

Research

Global habitat suitability models of terrestrial mammals

Carlo Rondinini^{1,*}, Moreno Di Marco¹, Federica Chiozza¹,
Giulia Santulli¹, Daniele Baisero¹, Piero Visconti^{1,2},
Michael Hoffmann^{3,4,5}, Jan Schipper⁷, Simon N. Stuart^{3,4,5,8,9},
Marcelo F. Tognelli^{6,10}, Giovanni Amori¹¹, Alessandra Falcucci¹,
Luigi Maiorano^{1,12} and Luigi Boitani¹

¹Global Mammal Assessment programme, Department of Biology and Biotechnologies, Sapienza Università di Roma, Viale dell'Università 32, 00185 Rome, Italy

²ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811, Australia

³IUCN, Rue Mauverney 28, 1196 Gland, Switzerland

⁴United Nations Environment Programme World Conservation Monitoring Centre, 219 Huntington Road, Cambridge CB3 0DL, UK

⁵Conservation International, and ⁶IUCN-CI Biodiversity Assessment Unit, Conservation International, 2011 Crystal Drive, Suite 500, Arlington, VA 22202, USA

⁷Big Island Invasive Species Committee, 23 E. Kawili Street, Hilo, HI 96720, USA

⁸Department of Biology and Biochemistry, University of Bath, Bath BA2 7AY, UK

⁹Al Ain Wildlife Park and Resort, PO Box 45553 Abu Dhabi, United Arab Emirates

¹⁰Instituto Argentino de Investigaciones de Zonas Áridas, CONICET CCT-Mendoza, C.C. 507, C.P. 5500 Mendoza, Argentina

¹¹CNR Institute for Ecosystem Studies, Viale dell'Università 32, 00185 Rome, Italy

¹²Department of Ecology and Evolution, University of Lausanne, Biophore Building, 1015 Lausanne, Switzerland

Detailed large-scale information on mammal distribution has often been lacking, hindering conservation efforts. We used the information from the 2009 IUCN Red List of Threatened Species as a baseline for developing habitat suitability models for 5027 out of 5330 known terrestrial mammal species, based on their habitat relationships. We focused on the following environmental variables: land cover, elevation and hydrological features. Models were developed at 300 m resolution and limited to within species' known geographical ranges. A subset of the models was validated using points of known species occurrence. We conducted a global, fine-scale analysis of patterns of species richness. The richness of mammal species estimated by the overlap of their suitable habitat is on average one-third less than that estimated by the overlap of their geographical ranges. The highest absolute difference is found in tropical and subtropical regions in South America, Africa and Southeast Asia that are not covered by dense forest. The proportion of suitable habitat within mammal geographical ranges correlates with the IUCN Red List category to which they have been assigned, decreasing monotonically from Least Concern to Endangered. These results demonstrate the importance of fine-resolution distribution data for the development of global conservation strategies for mammals.

Keywords: conservation priority setting; Red List; geographical range; range model; species distribution model; species richness

1. INTRODUCTION

Despite mammals being among the most intensively studied taxa, detailed large-scale information on their

distribution has been lacking, hindering conservation efforts. Broad maps of the extent of occurrence (i.e. the limit of the geographical range [1]) of terrestrial mammals have been produced in the past and have been used for elucidating general biogeographic patterns [2,3] and in global priority-setting analyses [4,5]. Although these latter studies have provided insightful hints on global conservation priorities for mammals, criticism of global biodiversity analyses

*Author for correspondence (carlo.rondinini@uniroma1.it).

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has been raised because the resolution of the geographical ranges used is too coarse to be useful on the local scale, which is the scale of conservation action [6]. A primary critique of such geographical range analyses is that species are not homogeneously distributed across their ranges, either because some habitats are not suitable for them or because they have no access [7]. On the other hand, the variable quality and incomplete coverage of available point locality data of mammal distributions have meant that their utility for global analyses has been quite limited [8].

To overcome the limitations of existing species datasets, it has been suggested that deductive habitat suitability models should be used [9]. These models, combining the geographical ranges and habitat preferences of species with environmental data such as vegetation and elevation, increase the resolution of the geographical range by helping to identify the unsuitable habitat within it [7,10]. Deductive models of this kind on a continental or sub-continental scale have been so far developed on a 1 km² resolution for Africa [11–13], Southeast Asia [14], Central America [15] and Europe (L. Maiorano *et al.* 2011, unpublished data). The use of these models for the identification of mammal conservation priorities demonstrated that the conservation of mammals requires more efforts than an analysis of their geographical ranges would tell.

The completion of the Global Mammal Assessment by the Species Survival Commission of the International Union for the Conservation of Nature (IUCN-SSC) at the end of 2008 [16] has provided an unprecedented opportunity to develop global distribution models for the entire mammalian fauna. The dataset, which received the input of thousands of mammal experts belonging to more than 30 Specialist Groups of the IUCN-SSC, is broadly based on the taxonomy published in Wilson & Reeder [17], updated with species described afterwards, and contains the geographical range and information on the habitat preferences of each mammal species, in addition to their conservation status. The entire dataset is publicly available through the IUCN Red List of Threatened Species [18].

We developed high-resolution, species-specific habitat suitability models for the terrestrial mammals based on the IUCN Red List, to estimate the extent of suitable habitat for each species and provide an improved baseline for the development of global conservation strategies for mammals. We validated the models of a subset of species, for which reliable point locality data were available. We conducted a global, fine-scale analysis of patterns of species richness, and investigated the biogeographic and ecological patterns underlying the observed difference between the extent of geographical ranges and the extent of suitable habitat for mammals. Our results demonstrate the importance of fine-resolution mammal distribution data and identify potential conservation bias in previous global prioritization exercises.

2. MATERIAL AND METHODS

(a) *Model development*

We used the geographical range (in ESRI shapefile format) and habitat preferences information obtained

from the IUCN Red List as a baseline for developing habitat suitability models for 5027 out of 5330 (94.3%) extant terrestrial (including coastal and flooded habitat) mammals. For 286 species we did not develop a habitat suitability model because the information on their habitat preferences was missing, or because they have a very small geographical range (less than 100 km²), in which case we preferred to use the entire range for the analysis. The 100 km² (equivalent to 10 × 10 km) range threshold was chosen heuristically based on the mismatch between the coastline boundaries used by the IUCN Red List for the species geographical ranges and those of the satellite maps used here to develop the habitat suitability models. The observed mismatch was in the order of magnitude of kilometres. If the mismatch is the same throughout the maps, for species with ranges below the 100 km² threshold the majority of the suitable habitat could be missed. For a further 17 species, there was no information available on the geographical range (electronic supplementary material, table S1); these species were excluded from the analysis.

For each species, we developed a habitat suitability model at 300 m resolution (*ca* 1.5 billion grid cells of size 0.09 km²) and limited to within the species' geographical range, to avoid extrapolating species' presence beyond their distribution limits. We focused on the following environmental variables: type of land cover, elevation and hydrological features. The type of land cover was mapped using Globcover v. 2.1 [19], a global, 300 m resolution map containing a legend of 63 classes based on the standard UN Land Cover Classification System (LCCS) [20]. The advantage of using an LCCS-based land-cover map is that the habitat preferences assessed against its legend can be easily applied to other similar maps in the future. The elevation map was produced by resampling (averaging) to 300 m the Shuttle Radar Topography Mission elevation [21], originally at 1 arcsecond resolution (approx. 90 m at the equator). The map of water bodies was produced by merging two sources: a 300 m wide buffer around the 210 class (water) of the Globcover for polygonal water bodies (lakes and large rivers), and the Vmap0 [22] linear permanent water map (converted to raster at 300 m resolution) for linear water bodies.

When known and recorded in the IUCN Red List, the information on the elevation range within which a species occurs is expressed as a minimum–maximum range in metres and as such used in the analysis. The rest of the information on habitat preferences, including the preferred habitat types, tolerance to human impact on natural habitat types and close relationship with water bodies are in the form of a textual description, and were extracted in two steps. First, we assigned each species to one or more broad habitat types (forest, shrubland, grassland, bare and artificial) and intersected this information with the suitability of flooded habitat and to the level of tolerance to human-impacted (degraded or mosaic) natural habitat types, to generate an automated classification of the classes of the land-cover map (electronic supplementary material, table S2). In the second step, applied only when detailed information on the habitat preference was available, if and where appropriate, we modified

manually the suitability of individual land-cover classes. In addition, we recorded whether the species' distribution should be restricted to within a small distance to water bodies.

We defined three levels of suitability for the land cover: high, corresponding to the primary habitat of a species, i.e. the preferred habitat where the species can persist; medium, corresponding to secondary habitat, i.e. habitat where a species can be found, but not persist in the absence of primary habitat; and unsuitable, where species are expected to be seldom or never found. All cells in the model inside the elevation range of the species retained the suitability score assigned to the land-cover map, while the other cells were classified unsuitable. In addition, for species whose distribution is restricted to within a small distance to water bodies, all cells farther than 1 km from water bodies were classified unsuitable; this 1 km threshold was chosen because of the potential spatial mismatch between the map of hydrological features and the maps of the other environmental variables. Models were developed in a Mollweide equal area projection (to represent and calculate areas accurately) using the free software GRASS GIS [23].

(b) Model evaluation

For a subset of 263 species, point locality data were available to evaluate the habitat suitability models. These data were derived from four different datasets. (i) The occurrence data of the African Mammals Databank [24], which were collected in 100 random localities in each of four countries (Morocco, Cameroon, Uganda and Botswana), for a total of 400 points, and consist of lists of species known to be present in a 1 km radius around the point (either by direct observation or by interview with residents and local wildlife professionals). (ii) The occurrence data of the Southeast Asian Mammals Databank [14], which were collected in 100 random localities in each of four countries (Thailand, Vietnam, Indonesia (Borneo) and the Philippines) and have otherwise similar characteristics as the African Mammal Databank point data. (iii) Further occurrence data that were collected for the Southeast Asian Mammals Databank and consist of a set of occasional (non-random) occurrences derived from various sources [14]. (iv) Further occurrence data that were extracted from the Global Biodiversity Inventory Facility [25]. The latter two datasets contain occasional data of various provenance and age. The subset chosen for the evaluation of mammal models included data collected in the last 20 years (1989–2009) and with a nominal positional error less than or equal to 1 km² (in the subsequent analysis, the positional error for these points was degraded to 1 km²). Only species with at least five separate occurrences (i.e. in different 1 km² cells) were considered for model evaluation.

To validate the habitat suitability models, we computed for each of the 263 species the proportion of 1 km² cells containing one or more occurrences and one or more 300 m cells with high and/or medium suitability (i.e. proportion of correctly predicted occurrences, or point prevalence). We compared this value

with the proportion of 1 km² cells with high or medium suitability within the range (i.e. the model prevalence across the range). If predicted suitable cells were distributed randomly with respect to species occurrences, the expectation would be that the point prevalence equals the model prevalence. When the point prevalence is higher than the model prevalence, the model is better than the geographical range at predicting occurrences, because it tends to correctly flag as unsuitable the cells that do not contain occurrences.

(c) Biogeographic, ecological and threat patterns

We used the habitat suitability models to map the global spatial pattern of terrestrial mammal species richness. In each cell, we summed all the species for which the cell was inside the geographical range and had medium or high suitability according to the model. We compared this value with the richness of terrestrial mammals calculated by overlaying the geographical ranges.

Species assigned to only one broad habitat type (forest, shrubland, grassland, bare and flooded) were considered habitat specialists, while the remaining species were considered habitat generalists. This classification, and the list of biogeographic realms where the species are found (extracted from the IUCN Red List), was used to analyse ecological and biogeographic patterns of range size and model prevalence. In addition, we analysed how the proportion of suitable habitat inside geographical ranges varied with the conservation status of species (IUCN Red List category). We performed all the analyses with the free-software POSTGRESQL database [26] and R environment for statistical computing [27].

3. RESULTS

(a) Model evaluation

A mean \pm s.d. of 33.8 ± 43.2 occurrences for each species was available to evaluate the models. On average, models predicted as suitable 54.8 ± 21.5 per cent of a species' geographical range, and predicted correctly 77.1 ± 16.8 per cent of the species occurrences. Point prevalence was consistently higher than model prevalence (figure 1); models predicted species occurrences better than the geographical ranges for 241 out of 263 species (91.6%), with no significant correlation between number of occurrences and model performance (Spearman rank correlation, $p = 0.19$). Point occurrences were available mainly for Afrotropical ($n = 83$), Indomalayan ($n = 75$), Nearctic ($n = 25$) and Palaearctic ($n = 19$) species. The other realms were marginally or not represented (Neotropical, $n = 3$; Australasian and Oceanian, $n = 0$). The remaining point occurrences corresponded to species occurring in more than one realm. Species with point occurrences were mainly forest specialists ($n = 68$, 25.9%) or habitat generalists ($n = 192$, 73.0%). The proportion of models that predicted occurrences better than ranges was non-significantly higher in forest specialists ($n = 65$, 95.6%) than in habitat generalists ($n = 173$, 90.1%).

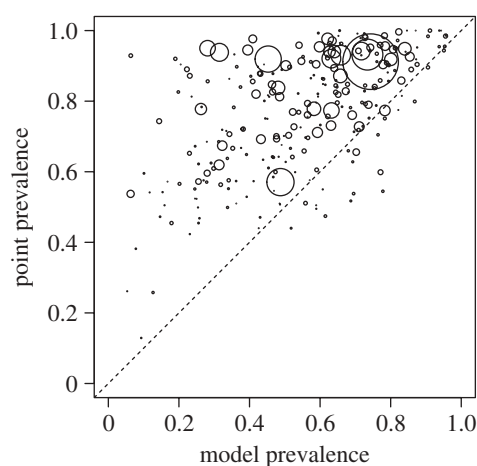


Figure 1. Validation of habitat suitability models for the 263 mammals with occurrence data. Each circle represents a species, and the size of the circle is proportional to the square root of the number of available occurrences for the species. Model prevalence: proportion of 1 km² cells containing habitat with medium or high suitability within the species' range. Point prevalence: proportion of points correctly predicted (i.e. falling in cells containing habitat with medium and/or high suitability for the species).

(b) Biogeographic patterns of suitable habitat

The mean terrestrial mammal richness (300 m resolution) was 56.67 ± 41.75 species based on the overlap of the whole geographical ranges (figure 2a), and 37.70 ± 33.24 species based on the overlap of the suitable areas inside species' geographical ranges (figure 2b). The peak of mammal richness (based on the overlap of suitable areas) was found in the Amazon basin (191 species estimated per cell); other tropical regions in Africa and Southeast Asia appeared less rich in species. In comparison, the richness estimated by geographical ranges smoothed differences within and among tropical regions (figure 2).

The mean difference per cell between the two estimators of species richness was 18.78 ± 20.78 , after excluding water basins from the calculation to avoid an overestimation (owing to the fact that the models classify water basins as unsuitable for most terrestrial species; figure 3a). Regions with the highest difference among the two estimators were found north and south of the Amazon basin, particularly in the Brazilian Cerrado and Atlantic Forest; in Central and Eastern Africa; and in Indochina.

The map of proportional difference among the two estimators of species richness (difference divided by richness estimated by geographical ranges) showed that in South China, Madagascar, and part of the Brazilian Cerrado, habitat suitability models estimate that species richness is one-fourth or less than that predicted by geographical ranges (figure 3b). For many other regions of the world, including the tropical Andes, the rest of the Cerrado, the African savannahs, most of central, south and Southeast Asia, part of the coastal areas in Australia, and scattered areas in Europe and North America, mammal richness predicted by habitat suitability models was approximately half of that predicted by geographical ranges. The difference was relatively smaller in regions that are highly

species-rich (tropical forests in the Amazon, Africa and Borneo) or species-poor (cold and hot deserts). The proportional difference equal to 1 observed in interior Greenland (figure 3b) was due to predicted richness of one species (the ermine, *Mustela erminea*) based on geographical ranges, and of zero species based on habitat suitability models.

The proportion of suitable habitat inside species' ranges changed depending on the biogeographic realm where they are found (Kruskal–Wallis $\chi^2 = 78.9$, d.f. = 7, $p < 0.0001$). Nearctic mammals ($n = 293$) had the highest proportion of suitable habitat within their geographical range (0.65 ± 0.24), and Oceanian mammals ($n = 11$) had the lowest (0.39 ± 0.41). Indo-malayan mammals had the second lowest ratio with 0.51 ± 0.27 (figure 4a).

(c) Ecological and threat patterns of suitable habitat

The percentage of suitable habitat inside mammal ranges varied depending on species habitat (Kruskal–Wallis $\chi^2 = 180.2$, d.f. = 5, $p < 0.0001$), from 59.8 ± 27.6 per cent for habitat generalists ($n = 2910$) to 13 ± 10 per cent for flooded habitat specialists ($n = 12$). Grassland specialists ($n = 112$) had the second lowest percentage of suitable habitat within the range (42 ± 26 ; figure 4b).

The percentage of suitable habitat inside mammal ranges varied with the conservation status according to the IUCN Red List (Kruskal–Wallis $\chi^2 = 81.7$, d.f. = 6, $p < 0.0001$), decreasing from 59 ± 26 for Least Concern species ($n = 3072$) to 48 ± 26 for Endangered species ($n = 429$; figure 4c). The only exception to this decreasing trend was Critically Endangered species, with a percentage of suitable habitat within the range of 52 ± 30 ($n = 142$). On the other hand, the decreasing trend of geographical range size was monotonic from Least Concern to Critically Endangered species (figure 4c).

4. DISCUSSION

Habitat suitability models greatly enhanced the resolution of mammal distribution analysis, which in previous global studies ranged between 10 000 and 20 000 km² [5,16]. This will benefit future global prioritization and conservation planning analyses. While our current resolution of 0.09 km² is limited by the resolution of maps of land cover and by the amount of computational effort required for map processing, these are likely to improve in the future owing to the increasing availability of high-precision satellite remote sensors and fast computational resources.

The habitat suitability models that we developed have a number of limitations. They may be affected by the variable, and potentially biased [28–31], knowledge of the species–habitat relationships, and of the geographical ranges that have been used to limit the extent of suitable habitat. It is very likely that the ranges of different species have been drawn at different resolution. For example, the ermine *Mustela erminea* is the only species whose range extends into interior Greenland. While this type of inaccuracy

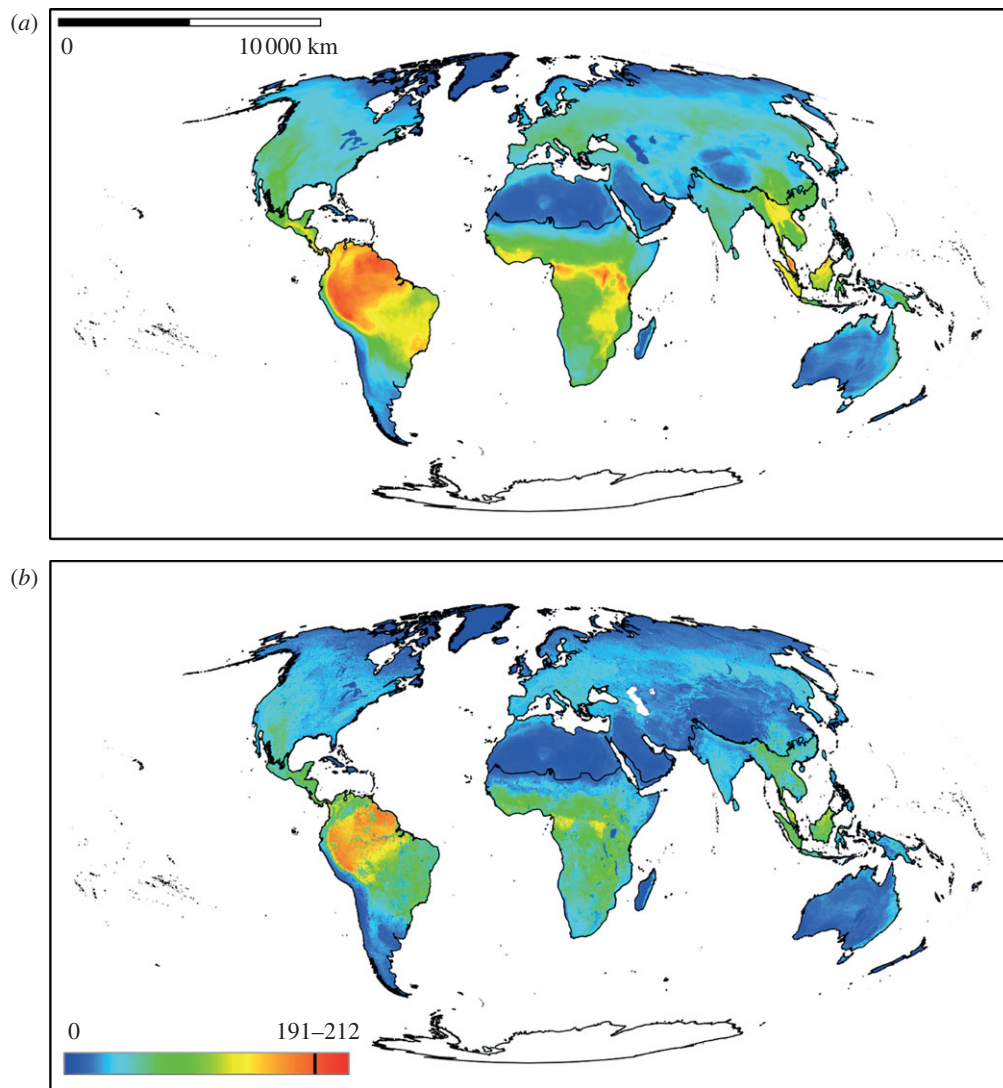


Figure 2. Mammal richness based on (a) geographical ranges and (b) habitat suitability models (high and medium suitability combined). Black lines on maps indicate biogeographic realms. The two upper limits on the scale bar indicate maximum richness based on habitat suitability models (191) and geographical ranges (212), respectively.

was corrected by our model (which indicated interior Greenland as unsuitable), other inaccuracies at the margins of species' ranges may have been overlooked if the habitat outside ranges is suitable. Our habitat suitability models also are based on a standard and restricted set of ecological variables equal for all mammals. They are therefore unlikely to take into account all of the most relevant variables limiting species distributions, and likely to still overestimate real distributions.

Habitat suitability models also are influenced by subjective methodological decisions, including on the baseline maps chosen to represent the ecological variables. Different maps (e.g. GLC2000 [32] or the anthropogenic biomes [33] for land cover) may produce different outcomes in terms of extent of suitable habitat. Here, the choice of Globcover was driven primarily by its resolution, higher than in the other available land-cover maps. In general, the availability of maps of environmental variables and the resolution at which environmental variables are mapped are limiting factors for the predictive power of habitat suitability models [34,35]. If limiting variables are not mapped, or some variables are not

mapped at the resolution at which species use their habitat, false presences and false absences (respectively) can be introduced in the models. These errors may be biased to particular types of land cover (e.g. fragmented habitat might be omitted as suitable habitat if existing maps are too coarse to identify small fragments), and can in turn result in geographical biases in the models [7,36,37]. When maps at higher resolution are available in the future, the higher level of detail will reveal small patches that are not resolved at the current analysis resolution of 300 m and will continue to refine the global picture of the distribution of suitable habitat for mammals. In addition, with increasing resolution of baseline maps, better consideration of the species-specific response to fragmentation [38] will be necessary.

Even with the acknowledged limitations, our models as a whole improve the knowledge on species distribution provided by geographical ranges. Point occurrences were available to evaluate the habitat suitability models for samples of species in two boreal and two austral biogeographic realms. Overall, habitat suitability models predicted known species occurrences

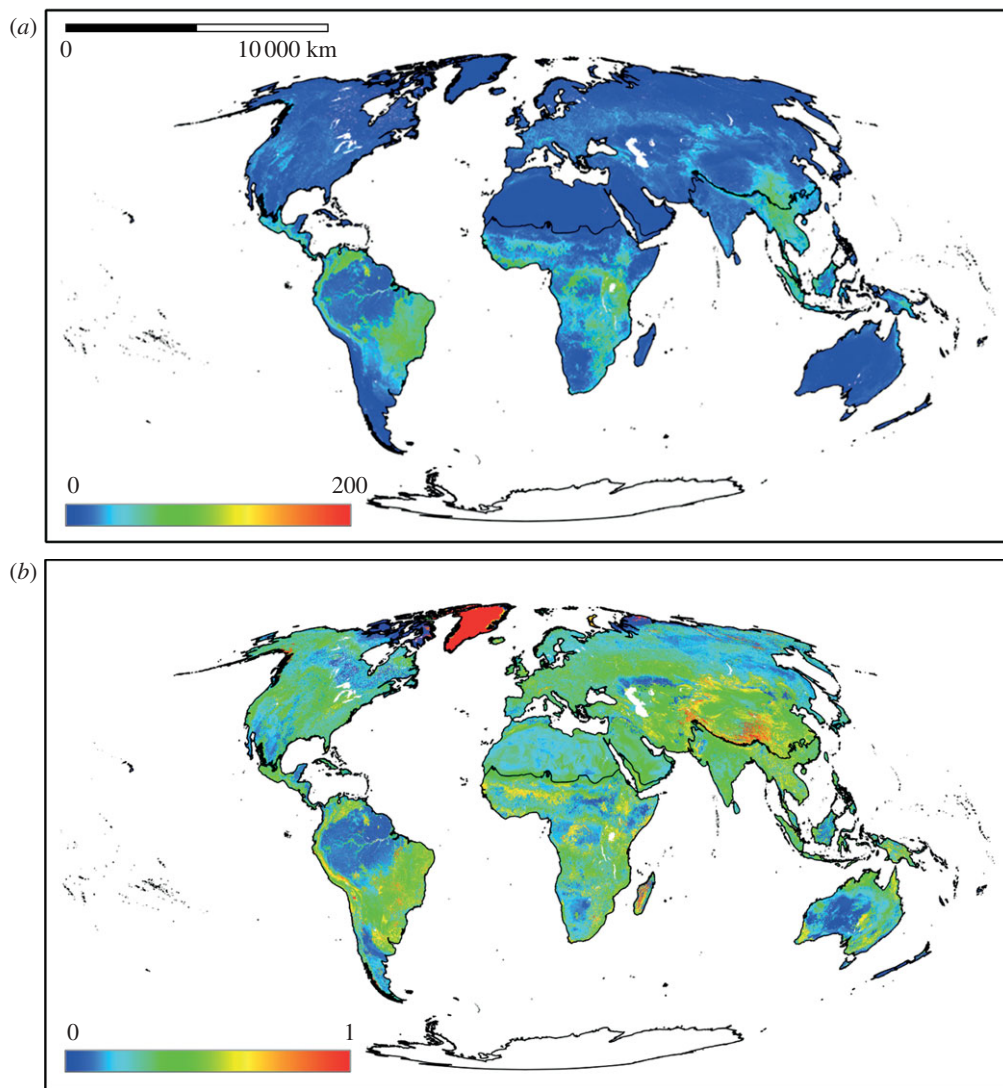


Figure 3. (a) Absolute and (b) relative difference of mammal richness estimated by geographical ranges and habitat suitability models. Absolute difference is represented as number of species. Relative difference is equal to absolute difference divided by the species richness estimated by geographical ranges. Black lines on maps indicate biogeographic realms.

better than geographical ranges particularly given that on average the suitable habitat according to our models occupied half of the range. The result of the validation was probably negatively affected by the resolution of point occurrences, which is coarser than that of the models (1 km² versus 0.09 km²). This can potentially obscure some fine-grained patterns of distribution of the suitable habitat. Also, most species for which point occurrences were available are habitat generalists. These tend to have a higher proportion of suitable habitat inside the range than habitat specialists, and the models for these species can be less sensitive in detecting habitat suitability than for habitat specialists [37]. If point occurrences for more habitat specialists were available, we would expect a further improvement of the model validation results.

The richness of mammal species estimated by the overlap of their suitable habitat is on average one-third less than that estimated by the overlap of their geographical ranges. Similar results are reported at the regional or continental level [11,14,15]. This has at least two general consequences. First, conservation assessments based on geographical ranges overestimate

the effectiveness of current protected areas, and underestimate the amount of conservation effort that is needed to fill their gaps. Such commission errors, which come with high conservation costs, occur when species may be listed as present in protected areas that overlap their mapped extent of occurrence but where they actually do not occur [4]. The consequences of this error can be substantial even on a large scale (e.g. the area to be protected to conserve mammals and amphibians across Africa is underestimated by 50% [11]). Second, they overestimate the number of different spatial options available for species conservation, because species distributions are more restricted and fragmented than geographical ranges represent.

The difference in mammal richness estimated through models or ranges is not even across the globe. The highest absolute difference is found in tropical and subtropical regions in South America, Africa and Southeast Asia that are not covered by dense forest. These regions would be expected to have high species richness based on the overlap of geographical ranges, but have been extensively converted to non-natural land cover. The relative difference in species richness

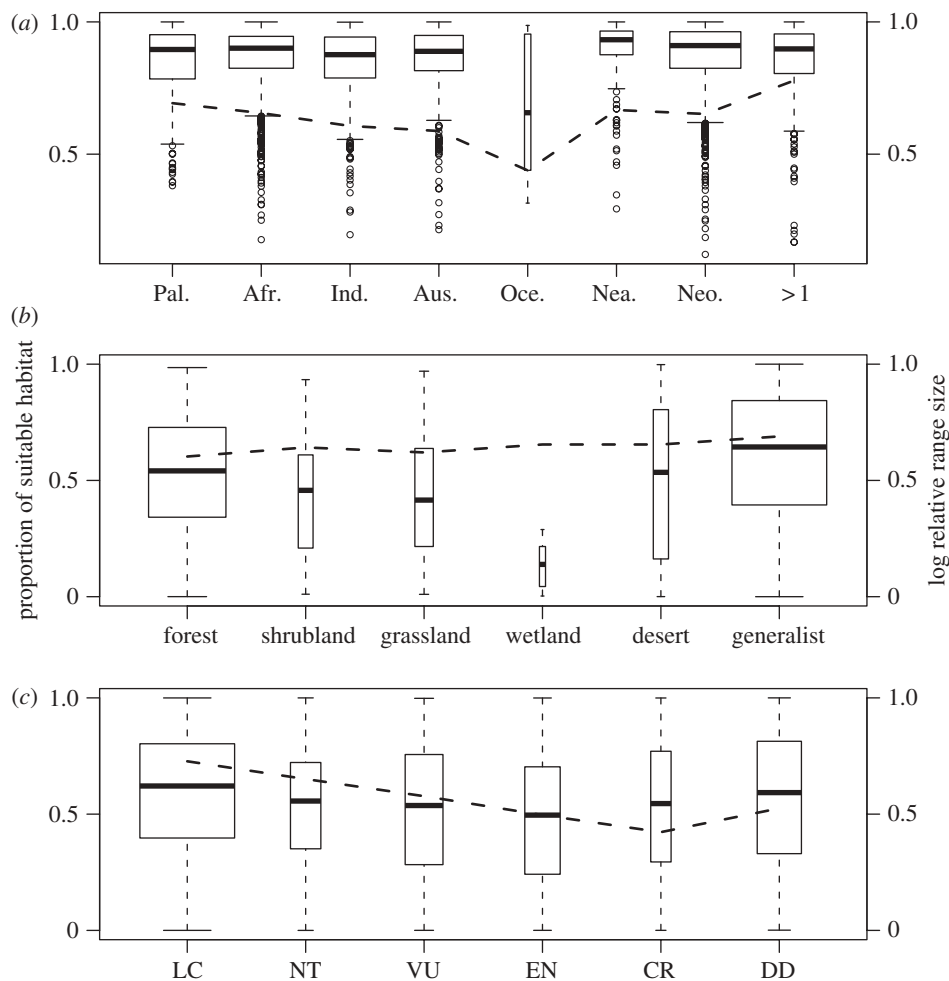


Figure 4. Tukey boxplots of the proportion of suitable habitat in mammal geographical ranges by (a) biogeographic realms (Pal., Palearctic; Afr., Afrotropical; Ind., Indomalayan; Aus., Australasian; Oce., Oceanian; Nea., Nearctic; Neo., Neotropical; >1: species distributed in more than one realm), (b) preferred habitat type and (c) IUCN Red List category, indicating increasing risk of extinction from low to extremely high (LC, Least Concern; NT, Near Threatened; VU, Vulnerable; EN, Endangered; CR, Critically Endangered). The dotted line represents the log size of species geographical ranges.

is consistently high throughout the globe, with the exceptions of tropical forests and cold and hot deserts. This in turn means that the overestimation of the effectiveness of conservation areas, and of the number of spatial options for conservation, is higher in regions with higher level of habitat conversion than in relatively more intact regions. This conclusion is reinforced by the evidence that the regions with the highest difference between richness estimated by models and by geographical ranges are also those where higher loss of mammal habitat is expected in the future [39].

Further, the proportion of suitable habitat inside mammal geographical ranges is variable, and this variation is reflected in differences among biogeographic realms and habitat types. Oceanian (and to a lesser extent, Indomalayan) mammals, whose ranges are smaller than those of the other mammals, have also disproportionately less suitable habitat within ranges, while Nearctic species have a much higher proportion of suitable habitat within range. This disproportion may cause conservation assessments to overestimate the distribution and underestimate the extinction risk of Oceanian and Indomalayan mammals when compared with mammals in other biogeographic realms.

The proportion of suitable habitat within mammal geographical ranges correlates with the IUCN Red List category to which they have been assigned, decreasing monotonically from Least Concern to Endangered. This is the case even if, as expected, the geographical range of mammals also decreases with increasing category of threat. Therefore, more threatened mammals have disproportionately less suitable habitat inside their range than less threatened mammals. A similar result was found by Jetz *et al.* [34] when comparing species range maps and well-studied survey locations of birds in Australia, North America and southern Africa. The only exception is with Critically Endangered mammals, whose small geographical ranges appear on average more suitable than those of the other threatened mammals. This may be an effect of two factors. First, given the geographical ranges of Critically Endangered species being very small, it is possible that the resolution of maps of environmental variables is not sufficient to identify the suitable habitat inside them. Second, the geographical ranges of Critically Endangered species are likely to have received higher attention than those of the other species, and to have been drawn at a

higher level of detail, including a more accurate exclusion of unsuitable habitat.

(a) Conservation implications

Habitat suitability models are far from being a perfect representation of species distributions [7]. Yet, the availability of point occurrence data is currently very limited, and this is unlikely to change substantially any time soon [8] (but see [39]). Geographical ranges based solely on expert knowledge, which involves implicit interpolations and, to some degree, extrapolations, are highly subjective and their level of detail is variable according to the geographical region where a species lives, the size of its range and its primary habitat. Habitat suitability models improve on geographical ranges because they make inference explicit, easy to evaluate quantitatively, and more uniform across species, thereby reducing bias in mapping species distribution. Furthermore, habitat suitability models allow an explicit validation, which should always be performed whenever species distribution maps are used for conservation purposes [37]. Habitat suitability models also can track changes in the extent of suitable habitat over time as maps of land-cover change are updated and can be used to make explicit predictions on future habitat loss [40], which can make conservation assessments proactive and more effective in preventing future threats.

The extent of suitable habitat estimated by habitat suitability models could be potentially used for re-assessing the conservation status of mammals under the criterion B of the IUCN Red List, but the current thresholds for criterion B are applicable either to the extent of occurrence (sub-criterion B1) or to the area of occupancy (sub-criterion B2). Therefore, either different thresholds or further research on the relationship between the extent of occurrence, the extent of suitable habitat and the area of occupancy are required to apply the criterion B appropriately.

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