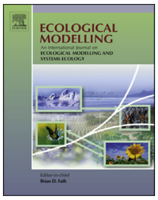
Ecological Modelling 320 (2016) 9–28

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



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

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ARTICLE INFO

Article history:
Received 2 January 2015
Received in revised form 6 September 2015
Accepted 7 September 2015

Keywords:
Species distribution modelling (SDM)
Chiroptera
Africa
Species richness
Range size rarity
Spatial resolution

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^2. 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.

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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http://dx.doi.org/10.1016/j.ecolmodel.2015.09.009
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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^2 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 cooccur. 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^2 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^2 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.,