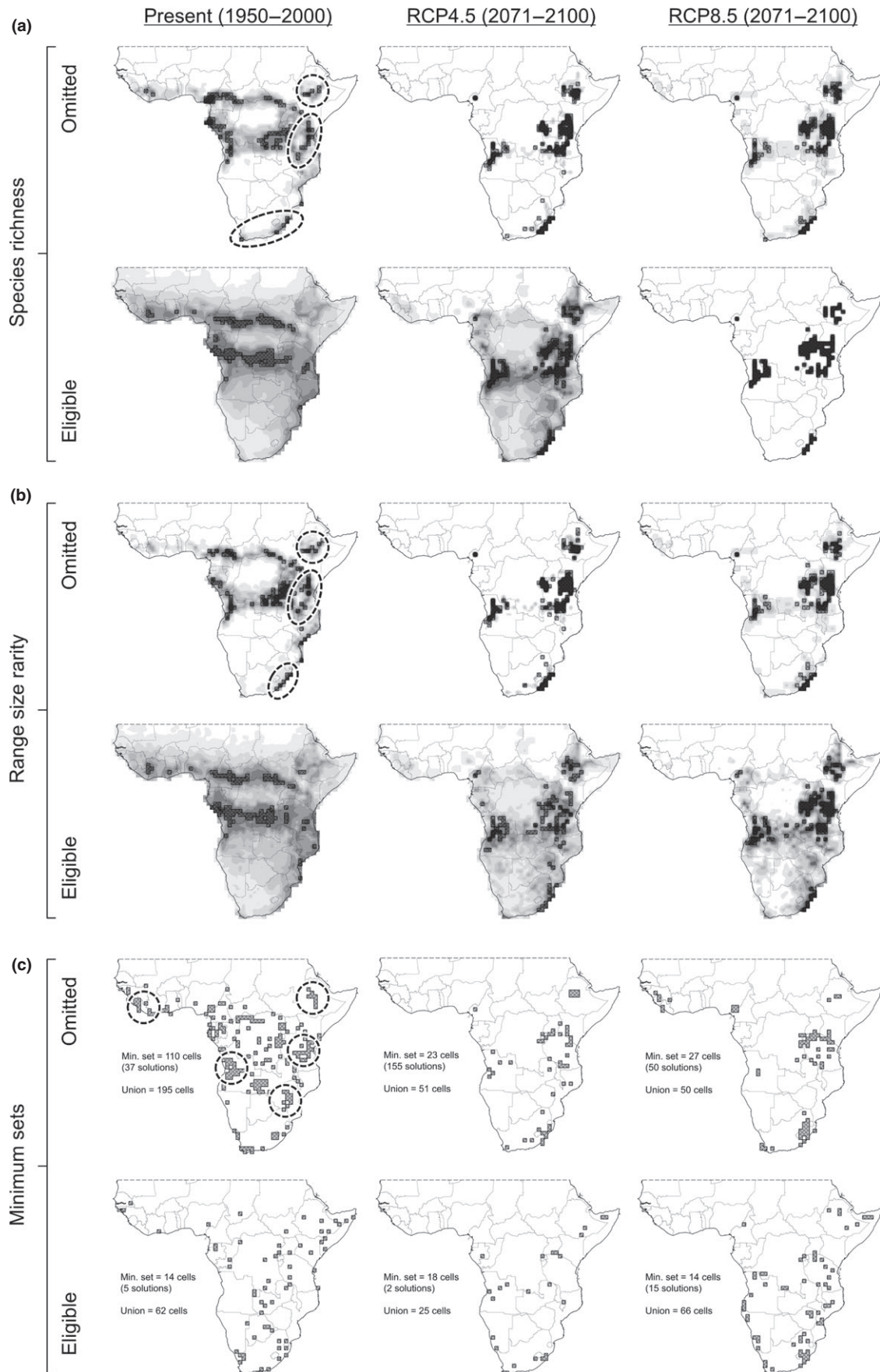
sites (Fig. S2). Similarly, while omitted species frequently lost all climate space at the 1° resolution, persistent populations tended to coincide with existing schemes (Fig. 4).

DISCUSSION

Natural habitats are changing at a rate unprecedented in human history. Faced with finite resources for addressing the decline of global biodiversity, it is necessary to locate priority sites for conservation investment (e.g. Olson & Dinerstein, 1998; Stattersfield *et al.*, 1998; Mittermeier *et al.*, 2004). Without global priorities, resources would be spread too thinly to have any meaningful impact on species conservation (Pimm *et al.*, 2001; Wilson *et al.*, 2006). Large-scale priority schemes, such as Biodiversity Hotspots, Endemic Bird Areas and Global 200 ecoregions, were developed directly from the available data on species occurrence (particularly local endemism) and threats, augmented by expert opinion. More recently, species distribution modelling (SDM) has become an almost ubiquitous technique in the conservation scientist's toolbox, accelerated in popularity by free Internet access to large databases of herbaria and zoological specimens (Graham *et al.*, 2004), digitized environmental data and a latent demand for predictive spatial models, particularly with respect to the impacts of anthropogenic climate change.

From simple envelope approaches, which employ concise rule sets to define species range boundaries (e.g. MDNE as employed here; BIOCLIM, Busby, 1991; HABITAT, Walker & Cocks, 1991; GARP, Stockwell & Peters, 1999), more complex modelling procedures have emerged (e.g. MARS and BRT, Friedman, 1991, 2001; MAXENT, Phillips & Dudik, 2008). Due to their superior capacity to fit the observed species data, housed within user-friendly desktop applications, such advances have been widely advocated (Elith *et al.*, 2006; Franklin, 2010). However, as the authors of these tools are the first to point out, model calibration must be underpinned by sufficient data on a species' distribution to avoid spurious predictions – a prerequisite that is, almost by definition, not fulfilled by many taxa of highest conservation concern, particularly at the coarse spatial resolutions dictated by species and climate data at global or continental scales.

In this study, we have highlighted that over half of the amphibian species in sub-Saharan Africa (excluding islands) have ranges too narrow for large-scale correlative SDM and that these species are disproportionately vulnerable, endangered or critically endangered on The IUCN Red List, with 92% of all such species being ineligible for modelling. This is

to be expected, given that range-size is a criterion in the Red Listing process, but the consequences have rarely been emphasized. Crucially for studies that infer conservation priorities from SDM, we find that the omitted species occupy significantly different niche space to eligible species: their observed distributions are characterized by higher annual rainfall with lower rainfall seasonality, by cooler and less seasonal temperatures and by more complex topography. This is consistent with previous studies (De Klerk *et al.*, 2002; Jetz & Rahbek, 2002; Ohlemüller *et al.*, 2008; Sandel *et al.*, 2011; Pyron & Wiens, 2013), which find that climatically and topographically diverse/distinct areas contain a disproportionate richness of narrow-ranging species.

Our results show that continental-scale correlative SDM is restricted to an unrepresentative sample of both current climate and future climate anomalies, and that this bias is counter to more traditional frameworks for identifying priority sites for conservation, which focus precisely on those taxa most likely to be omitted. Reverting to a simpler form of SDM – multidimensional niche envelopes – we find that conservation priorities derived empirically from the omitted species set generally exhibit higher congruence with existing priority schemes than those inferred from eligible species. In the future, sites occupied by omitted species are projected lower rates of warming. Many such sites, especially in eastern Africa, are projected to become increasingly important for the persistence of omitted and eligible species alike. Similarly at the ecoregion level, Iwamura *et al.* (2013) found that overlap between current and future climate space is highest within known centres of endemism, and Sandel *et al.* (2011) have shown that low climate velocities during the Late Quaternary coincide with contemporary hotspots for narrow-ranging birds, mammals and amphibians. These patterns are consistent with the theory that long-term climatic stability, combined with topographic complexity and geographic isolation, gives rise to, and may continue supporting, high rates of rarity and endemism (Fjeldså *et al.*, 1997; Platts *et al.*, 2013).

The projected future convergence of priority sites for narrow- and wide-ranging amphibians may therefore echo historical processes underlying contemporary biodiversity patterns. The 1° resolution used here is, however, too coarse to capture the variations in local climate, biotic interaction and adaptive potential that are ultimately central to species persistence under climate change (Hof *et al.*, 2010). Trivedi *et al.* (2008) found that coarse resolution models of high-altitude plants in Europe overestimated their thermal tolerance and thus underestimated mountain-top extinction. Conversely, Randin *et al.* (2009) found that topoclimatic refugia were better captured at finer scales, facilitating species

Figure 4 Spatial congruence between empirically derived amphibian priorities and three existing conservation priority schemes in western (a), eastern (b) and southern (c) Africa south of the Sahara, according to the partitions and schemes mapped in (d). Bar heights are the number (richness and rarity metrics) or percentage (minimum sets) of cells that coincide with existing schemes. Bar widths are proportional to the number of species still with suitable climate space by 2071–2100, under two emission pathways of IPCC-AR5. Underlying species distributions were mapped on 1° grids using multidimensional niche envelopes.

(a) Western Africa
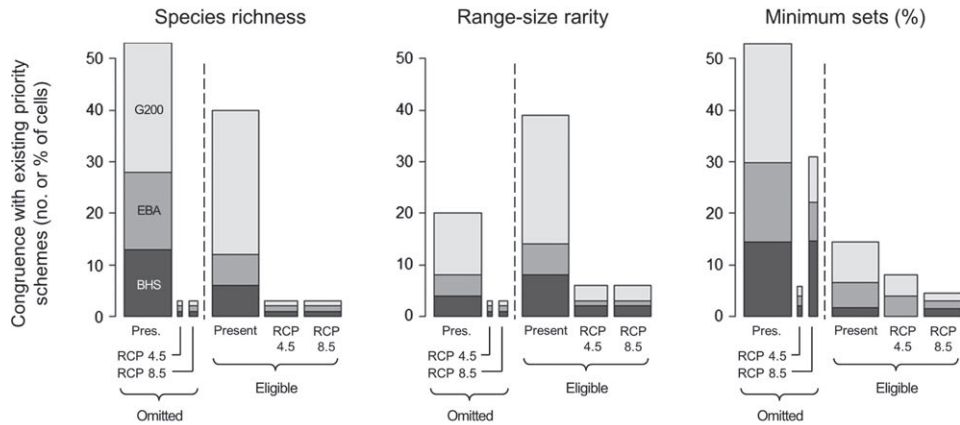
(b) Eastern Africa
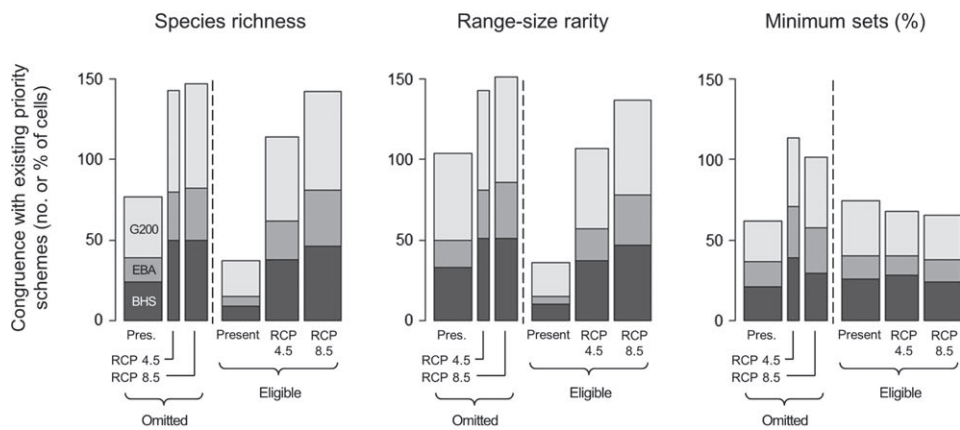
(c) Southern Africa
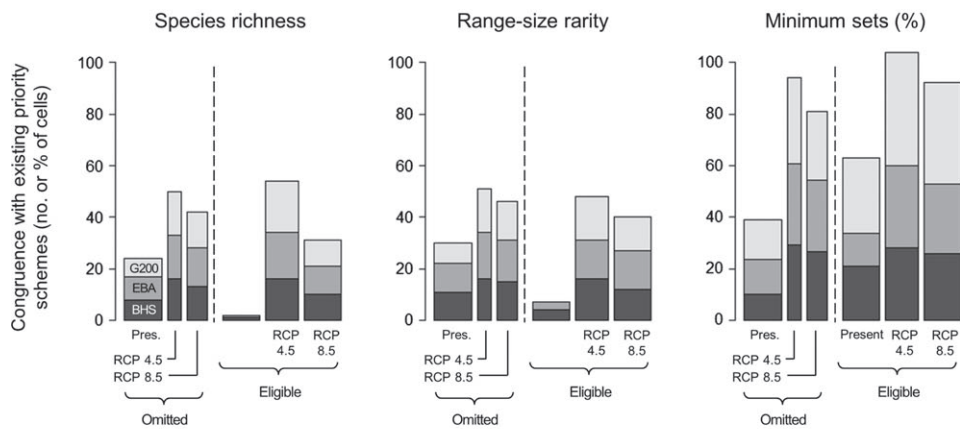
(d) Existing priority schemes
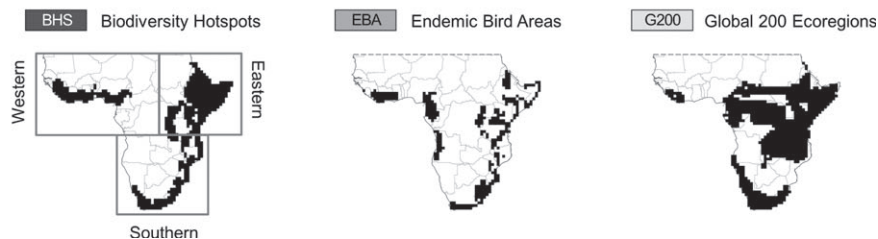
persistence (see also Franklin *et al.*, 2013). Our assumption of no intercell dispersal would need to be revised at finer scales, because narrow isotherms along altitudinal gradients facilitate species ability to track changing climates more locally (Loarie *et al.*, 2009), with the likely effect of further emphasizing the importance of existing, topographically complex, priority sites for conservation.

Most fundamentally for our analysis, a finer grid resolution would disaggregate spatially clustered occurrence records, increasing the proportion of species eligible for correlative SDM, albeit with increased spatial autocorrelation. We suggest that the convergence of conservation priorities for eligible versus omitted species under climate change is unlikely to be scale dependent in this regard, because sites of relative climatic stability would remain so, regardless of the species dichotomy. The effect of spatial scale on present-day, divergent priority metrics for omitted versus eligible species is more uncertain and would depend on how the disaggregation of distributional records varied between the two groups. A further consideration is that parameterizations for particular species models are also scale dependent, because the observed niche is shaped increasingly by non-climatic factors (e.g. biotic interactions, patch dynamics, habitat quality) at finer scales (Pearson & Dawson, 2003).

Our ability to investigate these uncertainties is limited by the fact that much of Earth's biodiversity is poorly documented, both in the quantity and in the quality of distributional records. In Africa, as elsewhere in the tropics, 1° (or at best 0.5°) grids are the operational default for continental-scale SDM, because much of the available species data are not reliably georeferenced at finer resolutions (Graham *et al.*, 2004; Wiens & Bachelet, 2010; Feeley & Silman, 2011). In specific regions where high-resolution species data are available, the issue of threatened species being omitted from modelling procedures remains pervasive. The Eastern Arc Mountains, for example, are among the best-documented sites in Africa (Feeley & Silman, 2011), yet two-thirds of threatened amphibians have fewer than ten records on a 10′ grid (Burgess *et al.*, 2007). Moreover, of the *c.* 500 plant species endemic to the Eastern Arc, none have sufficient herbarium data for correlative SDM on a 1° grid and, even at 30″ resolution, 90% are too narrow ranging to model (Platts *et al.*, 2013), the majority of these species being assessed as either threatened or scheduled for Red List assessment (Gereau *et al.*, 2010).

Novel approaches to address these challenges of spatial scale and narrow ranges, both within and beyond the field of SDM, are emerging. Current knowledge on species distributions can be systematically improved by iterative application of simple models and targeted fieldwork (Williams *et al.*, 2009; Platts *et al.*, 2010). Making the most of small sample sizes, Lomba *et al.* (2010) combine large numbers of bivariate models, built individually using all pairwise combinations of predictors. In contrast to a species-level focus, hierarchical approaches, combining species-specific and community models (Loarie *et al.*, 2008; Ovaskainen & Soininen, 2011), or

spatial modelling of climatically associated (Golicher *et al.*, 2008) or community-level (Ferrier & Guisan, 2006) species pools can help to detect shared patterns of response across narrow-ranging taxa. Simple measures of site exposure to different aspects of climate change, which do not rely on SDM, also provide indications of potential threats and opportunities for species present in such sites (Williams *et al.*, 2007; Ohlemüller *et al.*, 2008; Garcia *et al.*, 2014b).

These methods can be combined with biological trait-based assessments of species sensitivity (ability to cope in situ) and adaptive capacity (ability to escape by dispersal or evolution) to changing climatic conditions (Dawson *et al.*, 2011; Pearson *et al.*, 2014). For example, SDMs are increasingly complemented with trait-based vulnerability assessments (Heikkinen *et al.*, 2009; Garcia *et al.*, 2014a), while the IUCN is using physiological, ecological, genetic and functional characteristics, combined with simple measures of exposure to climate change (e.g. Garcia *et al.*, 2014b), to ascribe new measures of vulnerability to thousands of species for eventual inclusion in the Red List Categories and Criteria (IUCN, 2011; Foden *et al.*, 2013).

Through methods such as these, conservation planners may embrace valuable insights provided by popular SDM methodologies, while addressing their inherent limitations with respect to narrow-ranging species that have traditionally underpinned global allocation of conservation funds. Effective biodiversity conservation relies on our capacity to predict climate change impacts on all species, and not just those that fulfil biologically arbitrary occurrence thresholds required by one tool in the box. Our results suggest, however, that while current priorities can be highly sensitive to the exclusion of narrow-ranging taxa from SDM, likely strongholds for both narrow- and wide-ranging species under projected climate change are consistent with existing priority schemes. We conclude that while methods to tackle the rare species conundrum continue to advance, the focus on conserving habitat connectivity and ecological functioning at these sites ought to be maintained (Ricketts *et al.*, 2005; Hodgson *et al.*, 2009; Iwamura *et al.*, 2013; Pearson *et al.*, 2014).

REFERENCES

Ahrends, A., Rahbek, C., Bulling, M.T., Burgess, N.D., Platts, P.J., Lovett, J.C., Kindemba, V.W., Owen, N., Sallu, A.N., Marshall, A.R., Mhoro, B.E., Fanning, E. & Marchant, R. (2011) Conservation and the botanist effect. *Biological Conservation*, **144**, 131–140.

Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecological Society of America*, **93**, 1527–1539.

Balmford, A. & Gaston, K.J. (1999) Why biodiversity surveys are good value. *Nature*, **398**, 204–205.

Bateman, B.L., Murphy, H.T., Reside, A.E., Mokany, K. & VanDerWal, J. (2013) Appropriateness of full-, partial- and no-dispersal scenarios in climate change impact modelling. *Diversity and Distributions*, **19**, 1224–1234.

Bennie, J., Hodgson, J.A., Lawson, C.R., Holloway, C.T.R., Roy, D.B., Brereton, T., Thomas, C.D. & Wilson, R.J. (2013) Range expansion through fragmented landscapes under a variable climate. *Ecology Letters*, **16**, 921–929.

Burgess, N., Butynski, T., Cordeiro, N., Doggart, N., Fjeldsa, J., Howell, K., Kilahama, F., Loader, S., Lovett, J. & Mbilinyi, B. (2007) The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation*, **134**, 209–231.

Busby, J.R. (1991) BIOCLIM – a bioclimatic analysis and prediction system. *Nature conservation: cost effective biological surveys and data analysis* (ed. by C.R. Margules and M.P. Austin), pp. 64–68. CSIRO, East Melbourne, Vic., Australia.

Butchart, S.H.M., Walpole, M., Collen, B. *et al.* (2010) Global biodiversity: indicators of recent declines. *Science*, **328**, 1164–1168.

Chessel, D., Dufour, A.B. & Thioulouse, J. (2004) The ade4 package-I-One-table methods. *R News*, **4**, 5–10.

Da Fonseca, G.A.B., Balmford, A., Bibby, C., Boitani, L., Corsi, F., Brooks, T., Gascon, C., Olivieri, S., Mittermeier, R.A., Burgess, N., Dinerstein, E., Olson, D., Hannah, L., Lovett, J., Moyer, D., Rahbek, C., Stuart, S. & Williams, P. (2000) . . . following Africa's lead in setting priorities. *Nature*, **405**, 393–394.

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.

De Klerk, H.M., Crowe, T.M., Fjeldså, J. & Burgess, N.D. (2002) Patterns of species richness and narrow endemism of terrestrial bird species in the Afrotropical region. *Journal of Zoology*, **256**, 327–342.

Dolédec, S., Chesse, D. & Gimaret-Carpentier, C. (2000) Niche separation in community analysis: a new method. *Ecology*, **81**, 2914–2927.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36**, 27–46.

Early, R. & Sax, D.F. (2011) Analysis of climate paths reveals potential limitations on species range shifts. *Ecology Letters*, **14**, 1125–1133.

Elith, J., Graham, C.H., Anderson, R.P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.

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.

Ferrier, S. & Guisan, A. (2006) Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology*, **43**, 393–404.

Fjeldså, J., Ehrlich, D., Lambin, E. & Prins, E. (1997) Are biodiversity "hotspots" correlated with current ecoclimatic stability? A pilot study using the NOAA-AVHRR remote sensing data. *Biodiversity and Conservation*, **6**, 401–422.

Foden, W.B., Butchart, S.H.M., Stuart, S.N., Vié, J.-C., Akçakaya, H.R., Angulo, A., DeVantier, L.M., Gutsche, A., Turak, E., Cao, L., Donner, S.D., Katariya, V., Bernard, R., Holland, R.A., Hughes, A.F., O'Hanlon, S.E., Garnett, S.T., Şekercioğlu, Ç.H. & Mace, G.M. (2013) Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS ONE*, **8**, e65427.

Franklin, J. (2010) *Mapping species distributions*. Cambridge University Press, Cambridge, UK.

Franklin, J. (2013) Species distribution models in conservation biogeography: developments and challenges. *Diversity and Distributions*, **19**, 1217–1223.

Franklin, J., Davis, F.W., Ikegami, M., Syphard, A.D., Flint, L.E., Flint, A.L. & Hannah, L. (2013) Modeling plant species distributions under future climates: how fine scale do climate projections need to be? *Global Change Biology*, **19**, 473–483.

Friedman, J.H. (1991) Multivariate adaptive regression splines. *Annals of Statistics*, **19**, 1–67.

Friedman, J.H. (2001) Greedy function approximation: a gradient boosting machine. *Annals of Statistics*, **29**, 1189–1232.

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. & Araujo, M.B. (2014b) Multiple dimensions of climate change and their implications for biodiversity. *Science*, **344**, 1247579.

Gaston, K.J. (1994) *Rarity*. Chapman and Hall, London, UK.

Gereau, R.E., Taylor, C.M., Bodine, S. & Kindeketa, W.J. (2010) *Plant conservation assessment in the Eastern Arc Mountains and coastal forests of Tanzania and Kenya*. Available at: http://www.mobot.org/MOBOT/Research/tanzania/cepf.shtml/ (accessed 1 April 2014).

Golicher, D.J., Cayuela, L., Alkemade, J.R.M., González-Espinosa, M. & Ramírez-Marcial, N. (2008) Applying climatically associated species pools to the modelling of compositional change in tropical montane forests. *Global Ecology and Biogeography*, **17**, 262–273.

Graham, C.H., Ferrier, S., Huettman, F., Moritz, C. & Peterson, A.T. (2004) New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology & Evolution*, **19**, 497–503.

Hannah, L., Midgley, G.F., Lovejoy, T., Bond, W.J., Bush, M., Lovett, J.C., Scott, D. & Woodward, F.I. (2002) Conservation of biodiversity in a changing climate. *Conservation Biology*, **16**, 264–268.

Harrell, F.E., Lee, K.L., Califf, R.M., Pryor, D.B. & Rosati, R.A. (1984) Regression modelling strategies for improved prognostic prediction. *Statistics in Medicine*, **3**, 143–152.

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.

Hernandez, P.A., Graham, C.H., Master, L.L. & Albert, D.L. (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, **29**, 773–785.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hodgson, J.A., Thomas, C.D., Wintle, B.A. & Moilanen, A. (2009) Climate change, connectivity and conservation decision making: back to basics. *Journal of Applied Ecology*, **46**, 964–969.

Hof, C., Rahbek, C. & Araújo, M.B. (2010) Phylogenetic signals in the climatic niches of the world's amphibians. *Ecography*, **33**, 242–250.

Hof, C., Araújo, M.B., Jetz, W. & Rahbek, C. (2011a) Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*, **480**, 516–519.

Hof, C., Levinsky, I., Araújo, M.B. & Rahbek, C. (2011b) Rethinking species' ability to cope with rapid climate change. *Global Change Biology*, **17**, 2987–2990.

Hole, D.G., Willis, S.G., Pain, D.J., Fishpool, L.D., Butchart, S.H.M., Collingham, Y.C., Rahbek, C. & Huntley, B. (2009) Projected impacts of climate change on a continent-wide protected area network. *Ecology Letters*, **12**, 420–431.

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.

IUCN (2011) Guidelines for Using The IUCN Red List Categories and Criteria. Version 9.0. Prepared by the IUCN Standards and Petitions Subcommittee.

Iwamura, T., Guisan, A., Wilson, K.A. & Possingham, H.P. (2013) How robust are global conservation priorities to climate change? *Global Environmental Change*, **23**, 1277–1284.

Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science*, **297**, 1548–1551.

Kapos, V., Rhind, J., Edwards, M., Price, M.F. & Ravilious, C. (2000) Developing a map of the world's mountain forests. *Forests in sustainable mountain development: a state of knowledge report for 2000* (ed. by M.F. Price and N. Butt), pp. 4–9. CAB International, Wallingford.

Küper, W., Sommer, J.H., Lovett, J.C. & Barthlott, W. (2006) Deficiency in African plant distribution data – missing pieces of the puzzle. *Botanical Journal of the Linnean Society*, **150**, 355–368.

Liu, C., White, M. & Newell, G. (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography*, **40**, 778–789.

Loarie, S.R., Carter, B.E., Hayhoe, K., McMahon, S., Moe, R., Knight, C.A. & Ackerly, D.D. (2008) Climate change and the future of California's endemic flora. *PLoS ONE*, **3**, e2502.

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.

Lomba, A., Pellissier, L., Randin, C., Vicente, J., Moreira, F., Honrado, J. & Guisan, A. (2010) Overcoming the rare species modelling paradox: a novel hierarchical framework applied to an Iberian endemic plant. *Biological Conservation*, **143**, 2647–2657.

Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.

McClean, C.J., Lovett, J.C., Küper, W., Hannah, L., Sommer, J.H., Barthlott, W., Termansen, M., Smith, G.F., Tokumine, S. & Taplin, J.R.D. (2005) African plant diversity and climate change. *Annuals of the Missouri Botanical Garden*, **92**, 139–152.

Mittermeier, R.A., Gil, P.R., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J. & da Fonseca, G.A.B. (2004) *Hotspots revisited: Earth's biologically richest and most endangered ecoregions*. CEMEX, Mexico City, Mexico.

Moilanen, A., Wilson, K.A. & Possingham, H.P. (2009) *Spatial conservation prioritization*. Oxford University Press, Oxford.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

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.

Olson, D.M. & Dinerstein, E. (1998) The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conservation Biology*, **12**, 502–515.

Ovaskainen, O. & Soininen, J. (2011) Making more out of sparse data: hierarchical modeling of species communities. *Ecology*, **92**, 289–295.

Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.

Pearson, R.G., Stanton, J.C., Shoemaker, K.T., Aiello-lammens, M.E., Ersts, P.J., Horning, N., Fordham, D.A., Raxworthy, C.J., Ryu, H.Y., Mcnees, J. & Akçakaya, H.R. (2014) Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change*, **4**, 217–221.

Phillips, S.J. & Dudik, M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, **31**, 161–175.

Pimm, S.L., Ayres, M., Balmford, A. *et al.* (2001) Can we defy nature's end? *Science*, **293**, 2207–2208.

Platts, P.J., Ahrends, A., Gereau, R.E., McClean, C.J., Lovett, J.C., Marshall, A.R., Pellikka, P.K.E., Mulligan, M., Fanning, E. & Marchant, R. (2010) Can distribution models help refine inventory-based estimates of conservation priority? A case study in the Eastern Arc forests of Tanzania and Kenya. *Diversity and Distributions*, **16**, 628–642.

Platts, P.J., Gereau, R.E., Burgess, N.D. & Marchant, R. (2013) Spatial heterogeneity of climate change in an Afromontane centre of endemism. *Ecography*, **36**, 518–530.

Platts, P.J., Omeny, P.A. & Marchant, R. (2014) AFRICLIM: high-resolution climate projections for ecological applications in Africa. *African Journal of Ecology*. doi:10.1111/aje. 12180

Pressey, R.L., Hager, T.C., Ryan, K.M., Schwarz, J., Wall, S., Ferrier, S. & Creaser, P.M. (2000) Using abiotic data for conservation assessments over extensive regions: quantitative methods applied across New South Wales, Australia. *Biological Conservation*, **96**, 55–82.

Pyron, R.A. & Wiens, J.J. (2013) Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. *Proceedings of the Royal Society B*, **280**, 1471–2954.

Randin, C.F., Engler, R., Normand, S., Zappa, M., Zimmermann, N.E., Pearman, P.B., Vittoz, P., Thuiller, W. & Guisan, A. (2009) Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology*, **15**, 1557–1569.

R-Core-Team (2012) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. Available at: http://www.r-project.org/ (version 3.0.2).

Ricketts, T.H., Dinerstein, E., Boucher, T. *et al.* (2005) Pinpointing and preventing imminent extinctions. *Proceedings of the National Academy of Sciences USA*, **102**, 18497–18501.

Sandel, B., Arge, L., Dalsgaard, B., Davies, R.G., Gaston, K.J., Sutherland, W.J. & Svenning, J.-C. (2011) The influence of late quaternary climate-change velocity on species endemism. *Science*, **334**, 660–664.

Shoo, L.P., Storlie, C., Vanderwal, J., Little, J. & Williams, S.E. (2011) Targeted protection and restoration to conserve tropical biodiversity in a warming world. *Global Change Biology*, **17**, 186–193.

Sodhi, N.S., Bickford, D., Diesmos, A.C., Lee, T.M., Koh, L.P., Brook, B.W., Sekercioglu, C.H. & Bradshaw, C.J.A. (2008) Measuring the meltdown: drivers of global amphibian extinction and decline. *PLoS ONE*, **3**, e1636.

Stattersfield, A., Crosby, M.J., Long, A.J. & Wege, D.C. (1998) *Endemic Bird Areas of the world: priorities for biodiversity conservation*. BirdLife International, Cambridge, UK.

Stockwell, D. & Peters, D. (1999) The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographical Information Science*, **13**, 143–158.

Stockwell, D.R. & Peterson, A.T. (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling*, **148**, 1–13.

Trivedi, M.R., Berry, P.M., Morecroft, M.D. & Dawson, T.P. (2008) Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. *Global Change Biology*, **14**, 1089–1103.

Walker, P.A. & Cocks, K.D. (1991) HABITAT – a procedure for modeling a disjoint environmental envelope for a plant or animal species. *Global Ecology and Biogeography Letters*, **1**, 108–118.

Walsh, R.P.D. & Lawler, D.M. (1981) Rainfall seasonality: description, spatial patterns and change through time. *Weather*, **36**, 201–208.

Wiens, J.A. & Bachelet, D. (2010) Matching the multiple scales of conservation with the multiple scales of climate change. *Conservation Biology*, **24**, 51–62.

Wiens, J.J., Graham, C.H., Moen, D.S., Smith, S.A. & Reeder, T.W. (2006) Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. *The American Naturalist*, **168**, 579–596.

Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A. & Snyder, M.A. (2009) Niches, models, and climate change: assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences USA*, **106**(Suppl), 19729–19736.

Williams, P., Hannah, L., Andelman, S., Midgley, G., Araújo, M., Hughes, G., Manne, L., Martinez-Meyer, E. & Pearson, R. (2005) Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology*, **19**, 1063–1074.

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, J.N., Seo, C., Thorne, J., Nelson, J.K., Erwin, S., O'Brien, J.M. & Schwartz, M.W. (2009) Using species distribution models to predict new occurrences for rare plants. *Diversity and Distributions*, **15**, 565–576.

Wilson, K.A., McBride, M.F., Bode, M. & Possingham, H.P. (2006) Prioritizing global conservation efforts. *Nature*, **440**, 337–340.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H. & Guisan, A. (2008) Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, **14**, 763–773.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Comparison of Outlying Mean Index results for eligible versus omitted species.

Figure S2 Future climate anomalies and novel climates.

Figure S3 Variable contributions in MAXENT models.

Figure S4 Estimates of species richness and range-size rarity based on the eligible species set, compared for MAXENT predictions versus multidimensional niche envelopes.

Table S1 African amphibians included in the study, including range size and Red List status.

Table S2 Summary of IUCN Red List status for all amphibian species included in the study, detailed separately for eligible and omitted species.

Table S3 Environmental variable loadings and variance explained by the two-first axes of the Outlying Mean Index Analysis, on present-day climate and on future climate anomalies.

BIOSKETCH

Philip J. Platts is a Research Fellow at the University of York, UK. His recent work has focused on mountain forests in eastern Africa, their biological importance and the ecosystem services they provide.

Author contributions: N.D.B. and C.H. conceived the idea; P.J.P. and R.A.G. designed and implemented the analyses; L.H. and W.F. worked on the amphibian database; P.J.P., R.A.G. and N.D.B. led the writing; and all authors interpreted the results and commented on the text.

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