



# A high-resolution model of bat diversity and endemism for continental Africa



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## ABSTRACT

Bats are the second-most species-rich mammal group numbering more than 1270 species globally. Our knowledge of their geographic distributions and diversity patterns however is very limited – possibly the poorest among mammals – mainly due to their nocturnal and volant life history, and challenging fieldwork conditions in the tropics where most bat species occur. This knowledge gap obscures the geographic extent of ecosystem services provided by bats (i.e. pollination, seed dispersal and insect control), translates into inefficient conservation policies, and restricts macroecological analyses to coarse spatial resolutions. In contrast to the currently prevailing method of estimating species distributions using expert-drawn range maps, correlative species distribution models (SDMs) can provide estimates at very fine spatial grains and largely account for widespread sample bias as well as the prevalent Wallacean shortfall in species occurrence data. Very few such studies have hitherto been published that cover a large and complete taxonomic group with fine resolution at continental extent. Using an unparalleled amount of occurrence data, the MaxEnt algorithm and tailored solutions to specific modelling challenges, we created SDMs for nearly all 250 African bat species to explore emerging diversity patterns at a resolution of 1 km<sup>2</sup>. Predicted species richness generally increases towards the equator conforming to expectations. Within the tropical area of elevated richness, several pronounced richness peaks and lows stand out, hinting at a complex interplay of determining factors. Richness gradients are often steep, decreasing strongly away from streams, and especially so in savanna biomes. Species richness also seems positively associated with rugged terrain, in particular at lower elevations. Centres of endemism are found primarily at low latitudes near major elevational ranges. Overlap with hotspots of species richness is rather low, and confined to five or six topodiverse, relatively low lying areas between western Guinea and the East African coast. Several poorly sampled regions are identified that may represent rewarding future survey targets. Our results demonstrate the value of stacking SDMs to infer plausible continent-wide diversity gradients at a spatial resolution fine enough to directly inform conservation policies and to open up new avenues in macroecological research.

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## 1. Introduction

Current species extinction rates are about 1000 times higher than the likely speed of extinction before modern-day

human-induced land conversion and climate change (Pimm et al., 2014). A biodiversity loss of such dimension threatens ecosystem health and services (Luck et al., 2003; Cardinale et al., 2012). Halting this trend has been declared one of the Millennium Development Goals (United Nations, 2000), and strategic measures have been re-specified in the Aichi Targets to be achieved by 2020 (Secretariat of the Convention on Biological Diversity, 2014). Effective conservation and monitoring schemes however require sound knowledge of species distributions and related diversity patterns.

Despite collection efforts spanning two centuries, our current knowledge of species distributions remains severely affected by the Wallacean shortfall: occurrence data are sparse for the majority of

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known species, and often spatially biased towards more accessible regions and richer countries (Lomolino, 2004; Bini et al., 2006; Beck et al., 2013). Such data gaps make it impossible to infer species range sizes and frequently associated extinction threats based on point locality data alone, as distribution estimates based on the latter are confounded by uneven collecting intensity (Whittaker et al., 2005). Hence likely species occurrences need to be inferred with robust methods from better surveyed areas into undersampled regions.

The currently most common method to generate such data are expert-drawn range maps (Hortal, 2008), where species presence is inferred from a small set of general land cover maps using expert knowledge of species habitat preferences. Authors typically adhere to the precautionary principle and restrict range boundaries to the area enclosed by the outermost documented occurrence points (Schipper et al., 2008). These expert-drawn range maps are inherently restricted to a spatial resolution (grain) of 1° or coarser (Hurlbert and Jetz, 2007). This renders them inadequate for terrestrial conservation planning in practice, where cell sizes of 1–100 km<sup>2</sup> are commonly required, depending on the organism and local habitat heterogeneity (Seo et al., 2009; Boitani et al., 2011; Rondinini et al., 2011).

As a result, our knowledge of continental diversity patterns of large taxonomic groups is currently limited to a grain of 1° or coarser (Ceballos and Ehrlich, 2006; Grenyer et al., 2006; Schipper et al., 2008; Beck et al., 2012; Jetz et al., 2012a), even in the case of well-studied taxa such as birds (Orme et al., 2005; Davies et al., 2007; Jetz et al., 2012b). This knowledge gap frequently impedes efficient conservation planning and implementation at relevant spatial scales (Rondinini et al., 2006; Wohlgemuth et al., 2008). It also limits progress in macroecology as patterns of range size and species diversity may display different spatial structure at finer grains (Rahbek and Graves, 2001; Rahbek, 2005). Data with continental extent and comprising at least one complete – preferably large – taxonomic group are essential in addressing such questions (Jetz and Rahbek, 2002; Belmaker and Jetz, 2011; Beck et al., 2012).

The paucity of fine-grained continental diversity data also limits our knowledge of areas where many small-ranging species co-occur. Throughout this paper we refer to such centres of endemism as ‘rarity hotspots’ in the sense of range size (not abundance); the term ‘narrow endemism’ is largely synonymous (Gaston, 1994; Williams et al., 1996; Jetz et al., 2004). For instance, rarity hotspots identified at a grain of 1° may change once examined at finer grains, because range porosity is common (Hurlbert and White, 2005) and species distributions may hence be allopatric at the landscape scale. This is of significance to conservation planning as rarity hotspots often represent opportunities to efficiently allocate scarce resources (Reid, 1998). For macroecologists, rarity hotspots are of interest because they presumably indicate areas with a pronounced capacity to promote speciation (Endler, 1982; Haffer, 1982), species persistence (Mayr, 1963; Dynesius and Jansson, 2000), or both (Fjeldså and Lovett, 1997). Rarity hotspots should hence coincide with elevated levels of species richness; however, immigration, emigration or extinction in response to changing environmental conditions could lead to spatial incongruence of both hotspot types, casting rarity hotspots as the signature of historical processes within current richness patterns (Jetz et al., 2004). So far most studies addressing this issue with continental to global extent concluded that congruence among hotspots of richness and rarity is low (e.g. Ricketts, 2001; de Klerk et al., 2002; Orme et al., 2005; Ceballos and Ehrlich, 2006; Lamoreux et al., 2006). These studies however were all carried out using a grain of 1° or coarser.

In contrast to expert-drawn range maps and another common method (gridded survey data, see e.g. Araújo et al., 2005; Hawkins et al., 2008), statistical species distribution models (SDMs) can

produce estimates at fine grain while also covering a large geographic extent. They involve less subjectivity than range maps, can arguably identify more complex ecological niches than human experts, and yield transparent predictions beyond the documented range (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005; Franklin, 2009; Elith and Leathwick, 2009). Compiling the required comprehensive and high-quality occurrence data however is still a very laborious task (Larsen and Rahbek, 2003; Boakes et al., 2010; Beck et al., 2013). Hence very few SDM-based studies have been carried out that cover large extents at high spatial resolution and comprise a large and complete taxonomic group (Beck et al., 2012).

Here we set out to model such SDM-derived richness and rarity patterns for nearly all recognized bat species occurring in continental Africa. Relative to its size, Africa has been particularly poorly surveyed to date (Martin et al., 2012). This relative neglect, coupled with rapid human population growth and – often coinciding – high biodiversity values in many areas (Balmford et al., 2001; Hartley et al., 2007), renders Africa’s conservation planning particularly vulnerable to the effects of the Wallacean shortfall (Bini et al., 2006). Continental Africa also corresponds to one of the main biogeographic realms (Cox, 2001; Kreft and Jetz, 2010), with the surrounding water and desert isthmus forming a near-complete natural range boundary for most terrestrial species, and thus a logical modelling extent.

Bats (Chiroptera) represent the second-largest mammalian order globally numbering more than 1270 species (J. Fahr, unpublished data). About 20% of all presently recognized bat species occur in continental Africa, where in turn they account for about 20% of all mammals (Happold and Happold, 2013). About one third of all African bat species are classified as threatened or data deficient in the current IUCN Red List (Mickleburgh et al., 2002; IUCN, 2014). Improved knowledge of their geographic distribution at a finer grain is therefore fundamental to devise timely conservation plans. Fine-grained data of species diversity and range size rarity representing such a large taxonomic group also opens up exciting new avenues of macroecological research, including studies spanning a range of spatial grains.

As the only mammal group capable of powered flight, bats have strong dispersal capacities and successfully colonized all continents except Antarctica (Springer et al., 2011). Both theory and empirical evidence suggest that, compared with less mobile species, the currently realized distributions of bats resemble closely their potential distributions (Munguía et al., 2008). As pollinators, seed dispersers and insect predators bats constitute key players in many ecosystems and contribute substantial ecosystem services to humans (Kunz et al., 2011). They have further been implicated as reservoirs of various diseases relevant to human health (Calisher et al., 2006; Olival et al., 2012; Moratelli and Calisher, 2015). However, due to their nocturnal nature and active flight style, our knowledge of their geographic distributions is low compared with other mammals and certainly compared with birds. Moreover, bat diversity peaks in the tropics where fieldwork conditions are especially challenging. As a result, little is known about continental richness and endemism patterns of bats at grains finer than the 1° inherent to expert-drawn range maps (e.g. Ramos Pereira and Palmeirim, 2013).

We chose a grain of 1 km<sup>2</sup> as this approximates the one at which bat species presumably discriminate and utilize essential habitat resources, and which thus represents the “natural scale of resolution for an SDM” (Austin and van Niel, 2011). Various telemetry studies found home ranges of species to encompass 1 km<sup>2</sup> or less (Davidson-Watts and Jones, 2005; Kerth and Melber, 2009; Weber et al., 2009; Monadjem et al., 2009). Also, while other bat species have been found to forage at larger distances away from their day roosts (up to several tens of kilometres), these were highly selective in terms of habitat use within their home range (Marques et al.,

2004; Russo et al., 2005; Daniel et al., 2008; Popa-Lisceanu et al., 2009; Razgour et al., 2011; Rainho and Palmeirim, 2011; Lehmkuhl Noer et al., 2012; Zeale et al., 2012; Rollinson et al., 2013). At a landscape scale, these findings are corroborated by forest dwelling bats occurring in narrow gallery forests surrounded by vast stretches of atypical (open savanna) habitat (Fahr and Kalko, 2011).

While reviewing the state of the art of current SDM techniques, we found that continent-wide studies tend to follow a one-size-fits-all philosophy. For instance, an exposition of how exactly the selected environmental variables relate to the studied taxon at the chosen spatial grain is rarely provided. Attempts to optimize the frequent trade-off between retaining a large sample size and achieving statistical independence of densely clustered species occurrence records seem rare. How best to transform a species' potential distribution estimate into a plausible approximation of its currently realized geographic distribution remains a largely unresolved issue that may also benefit from a more customized approach. Against this background we have devoted a considerable portion of this study to finding informed solutions to these and other methodological challenges in order to obtain plausible distribution estimates for (nearly) all African bats despite a massive Wallacean shortfall.

The main aim of this study was to create the first high-resolution species richness prediction for African bats across the entire continent. Our second aim was to generate a corresponding map of summed range size rarity ('endemism'). The third aim was to evaluate the amount of spatial congruence between hotspots of these two patterns.

## 2. Methods

### 2.1. Species data compilation

A total of 54 natural history collections were accessed up to July 2008 via GBIF, MaNIS, Arctos, individual museum websites, and via direct communication with curators (see Appendix A). We complemented these records with (largely unpublished) West African field data collected by one of us (J.F. and colleagues) since 1989 as well as occurrence data extracted from about 2000 publications (see <http://afribats.myspecies.info/biblio> for full list). Records from Bioko and islands off the coast of Tanzania were included but those pertaining to other offshore islands (>50 km from the coast) were excluded. To ensure standardized and topical species identification and locality names as well as spatiotemporal accuracy of records, we identified specimens referred to multiple times (possibly under a different name) in the literature and/or museum catalogues and assigned it a common, updated taxonomic determination and identical geographic coordinates (see Appendix B).

We followed the taxonomy of Simmons (2005), with some changes reflecting more recent studies describing new species or removing synonymies except in the following circumstances (for details see Appendix C). First, if some (inconclusive) support was found in either the literature or unpublished datasets that two or more allopatric populations of a given species may in fact constitute separate species, we tentatively produced separate SDMs for these populations. If the resulting predictions showed no or only little geographic overlap, we treated these populations as distinct species for the purposes of this study. For even if such disjoint populations represent a single species, their habitat preferences apparently differ considerably, suggesting some non-stationarity. As stationarity is a central assumption for SDMs, separate models are preferable (Pearman et al., 2010; Gonzalez et al., 2011). Note that in case of fully allopatric populations this decision should not affect derived gradients of species richness (Fjeldså, 2003). Secondly, if the literature suggested or demonstrated that a taxon

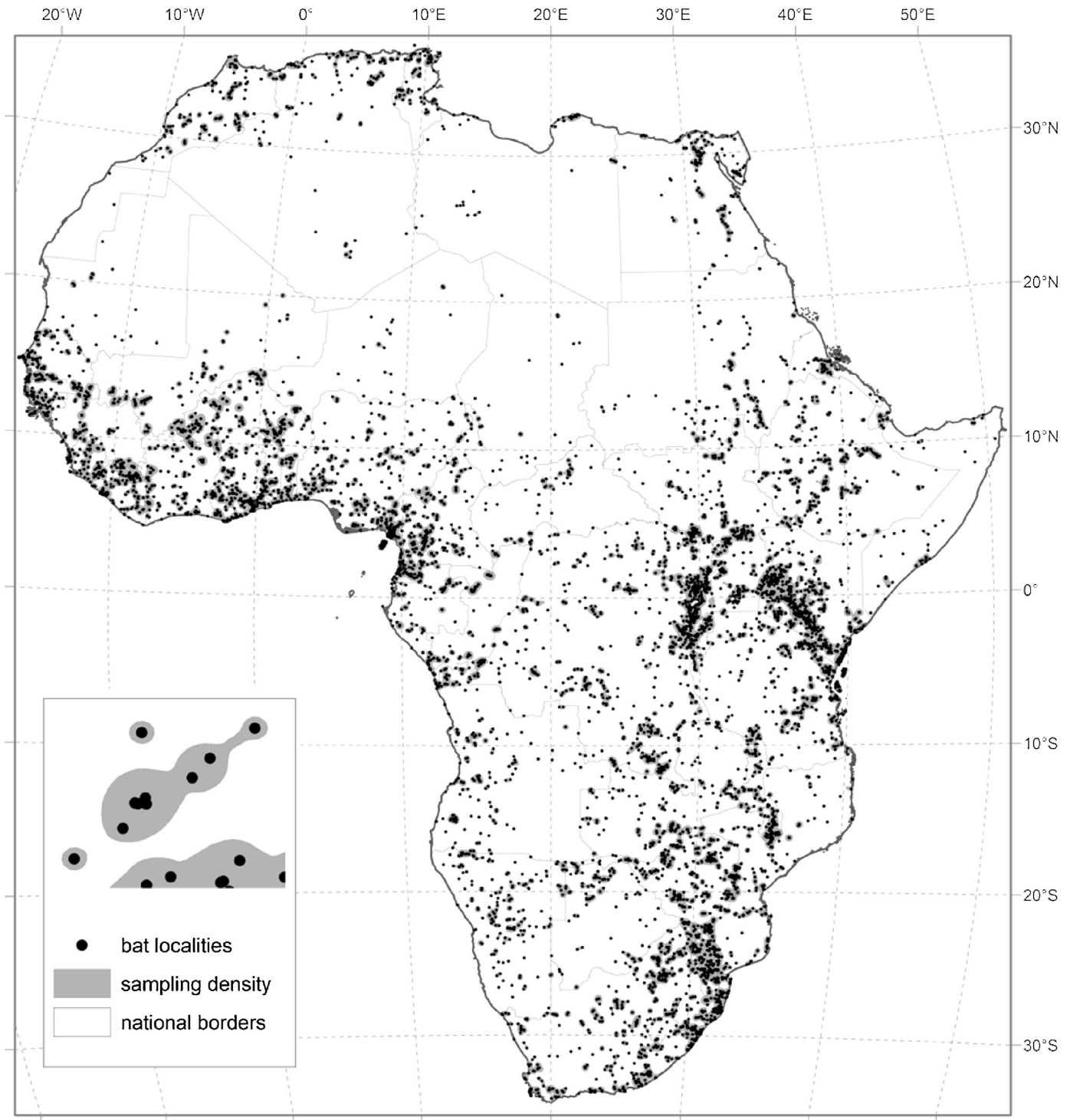
comprised several cryptic species without disentangling the vast majority of affected known records (e.g. Taylor et al., 2012), we retained the single species status but marked it as a species complex (in Appendix C). We consider this approach preferable to the alternative treatment of excluding all affected records entirely. We do exclude however the entire family Miniopteridae since the current taxonomy of African taxa is largely unresolved and likely to comprise a disproportionate level of cryptic diversity (Christidis et al., 2014). Moreover, traditionally defined species boundaries in this group are probably suffering from particularly high levels of phenetic similarity unrelated to real species boundaries (Appleton et al., 2004).

Following the taxonomic scheme outlined above we distinguished 241 bat species, of which 199 (83%) are endemic to continental Africa and another 13 species (5%) also occur on nearby islands (including Madagascar). We refer to this group of 212 species (88%) as 'African endemics' throughout this paper. The documented range of the remaining 29 species (12%) extends beyond Africa into Europe or Asia, sometimes covering only a small fraction of Africa. In the main text we only present patterns obtained by overlaying predicted distributions of all 241 bat species; corresponding results for the reduced set of species are provided as supplementary information.

Our compiled species occurrence data comprised about 9200 point localities (see Fig. 1), which rendered some 27,000 unique species-locality combinations of which 93% could be georeferenced with sufficient accuracy as specified in Section 2.2 and Appendix B.

### 2.2. Species data selection

Spatiotemporal accuracy and taxonomic topicality of compiled presence records varied considerably reflecting the diversity of data sources; older literature for instance often provided geographically valuable but relatively imprecise locality information. To adequately infer habitat suitability given the limited temporal coverage of vegetation and land cover predictors as well as the fine grain employed in this study, we trained models only with records featuring a spatial uncertainty lower than 5 km and a collection date more recent than 1960. The median spatial accuracy of all admitted training localities was 1.3 km, which we regard as reasonably close to the spatial grain at which SDMs were built (1 km<sup>2</sup>). We considered not only the accuracy of a given locality's centre point but also its spatial extent. Localities plotting to areas with high spatial heterogeneity (e.g. mountain slopes) or likely major land cover change before 2000 (e.g. vicinity of large cities, plantations) were examined in Google Earth™, and usually subjected to a much stricter spatial and/or temporal threshold. For about 10% of training localities, we accepted a spatial accuracy of less than 5). W km after manual inspection, because they either constituted the only indication of a species' presence in a severely undersampled region or markedly increased the sample size in case of rarely recorded species. The strict condition was that each of these localities was located somewhere within an area that featured rather homogenous environmental conditions in terms of our predictor set (see Appendix B for full georeferencing details). We concede that a closer spatiotemporal match is desirable as it would yield a more precise species-environment relationship. Enforcing stricter uncertainty and topicality thresholds however would have conflicted with a second aim: retaining a sufficient number of training localities to obtain robust models. With stricter thresholds, sample sizes would have dropped considerably for most species, including many rare ones. Geographic regions would also have been affected unequally, with those difficult to access or characterized by recent political instability losing the vast majority of records, e.g. many records from the Democratic Republic of Congo (DRC).



**Fig. 1.** Spatial distribution of all georeferenced bat occurrences (black dots) and the surrounding sampling effort as quantified by the kernel density estimate (grey area), which we used as custom background for species distribution modelling (SDM) with MaxEnt (see Section 2.4 and Appendix D for details).

While the use of a target group background (see Section 2.4) largely controlled for survey bias, it did not ensure that records were statistically independent. As this is a fundamental assumption of correlative SDMs, we applied a spatial filter to ensure a minimum distance between presence localities used to train individual SDMs (Legendre and Legendre, 1998; Boria et al., 2014). The removal of spatially ‘too close’ presence localities however can lead to the loss of valuable information on the species’ niche when the discarded localities vouch for the suitability of ‘very different’ habitat. In

fine-grained studies and/or spatially very heterogeneous environments this may substantially reduce the accuracy and robustness of SDMs, especially in case of rarely collected species. We therefore devised a novel approach that ensured that presence localities situated geographically ‘too close’ to each other were retained if their distance in environmental space was sufficiently large.

The first step of this approach was to generate a map that delineated classes of ‘very different’ habitat. To this end we performed an iterative unsupervised classification (ISODATA; Ball and Hall,

1965) of the first eight principal components extracted from the set of our environmental predictors, choosing the optimal number of classes based on maximized multidimensional dissimilarity (see Appendix G for details). Next, for each species, we identified all presence points situated in the same habitat class and also within the same cell of a superimposed hexagonal grid, and retained that record with the lowest spatial uncertainty. In case of parity, we favoured the record featuring (1) the more recent collection date, (2) a less disturbed habitat (i.e. situated in a protected area), (3) or more available auxiliary information (in this order). As the use of a single hexagonal grid would have permitted two spatially close records to be retained if situated just across the grid cell border, we repeated the above selection process two more times using two different, spatially offset hexagonal grids (see Appendix G for details). We chose hexagonal grids that measured 40 km in diameter and together ensured a minimum distance between same-habitat records of about 20 km. While this distance remains an arbitrary choice it seems adequate to control for most of the spatial autocorrelation arising from biological processes such as dispersal and biotic interactions (Austin, 2002; Dormann, 2007b). It also resembles in magnitude the spatial filters applied in other SDM studies (Mateo et al., 2012; Benito et al., 2013).

We built final SDMs using all retained records rather than splitting them into training and test data in order to maximize information content (Fielding and Bell, 1997). We attempted to build SDMs for all species, even if very few training localities were available, as our chosen SDM method (MaxEnt) has been found to be relatively insensitive to sample sizes as low as 10 (Wisz et al., 2008), and has produced “useful” results with “high success rates” based on as few as three to five occurrences (Hernandez et al., 2006; Pearson et al., 2007; Ochoa-Ochoa et al., 2009; Vasconcelos et al., 2012; Brown et al., 2014; see also Appendix G). In fact, when working with such small sample sizes, sample bias can constitute a larger problem than sample size (Phillips et al., 2009). We also lowered model complexity by raising the regularization parameter (as described in Section 2.4), which has been found to improve the performance of MaxEnt models when sample size is small (Anderson and Gonzalez, 2011; Shcheglovitova and Anderson, 2013). In addition, SDM predictions based on less than five presence localities received a particularly conservative expert-guided biogeographic clip (see Section 2.5).

For 15 rarely collected species no (reasonable) SDM could be produced (marked as such in Appendix C), of which ten species are known from a single site only. For these 15 species (about 7%) we used a different method to represent their geographic distribution: we determined which GLC2000 land cover classes (Mayaux et al., 2004) were within the spatial uncertainty radius associated with a given record, and then used the area occupied by these land cover classes, confined to a radius of 10 km around the record's georeferenced centre, to represent the species' predicted distribution. Throughout the rest of this paper we refer to these predictions as 'buffer models'.

### 2.3. Environmental predictors

Accurate inference of habitat suitability requires predictor variables that are both relevant and comprehensive enough to effectively capture habitat as perceived by the target organism (Austin, 2002; Dormann, 2007a; Elith and Leathwick, 2009). Both temperature and rainfall conditions are known to impose limits on the ability of bats to forage for food (Erickson and West, 2002), and to survive prolonged hibernation periods or seasonal heat (Hope and Jones, 2012). These climatic factors may also act indirectly by limiting the availability of essential resources (Stevens, 2013). To allow inference of such species-specific physiological constraints we used WorldClim 1.4 precipitation and temperature

data (Hijmans et al., 2005). We computed 10 climatic predictor variables using directly the basic data layers named monthly minimum temperature, monthly maximum temperature, and monthly total precipitation. These comprise 12 monthly datasets each, that in turn represent the respective monthly mean across the covered time period (several decades). For each of the three basic variables we stacked the 12 monthly datasets and calculated the minimum, maximum and standard deviation per grid cell. The nine resulting predictor variables effectively summarized potentially limiting conditions in terms of monthly cold, heat and rainfall conditions that bats will encounter during a typical year in a particular grid cell, both in terms of absolute stress (minima, maxima) and seasonal stress (standard deviation). As rainfall influences resource availability of both insectivorous and frugivorous bat species (Erickson and West, 2002), we also summed the monthly precipitation data to obtain a 10th climatic predictor representing the multi-year average of total annual precipitation.

Within such climatic limits, habitat suitability for bats is further constrained by a range of specific resource requirements, primarily the presence of suitable roost sites and foraging habitat. Because such microhabitat features (e.g. Regnery et al., 2013) require extremely fine-grained datasets that are still under development (e.g. Estes et al., 2010) and not yet available at continental extent, we resorted to the use of proxy variables (Elith and Leathwick, 2009).

Many African bat species depend on caves and rock crevices as day roosts (Happold and Happold, 2013). Such structures are more likely to be found in rugged terrain – irrespective of absolute elevation. To represent areas featuring such suitable roost conditions we computed two ruggedness indices from the SRTM30 V2 dataset (Farr et al., 2007). Specifically, we extracted the range within a  $3 \times 3$  cells neighbourhood as well as the variance within a  $9 \times 9$  cells neighbourhood using moving window analysis. Both predictor variables were  $\log_e$  transformed, multiplied by 10 and then converted from float to integer format to minimize data storage. The two different neighbourhood sizes were chosen to account for differences in how cave-dwelling bats perceive the landscape. In addition, we associated the smaller neighbourhood with elevational range (rather than variance) as proxy for the likelihood of cliffs, which are particularly important to some crevice-roosting bat species.

Freshwater availability is another important predictor of habitat suitability for many bat species, in particular in (seasonally) hot and dry regions, as evaporative water loss during foraging activities must be replenished (Rainho and Palmeirim, 2011). Further, bats have been found to prefer the proximity of water and/or riverine vegetation where insect abundance tends to be higher (Hagen and Sabo, 2011). We developed a freshwater proximity predictor based on a combination of the SWBD (USGS EROS Center, 2002) and HydroSHEDS datasets (WWF WCP, 2007). Specifically, we assigned all cells representing water surfaces (lakes and rivers) the maximum value, all cells further than 10 km from such features the minimum value, and cells with intermediate distances a linearly interpolated value (Gschweng et al., 2012). The threshold distance of 10 km was chosen as known home ranges (see Section 1) are probably smaller for the majority of African bats.

The foraging ability of bats strongly depends on the structural composition of vegetation: dense forests can only be accessed by highly manoeuvrable species equipped with an adequate sensory system, whereas efficient foraging in more open space environments requires fast flight and a sensory system to detect prey at large distances (Norberg and Rayner, 1987; Neuweiler, 1989). As a result, bat species differ tremendously in their tolerance to the structural clutter of vegetation (Fahr and Kalko, 2011; Jung et al., 2012). We selected the main layers of the MODIS Vegetation Continuous Fields dataset Collection 3 Version 3 (Hansen et al.,

2003) – tree cover, herb cover and bare ground – to represent such differences in physical vegetation structure across Africa.

Bats feed on a variety of animals and plants and are often highly specialized on specific resources. These tend to be associated with specific vegetation types as well as specific abiotic land cover characteristics in terms of soil and rock type. To represent such potentially habitat-defining conditions we used two spectral reflectance bands derived primarily from SPOT VEGETATION data (Mayaux et al., 2004) as further environmental predictors. The first band is centred on the red spectrum, i.e. the absorption peak of the chlorophyll, whereas the second band captures the emission in the near-infrared spectrum, i.e. the maximum vegetation spectral reflectance (Vancutsem et al., 2007). We did not combine both variables into a single measure such as the NDVI in order to avoid the associated saturation effect and subsequent loss of information at very high and low reflectance levels (Foody et al., 2001).

When selecting these ecologically relevant predictors, we purposefully avoided the use of categorical variables (e.g. vegetation types, land cover classes) as these datasets are typically general-purpose products using thematic categories poorly suited for a specific target taxon; moreover, they do not capture gradual changes in habitat suitability and contain additional classification errors (Bradley and Fleishman, 2008; Cord et al., 2014). Further details on how we produced environmental predictors are provided in Appendix E.

To facilitate easier evaluation of model plausibility we did not transform predictors (except for the topographical ones as described above), also because MaxEnt internally rescales all derived features to the interval [0,1] (Merow et al., 2013). We accepted substantial multicollinearity between some predictors (see Appendix F) for several reasons: (a) we were not interested in evaluating relative individual predictor importance but in robust habitat suitability predictions (Graham, 2003; Dormann et al., 2013), (b) our preliminary SDMs showed that the chosen algorithm (MaxEnt) was rather insensitive to multicollinearity, which is in agreement with Elith et al. (2010b) and Kramer-Schadt et al. (2013), (c) a small difference between highly correlated variables may in some cases still carry a biologically important signal, such as the one here between the two SPOT-derived variables ( $r=0.935$ ,  $P<0.0001$ ), which would yield an NDVI map (Oindo and Skidmore, 2002), and (d) substantial multicollinearity is inevitable when predictors are spatially autocorrelated (Legendre and Legendre, 1998) and may even be beneficial in some situations (Naimi et al., 2011).

#### 2.4. Statistical model

We used MaxEnt version 3.3.3e (Phillips et al., 2006; Elith et al., 2010b) to statistically infer the ecological niche of species and to estimate their currently realized distributions. MaxEnt does not require absence data, which are nearly impossible to obtain for mobile species such as bats. MaxEnt outperformed most alternative methods in a large study using independent validation data (Elith et al., 2006; but see Peterson et al., 2008), in part because it can fit reasonable models even if sample size is small (Wisiz et al., 2008).

MaxEnt contrasts environmental conditions of sites where a species has been found with those of a random sample across the entire study area (Phillips et al., 2006; Merow et al., 2013). Bat occurrence sites however are distributed non-randomly across Africa, as collectors tend to restrict sampling to areas of special interest and/or those easy to access (see Fig. 1). As the geographic bias in occurrence data brought about environmental bias too (see Appendix D), we employed a target group (TG) background to mirror and thus neutralize it (Ponder et al., 2001; Phillips et al., 2009; Merow et al., 2013). The total set of localities from where bat species have been reported is a reasonable definition of this

TG background (Platts et al., 2008; Phillips et al., 2009; Williams et al., 2010). To account for the fact that the area sampled de facto is usually larger than just the locality from where a bat is reported (because of local movement by both bats and collectors), we enlarged the area around occurrence points beyond the respective 1 km<sup>2</sup> cells. Specifically, we expanded the TG background so that it varied in size between about 10 and 30 km around each presence point using a spatial kernel density estimate (see Appendix G for details; also see (López-González et al., 2012)). We employed the same background data in all species models. To ensure adequate sampling across this large background area, we increased the number of points to 100,000 and maximum iterations to 10,000. As MaxEnt's logistic output format is robust to differences in the number of background points relative to the number of presence points used, we refrained from down-weighting the background data (Phillips and Dudík, 2008; Elith et al., 2010a). To avoid model overfitting when presence points are few, MaxEnt not only reduces the type and number of features employed but also employs so-called regularization (Phillips and Dudík, 2008; Merow et al., 2013). Default regularization settings however produced implausible – usually too restrictive – predictions. Based on extensive experiments with different regularization values for a diverse subset of bat species with well-known habitat requirements we raised the regularization multiplier to 2.5 (Anderson and Gonzalez, 2011). This value resembles in magnitude those found adequate by Razgour et al. (2011) as well as Radosavljevic and Anderson (2013). It has also been suggested by Elith et al. (2010a) “to fit more general models”.

Models were trained with the kernel-based TG background and then projected to entire continental Africa. As this entailed the possibility of encountering novel environments not found in the training data, we set MaxEnt to employ ‘clamping’ and ‘fade by clamping’ (Elith et al., 2010b; Anderson and Gonzalez, 2011). We used the same TG background for all species, because even coarse estimates of current distribution patterns are still unreliable for many species: new presence records continue to be discovered thousands of kilometres away from known localities (e.g. Fahr and Ebigbo, 2003; Bendjeddou et al., 2013). It was hence impossible to determine and use an adequate ‘regional’ species-specific background (VanDerWal et al., 2009; Anderson and Raza, 2010; Barve et al., 2011).

#### 2.5. Post-processing

To obtain species richness values per grid cell we converted each species' continuous logistic MaxEnt output into a binary map. Currently no consensus exists on a single best approach to choosing an adequate threshold, in part because this decision depends on the study aim and dataset characteristics (see Appendix H for a short discussion). Given the fine grain of our study, the low (continental) prevalence of most species, and the recent recommendation to favour restrictive thresholds when stacking binary SDMs to compute species richness (Benito et al., 2013), we selected the highest threshold among all those provided by MaxEnt as a starting point. We then lowered or raised this threshold using expert knowledge about the species' position on the generalist-specialist continuum in terms of habitat requirements. At the same time we aimed at retaining presence predictions near confirmed presence sites while excluding areas with very implausible habitat (Young et al., 2009; Anderson and Gonzalez, 2011). Additional occurrence data that were not used for model building due to age or spatial inaccuracy provided valuable context information at this stage (Platts et al., 2008). Given that this multi-criteria approach involved some subjectivity we provide all chosen thresholds in Appendix C, together with their deviation from the highest MaxEnt threshold.

As we aimed to estimate realized rather than potential species distributions (Jiménez-Valverde et al., 2008; Saupe et al., 2012), we removed predicted but unconfirmed patches if they were deemed too isolated from the core areas of confirmed presence. For instance, several species endemic to southern Africa were also predicted in the opposite hemisphere (North Africa), reflecting the similarity of climates and biomes. The decision to remove such patches was based on expert knowledge of a species' dispersal capacity and major biogeographic barriers (Papeş and Gaubert, 2007; Koleff et al., 2008; Young et al., 2009; Platts et al., 2010; Graham et al., 2010; Williams et al., 2010; Vasconcelos et al., 2012; Greve et al., 2012). Of the remaining patches of predicted presence we usually retained all those situated in areas not surveyed for bats before (as quantified by our kernel density estimate of sampling effort, see Fig. 1).

## 2.6. Model evaluation

We report AUC values for each SDM based on fractional predicted area (Wiley et al., 2003; Phillips et al., 2006; Elith et al., 2006; see Appendix C) but recommend interpreting these (see Section 4.8) as an amalgamated measure of discrimination capacity, prevalence, model complexity, and even sample size (Lobo et al., 2008; Warren and Seifert, 2011; Jiménez-Valverde, 2012; Radosavljevic and Anderson, 2014; Boria et al., 2014; Fourcade et al., 2014). To assist in this interpretation we also report sample size and the effective number of features used (see Appendix C) as measures of model complexity (Yackulic et al., 2013). While the context-dependency of AUC values impedes their interpretation in absolute terms – including a comparison across species – (Jiménez-Valverde et al., 2013), they can still be informative if assessed in relative terms for each species separately. We therefore created additional test SDMs for each species employing cross-validation and resampling using random partitioning (see Appendix I for details). We then computed both the standard deviation of AUC values associated with the test SDMs as well as the difference between the AUC values of our final SDM (using all presence data available) and the (mean) AUC values of the test SDMs (see Appendix C). A low AUC standard deviation and/or small difference between AUC values of the full and test models can be considered an indication of model robustness.

As a measure of model calibration success we report omission errors. In addition, given the mobility of bats, we adopt a more generous view and provide those obtained when expanding the predicted range boundary by up to 10 km (see Appendices C and J; Merow et al., 2013). We further include two “maps of ignorance” that quantify certain aspects of uncertainty residing in species richness estimates that are based on summed binary SDMs (Pearson et al., 2006; Rocchini et al., 2011). The first (see Appendix K) shows the reduction in species richness per grid cell as a result of species-specific biogeographic clipping (see above). The second map (see Appendix L) shows the number of species affected by clamping and thus identifies areas of elevated uncertainty due to the presence of unsampled environmental conditions.

## 2.7. Species richness and range size rarity

We calculated species richness by summing 226 binary SDMs plus 15 buffer models for species without SDMs. Range sizes were measured by counting the number of predicted 1 km<sup>2</sup> presence cells. We created the map of summed range size rarity by first weighting the presence cells of each species by the inverse of its predicted continental prevalence, and then computing the sum of these scores on a cell by cell basis (Kershaw et al., 1995; Blackburn and Gaston, 1996; Williams et al., 1996). As a second measure, and

merely to adequately compare the amount of overlap between richness and rarity hotspots of bats with results of two other studies, we also computed a map of species richness using the quartile of species with the smallest range sizes to serve as alternative measure of ‘endemism’. Both measures, species richness and summed range size rarity, were also calculated for African endemics only ( $n = 212$ ).

## 2.8. Congruence of hotspots

To evaluate the spatial congruence of peaks in richness and summed range size rarity, we first specified a common size (i.e. number of cells) for both hotspot types. Previous analyses have shown that in terrestrial biomes the richest 1–5% of land area can harbour a substantial portion of species (Prendergast et al., 1993; Myers et al., 2000; Orme et al., 2005; Ceballos and Ehrlich, 2006). We therefore measured the congruence of the two hotspot types at both the 1% and 5% size level. Where exact percentages were impossible, we rounded following the method of (Prendergast et al., 1993). The degree of hotspot overlap was determined in ArcGIS 10.0 (ESRI, 2011) by counting the number of cells belonging to either and both hotspot types. This procedure was repeated using the range size rarity hotspots inferred from the quartile of species with the smallest range. Finally, we also carried out this hotspot congruence analysis using only the 212 (about 88%) African endemics.

## 3. Results

### 3.1. Distribution models

We obtained plausible MaxEnt distribution models for 226 species (94% of all species considered). Quality control and spatial filtering reduced the initially available number of localities for each species on average by approximately 40%. A quarter of SDMs were thus trained with 10 localities or less; half the SDMs were based on 25 or more localities (see Appendix C for details).

Omission rates of 1 km<sup>2</sup> SDMs using the full training data were relatively high (median 7.2%). When buffering predicted range boundaries by 10 km however, omission rates were very low (median 0.2%; see Appendix J for details).

Most SDMs obtained can be considered robust, as AUC values of test SDMs dropped by only 3.4% (median) and 4.7% (mean) when compared with the species' AUC value obtained using the full training SDM (Appendix C). As expected from theory (see Section 2.6), we find absolute AUC values strongly correlated with the prevalence of species (Spearman's rho:  $-0.86$ ), and – to a lesser degree – with sample size of training points ( $-0.68$ ), model robustness ( $-0.60$ ) and model complexity in terms of the number of features used ( $-0.55$ ) (see Appendix M).

Bat occurrence data exhibited substantial geographic sampling bias (see Fig. 1), but our TG background effectively controlled for it (see Appendix F). Only 3% of continental Africa was perceived by MaxEnt as featuring an unknown environment, and a mere six SDMs contained areas affected by clamping that were larger than 1% of the species' predicted range (Appendix C). These areas of high model uncertainty were located primarily in the hottest parts of the Sahara with two other, much smaller, patches situated along the very wet West African coast (Appendix L). As shown in Appendix K, biogeographic clipping primarily removed predictions into areas with insular character (e.g. Tibesti Mts in Chad) and/or areas featuring habitat also found in the opposite hemisphere. While this, as intended, resulted in substantially lower richness values in such places, it did not change the general pattern of species richness much: 92% of the study area experienced a net reduction in species richness by at most three species.

### 3.2. Species richness

Predicted richness of all 241 species considered in this study is generally highest near the equator (nearly all of the richest 5% of cells are located within 10°N and 10°S), and lowest in subtropical (desert) zones, where some areas are predicted to have no bat species at all (Fig. 2). Six distinct regional hotspots emerge that harbour the vast majority of the richest 0.1% of cells: the area to the south and east of Lake Volta (Ghana and Togo), the area between Onitsha in Nigeria and south-central Cameroon, the Batéké Plateau area in Congo-Brazzaville, south-eastern Kenya near Lake Victoria, south-western Ethiopia with parts of neighbouring South Sudan, and the northern Albertine Rift along the border of Uganda and the DRC. The latter area contains all cells with richness surpassing 74 species including the maximum (84) on the Semliki River south-west of Lake Albert. Pronounced regional hotspots also form at intermediate richness levels (e.g. the Nuba Mts in Sudan and around Lake Kariba on the Zambezi River). Predicted richness gradients can be very steep: especially in savanna biomes predicted richness often varies by 30 species over distances as short as 20 km – and sometimes even over distances of 2 or 3 km only (e.g. in Senegal and Zimbabwe). At such landscape scales, richness appears to positively correlate with an area's proximity to either the hydrological network or steep sloping terrain (see inset of Fig. 2).

The pattern obtained for the 212 African endemics is qualitatively very similar except that species richness is substantially lower across North Africa, rendering large parts of the Sahara desert void of bats (see Appendix N).

### 3.3. Range size rarity

Predicted range sizes vary among bat species by more than five orders of magnitude, ranging from about 200 km<sup>2</sup> (continental prevalence 0.001%), representing species known from only a single locality, to over 14,000,000 km<sup>2</sup> (prevalence 49%). The predicted median range size is about 1,500,000 km<sup>2</sup> (prevalence 5.16%; see Appendix C for species data).

The summed range size rarity map shows six hotspot regions: (1) the hills between western Guinea and western Ivory Coast and parts of the Liberian coast, (2) the Mt Cameroon area including the western escarpment of the Bamenda Highlands (Fig. 3, inset) – slightly less pronounced, this hotspot extends also southwards into Equatorial Guinea, (3) the area between northern Gabon and the Congo River, (4) the Eastern Arc Mts in Tanzania and adjacent coastal areas, (5) the Ethiopian highland, in particular the western part, and (6) the Albertine Rift between Lake Albert and Lake Tanganyika including the Kivu region to the west. The latter rarity hotspot may seem less pronounced in Fig. 3 but it is of primary rank as it holds more endemic species as the one in Cameroon. These species do not show up as strongly as they potentially could because reasonable SDMs could not be produced given the paucity of presence records. The higher level of rarity in the southern parts of Ivory Coast and Ghana represents a rarity hotspot of secondary rank. This area does not contain any endemic bat species; its rarity score is driven by a relatively high number of species with intermediate range sizes. Outside these six regions a dozen very small rarity hotspots can be discerned (brown 'speckles' in Fig. 3); in most cases these represent species accounted for using a buffer model instead of an SDM. These rarity hotspots are thus qualitatively different from the larger ones described above, as the buffer models do not interpolate between or extrapolate beyond known occurrences, and often represent the only documented presence localities for a species. By contrast, hotspots surrounded by moderate levels of rarity (orange and yellow areas in Fig. 3) typically involve more than one relatively rare species.

In North Africa predicted rarity hotspots are largely based on species whose geographic ranges extend into Europe or Asia. If these 29 species are excluded, only the hotspot in eastern Libya persists; the pattern in sub-Saharan Africa remains essentially unchanged (Appendix O).

### 3.4. Congruence of richness and rarity hotspots

If richness and rarity hotspots are defined as the 1% of cells containing the highest species richness and summed range size rarity score, respectively, spatial congruence of both amounts to 7.3% of their joint area. Relaxing the hotspot definition to comprise the highest ranking 5% of cells increases their spatial congruence considerably to 42.0%. Results of an exploratory analysis using intermediate and larger hotspot sizes suggest a robust, slightly curvilinear relationship, which remains similar when the analysis is repeated for African endemics (see Appendix P). In that case however, congruence of richness and rarity hotspots at the 1% and 5% levels is consistently higher (18.4% and 54.3%, respectively).

Richness and rarity hotspots coincide at the 1% size level in only five regions. The largest comprises the lower slopes of Mt Cameroon, the hills to the north and east, and the western escarpment of the Bamenda Highlands (Fig. 4a). A second area of congruence, much smaller and fragmented, extends from south-central Cameroon to south-eastern Gabon. Other shared hotspots are located in West Africa between south-western Guinea and central Liberia, in the Albertine Rift between the Ruwenzori Mts and Lake Kivu, and in East Africa between the Udzungwa Scarp Mts in Tanzania and the Malindi region in Kenya (Fig. 4).

If hotspots are defined as the highest ranking 5% of cells, a much larger area of congruence is discernible (see yellow areas in Fig. 4). In West Africa, the overlapping area now comprises half of Liberia and a second large hotspot emerges that covers most of southern Ivory Coast, southern Ghana and parts of Togo. The Mt Cameroon area of congruence now extends into Equatorial Guinea, northern Gabon and southern Nigeria. Along the eastern edge of the Congo basin, a new area of congruence can be observed, and the one in the Albertine Rift Valley now extends into western Uganda and far west into the Congo basin. Parts of the Kenyan highlands as well as south-western Ethiopia now also harbour some (small) areas of congruence. Notably, at this less strict specification of hotspot size, hotspot congruence in the Eastern Arc Mts (Fig. 4c) and south-eastern Gabon increases only marginally.

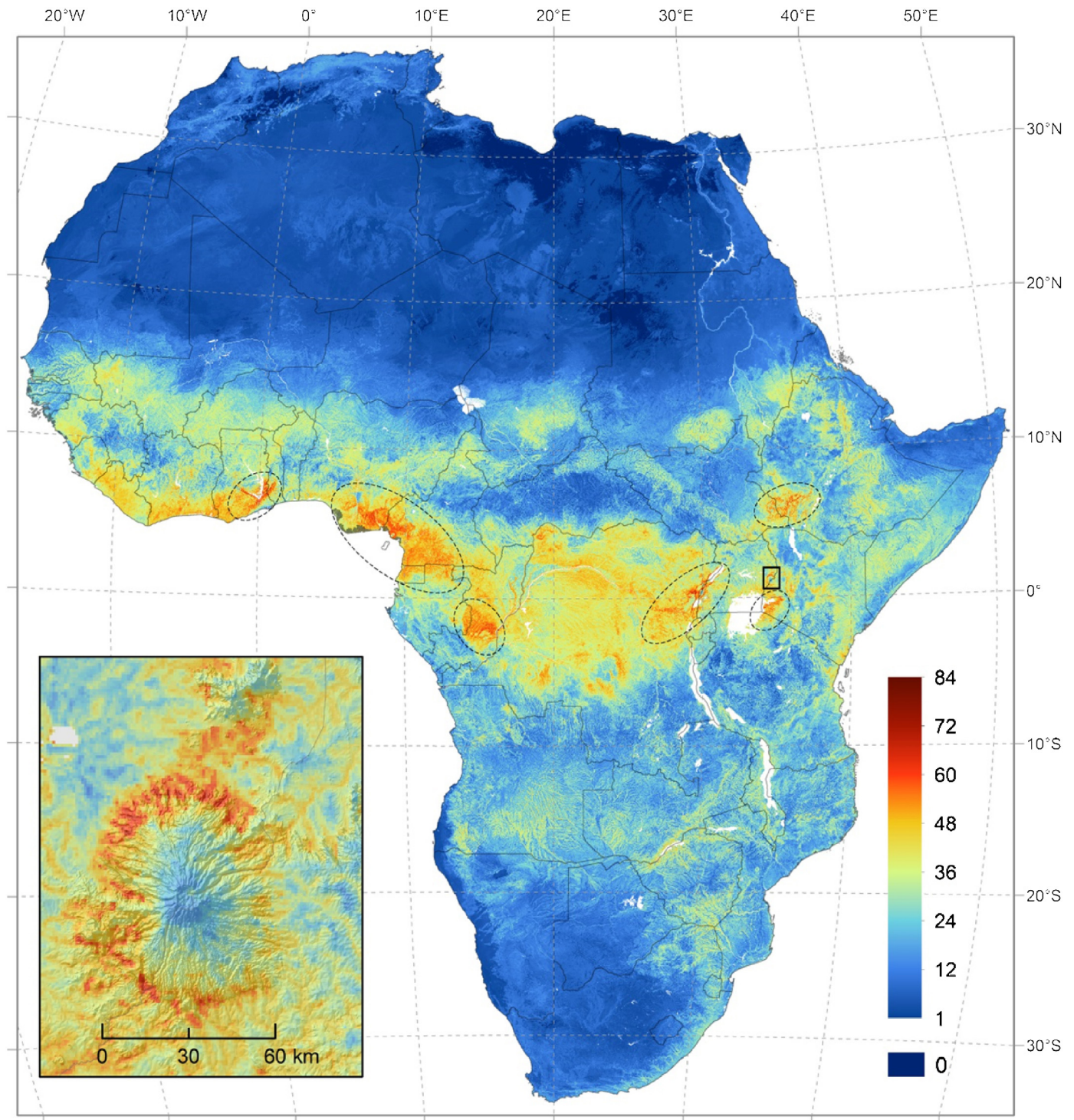
When the 29 species whose geographic ranges extend beyond continental Africa are excluded from this analysis, the pattern of spatial congruence of richness and rarity hotspots is nearly identical if the highest ranking 5% of cells are used to define hotspots (congruence in the central Congo Basin increases slightly). If hotspots are defined as the top 1% of cells however, both hotspot types also coincide in parts of southern Ivory Coast and southern Ghana, in the coastal hills of Cameroon and Equatorial Guinea, as well as in the North Kivu province of eastern DRC (see Appendix Q).

## 4. Discussion

### 4.1. Opportunities arising from stacked fine-grained SDMs

High resolution species diversity data that comprise large taxonomic groups and continental extents are of major interest to macroecological research yet they are still extremely scarce (Beck et al., 2012). Here we present the first fine-grained model of continental African bat richness. Such diversity data will advance our understanding of the role local processes play in generating large-scale macroecological patterns (Levin, 1992; Belmaker and Jetz, 2011), and open new avenues exploring the effects of scale on



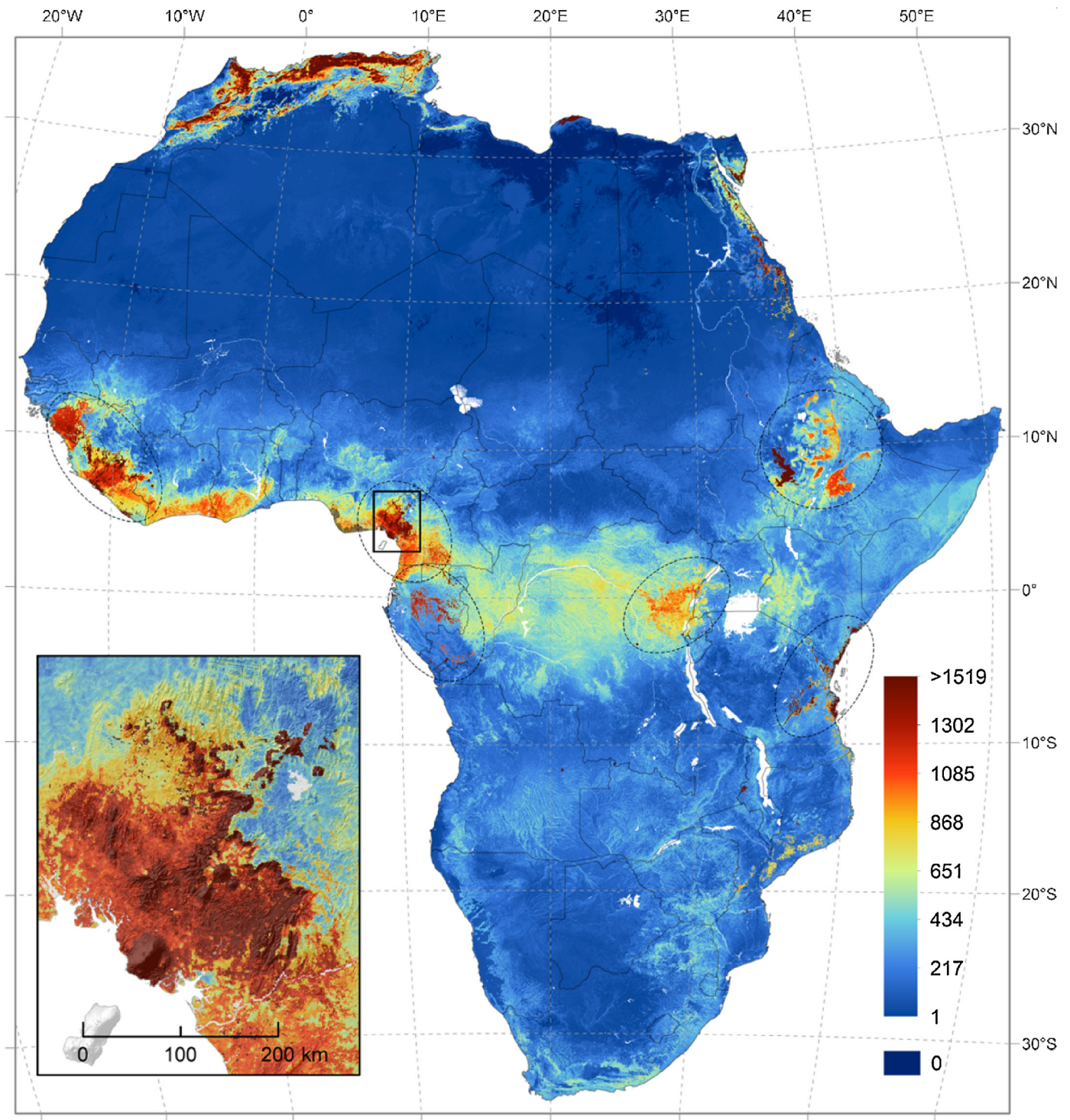


**Fig. 2.** Predicted species richness of African bats ( $n = 241$ , excluding *Miniopterus* spp.) at  $1 \text{ km}^2$  spatial grain. The inset shows the area around Mt Elgon and illustrates the apparent association of richness with the hydrological network and/or steep sloping terrain; topography shown by hill-shading (SRTM). Dotted ellipses indicate the six richness hotspots mentioned in the text.

species richness (Rahbek, 2005) across grains orders of magnitude finer than the  $1^\circ$  resolution still common in continental studies (Rahbek and Graves, 2001; Grenyer et al., 2006). Conservation planning too stands to benefit from such fine-grained diversity data given the often rather small extent of management units, increasingly fragmented landscapes, and shifting species ranges in response to climate change (Trivedi et al., 2008; Randin et al., 2009).

In contrast to richness estimates generated using macroecological theory (e.g. Buckley and Jetz, 2007) we derived species richness by stacking the modelled ranges of individual species. This approach also allowed us to create the first summed range size rarity map for African bats.

The underlying fine-grained large-extent data on species range sizes, range configuration and assemblage composition should be of high value to devise efficient conservation strategies

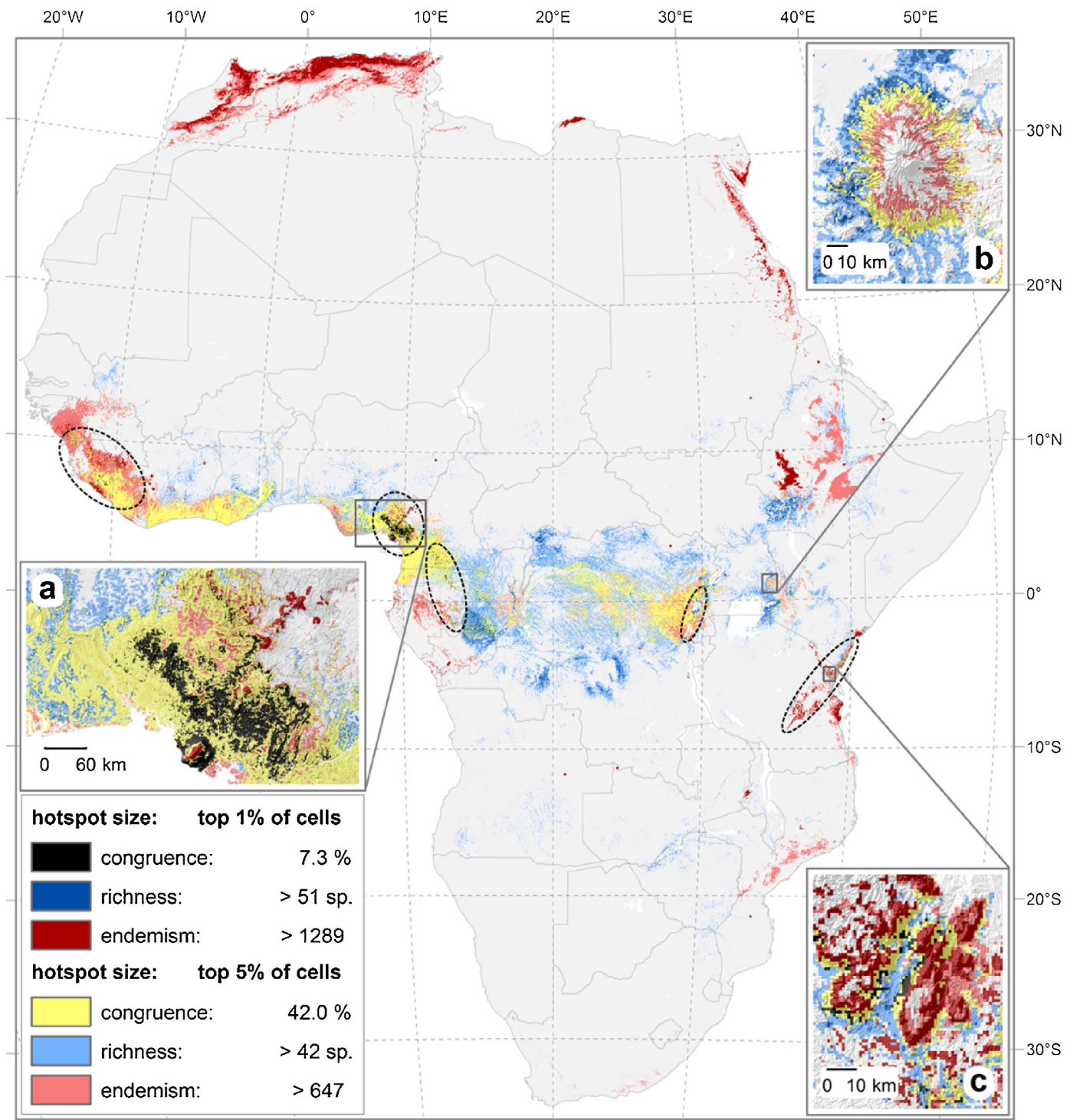


**Fig. 3.** Predicted endemism pattern of African bats ( $n=241$ , excluding *Miniopterus* spp.) at  $1\text{ km}^2$  spatial grain. Endemism was quantified here by summing the range size rarity scores of all species predicted to occur in a given cell. The inset zooms in on the pattern along the Cameroon volcanic line; topography shown by hill shading (SRTM). Due to the strong skewness of the distribution, data are mapped with a linear colour stretch truncated at one standard deviation (1519). Dotted ellipses indicate the six range size rarity hotspots mentioned in the text.

based on the principle of complementarity and/or focused on rare (often threatened) species, especially when targeting data-poor regions (Araújo et al., 2005). Similarly, the data may help select an optimal set of monitoring sites to inform so-called ‘essential biodiversity variables’ that have recently been proposed to harmonize global biodiversity monitoring (Pereira et al., 2013).

#### 4.2. Species richness patterns

The possibly most striking pattern in our results is the ubiquity of steep richness gradients over only a few kilometres (Fig. 2). This phenomenon can be observed across the entire study area except in very arid regions lacking freshwater resources, and it is most pronounced in tropical savannas. It seems positively correlated with



**Fig. 4.** Spatial congruence between hotspots of species richness and endemism (quantified here as summed range size rarity). If hotspots are defined as the highest ranking 1% of cells, the area of congruence is very small (shown in black and surrounded by dotted ellipses). If hotspots are defined as the highest ranking 5% of cells, the area of congruence is considerably larger (in yellow). Areas shown in blue and red depict those richness and endemism hotspots, respectively, that do not overlap – neither at the 1% nor at the 5% hotspot size level. (For interpretation of reference to color in this figure legend, the reader is referred to the web version of this article.)

the proximity to streams and lakes although occasionally amplified by rugged terrain in the vicinity of the hydrological network. An association of bat richness with freshwater resources is ecologically plausible. A strong affinity of bats to water bodies has not only been found in semi-arid Mediterranean regions (Carmel and Safriel, 1998; Scott et al., 2010; Razgour et al., 2010; Rainho and Palmeirim, 2011; Lisón and Calvo, 2011) but also in central Europe,

where water is not a limiting resource (Ciechanowski, 2002; Scott et al., 2010; Zeale et al., 2012). In (sub)tropical savanna habitats, it may also be the structurally complex riparian vegetation that constitutes the essential habitat element rather than water per se (Rautenbach et al., 1996; Aguirre, 2002; Milne et al., 2006). In Swaziland, Monadjem and Reside (2008) found that species richness in riparian habitat was twice as high as in the surrounding

savanna and that community composition between both habitat types was very different (the non-riparian community being a subset of the riparian one). In northern Ivory Coast, [Fahr and Kalko \(2011\)](#) found high species richness in gallery forests situated in a naturally fragmented forest-savanna mosaic. Their results suggest that the relative permeability and linear arrangement of these forests allow bat species specialized on forest, open savanna and edge vegetation alike to use such habitat. Further, gallery forests along large rivers may connect populations of forest species over several hundred kilometres with more isolated populations in the forest-savanna mosaic. Together, these studies demonstrate how strongly bat species select for specific habitat over short distances. The signature of the hydrological network in our fine-grained richness prediction seems therefore plausible.

Species richness also appears to be positively associated with moderately rugged terrain (topodiversity over very short distances), although the strength of the relationship seems to decrease with increasing elevation and forest cover (see e.g. Sierra Leone, central Albertine Rift, south-western Ethiopia, northern Mozambique, and also the inset in [Fig. 2](#)). Such a topographic signal is ecologically plausible too: at the landscape-scale (spanning a few km) rugged terrain increases the likelihood of suitable roost sites for cave-dependent species, and these constitute roughly a third of all African bats ([Happold and Happold, 2013](#)). In fact, Mt Nimba in West Africa was recently found to boast Africa's highest richness of hipposiderid species (a largely cave-dependent family; [Monadjem et al., 2013](#)). Low richness levels in areas with very little topodiversity, e.g. on the Batéké Plateau north of Kinshasa and along the Nile flats in South Sudan, reinforce the notion of a positive association between bat richness and rugged terrain. The proximity of a major elevational range however does not seem to co-determine the location of bat richness hotspots – in contrast to hotspots of range size rarity (see Section 4.6). For instance, elevational differences above 500 m within a radius of 100 km do not exist in many species-rich areas such as southern Ivory Coast or the northern, western and southern rim of the Congo Basin.

Within the tropical zone, predicted richness frequently peaks near the base of mountains and escarpments; on mountains with a relatively dry base (e.g. Mt Elgon, Kenya) this peak tends to be slightly further upslope – but still near the base – than on those with a wet base (e.g. Mt Cameroon). The pattern would agree with the one found by [McCain \(2007\)](#) and [Curran et al. \(2012\)](#), as would the apparent mid-elevation richness peak for the Atlas Mts (temperate zone, dry base).

Our predicted bat richness pattern agrees broadly with the one that [Monadjem et al. \(2010\)](#) and [Schoeman et al. \(2013\)](#) have presented for southern Africa, in that bat richness is high in topodiverse areas between Lesotho and Malawi and low in the drier western region. For both Angola and northern Mozambique however we predict relatively higher levels of richness. This difference is most likely due to the smaller geographic extent of these studies which impedes inference of the full ecological niche of those species whose geographic ranges extend only marginally into the study areas. Consequently, richness patterns reported in these and other fine-grained regional studies of African bats ([Pio, 2010](#); [Leach et al., 2013](#)) only comprise about two thirds of the regional species pool.

The predicted peak of African bat richness near the equator is in agreement with (coarse-grained) latitudinal studies of New World bat richness ([Willig and Lyons, 1998](#); [Stevens, 2004](#); [Tello and Stevens, 2010](#); [Ramos Pereira and Palmeirim, 2013](#); [Arita et al., 2014](#)). Interestingly though, our fine-grained analysis also predicts several small patches of high richness (belonging to the top 1% of cells) at latitudes as high as 25°S (in Kruger National Park, South Africa). Here we do not evaluate our results in light of macroecological hypotheses as we intend to present quantitative analyses in separate papers. Instead, we have focussed on assessing the

plausibility of predicted patterns in light of field-based data and with reference to other published patterns rather than hypotheses of species richness gradients.

#### 4.3. Potential sampling artefacts

The species richness model presented here ([Fig. 2](#)) features several areas within tropical Africa where richness is substantially lower relative to their surroundings. The most obvious of these apparent coldspots comprises most of the Central African Republic (CAR), but several others – albeit smaller in size – can be discerned. Some of these seem plausible such as very dry north-western Kenya and the cold highlands of Ethiopia. Those situated in relatively flat areas, too, e.g. the Nile River plain in South Sudan and the coastal flats in southern Somalia, could be explained invoking the apparent association of richness with rugged terrain discussed above. The large coldspot in the Central African Republic however, the smaller one comprising eastern Guinea and north-western Ivory Coast, as well as the mosaic of apparent coldspots extending from north-eastern Angola to central Tanzania and southwards into Mozambique, all seem rather implausible: they comprise tropical forest-savanna mosaics or woodlands ([Olson et al., 2001](#); [Mayaux et al., 2004](#)), and feature an intermediate tree cover of about 30–50%. Large-scale human activities too (e.g. major deforestation or rapid urbanization) are relatively rare in these areas according to Google Earth™ imagery. While some riparian areas within these coldspots are predicted to reach intermediate richness levels, it still seems odd that bat richness (away from streams) in such centrally located environments (in terms of vegetation cover, climate, topodiversity and geography) should be as low as along the southern rim of the Sahara desert.

We therefore inspected sampling effort more closely and found that these coldspots are all associated with the same three habitat classes (10, 11 and 19) – out of 68 characterizing bat habitat across continental Africa (see [Appendix G](#)). We also found that sampling effort in these habitat classes has not been as intense as in other classes representing savanna and forest biomes (see [Appendix R](#)). At the same time, although environmental conditions in these classes were obviously sufficiently unusual to form distinct habitat classes, MaxEnt interpreted these environments as very familiar – especially the riverine elements (see [Appendix S](#)). The reason for this may have been the intermediate position of these three classes in terms of climate, topodiversity and land cover compared with continental Africa. The coincidence of these two factors may well have caused MaxEnt to underestimate relative habitat suitability in most parts of these habitat classes. Note that we examined whether the carefully prepared kernel-enhanced TG background successfully controlled for uneven sampling effort across Africa ([Appendix D](#)). The assessment however was made using mean continental values; strong regional sampling bias (e.g. in the habitat areas discussed here) may thus have escaped notice. It hence seems likely that most of the CAR, parts of Guinea and Ivory Coast, the miombo woodlands in Angola and north-western Zambia, as well as the coastal forests in central Mozambique, harbour a higher species richness than currently predicted.

#### 4.4. Targets for future surveys

All coldspots discussed above represent rewarding targets for future surveys because the few sampling sites in the past have revealed surprisingly heterogeneous bat faunas given the distinct, relatively homogenous environment these areas represent (see [Appendix R.2](#)). A second set of promising survey targets are apparently species-rich but hitherto unvisited areas. These include a hilly region in western Mali, the Batéké Plateau area in Congo Brazzaville, and the steep valleys of south-western Ethiopia, all of which have

largely been ignored by past surveys (also see [Appendix T](#)). Recent studies have shown the relative success of SDM-directed survey campaigns aimed at discovering new populations ([Greaves et al., 2006](#); [Rebello and Jones, 2010](#); [Costa et al., 2010](#); [Newbold et al., 2010](#); [Searcy and Shaffer, 2014](#)), or even new species ([Raxworthy et al., 2003](#)). In this context, the map showing areas predicted to support more bat species than we deemed likely given biogeographic dispersal barriers could also be informative ([Appendix K](#)). Further, these areas are all predicted to display steep richness gradients over short distances – a pattern future fieldwork could validate too. Finally, we draw attention to several regions in sub-Saharan Africa that have been systematically neglected by past natural history collectors, possibly due to reduced accessibility: southern Botswana, south-east Angola, southernmost and north-east Mozambique, eastern CAR, south-central Chad and central Somalia (see [Fig. 1](#)). These gaps largely coincide with those of other taxa, including ticks ([Cumming, 2002](#)), birds ([Reddy and Dávalos, 2003](#)), plants ([Küper et al., 2006](#)), palms ([Blach-Overgaard et al., 2010](#)), and dragonflies ([Clausnitzer et al., 2012](#)).

#### 4.5. Species richness calibration

Our estimate of bat richness constitutes an upper bound to richness for at least two reasons. Individual SDMs could not account for all potentially constraining factors due to unavailable knowledge or data ([Hirzel and Le Lay, 2008](#)). Second, species richness itself may be constrained by environmental conditions (e.g. [Boucher-Lalonde et al., 2013](#)), which our approach of stacking individual SDMs cannot account for. However, the aim of the present paper is to infer plausible gradients of species richness; absolute levels of species richness are of secondary interest ([Vasconcelos et al., 2012](#)). We therefore do not assess calibration success systematically here but merely provide a general indication – also for lack of a sufficiently high number of exhaustively sampled fine-grained ground truth data to carry out a full validation exercise.

Overall, absolute richness values seem rather realistic in most cases: for some inhospitable areas (e.g. sand dunes in north-western Sudan) our richness estimate is zero. For an intensively sampled forest-savanna mosaic in Comoé NP (Ivory Coast) some 45 km<sup>2</sup> in size, our prediction of 58 species (for the entire area) is close to the estimated species richness of 60–62 (observed: 55) reported by [Fahr and Kalko \(2011\)](#). Similarly, our richness prediction for the entire NP (72) is very close to their estimated range (65–71). For an equally intensively sampled rain forest area in Taï NP (Ivory Coast) about 6 km<sup>2</sup> in size, the fieldwork derived richness estimate of [Fahr and Kalko \(2011\)](#) is 41–44 species (observed: 39) whereas our distribution models predict the presence of 47 species. For the entire Taï NP however, our prediction (61) deviates substantially from the range (44–50) estimated by these authors. Our model also appears to overestimate richness at the highest elevations, as it predicts 10–15 species to occur at 4100 m a.s.l. (in the mountains of the Albertine Rift even more species), whereas this elevation is given as the currently known limit to bat distributions in the review by [McCain \(2007\)](#). The data we compiled for this study, too, do not contain records of bat occurrence above this elevation.

Temporary absence of bat species in areas principally both suitable and accessible is common, even at the fine grain chosen here. Reasons include local population dynamics, interactions with other species, nomadism or migratory behaviour and stochastic events. Yet, this should be of little concern for evaluating model calibration, as the SDMs presented here were designed to estimate the currently realized geographic distribution of a species regardless of temporary absence – and field-based presence data convey the same information.

#### 4.6. Range size rarity patterns

Hotspots of summed range size rarity ('rarity hotspots') appear generally associated with areas of higher topodiversity and tend to be located near major elevational ranges that constitute 'continental islands'. This finding is in agreement with theory and previous empirical studies ([Diamond and Hamilton, 1980](#); [Fjeldså and Lovett, 1997](#); [Jetz and Rahbek, 2002](#); [Jetz et al., 2004](#)). Most rarity hotspots are situated near the equator but some less pronounced ones can also be found at higher latitudes, e.g. in Libya and central Mozambique. Rarity hotspots seem also more dispersed than richness hotspots ([Fig. 4](#)), as found for birds globally ([Orme et al., 2005](#)). Mountains, in particular tropical ones, have previously been identified as rarity hotspots around the globe for a range of taxa including mammals, birds, amphibians, lizards and plants, both at coarse grains with continental-to-global extents ([Jetz and Rahbek, 2002](#); [Ceballos and Ehrlich, 2006](#); [Rahbek et al., 2007](#); [Sandel et al., 2011](#)) and at fine grains with regional extents ([Young et al., 2009](#); [Raes et al., 2009](#); [Bell et al., 2010](#)).

Few studies have examined this relationship for bats. [Tello and Stevens \(2010\)](#) found that New World bats with small range sizes primarily occur in the mountain ranges extending from central Mexico to central Peru – but much less so in the tropical mountains of the Guiana Shield. In a finer grained study of Mexican bats (using a grain of 0.25° instead of 1°), [Vázquez and Gaston \(2004\)](#) found a more pronounced association of rarity hotspots with tropical mountains, but uncertainty remained as only 11% of bat species analyzed were fully endemic to the country. We note that the majority of African bat species recently described as new to science (see [Appendix C](#)) – most with presumably small ranges – were found in highly topodiverse areas.

Comparing the continental rarity pattern of bats with those reported for other African taxa is challenging for at least three reasons. One, different methods have been used to quantify rarity based on range size (applying weights vs. choosing species subsets; adjusting for local richness or not). Two, hotspot size definitions vary because they are ultimately an arbitrary choice. Three, our spatial grain is two orders of magnitude finer than in previous continental studies. With these caveats in mind, some general observations can be made.

Most rarity hotspots of bats coincide with those of other taxa, especially the Mt Cameroon area, the Albertine Rift and Kivu area, and the Eastern Arc Mts including the adjacent coast. All three constitute major continental rarity hotspots and rank globally among the top 'centres of endemism' for many taxa ([Lovett et al., 2000](#); [Linder, 2001](#); [Brooks et al., 2001](#); [de Klerk et al., 2002](#); [Fjeldså, 2003](#); [Jetz et al., 2004](#); [Küper et al., 2004](#); [Orme et al., 2005](#); [Ceballos and Ehrlich, 2006](#); [Schipper et al., 2008](#); [Sandel et al., 2011](#)). The Ethiopian rarity hotspot predicted in our study has also been identified as such for mammals, snakes, amphibians and birds, but not for plants ([Küper et al., 2004](#)); for birds it depends on how the size of the hotspot is chosen ([Fjeldså, 2003](#)). Other rarity hotspots frequently reported are the Kenyan highlands, parts of Somalia, western Angola, the Katanga area, the coastal escarpments of Namibia and South Africa, and the area between southern Malawi and western Zimbabwe. None of these emerge as major rarity hotspots for bats (given the measure of rarity used here) except for the latter region, for which we predict a moderately pronounced rarity hotspot. Finally, the rarity hotspot between western Guinea and western Ivory Coast, which contains the highest number of strictly endemic bat species (10), has also been reported as a major rarity hotspot for amphibians ([Brooks et al., 2001](#); [Penner et al., 2011](#); [Sandel et al., 2011](#)) and plants ([Küper et al., 2004](#)), but not for mammals ([Ceballos and Ehrlich, 2006](#); [Schipper et al., 2008](#); [Sandel et al., 2011](#)). For birds, too, this hotspot is rarely predicted

(Fjeldså, 2003; Orme et al., 2005; Sandel et al., 2011), except when geometric range size constraints are incorporated (Jetz et al., 2004).

#### 4.7. Congruence of hotspots

The amount of spatial overlap between richness and rarity hotspots of African bats varies substantially depending on the definition of hotspot size and the range size rarity measure used. Overlap is relatively small (7%) if a strict hotspot definition is employed (the highest ranking 1% of cells) and quite large (42%) when a more liberal definition is used (the top 5% of cells). In both cases however, richness and rarity hotspots coincide primarily in topodiverse humid areas situated near major elevational ranges (Fig. 4). In some regions both hotspot types barely overlap (e.g. in Ethiopia and the Kenyan highlands), whereas they do extensively in other regions (e.g. West Africa and Mt Cameroon area, see Fig. 4a). Local elevational gradients often show rarity hotspots centred at slightly higher elevations than richness hotspots, for instance on Mt Elgon in Uganda (Fig. 4b) and in the Usumbara Mts of northern Tanzania (Fig. 4c). Across continental Africa however, both hotspot types are situated at approximately the same elevation as a number of highly endemic species occur in low lying coastal regions near the equator. Overall, areas of congruence have a median elevation of 302 m and 397 m (with hotspot size defined as the highest ranking 1% and 5% of cells, respectively).

To adequately compare our results with other studies, we also calculated the degree of overlap using hotspots defined as the highest ranking 2.5% of cells. Using this definition, richness and rarity hotspots for bats show an overlap of 25% – markedly more than the 18% found for non-volant mammals (Ceballos and Ehrlich, 2006) and the 10% found for birds (Orme et al., 2005). The overlap is even higher (~35%) when only bat species endemic to Africa are considered (Appendix P). Given that the aforementioned studies were carried out with a grain of 1° we expected that hotspot overlap would be generally lower in our fine grained study: ranges of widespread species tend to have substantial porosity (Hurlbert and White, 2005), and fine-grained distribution maps are better than coarse-grained ones in delineating potentially allopatric distribution patterns and thus separating richness patterns of wide- and narrow-ranging species. We hence recomputed hotspot congruence for bats using not only the same hotspot size definition as the aforementioned studies but the same rarity measure too: species richness of the smallest range size quartile. Overlap at the 2.5% level was now reduced to 8%, i.e. slightly smaller than the one found in birds and about half the overlap reported for non-volant mammals (see Appendix P). Birds are similar to bats in terms of mobility (see also Ricketts, 2001), and range sizes of non-volant mammals are typically smaller than those of bats (Vázquez and Gaston, 2004), which increases the likelihood of higher hotspot congruence in that group. Against this background, we conclude that the magnitude of hotspot congruence predicted here for African bats is plausible.

#### 4.8. SDM challenges and solutions

To achieve our aim of creating plausible and robust SDMs we paid special attention to a number of methodological issues including (1) selecting predictors relevant to the target organism, (2) threshold setting when converting MaxEnt outputs to binary predictions plus subsequent biogeographic clipping, (3) reducing sample bias without overly reducing sample size, and (4) evaluating models using more criteria than a high AUC value.

When selecting environmental predictors, we followed two principles: to only use reasonably proximal variables (Austin, 2002), i.e. those that are likely to affect the biological fitness of bats relatively directly, and to ensure that the final variable set describes comprehensively the diverse ecological requirements of

bats in terms of ecophysiology, habitat characteristics and resource availability. We are confident to have achieved both aims within the limits of currently available (remotely sensed) data. Still, our selection remained incomplete as we did not include predictors representing food resources, nor biotic interactions in general. However, neither are species-specific requirements sufficiently known for most bats, nor are such data available (yet) at a pan-African extent and sufficiently fine grain. For similar reasons, we also chose to train all SDMs with the same set of predictors – with the exception of a few high-flying species (marked as such in Appendix C) for which we omitted the freshwater proximity predictor to mitigate sampling bias effects since these species have been predominantly caught when descending to drink from open water bodies.

Our environmental predictors calculated directly from WorldClim data were in part identical with the BioClim variables that Hijmans et al. (2005) provide as a complementary dataset. We decided against using the entire set because composite variables such as “minimum rainfall of hottest month” tend to have steeper gradients than pure rainfall or heat variables (Elith et al., 2010a). Yet, to what degree they directly (functionally) constrain habitat suitability is often unclear. The inclusion of such complex predictors of uncertain relevance raises the risk of training models based on spurious correlations and may thus result in overfitted models (Peterson and Nakazawa, 2008). Several BioClim ratio variables also contain regions with very abrupt and step-like rather than gradually changing values, especially in very dry areas; we preferred avoiding the risk of training models with partially unrealistic environmental gradients.

Seasonally changing climatic conditions may constrain bat distributions in two ways: extreme heat or cold constitute ecophysiological limits (Arlettaz et al., 2000; Welbergen et al., 2008), whereas generally high variability around mean conditions may be thermoregulatory costly but not render the specific locality inhabitable. In addition to climatic minima and maxima we hence included standard deviation of rainfall and temperature variables into our predictor set, as this measure of spread provides a more robust quantification of seasonal climatic variability than for instance range (which MaxEnt could still infer by combining the linear features derived from the original climatic minima and maxima variables). With this purpose in mind, we deemed it acceptable to use the standard deviation statistic even though data were usually not distributed normally.

Several African bat species are known to migrate. We could have modelled these species by aggregating multi-temporal SDMs (see e.g. Reside et al., 2010; Gschweng et al., 2012). Unfortunately, this was not an option for two main reasons. First, while migratory or nomadic behaviour has been reported for nearly 10% of African bats, we still know very little about the migratory tendency of the remaining 90% of species (Happold and Happold, 2013). Second, for the vast majority of species the number of known presence localities is currently too small to split into temporally stratified SDMs. We therefore disregarded the migratory status of species in this study.

To convert MaxEnt's continuous habitat suitability output into a binary classification of a species' realized distribution, we employed a threshold-setting approach that integrated MaxEnt's suite of default thresholds, expert knowledge, and the spatial distribution of sampling effort around the predicted presence areas. Selected thresholds were about equally often the frequently advocated statistics of ‘equal sensitivity and specificity’, ‘maximized sum of sensitivity and specificity’ and ‘10 percent training data’. For a considerable number of SDMs we deemed the use of a much lower or much higher threshold than any of the above more adequate. This species-specific threshold setting contrasts with the common practice of using a single threshold criterion for all SDMs, but

agrees with recommendations for real world datasets (Bean et al., 2012) and calls to consider the limited content of the confusion matrix (Meynard and Kaplan, 2013). Expert knowledge and context information (e.g. sampling effort) also served as our primary tools to account for evolutionary origin and dispersal limitations. Here we used species-specific biogeographic clips (see Section 2.5 and Appendix K) since methods to incorporate range dynamics more formally into correlative SDMs are still under development (Schurr et al., 2012).

To control for bias in the occurrence data, we used a target group (TG) background of continental scope (Phillips et al., 2009). This ensured consideration of the complete length of relevant environmental gradients when identifying a species' niche (Thuiller et al., 2004). This decision however may also have caused MaxEnt to produce unnecessarily simple models for species with small ranges (VanDerWal et al., 2009; Anderson and Raza, 2010; Vale et al., 2014) whenever models for regional endemics were at least partially trained with background data representing some inaccessible areas in distant parts of Africa (Barve et al., 2011; Merow et al., 2013). Unfortunately, for most African bat species very little is known about where the 'accessible' area ends, and beyond which background data should not be used for model training – the distance from documented presences may be quite large given their high mobility. Further, preliminary tests using a species-specific, 'regional' instead of continental TG background produced ambiguous results. For some species, mostly local endemics, predictions displayed more spatial structure over shorter distances in agreement with results of VanDerWal et al. (2009); for other species, predictions suggested implausible presence far beyond the currently known geographic range. Against this background we considered it advisable to create all SDMs using the same continental TG background.

Finally, assessing the performance of SDMs involves measuring both discrimination and calibration success (Pearce and Ferrier, 2000). Neither aspect can be fully measured if absence data are lacking as in this case commission errors remain unknown. They are however required to build calibration plots and to compute discrimination measures (Jiménez-Valverde et al., 2013) such as the AUC (Fielding and Bell, 1997). As a workaround, the discrimination ability of SDMs built with presence/background data has been commonly evaluated with the AUC metric using fractional predicted area instead of commission error (Wiley et al., 2003; Phillips et al., 2006; Elith et al., 2006). While AUC is free of the subjectivity inherent to threshold-dependent discrimination measures such as TSS (Allouche et al., 2006), it has some serious shortcomings when used to evaluate presence-only SDMs, primarily due to its rank-based character (see Appendix I for a brief discussion). The two shortcomings most relevant to the present study are that AUC actually measures many model aspects and not just discrimination ability, and that AUC assumes equal importance of omission and commission errors. When modelling with background instead of true absence data however, commission error will be overestimated by design and therefore should have a lower weight (Raxworthy et al., 2003; Peterson et al., 2008; Jiménez-Valverde et al., 2013). Nonetheless, as outlined by the latter authors, a limited species-specific assessment of model discrimination success is possible when AUC, model complexity and prevalence values (see Appendix C) are evaluated jointly and in the context of the specific statistical distribution of predicted habitat suitability values.

Evaluating calibration success without independent validation or absence data is just as challenging as measuring discrimination success under such conditions, and hence a largely unresolved issue (Ward et al., 2009; Jiménez-Valverde et al., 2013). Phillips and Elith (2010) proposed the use of POC plots. This method however requires at least a rough estimate of each species' prevalence in

the study area. For most African bat species this is not known, and certainly not at the fine grain employed in our study.

## 5. Conclusions

We have created state-of-the-art SDMs for a large taxonomic group and demonstrated that by stacking these a plausible model of fine-grained continental species diversity and endemism patterns can be obtained despite often scarce and biased occurrence data (the so-called 'Wallacean shortfall').

Our model suggests that African bat species richness (1) generally increases towards the equator, (2) varies substantially within the equatorial zone of elevated richness, often showing a positive association with high topodiversity at relatively low elevations, and (3) accommodates surprisingly steep gradients over a few kilometres, especially near rivers in savanna biomes. Centres of endemism (hotspots of summed range size rarity) are mostly found in or near areas characterized by substantial elevational ranges – on tropical mountains often at higher elevations than hotspots of species richness. Spatial congruence between richness and rarity hotspots is relatively low although this depends on the definition of both rare species and hotspot size.

Our approach in general, and the presented model in particular, should prove valuable for a range of applications because the maps of African bat diversity and endemism presented here constitute one of the few published datasets featuring high spatial resolution, large geographic extent, and broad taxonomic scope.

Owing to these properties, and in combination with the underlying individual SDMs, the model may help optimize protected area networks, support survey planning, and feed into biodiversity monitoring schemes. The generated data also lend themselves to a range of macroecological analyses, including tests of hypotheses across spatial grains finer than the common limit of 1° as well as studies distinguishing taxonomic subsets and functional groups.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2015.09.009>.

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