

Macroecological conclusions based on IUCN expert maps: A call for caution

K. Matthias B. Herkt^{1,2}  | Andrew K. Skidmore² | Jakob Fahr^{1,3,4} 

¹Institute of Evolutionary Ecology and Conservation Genomics, University of Ulm, Albert-Einstein-Allee 11, Ulm, 89069, Germany

²Faculty of Geo-Information Science and Earth Observation, University of Twente, PO Box 217, Enschede, 7500 AE, The Netherlands

³Department of Migration and Immunology, Max Planck Institute for Ornithology, Am Obstberg 1, Radolfzell, 78315, Germany

⁴Zoological Institute, TU Braunschweig, MendelssohnstraÙ 4, Braunschweig, 38106, Germany

Correspondence

K. Matthias B. Herkt, Institute of Evolutionary Ecology and Conservation Genomics, University of Ulm, Albert-Einstein-Allee 11, Ulm, 89069, Germany. Email: matthias.herkt@gmail.com
Jakob Fahr, Department of Migration and Immunology, Max Planck Institute for Ornithology, Am Obstberg 1, Radolfzell, 78315, Germany. Email: jakob.fahr@gmail.com

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Abstract

Aim: International Union for Conservation of Nature (IUCN) expert maps are increasingly used in macroecological research. However, they have not been produced for this purpose. Macroecological insights based exclusively on this type of data could therefore be misleading. Here we compare, for a large taxonomic group (bats) and an entire biogeographical realm (Africa), the species-specific discrepancies between IUCN maps and species distribution models (SDMs) that approximate the complete geographical range of species. We then examine the implications for a typical macroecological analysis that explores environmental correlates of species richness.

Location: Continental Africa.

Time period: Around 2000.

Taxa: Bats (Chiroptera).

Methods: We measure disagreement between IUCN expert maps and SDMs at both the species (geographical ranges) and the aggregated level (range size–frequency distributions and species richness). We further quantify the difference in absolute and relative weight assigned to three variables hypothesized to drive species richness: primary productivity, climatic seasonality and environmental heterogeneity.

Results: Location, shape and size of individual species' ranges, derived richness patterns and range size–frequency distributions differ substantially. SDMs predict larger and more complex geographical ranges, and species' range sizes vary less. The spatial congruence of richness hotspots among both datasets is only 42%. These discrepancies are large enough to alter the absolute explanatory power of environmental correlates, whereas the redundancy in the variation explained increases markedly when richness is inferred using SDM-based estimates of complete species ranges.

Main conclusions: IUCN expert maps differ considerably and systematically from SDMs built to estimate complete species ranges, primarily because of their intentional greater sensitivity to geographical sampling bias. This property is desirable in a conservation context but unwanted in most macroecological analyses. We therefore caution against the use of IUCN expert maps in macroecology and recommend at least gauging the robustness of results using additional range estimates designed to approximate the complete geographical range of species.

KEYWORDS

Africa, bats (Chiroptera), environmental drivers, extent of occurrence, geographical range, IUCN expert maps, macroecology, species distribution models, species richness, Wallacean shortfall

1 | INTRODUCTION

Macroecology aims to identify biotic patterns extending across large geographical, temporal and phylogenetic extents and to understand the underlying processes that determine large-scale assemblage characteristics (Beck et al., 2012; Brown & Maurer, 1989). Key variables of interest are species diversity patterns and geographical range properties. To investigate these phenomena, accurate estimates of the complete geographical range of species are a fundamental requirement. Unfortunately, despite two centuries of sampling biodiversity around the globe, occurrence data for most known species are scarce, and taxonomic, temporal and geographical biases abound; a situation called the Wallacean shortfall (Jetz, McPherson, & Guralnick, 2012; Lomolino, 2004). Methods are therefore needed that infer species' complete geographical ranges from such patchy occurrence data. Several approaches are currently being used, each rendering a map with particular characteristics (McPherson & Jetz, 2007).

The traditional and still most common method is to manually draw a simplified polygon around known occurrence localities using expert knowledge of a species' habitat preference and auxiliary environmental information, such as a categorical land cover map (Hawkins, Rueda, & Rodríguez, 2008). Given the rather high level of abstraction involved, deduced range boundaries typically ignore most of the internal structure as well as spatial outliers (Brown, Stevens, & Kaufman, 1996).

The most comprehensive repository of such expert maps is provided by the International Union for the Conservation of Nature (IUCN) and its partner, BirdLife International. At present, IUCN expert maps are available for birds (Butchart et al., 2004), amphibians (Stuart et al., 2004), mammals (Schipper et al., 2008) and reptiles (Böhm et al., 2013), and they are being used increasingly for macroecological research (see Supporting Information Appendix S1), often because they are the only source of occurrence information readily available.

These IUCN expert maps, however, were created with a specific purpose in mind, namely to guide conservation efforts, and for this reason have been drawn adhering to the precautionary principle. Experts involved were asked to restrict presence predictions to those areas with presumably suitable habitat where the species is known rather than suspected to occur, and generally to disregard areas far beyond the polygon connecting confirmed presence localities (such areas can be recorded as 'possibly extant', but this option is rarely made use of; IUCN Standards and Petitions Subcommittee, 2014; Schipper et al., 2008). IUCN expert maps consequently underestimate systematically the complete geographical range (*sensu* extent of occurrence; see Gaston & Fuller, 2009) of many species, especially in poorly surveyed regions such as the species-rich tropics—even in case of well-studied taxa (Ficetola et al., 2014; Pineda & Lobo, 2012). In a conservation context, this is desirable because erroneously assumed presences of a species are usually more costly than falsely predicted absences. For macroecological research, however, such purpose-specific expert maps are conceptually inadequate. Instead, general-purpose maps are needed that attempt to depict the complete range of species in order to identify fundamental patterns and processes successfully.

Given that few such maps exist for large geographical extents and taxonomic groups, macroecologists may be tempted to use IUCN expert maps nonetheless. Here, we explore empirically the consequences of doing so, using carefully crafted species distribution models (SDMs) as a reference dataset depicting the complete range of species. SDMs are capable of inferring the full geographical range of a species from a set of presence localities and use explicit rules or statistical correlations based on a species' position in ecological rather than geographical space (Dormann et al., 2012; Elith & Leathwick, 2009). This is a conceptual benefit (see Discussion), and it makes range estimates easier to reproduce. Creating plausible general-purpose SDMs is not without caveats, however, and compiling high-quality species presence data can be very time consuming (Boakes et al., 2010). Expert maps and SDMs have previously been evaluated for agreement at both the individual and aggregated (i.e. species richness) level, but to our knowledge only Vasconcelos, Rodríguez, & Hawkins (2012) examined a large taxonomic group (amphibians) across an entire biogeographical realm (the New World) and used IUCN expert maps. Their SDMs, however, as the authors concede, predicted implausibly large range sizes, and for species-rich South America only the most frequently recorded species (top 22%) were analysed.

We compare IUCN expert maps with SDMs created to depict complete ranges of species, using as our study system nearly all African bat species. Continental Africa comprises long environmental gradients and multiple biomes, both essential requirements for macroecological analyses (Fahr & Kalko, 2011; Rahbek, 2005). Its boundaries also align with a biogeographical realm as defined by Kreft & Jetz (2010), which maximizes the proportion of endemics and thus minimizes the potential imprint of evolutionary processes originating outside the study area (Ricklefs, 2004). At the same time, Africa has been especially poorly surveyed to date relative to its size (Martin, Blossey, & Ellis, 2012), which makes drawing expert range maps a particular challenge. Bats comprise c. 20% of all mammals in Africa as well as globally (Happold & Happold, 2013), yet they constitute perhaps the least known mammal group in terms of geographical range as a result of their nocturnal nature and active flight. They therefore resemble the vast majority of known species more closely in terms of available occurrence data and knowledge than birds, amphibians and large mammals, which many macroecological studies investigate.

The overall aim of our study is to quantify the consequences of using IUCN expert maps for macroecological analyses—an application area for which they were not created. As reference distribution data, we use carefully crafted SDMs that approximate complete species ranges (see Figure 1 for an illustrative example). For each species, we measure the discrepancy between the two range estimates in terms of size, location and shape. We also compare the range size–frequency distributions (RSFDs; Gaston, 1998) obtained by each method and assess the agreement between species richness patterns, including the location of richness hotspots. Finally, we measure the degree to which correlative drivers of species richness change in terms of both absolute and unique explanatory power when species richness is based on the reference SDMs instead of IUCN expert maps.

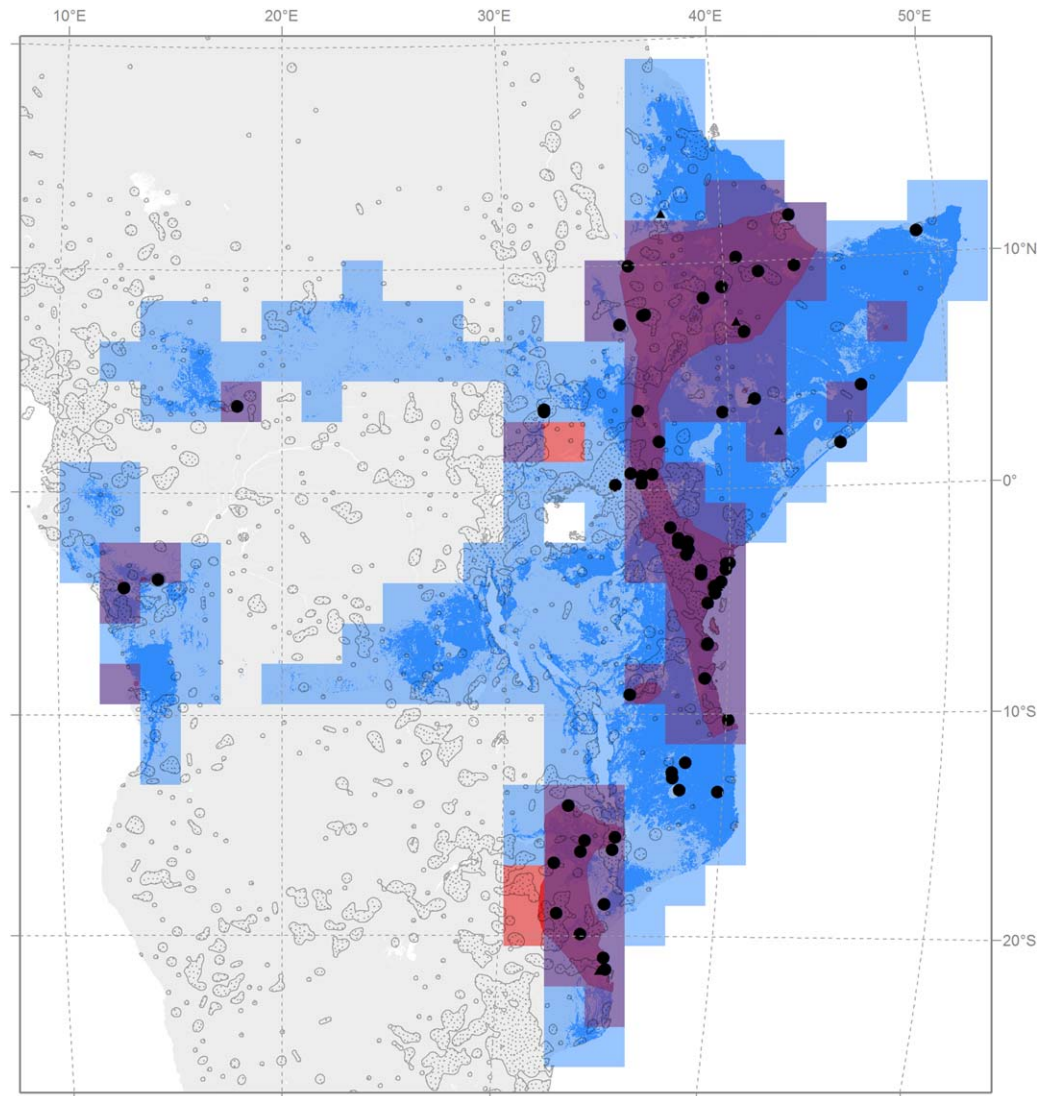


FIGURE 1 Divergent geographical range estimates for the relatively well-understood and frequently collected bat species *Triaenops persicus* *afer*. Areas in red and blue indicate presence predictions by only the International Union for Conservation of Nature (IUCN) expert map or the species distribution model (SDM), respectively; areas of agreement are shown in purple. Black circles mark confirmed presence localities ($n = 67$). Black triangles represent published presence localities that did not qualify as SDM training data but may serve as fuzzy validation data. Stippled grey polygons delineate a kernel density-based estimate of past sampling effort based on all known presence localities of African bats. To ensure an appropriate comparison, IUCN polygon maps (including a few small circles representing spatial outliers) were rasterized at 1 km^2 and then upscaled to the appropriately coarse resolution of $200 \text{ km} \times 200 \text{ km}$. The original fine-grained (1 km^2) SDM was also upscaled to match this grain (applying a minimum area requirement; see Methods). These two original datasets are discernible in the figure as slightly darker red and blue areas, respectively, with overlapping areas in slightly darker purple. An extensive interpretation of this figure is provided in Supporting Information Appendix S16

2 | METHODS

2.1 | Species distribution data

We assembled occurrence data for all African bat species from 54 natural history collections, > 2,000 publications and field data collected by J.F. and colleagues. After meticulous georeferencing and quality assurance checks, > 9,000 localities were available to train SDMs. To constrain the temporal mismatch with environmental pre-

dictor data, we did not use presence records older than 1960 when training SDMs (with very few exceptions; see Appendix G of Herkt, Barnikel, Skidmore, & Fahr, 2016). We created SDMs using a grain of 1 km^2 because bats respond to environmental gradients at this or a finer spatial resolution (references in Herkt et al., 2016). We used MaxEnt (version 3.3.3e; Phillips, Anderson, & Schapire, 2006) as the SDM algorithm and 18 environmental predictors, all of potentially high biological relevance to African bat species. These comprised

temperature and precipitation conditions (annual extremes and SDs), topographic ruggedness, distance to large freshwater bodies, structural composition of vegetation, and two remotely sensed images of red and near-infrared spectral reflectance representing variation in vegetation density and abiotic land cover characteristics. We evaluated SDMs in terms of discrimination success and model robustness using AUC values and the continuous Boyce index (CBI; Hirzel, Le Lay, Helfer, Randin, & Guisan, 2006), paying special attention to SDMs of rarely recorded species (details in Supporting Information Appendix S2). We then converted predictions to binary format using the highest statistical threshold provided by MaxEnt (with some exceptions) and removed very isolated presence patches not containing a confirmed presence record, such as those located in the opposite hemisphere (see Supporting Information Appendix S3 for further details on SDM production, and Herkt et al., 2016 for a full account). Expert maps were retrieved from the IUCN Red List data portal (www.iucnredlist.org; accessed 19 April 2013). We treated both IUCN presence categories 'extant' and 'probably extant' as presence (16% of species were mapped using in part the latter category, which enlarged concerned ranges by 8%). Other presence categories did not exist in the data; origin and seasonality were 'native' and 'resident', respectively, for all range fragments of all species. We rasterized polygons to match the SDM data regarding spatial grain (1 km²), equal area projection, geographical extent and water body mask. The IUCN expert maps were based on the taxonomy of Simmons (2005), whereas our SDMs were created using an updated taxonomy that accounts for 55 taxa that have since been described as new, removed from synonymies or otherwise changed status (see Appendix C of Herkt et al., 2016 for full details). For the present study, we reconciled both taxonomies as much as possible (see Supporting Information Appendix S4). Species known from fewer than five presence localities were disregarded even in case of unambiguous taxonomy. As a result, our analysis considers 183 (82%) of the 224 continental African bat species distinguished in the IUCN dataset.

2.2 | Spatial grain of comparison

Expert maps of even the best known species cannot represent the spatial discontinuities (incomplete range filling) characterizing most species distributions at grains finer than 2° or at most 1° (Hurlbert & Jetz, 2007). To ensure an appropriate comparison, we therefore upscaled both the rasterized IUCN expert maps and the original SDMs to a grain of 200 km × 200 km. Results obtained for a representative subset of species confirmed that such a coarse grain was required for upscaled SDMs to display range boundaries visually approximating the generalization level of expert maps (Supporting Information Appendix S5). Fine-grained SDMs tend to predict range boundaries that meander much more than those of expert maps over distances shorter than 200 km, and are characterized by many isolated presence patches beyond the main distribution area. When upscaled, such fuzzy boundary areas tend to expand disproportionately relative to the species' core range area. To mitigate this effect, only coarse-grained cells (40,000 km²) that comprised at least 200 km² of fine-grained predicted presence area were treated as presence. We chose this specific thresh-

old because below this value, median range filling (across all species) increased strongly, whereas above this threshold it increased at a noticeably lower rate (Supporting Information Appendix S6-1). Also, when this minimum area requirement was not applied to upscale SDMs, species ranges extended far beyond suitable biomes (Supporting Information Appendix S6-2). We verified that the imposed minimum area requirement did not increase the difference between upscaled SDMs and IUCN expert maps (Supporting Information Appendix S6-3).

2.3 | Discrepancies in species ranges

For each species, we compared ranges in terms of size, shape and location. Agreement in size was measured as the absolute difference in continental prevalence predicted by either method. Agreement in shape was quantified as the difference between the compactness of each range (with the latter calculated as the range area divided by the area of a circle with the same perimeter). Agreement in location was measured as the difference between geographical centroids of each range, applying the mean centre tool in ArcMap 10.2 (www.esri.com). We computed the four elements of the confusion matrix, positive agreement (Cicchetti & Feinstein, 1990) and two common similarity measures (Cohen, 1960; Jaccard, 1901). Given the limitations of Cohen's Kappa metric, we also calculated quantity and allocation disagreement (Pontius & Millones, 2011) as well as the true skill statistic (TSS), which, unlike κ , is not sensitive to differences in prevalence (Allouche, Tsoar, & Kadmon, 2006) and therefore permits summary statistics across species. As a measure of accuracy rather than agreement, however, TSS requires one dataset to represent the 'truth'. We therefore report three different TSS values: the first considers the expert map to be true, the second the SDM, and the third represents the simple mean between the two TSS values. Given that disagreement over short distances may be acceptable for some macroecological questions, we further report fuzzy κ as implemented in the map comparison kit (Visser & de Nijs, 2006) using a linear decay function with slope of 0.5 (i.e., measuring distance-weighted similarity of cells up to 400 km away from the focal cell). Likewise, we report fuzzy versions of the Jaccard index using three inverse distance-weighting schemes to represent vague similarity (Barbosa, 2015). As an integrative measure of disagreement in range location and shape irrespective of differences in range size, we computed the earth mover's distance (EMD; Rubner, Tomasi, & Leonidas, 2000) using the package 'emdlist' (Urbanek & Rubner, 2013), the FastEMD version 3 algorithm (Pele & Werman, 2009) and the geographical distance calculation provided in the package 'move' (Kranstauber, Smolla, & Safi, 2016) for R version 3.1.1 (R Core Team, 2014). To evaluate the theoretical expectation that richness patterns based on IUCN expert maps are more dependent on, and thus more correlated with, past sampling effort than SDM-based richness estimates, we computed Pearson's r between each richness estimate and the amount of area effectively sampled for bats within each 40,000 km² (presented by Herkt et al., 2016). We summarized species-specific discrepancies between SDMs and IUCN expert maps by comparing the derived RSFDs, and examined their similarity using a two-sided Wilcoxon rank-sum test. Skewness and kurtosis were measured using the type 3 definition in the R package 'e1071' (Meyer et al., 2014).

2.4 | Discrepancies in species richness and hypothesized drivers

We summed the number of species in each cell for the two datasets and compared the resulting richness maps both visually and in terms of cell-based correlation (Pearson's r). We further assessed the spatial congruence of the richest 5% of cells in either dataset, which is an arbitrary but commonly chosen definition of richness hotspots (e.g., Grenyer et al., 2006; Hurlbert & Jetz, 2007), by measuring the proportion of spatial overlap and mapping their locations. In a final step, we assessed the extent to which support for three common hypotheses explaining species richness changed when species richness was inferred from SDMs instead of IUCN expert maps. We represented each hypothesis using a single environmental variable. The productivity hypothesis (Wright, 1983) was quantified using log-transformed annual net primary productivity (NPP). The seasonality hypothesis (Carrara & Vázquez, 2010) was expressed as the SD of intra-annual actual evapotranspiration (AET). The environmental heterogeneity hypothesis (reviewed by Stein, Gerstner, & Kreft, 2014) was represented by a log-transformed synthetic measure of topographic and land cover diversity (see Supporting Information Appendix S7 for a summary of each hypothesis as well as the sources used and processing steps performed to prepare the proxy variables). We identified the best model representing each hypothesis by fitting a series of univariate linear regression models (allowing terms up to the third polynomial) and selecting the model with the highest adjusted R^2 (Legendre & Legendre, 1998). We assessed the support for hypothesized drivers (a) by measuring the richness source-dependent difference in absolute effect size (adjusted R^2) for each hypothesis separately, and (b) by comparing the relative explanatory power attributed to each hypothesis (adjusted R^2) in a variation partitioning analysis (Bocard, Legendre, & Drapeau, 1992; Legendre & Legendre, 1998; Peres-Neto, Legendre, Dray, & Borcard, 2006). To present results for the latter (Figure 5), we used the program euler APE v.3 (Micallef & Rodgers, 2014). Computations were carried out in R version 3.1.1 (R Core Team, 2014) using the varpart function of the vegan version 2.0–10 package (Oksanen et al., 2013). Robustness and significance of results were tested using the script provided by Tello & Stevens (2010; Supporting Information Appendix S8). Finally, we repeated the exemplary macroecological regression analysis excluding all SDMs with below-median performance in terms of both CBI and drop in AUC (details in Supporting Information Appendices S2, S9, S10 and S11).

3 | RESULTS

All SDMs had sufficient discriminatory capacity and were robust enough to serve as useful estimates of species' complete geographical ranges (CBI 0.91 ± 0.14 and drop in $AUC_{(training - test)}$ $3.47 \pm 3.05\%$; median and 1 SD ; see Supporting Information Appendices S2 and S9 for further details).

IUCN expert maps differ substantially from SDM-based estimates of species' complete ranges. Estimated range sizes are about half of what SDMs predict (median continental prevalence 0.08 vs. 0.16). They are also more compact than SDMs (median compactness 0.24 vs.

0.17). Median range centre points differ by 300 km and for 10% of species by > 800 km. Consequently, common cell-based concordance metrics, such as positive agreement (median = 0.65), the Jaccard coefficient (median = 0.48) and κ (median = 0.58), indicate mediocre agreement only. Allocation disagreement (median = 0.09) is slightly larger than quantity disagreement (median = 0.06). Controlling for differences in the continental prevalence of species, TSS rates the accuracy of IUCN expert maps as 0.50 (median) if SDMs depict the true ranges of species, and it puts the accuracy of SDMs at 0.80 (median) in the reverse case. Giving equal credence to both methods results in a mean TSS of 0.64 (median). As expected from theory, agreement increases moderately when predicted range boundaries are treated less firmly: fuzzy κ with linearly decreasing weights up to a distance of 400 km equals 0.65 (median), and the fuzzy Jaccard index with squared inverse distance weights applied is 0.57 (median; see Supporting Information Appendix S9 for detailed results).

As shown in Figure 2, disagreement on range size is positively correlated (Pearson's $r = .64$) with disagreement on range location and shape (evaluated jointly using the EMD). The EMD is generally largest for those species known from the fewest localities, but there is also considerable disagreement for many species belonging to the most frequently recorded quartile. Overall, the number of a species' presence localities is only weakly correlated with EMD ($r = -.13$) and absolute range size disagreement ($r = .20$). This correlation is slightly stronger (and turns negative) when range size discrepancies are divided by the species' predicted (mean) absolute range size to remove the influence of the latter ($r = -.34$).

As shown in Figure 3, the RSFD of IUCN expert maps is characterized by a stronger positive skewness (1.59) compared with the RSFD of SDMs (1.01) and by a higher leptokurtosis (2.18 vs. 0.23). In other words, IUCN expert maps show generally smaller ranges (inset in Figure 3) but greater range size differences among species.

Mean continental species richness is substantially lower (-29% ; 22 vs. 31) when based on summed IUCN expert maps (Figure 4a) compared with summed SDMs (Figure 4b). More importantly, pronounced regional differences can be discerned (Figure 4c), with IUCN expert maps predicting richness levels that deviate from SDM-based richness by as much as -91% (central Somalia: 3 vs. 33) and $+43\%$ (northwest Egypt: 7 vs. 3). As a result, although the correlation between both richness estimates is strong across entire continental Africa ($r = .89$), there is major disagreement on which cells constitute the richest 5% (κ and mean TSS both 0.42). The IUCN expert maps allocate these along an almost straight line connecting Liberia with coastal Tanzania, whereas the SDMs suggest geographically more dispersed richness peaks, with two additional hotspots in south-western Ethiopia and central Congo-Brazzaville (Figure 4d). Also, past sampling effort is clearly more correlated with the species richness estimate derived from IUCN expert maps than with the one based on SDMs ($r = .66$ vs. $r = .54$; both p -values < 0.001 , d.f. = 812).

The differences between the two species richness estimates changed the results of our analyses of correlative richness drivers (also see Supporting Information Appendices S7 and S8). When richness is

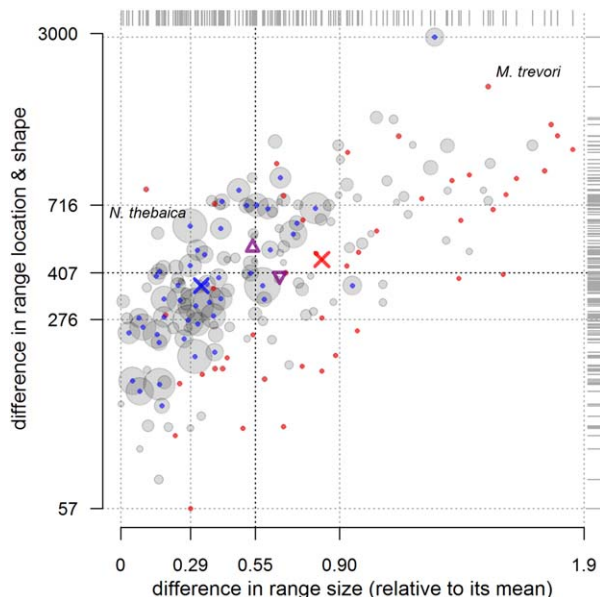


FIGURE 2 Disagreement between IUCN expert maps and species distribution models (SDMs) in terms of range size (measured as continental prevalence) and a joint evaluation of range location and shape (measured as EMD). Given that absolute range size disagreement is more likely to be found for species with large ranges than for those with small ranges, range size differences are shown relative to the mean range size estimated by both IUCN expert maps and SDMs. Circle size reflects the number of presence localities (n). Blue and red circle centres mark the quartile of species with the highest and lowest n , respectively, and the blue and red cross each group's median disagreement. The upward- and downward-pointing triangles indicate median disagreement for the group with the second-highest and second-lowest n , respectively. Dotted lines mark quartile boundaries of the two dimensions of disagreement. The figure shows that in both dimensions the disagreement is highest for species known from a few localities only (e.g., *Mops trevori*), whereas many frequently recorded species (e.g., *Nycteris thebaica*) also show a surprisingly strong disagreement in terms of range location and shape (earth mover's distance)

based on complete species ranges as estimated by the SDMs instead of inferred using IUCN expert maps, support for the heterogeneity hypothesis nearly doubles (adjusted $R^2 = .29$ vs. $.18$), and it increases for the seasonality hypothesis by a similar amount (adjusted $R^2 = .49$ vs. $.34$). Only the productivity hypothesis retains its level of support (adjusted $R^2 = .80$ vs. $.77$). However, the fraction of variation in richness explained exclusively by the productivity hypothesis is much smaller when SDMs are used (27%) instead of IUCN expert maps (41%). Conversely, 54% of the total variation can be attributed to more than one of the hypotheses tested here if richness is based on SDMs, compared with 36% if IUCN expert maps are used (Figure 5). The former data type therefore entails the (remote) possibility that seasonality explains 50% of total variation; more than the productivity hypothesis. These discrepancies remain at least as large when the 13% of species with the poorest performing SDMs are excluded from analysis (Supporting Information Appendices S10 and S11).

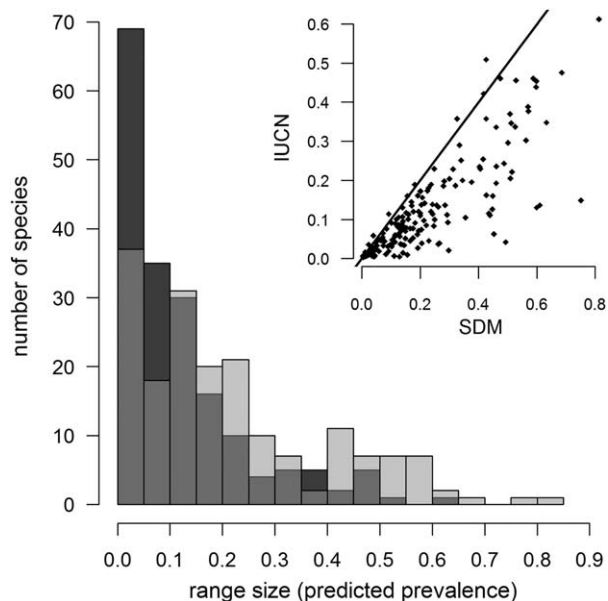


FIGURE 3 Range size–frequency distributions (RSFDs) of African bats ($n = 183$) derived from IUCN expert maps (dark grey) and species distribution models (SDMs; light grey), with the proportion of agreement depicted in medium grey. Range size is measured as the predicted continental prevalence at a grain of $200 \text{ km} \times 200 \text{ km}$. Note that although both range estimation methods suggest range sizes to be smaller than the mean for the majority of species, IUCN expert maps depict ranges that are generally smaller while also less similar in size. Inset: scatterplot of range sizes (measured as above) as estimated by SDMs and IUCN expert maps

4 | DISCUSSION

4.1 | Diverging estimates of species geographical ranges

IUCN expert maps are created following the precautionary principle (IUCN Standards and Petitions Subcommittee, 2014) and for this reason they tend to underestimate the complete geographical range of all but the best known species. This is desirable when they are used to guide conservation decisions, which is their intended application area. Macroecologists, however, require data on the complete geographical range of species. We therefore argue that it is inappropriate to use IUCN expert maps in macroecological analyses whenever the study area has been poorly sampled or the species' habitat requirements are poorly understood. To our knowledge, the present study is the first to present this argument explicitly and the first to measure the postulated discrepancies and implications using a large empirical dataset covering an entire biogeographical realm.

We found that IUCN expert maps of African bats differ substantially from carefully crafted SDMs designed to depict species' complete ranges. Range centroids typically differ by 300 km, and SDMs predict ranges about twice as large and less compact. Common measures of map concordance, such as positive agreement, κ , TSS and Jaccard coefficient, also indicate only moderate agreement (0.48–0.65), as do those measures that tolerate some spatial

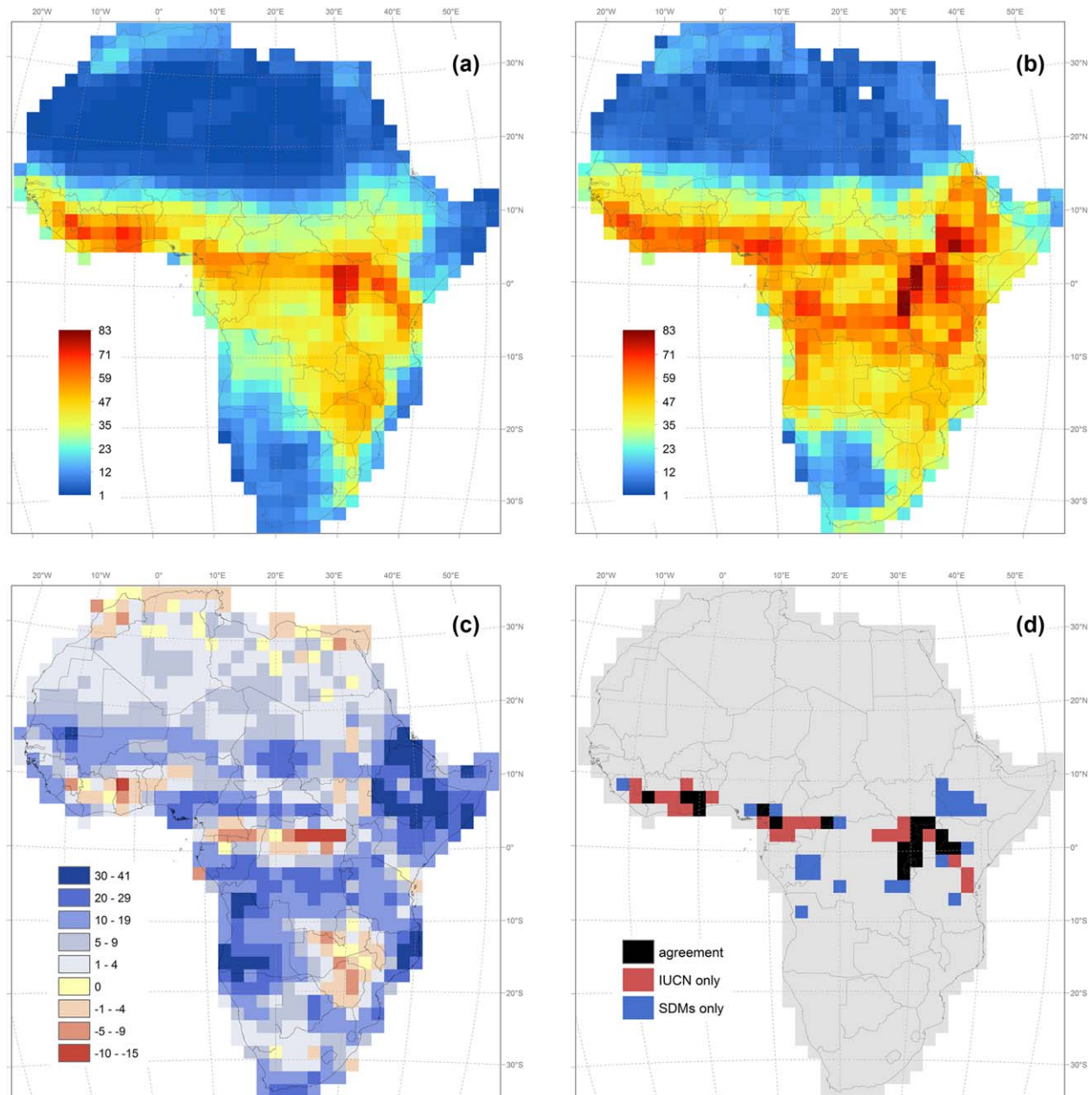


FIGURE 4 Species richness of African bats ($n = 183$) at the $200 \text{ km} \times 200 \text{ km}$ grain based on (a) summed IUCN expert maps and (b) species distribution models (SDMs). (c) The net difference; positive values (in blue) indicate areas where SDMs predict higher species richness than IUCN expert maps, whereas negative values (in red) denote the opposite. (d) The (dis)agreement of richness hotspots when these are defined as the 5% most species-rich cells. Maps are in Lambert azimuthal equal area projection centred on $5^\circ \text{ N } 20^\circ \text{ E}$

discrepancy (fuzzy κ and fuzzy Jaccard) or summarize differences across the entire study area (EMD).

Not all of this disagreement, however, may be attributable to the special-purpose character of IUCN expert maps; we used a different method (SDMs) to estimate the complete geographical range of species, and we do not know for certain how closely these SDMs reflect reality because we lack truly independent validation data. We discuss these interrelated issues in the following paragraphs.

Clearly, to measure only the spatial net effect of applying the precautionary principle when drawing expert maps, the straightforward comparison would have been to use general-purpose expert maps instead of SDMs. However, few such maps exist for a similarly large taxonomic group and region, and those maps available (e.g., Galster, Burgess, Fjelds , Hansen, & Rahbek, 2007) are typically built with expert-informed interpolation restricted to relatively common species and to the area between, not beyond, confirmed presence localities.

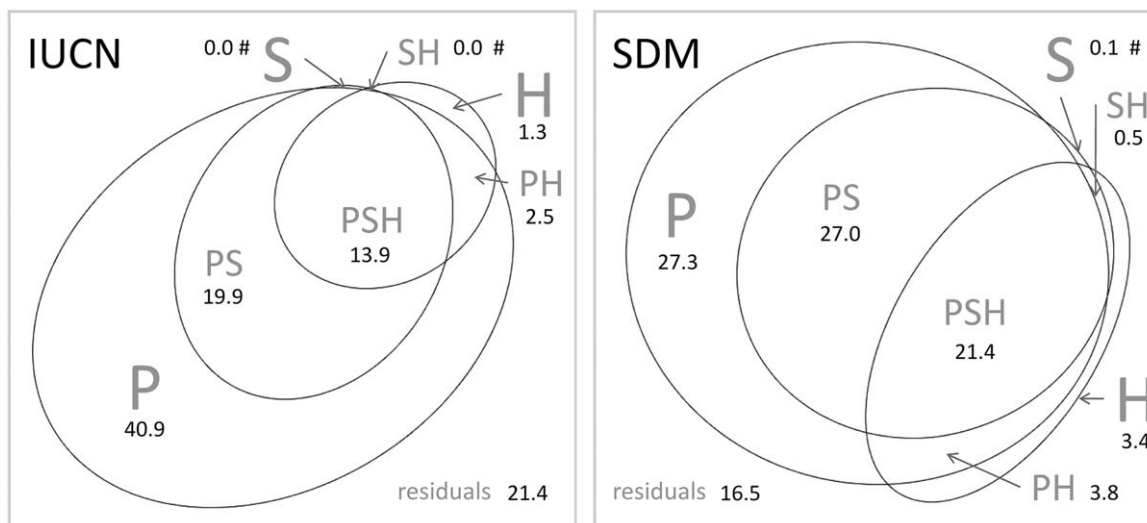


FIGURE 5 Variation in African bat species richness explained by one or several of the three hypotheses tested here (H = environmental heterogeneity; P = primary productivity; S = climatic seasonality) when species richness is derived by summing either IUCN expert maps (left) or species distribution models (SDMs; right). Ellipses are proportional in size to the variance attributable to the respective partition. A hash symbol (#) denotes values not different from random (see Supporting Information Appendix S8). Note that support for the productivity hypothesis in isolation is substantially reduced when SDMs are used in place of IUCN expert maps to compute richness, and that in this case the amount of variance explained by more than one hypothesis increases from 36 to 53%

Given that many regions, especially in the species-rich tropics, are still severely undersampled, these maps thus tend to fall short of estimating the complete range of species as well.

We therefore use SDMs as a reference dataset. SDMs are less sensitive to geographical gaps in sampling effort (illustrated in Figure 1) because they depend primarily on training data that comprise range margins in ecological rather than geographical space (Graham & Hijmans, 2006). The process of creating SDMs is also less opaque compared with expert maps. On the other hand, SDMs tend to predict potential rather than realized species distributions, because not all range-constraining factors (in particular, biotic interactions and dispersal limitations) are known or quantifiable for model training (Jiménez-Valverde, Lobo, & Hortal, 2008). SDMs may also misconstrue a species' current distribution if its ecological niche preference is not constant across its entire range (Elith, Kearney, & Phillips, 2010), and the use of an overly liberal threshold when converting relative habitat suitability predictions to binary format can cause range overestimation. We have therefore taken great care to control for these issues as much as possible when generating SDMs. To limit range overprediction, (a) we used predictor variables that comprised not only climatic conditions but also topography, hydrology, vegetation structure and land cover information derived from remote sensing, (b) we removed predicted presence areas implausibly far from confirmed presence localities (e.g., in the opposite hemisphere), (c) we selected a study taxon that is very mobile and thus likely to satisfy the assumption of constant range-wide habitat preferences, and (d) we created binary maps using a conservative threshold for most species (see Supporting Information Appendix S3 for more, and Herkt et al., 2016 for full details). Contrary to most continental studies, we also built SDMs using a spatial grain fine enough to capture environmental variation at the landscape scale. Finally, when upscaling these fine-grained SDMs to a grain coarse enough for an

adequate comparison with expert maps, we required the fine-grained presence area to amount to at least 200 km² before accepting the species as present in the coarser cell. This rule reduced predicted ranges markedly (Supporting Information Appendix S6–2); in some areas even to the point that SDM-based richness was lower than the one derived from IUCN expert maps (Figure 4c).

We are thus confident that the coarse-grained SDMs used here approximate the true geographical ranges of African bats rather well and that major range overestimation is unlikely. In their ground-validated study of Mexican amphibians, Pineda & Lobo (2012) found that SDMs generally do overestimate range size at a spatial grain of 2°, whereas IUCN expert maps tend to underestimate it. However their SDMs were trained using only climatic predictors, and potentially important dispersal limitations were not accounted for.

Yet, before concluding that the observed discrepancies are primarily the result of the special-purpose character of IUCN expert maps, two methodological limitations of the expert mapping approach in general must also be considered as potential explanations. First, the analytical ability of human experts is rather limited when capturing and synthesizing the complex interplay of multiple environmental factors that determine a species' habitat suitability (Levin, 1992). Mapping the geographical range of habitat generalists is thus a greater challenge than mapping habitat specialists (Stockwell & Peterson, 2002). Second, it is very difficult to draw accurate expert maps at a spatial grain finer than c. 1° (Hurlbert & Jetz, 2007). Range-determining factors only discernible at the landscape scale (e.g., proximity to streams) may thus have remained unaccounted for in the IUCN expert maps. However, there is no reason to assume that these two methodological limitations of expert maps in general lead to range underestimation more often than to range overestimation. They are thus unlikely to cause IUCN expert maps to depict consistently smaller ranges than SDMs.

This leaves the special-purpose character of IUCN expert maps as the most likely explanation, and our data support this empirically; when richness is computed by stacking IUCN expert maps instead of SDMs, the correlation with sampling effort is significantly stronger. This makes sense given that IUCN expert maps exclude by design un(der)sampled regions (at least outside the minimum convex polygon) even if environmental conditions are deemed suitable by the expert. A second indication of prevailing range underestimation by IUCN expert maps is the high percentage of species (c. 85%) for which presence records were found outside expert-delineated ranges in two large studies (Pineda & Lobo, 2012; Ficetola et al., 2014). We also note that Graham & Hijmans (2006) report a similar fraction of species with underestimated ranges even though they studied a well-sampled region and used general-purpose expert maps. These results show that current expert maps, especially those of the IUCN, require regular updates (Rondinini et al., 2014) and that they tend to underestimate currently realized species ranges.

4.2 | Implications for macroecological research

Systematic disagreement at species level affects variables of macroecological interest. In testimony of this, we found the SDM-based RSFD to be half as skewed as and more even than the RSFD of IUCN expert maps (Figure 3). The two species richness patterns also differ considerably. Richness hotspots are disagreed upon more often than not (Figure 4d), and SDMs predict much higher species richness in notoriously undersampled regions, such as Angola, Eritrea, Ethiopia, Somalia and Mozambique (Figure 4c). Interestingly, disagreement on richness is strongest in cells with intermediate predicted richness levels (Supporting Information Appendix S12). This contrasts with results of Pineda & Lobo (2012), who found the largest discrepancies in the richest cells, but we regard our result as plausible because cells with intermediate richness contain a large proportion of wide-ranging (generalist) bat species, whose ranges are typically hardest to predict.

Tackling the key question of whether the observed disagreement on richness patterns is large enough to lead to quite different macroecological conclusions, we investigated the degree to which correlative environmental drivers of species richness change in terms of both their absolute and relative explanatory power in response to using either richness dataset. Although the productivity hypothesis receives the most support, regardless of which species richness dataset is used, the environmental heterogeneity and climatic seasonality hypotheses both gain correlative strength when SDMs approximating complete species ranges are used instead of IUCN expert maps. Furthermore, in this case redundancy among hypotheses is notably higher; 53% of variation (as opposed to 36%) can now be explained by more than one of the hypotheses tested here (Figure 5). Overall, the magnitude of change in support of hypothesized richness drivers seems disconcertingly high even if we consider the rather simple, univariate representations of hypotheses.

Given our conceptual arguments and empirical findings, we thus recommend using IUCN expert maps for macroecological analyses only when the ecology of the taxon is well understood and the region does

not contain major geographical sampling gaps. We have shown that for African bats these conditions do not hold. Although IUCN expert maps may be appropriate for macroecological analyses if the focus is on much better sampled taxa, such as birds, large mammals and perhaps amphibians in Europe or North America, this seems unlikely for many other taxa and regions.

We also explored whether a high number of known presence localities would cause IUCN expert maps to approximate the complete range of a species (i.e., to resemble the SDM). Our results are sobering, in that disagreement on range size is strong even for species known from > 60 localities (the median across all 183 species analysed; see Supporting Information Appendix S13). Only when we account for the fact that larger ranges require more presence localities to be delineated correctly (and divide range size discrepancies by the species' predicted mean absolute range size) do we observe a relationship conforming to our expectation that discrepancies are smaller for more frequently found species (Supporting Information Appendix S13). Yet, even when standardized this way, above-median discrepancies in range size remain for nearly one-third of species known from at least 60 localities. Likewise, disagreement in the shape and location of species' geographical ranges (quantified as EMD) is widespread among all species except those known from > 300 localities (Supporting Information Appendix S14). Furthermore, disagreement on range size is broadly proportional to absolute range size (Supporting Information Appendix S15). Given that most rarely collected species have small estimated ranges, it thus seems likely that results would be similar had we restricted our analyses to species known from, for example, at least 10 localities (instead of at least five).

A caveat of our study is that we relied on a single SDM algorithm (MaxEnt) to estimate the complete geographical range of species. However, algorithm choice is but one of several factors influencing prediction success, and it can lose primacy when an evaluation metric other than AUC is used (Tessarolo, Rangel, Araújo, & Hortal, 2014). Furthermore, MaxEnt was found to perform well even when compared with ensemble approaches (Aguirre-Gutiérrez et al., 2013), and we carefully attended to a range of modelling challenges when generating the SDMs (Herkt et al., 2016). In brief, we are confident that the SDMs used here approximate complete species ranges sufficiently well to warrant a first call for caution on using IUCN expert maps in macroecology, and we hope to have stimulated further research on this topic.

The broader implication of our findings is that at present few species' geographical range datasets are appropriate for use in macroecology. We therefore commend projects such as 'Map of Life' (Jetz et al., 2012) that offer a synthetic overview of the available distribution data. Such knowledge integrating platforms help to facilitate efficient updates of range estimates as new occurrence data come in, and permit ad hoc validation of predictions made by different range estimation methods. To provide macroecologists with adequate geographical range estimates, we propose (a) to enrich existing IUCN expert maps by making much more use of the 'possibly extant' field, thus facilitating their use as general-purpose maps of some sort, and (b) to create SDMs akin to those used here to be used as a complementary or

alternative dataset to general-purpose expert maps. Although current correlative SDM techniques are certainly not perfect, they yield transparent predictions into undersampled regions and can provide insights at much finer grain than hand-drawn expert maps. When such SDMs are combined in a hierarchical framework with expert maps (and possibly atlas data and point locality records too), multiple range boundaries could be inferred, each associated with a different confidence level reflecting the amount of congruence with other data types. Macroecologists could then choose the geographical range dataset that most suits their needs.

5 | CONCLUSIONS

Here we have shown, for a large taxonomic group, that macroecological insights change when SDMs built to estimate the complete geographical range of species are used instead of the frequently used IUCN expert maps. We attribute the observed differences in geographical range size, shape and location as well as the derived richness patterns primarily to the precautionary principle that underpins IUCN expert maps and renders them relatively sensitive to geographical variation in sampling effort, which is a common situation in most parts of the world. We therefore caution against basing macroecological analyses on this type of data and recommend using an SDM approach, with subsequent map refinement using expert knowledge. We conclude on both conceptual and empirical grounds that only in the case of easily found taxa and very well-sampled regions can IUCN expert maps be expected to delineate a species' full geographical range and thus adequately inform macroecological analyses.

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DATA ACCESSIBILITY

Both sets of species distribution estimates compared in this study (IUCN expert maps and SDMs), the two resulting species richness maps, the geographical distribution of sampling effort and the three maps of environmental 'drivers' included in our macroecological analysis are available as raster grids (at 200 km × 200 km spatial resolu-

tion) from the PANGAEA database: <https://doi.pangaea.de/10.1594/PANGAEA.871515>.

AUTHOR CONTRIBUTIONS

J.F. conceived the study, K.M.B.H. and J.F. compiled the data, K.M. B.H. analysed the data and wrote the first draft, and all authors contributed substantially to revisions of the manuscript.

REFERENCES

- Aguirre-Gutiérrez, J., Carvalheiro, L. G., Polce, C., van Loon, E. E., Raes, N., Reemer, M., & Biesmeijer, J. C. (2013). Fit-for-purpose: Species distribution model performance depends on evaluation criteria – Dutch Hoverflies as a case study. *PLoS One*, 8, e63708.
- 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.
- Barbosa, A. M. (2015). fuzzySim: Applying fuzzy logic to binary similarity indices in ecology. *Methods in Ecology and Evolution*, 6, 853–858.
- Beck, J., Ballesteros-Mejia, L., Buchmann, C. M., Dengler, J., Fritz, S. A., Gruber, B., ... Dormann, C. F. (2012). What's on the horizon for macroecology? *Ecography*, 35, 673–683.
- Boakes, E. H., McGowan, P. J. K., Fuller, R. A., Chang-Qing, D., Clark, N. E., O'Connor, K., & Mace, G. M. (2010). Distorted views of biodiversity: spatial and temporal bias in species occurrence data. *PLoS Biology*, 8, e1000385.
- Bocard, D., Legendre, P., & Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, 73, 1045–1055.
- Böhm, M., Collen, B., Baillie, J. E. M., Bowles, P., Chanson, J., Cox, N., ... Rhodin, A. G. (2013). The conservation status of the world's reptiles. *Biological Conservation*, 157, 372–385.
- Brown, J. H., & Maurer, B. A. (1989). Macroecology: The division of food and space among species on continents. *Science*, 243, 1145–1150.
- Brown, J. H., Stevens, G. C., & Kaufman, D. M. (1996). The geographic range: Size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, 27, 597–623.
- Butchart, S. H. M., Stattersfield, A. J., Bennun, L. A., Shutes, S. M., Akçakaya, H. R., Baillie, J. E. M., ... Mace, G. M. (2004). Measuring global trends in the status of biodiversity: Red List indices for birds. *PLoS Biology*, 2, e383.
- Carrara, R., & Vázquez, D. P. (2010). The species-energy theory: A role for energy variability. *Ecography*, 33, 942–948.
- Cicchetti, D. V., & Feinstein, A. R. (1990). High agreement but low kappa: II. Resolving the paradoxes. *Journal of Clinical Epidemiology*, 43, 551–558.
- Cohen, J. (1960). A coefficient of agreement for nominal scales. *Educational and Psychological Measurement*, 20, 37–46.
- Dormann, C. F., Schymanski, S. J., Cabral, J., Chuine, I., Graham, C., Hartig, F., ... Singer, A. (2012). Correlation and process in species distribution models: Bridging a dichotomy. *Journal of Biogeography*, 39, 2119–2131.
- Elith, J., Kearney, M. R., & Phillips, S. J. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, 1, 330–342.
- Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40, 677–697.
- Fahr, J., & Kalko, E. K. V. (2011). Biome transitions as centres of diversity: Habitat heterogeneity and diversity patterns of West African bat assemblages across spatial scales. *Ecography*, 34, 177–195.

- Ficetola, G. F., Rondinini, C., Bonardi, A., Katariya, V., Padoa-Schioppa, E., & Angulo, A. (2014). An evaluation of the robustness of global amphibian range maps. *Journal of Biogeography*, *41*, 211–221.
- Galster, S., Burgess, N. D., Fjeldså, J., Hansen, L. A., & Rahbek, C. (2007). One degree resolution databases of the distribution of mammals in Sub-Saharan Africa. Retrieved from: <http://macroecology.ku.dk/resources/african-vertebrates>. Last accessed 7 March 2016.
- Gaston, K. J. (1998). Species-range size distributions: Products of speciation, extinction and transformation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *353*, 219–230.
- Gaston, K. J., & Fuller, R. A. (2009). The sizes of species' geographic ranges. *Journal of Applied Ecology*, *46*, 1–9.
- Graham, C. H., & Hijmans, R. J. (2006). A comparison of methods for mapping species ranges and species richness. *Global Ecology and Biogeography*, *15*, 578–587.
- Grenyer, R., Orme, C. D. L., Jackson, S. F., Thomas, G. H., Davies, R. G., Davies, T. J., ... Ding, T. S. (2006). Global distribution and conservation of rare and threatened vertebrates. *Nature*, *444*, 93–96.
- Happold, M., & Happold, D. C. D. (2013). *Mammals of Africa. Volume IV. Hedgehogs, shrews and bats*. London: Bloomsbury.
- Hawkins, B. A., Rueda, M., & Rodríguez, M. Á. (2008). What do range maps and surveys tell us about diversity patterns? *Folia Geobotanica*, *43*, 345–355.
- Herk, K. M. B., Barnikel, G., Skidmore, A. K., & Fahr, J. (2016). A high-resolution model of bat diversity and endemism for continental Africa. *Ecological Modelling*, *320*, 9–28.
- Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C., & Guisan, A. (2006). Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling*, *199*, 142–152.
- Hurlbert, A. H., & Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences USA*, *104*, 13384–13389.
- IUCN Standards and Petitions Subcommittee. (2014). Guidelines for using the IUCN Red List categories and criteria. Version 11. Prepared by the Standards and Petitions Subcommittee. Retrieved from: <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>. Last accessed 27 March 2015.
- Jaccard, P. (1901). Étude comparative de la distribution florale dans une portion des Alpes et des Jura. *Bulletin Del La Société Vaudoise Des Sciences Naturelles*, *37*, 547–579.
- Jetz, W., McPherson, J. M., & Guralnick, R. P. (2012). Integrating biodiversity distribution knowledge: Toward a global map of life. *Trends in Ecology and Evolution*, *27*, 151–159.
- Jiménez-Valverde, A., Lobo, J. M., & Hortal, J. (2008). Not as good as they seem: The importance of concepts in species distribution modelling. *Diversity and Distributions*, *14*, 885–890.
- Kranstauber, B., Smolla, M., & Safi, K. (2016). Similarity in spatial utilization distributions measured by the Earth Mover's Distance. *Methods in Ecology and Evolution*, *8*, 155–160.
- Kreft, H., & Jetz, W. (2010). A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography*, *37*, 2029–2053.
- Legendre, P., & Legendre, L. (1998). *Numerical ecology* (2nd ed.). Amsterdam: Elsevier.
- Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology*, *73*, 1943–1967.
- Lomolino, M. V. (2004). Conservation biogeography. In M.V. Lomolino and L.R. Heaney (Eds.) *Frontiers of biogeography: New directions in the geography of nature* (pp. 293–296). Sunderland, MA: Sinauer Associates, Inc.
- Martin, L. J., Blossey, B., & Ellis, E. (2012). Mapping where ecologists work: Biases in the global distribution of terrestrial ecological observations. *Frontiers in Ecology and the Environment*, *10*, 195–201.
- McPherson, J. M., & Jetz, W. (2007). Type and spatial structure of distribution data and the perceived determinants of geographical gradients in ecology: The species richness of African birds. *Global Ecology and Biogeography*, *16*, 657–667.
- Meyer, D., Dimitriadou, E., Hornik, K., Weingessel, A., Leisch, F., Chang, C.-C., & Lin, C.-C. (2014). Package "e1071". Misc Functions of the Department of Statistics (e1071). Version 1.6–4. Retrieved from: <http://cran.r-project.org/web/packages/e1071>. Last accessed 20 May 2015.
- Micallef, L., & Rodgers, P. (2014). eulerAPE: Drawing area-proportional 3-Venn diagrams using ellipses. *PLoS One*, *9*, e101717.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., Simpson, K. L., ... Wagner, H. (2013). Community Ecology Package "vegan". Retrieved from: <http://cran.r-project.org>. Last accessed 8 October 2014.
- Pele, O., & Werman, M. (2009). Fast and robust earth mover's distances. In: ICCV 2009 (pp. 460–467). Kyoto, Japan.
- Peres-Neto, P. R., Legendre, P., Dray, S., & Borcard, D. (2006). Variation partitioning of species data matrices: Estimation and comparison of fractions. *Ecology*, *87*, 2614–2625.
- Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*, 231–259.
- Pineda, E., & Lobo, J. M. (2012). The performance of range maps and species distribution models representing the geographic variation of species richness at different resolutions. *Global Ecology and Biogeography*, *21*, 935–944.
- Pontius, R. G. J., & Millones, M. (2011). Death to Kappa: Birth of quantity disagreement and allocation disagreement for accuracy assessment. *International Journal of Remote Sensing*, *32*, 4407–4429.
- R Core Team (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rahbek, C. (2005). The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, *8*, 224–239.
- Ricklefs, R. E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, *7*, 1–15.
- Rondinini, C., Di Marco, M., Visconti, P., Butchart, S. H. M., & Boitani, L. (2014). Update or outdate: long-term viability of the IUCN Red List. *Conservation Letters*, *7*, 126–130.
- Rubner, Y., Tomasi, C., & Leonidas, J. G. (2000). The Earth Mover's Distance as a metric for image retrieval. *International Journal of Computer Vision*, *40*, 99–121.
- Schipper, J., Chanson, J. S., Chiozza, F., Cox, N. A., Hoffmann, M., Katariya, V., ... Young, B. E. (2008). The status of the world's land and marine mammals: Diversity, threat and knowledge. *Science*, *322*, 225–230.
- Simmons, N. B. (2005). *Order Chiroptera. Mammal species of the world: A taxonomic and geographic reference* (pp. 312–529). Baltimore, MD: Johns Hopkins University Press.
- Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, *17*, 866–880.

- Stockwell, D. R. B., & Peterson, A. T. (2002). Effects of sample size on accuracy of species distribution models. *Ecological Modelling*, *148*, 1–13.
- Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S. L., Fishman, D. L., & Waller, R. W. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science*, *306*, 1783–1786.
- Tello, J. S., & Stevens, R. D. (2010). Multiple environmental determinants of regional species richness and effects of geographic range size. *Ecography*, *33*, 796–808.
- Tessarolo, G., Rangel, T. F., Araújo, M. B., & Hortal, J. (2014). Uncertainty associated with survey design in species distribution models. *Diversity and Distributions*, *20*, 1258–1269.
- Urbanek, S., & Rubner, Y. (2013). Package “emdist”. Earth Mover's Distance. Version 0.3–1. Retrieved from: <http://www.rforge.net/emd>. Last accessed 30 January 2014.
- Vasconcelos, T. S., Rodríguez, M. Á., & Hawkins, B. A. (2012). Species distribution modelling as a macroecological tool: A case study using New World amphibians. *Ecography*, *35*, 539–548.
- Visser, H., & de Nijs, T. (2006). The map comparison kit. *Environmental Modelling & Software*, *21*, 346–358.
- Wright, D. H. (1983). Species-energy theory: An extension of species-area theory. *Oikos*, *41*, 496–506.

BIOSKETCHES

MATTHIAS HERKT is a PhD student interested in detecting and understanding biogeographical and macroecological patterns. He enjoys spatial analyses at the landscape scale and harnessing the benefits

of remote sensing data in the context of species distribution modelling.

ANDREW SKIDMORE is Professor of Spatial Environmental Resource Dynamics at the University of Twente, Faculty of ITC. His interest in research relates to spatial ecology, including fragmentation and climate change, hyperspectral remote sensing and image processing and, more generally, techniques for handling geo-information.

JAKOB FAHR is broadly interested in factors explaining the distribution and abundance of species across spatial scales, ranging from the movement ecology of individuals to community ecology and up to biogeographical patterns found on continental scales. Most of his research uses bats as the study system.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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