

Journal of Applied Ecology

MS MARSYA CHRISTYANTI SIBARANI (Orcid ID : 0000-0003-0942-139X)

Article type : Research Article

Handling Editor: Johan du Toit

Title

Measuring the surrogacy potential of charismatic megafauna species across taxonomic, phylogenetic and functional diversity on a megadiverse island

Author details

Marsya C. Sibarani¹, Moreno Di Marco^{2,3}, Carlo Rondinini⁴ and Salit Kark¹

¹The Biodiversity Research Group, The School of Biological Sciences, Centre for Biodiversity & Conservation Science, The University of Queensland, Brisbane, QLD 4072, Australia

²Centre for Biodiversity and Conservation Science, The University of Queensland, Brisbane, QLD 4072, Australia

³CSIRO Land & Water, Brisbane, QLD 4001, Australia

⁴Global Mammal Assessment Program, Department of Biology and Biotechnologies, Sapienza Università di Roma, Rome I-00185, Italy

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/1365-2664.13360

This article is protected by copyright. All rights reserved.

Corresponding author

Marsya Sibarani

School of Biological Sciences, The University of Queensland, Brisbane, QLD 4072,

Australia

marsyachr@gmail.com

Abstract

1. Conservation organisations and governments often use charismatic megafauna as surrogates to represent broader biodiversity. While these species are primarily selected as “flagships” for marketing campaigns, it is important to evaluate their surrogacy potential, i.e., the extent to which their protection benefits other biodiversity elements. Four charismatic megafauna species are used as surrogates in the megadiverse island of Sumatra: the Sumatran tiger *Panthera tigris sumatrae*, Sumatran elephant *Elephas maximus sumatranus*, Sumatran orangutan *Pongo abelii* and Sumatran rhinoceros *Dicerorhinus sumatrensis*. We examined how well each of these species performed in representing the distribution of all co-occurring terrestrial mammal species on the island, and the priority areas for the conservation of three facets of mammalian biodiversity (taxonomic, phylogenetic and functional).
2. We used habitat suitability models to represent the distribution of 184 terrestrial mammal species, 160 phylogenetic groups and 74 functional trait groups. We then identified priority conservation areas using the spatial prioritisation software Zonation.
3. We found that the habitat overlaps between each of the four charismatic species and the other mammal species varied, ranging from a mean of 52% (SD = 27%) for the tiger to 2% (SD = 2%) for the rhino. Combining the four species together only improved the representation levels marginally compared to only using the tiger. Among the four charismatic megafauna species, the extent of suitable habitat of Sumatran tiger covered

the highest proportion of priority conservation areas. The Sumatran tiger also outperformed most of other mammal species with similar range sizes.

4. We found that some of the top-ranked conservation areas for taxonomic (28%), phylogenetic (8%) and functional diversity (19%) did not overlap with any of the charismatic species' suitable habitat.
5. *Synthesis and applications.* Wide-ranging charismatic species can represent broader mammalian biodiversity, but they may miss some key areas with high biodiversity importance. We suggest that a combination of systematic spatial prioritisation and surrogacy analyses are important in order to determine the allocation of conservation resources in biodiversity-rich areas such as Sumatra, where an expansion of the protected area network is required.

Abstrak

1. Organisasi konservasi dan pemerintah seringkali menggunakan megafauna karismatik sebagai spesies pengganti untuk merepresentasikan biodiversitas yang lebih luas. Walaupun spesies pengganti biasanya memiliki peran utama sebagai “*flagship*” untuk kampanye, penting juga untuk mengetahui apakah perlindungan spesies tersebut dapat memberikan keuntungan bagi aspek biodiversitas lainnya. Empat megafauna karismatik digunakan sebagai spesies pengganti di Pulau Sumatera, yaitu harimau sumatera *Panthera tigris sumatrae*, gajah sumatera *Elephas maximus sumatranus*, orangutan sumatera *Pongo abelii* dan badak sumatera *Dicerorhinus sumatrensis*. Kami mengevaluasi bagaimana keempat spesies tersebut merepresentasikan distribusi spesies mamalia terrestrial lainnya di Sumatera dan area prioritas untuk konservasi tiga aspek keanekaragaman hayati (taksonomik, filogenetik, dan fungsional).
2. Kami menggunakan pemodelan kesesuaian habitat untuk merepresentasikan distribusi

184 spesies mamalia terestrial, 160 kelompok filogenetik, dan 74 kelompok karakteristik fungsional. Kami kemudian mengidentifikasi area konservasi prioritas menggunakan perangkat lunak Zonation.

3. Tumpang-tindih habitat di antara keempat spesies karismatik dan spesies mamalia lainnya bervariasi, berkisar dari rerata 52% (SD = 27%) untuk harimau hingga 2% (SD = 2%) untuk badak. Menggabungkan distribusi keempat spesies hanya sedikit meningkatkan tumpang-tindih habitat dibandingkan jika hanya menggunakan harimau. Di antara keempat spesies karismatik, habitat yang sesuai bagi harimau sumatera melingkupi area konservasi prioritas dengan proporsi tertinggi. Harimau sumatera juga mengungguli sebagian besar mamalia lain yang memiliki luas habitat yang serupa.
4. Beberapa area konservasi prioritas untuk keanekaragaman taksonomik (28%), filogenetik (8%), dan fungsional (19%) tidak bertumpang-tindih dengan habitat spesies karismatik mana pun.
5. *Sintesis dan aplikasi*. Spesies karismatik dengan distribusi yang luas dapat merepresentasikan keanekaragaman mamalia, tetapi dapat juga melewati beberapa area yang penting untuk konservasi biodiversitas. Kombinasi antara analisis spasial untuk menentukan prioritas konservasi dan analisis surogasi merupakan hal yang penting untuk menentukan alokasi sumber daya konservasi di area yang kaya akan biodiversitas, seperti Sumatera, di mana perluasan kawasan konservasi diperlukan.

Keywords

Functional diversity, phylogenetic diversity, spatial conservation prioritisation, Sumatran elephant, Sumatran orangutan, Sumatran rhinoceros, Sumatran tiger, surrogate species

Introduction

Conserving all biodiversity features at the same time is not feasible due to limited resources, hence conservation efforts must be strategically planned and prioritised (Bottrill et al., 2008; Joseph, Maloney, & Possingham, 2009). One conservation strategy that is often applied is to employ a species or group of species, in many cases large and charismatic species, as flagships. A flagship species is “a species used as the focus of a broader conservation marketing campaign based on its possession of one or more traits that appeal to the target audience” (Verissimo, MacMillan, & Smith, 2011). However, most of the campaigns primarily seek funds directly for the flagships and are rarely aimed to benefit other biodiversity (Smith, Verissimo, Isaac, & Jones, 2012). Considering limited resources for conservation and the vast range of biodiversity that require protection, conserving flagship species in their natural habitat has a great potential to contribute to the persistence of biodiversity, when properly planned.

While flagship species do not necessarily act as umbrella species—species whose conservation confer protection to a large number of co-occurring species (Roberge & Angelstam, 2004) —charismatic megafauna may serve as both flagship and umbrella (Caro, 2010). However, previous work has shown mixed results as to whether charismatic megafauna species are effective surrogates for biodiversity. Andelman & Fagan (2000) reported little evidence for the effectiveness of various surrogate schemes, including charismatic species, for regional species conservation in the United States. Similarly, Williams et al. (2000) found that areas identified based on the distribution of flagship species do not perform better in representing the diversity of mammals and birds than areas identified from randomly selected species. In contrast, conservation networks for jaguar *Panthera onca* in Latin America represent substantial proportion of high quality habitats for other terrestrial mammals (Thornton et al., 2016), and the giant panda *Ailuropoda melanoleuca* is an effective

Accepted Article
surrogate for endemic mammal and bird species in China (Li & Pimm 2016). In Africa, the priority conservation areas for the African “Big Five” species highly represent priority areas for the other mammals, yet provide poor representations for amphibians, reptiles, invertebrates and plants (Di Minin & Moilanen, 2014).

Most evaluations of surrogate species focused on their representation of taxonomic diversity. However, taxonomic diversity alone does not capture other important facets of biodiversity, such as phylogenetic diversity—the distinctiveness among species based on their evolutionary history (Faith, 1992)—and functional diversity—the distribution of species in a multidimensional niche space defined by their life-history traits (Petchey & Gaston, 2006). This limits the global understanding of surrogacy potential for charismatic species because different facets of biodiversity often show non-congruent spatial patterns. For example, global mammal hotspots defined using taxonomic, phylogenetic and functional diversity are not spatially congruent (Mazel et al., 2014). Similarly, there is only 4.6% overlap among the top priority conservation areas for mammal conservation across the three facets (Brum et al., 2017). On a country scale, functional diversity of birds in France is underrepresented in protected areas, whereas taxonomic diversity is overrepresented (Devictor et al., 2010).

Sumatra is a part of the Sundaland biodiversity hotspot, where the use of charismatic megafauna to guide conservation efforts is a common practice (MoF, 2007; PHKA, 2015; Soehartono et al., 2007; Soehartono, Susilo, et al., 2007; Soehartono, Wibisono, et al., 2007). The protected area coverage of Sumatra requires an expansion from the current ~11% to 17% to achieve the commitments set under the Convention on Biological Diversity’s Aichi Target 11, assuming proportional allocation to land area across the major islands in Indonesia. Conservation efforts in Sumatra have been largely targeted towards four charismatic megafauna species: the Sumatran tiger *Panthera tigris sumatrae*, the Sumatran elephant

Elephas maximus sumatranus, the Sumatran orangutan *Pongo abelii* and the Sumatran rhinoceros *Dicerorhinus sumatrensis*. Conservationists often propose that these large mammals have an umbrella effect, and that saving them will also save a number of other co-occurring species. However, this proclaimed umbrella effect remains largely untested, especially when it comes to multiple facets of biodiversity, such as functional and phylogenetic diversity. In this work, we addressed this important shortfall and evaluated whether the available habitat for four flagship species in Sumatra is representative of the taxonomic, functional and phylogenetic mammal diversity (hereafter “surrogacy potential”).

Our first aim was to measure the habitat overlap between the four charismatic species of Sumatra and the other native terrestrial mammal species on the island. The second aim was to identify the priority areas for mammal conservation in Sumatra based on taxonomic, phylogenetic and functional diversity, and to assess how much these areas would benefit from the protection of the four charismatic species.

Materials and Methods

Study region

Sumatra is one of the largest islands in Indonesia with a total area of 430,000 km² (GADM, 2009). The island is surrounded by many smaller satellite islands, yet this study focused only on the main island (Fig. 1). Forest land use zones are divided into three functions: biodiversity conservation (10.6% of the island), water system protection (13%) and production (35.6%). Other land uses (40.8% of the island) include agriculture land and settlements (Margono, Turubanova, Zhuravleva, Potapov, & Tyukavina, 2012). Between 1990–2010, an estimated 7.5 million hectares of primary forest in Sumatra were cleared and 2.3 million hectares have been degraded, leaving only 30% of Sumatra covered by primary

forest in 2010 (Margono et al., 2012). The human population of Sumatra in 2010 was 50.6 million, with a growth rate of 14.5% between 2000 and 2010 (BPS 2012).

Mammal distribution data

We obtained the list of native terrestrial mammal species in Sumatra using (i) the search tool on IUCN Red List of Threatened Species website (www.iucnredlist.org) and (ii) the IUCN geographic distribution ranges for terrestrial mammals (IUCN, 2016). Because the two lists did not return the same number of species, we merged them and checked the species information pages on the IUCN Red List website to filter species that occur in Sumatra (excluding species that only occur on satellite islands). This resulted in 193 mammal species being listed, including the four surrogate species (see Appendix S1 in Supporting Information).

Given the lack of comprehensive occurrence data for developing statistical distribution models for all species, we used deductive (expert-driven) habitat suitability models to represent species' distributions on the island (Rondinini et al., 2011). Habitat suitability models have been used in a number of other studies on a regional (e.g., Thornton et al. 2016) and global scale (e.g., Brum et al. 2017), where comprehensive occurrence data were unavailable. Rondinini et al. (2011) assessed species' habitat suitability by considering species habitat preferences for three environmental variables: the types of land cover, elevation range and hydrological features. The resulting deductive models consist of three classes of habitat suitability (Rondinini et al., 2011):

- (i) high habitat suitability, representing the primary habitat where the species can persist;
- (ii) medium habitat suitability, representing secondary habitat where the species can be found, yet cannot persist without the primary habitat; and

(iii) low habitat suitability, representing areas where the species are generally not found or unlikely to occur.

In the spatial prioritisation analysis, we only used areas of high habitat suitability to represent the occurrence of the species (hereafter “extent of suitable habitat”) because we intended the resulting conservation area systems to include areas where species are most likely to persist. Of the 193 native terrestrial mammal species in Sumatra, the two recently split orangutan populations (Nater et al., 2017) were considered as one species, and eight species were not modelled by Rondinini et al. (2011); therefore, our analysis included a total of 184 species (including the four charismatic species).

Assessing the representation of mammal species by the charismatic megafauna

We assessed the surrogacy potential of charismatic megafauna species by overlaying their extent of suitable habitat with that of all other mammals. Representation was calculated as the proportion of a species’ extent of suitable habitat overlapping with the habitat of each charismatic megafauna species. We performed all spatial data processing using the R packages ‘sp’ (Pebesma & Bivand, 2005) and ‘raster’ (Hijmans & van Etten, 2012) in R version 3.4.1 (R Development Core Team, 2008).

Assessing the representation of priority areas based on multiple facets of biodiversity

We identified conservation priority areas using the Zonation v.4 software (Moilanen et al., 2014). The input data for Zonation analysis are raster maps of biodiversity features (e.g., species and habitat types) which represent their spatial distribution. The Zonation algorithm starts from the full extent of the landscape of interest, and then iteratively removes areas with the lowest value for conservation based on the occurrence level of biodiversity features

(Moilanen et al., 2005). This iterative removal process generates a map showing a hierarchic ranking of conservation priorities throughout the landscape (Moilanen, Kujala, & Leathwick, 2009). Each raster cell of the output map contains a rank of conservation priorities ranging between 0 (lowest priority) and 1 (highest priority) that can be visualised as a hierarchical zoned map of top priority areas for conservation. Zonation has already been used for assessing umbrella effects of surrogate species (Di Minin & Moilanen, 2014) and examining congruency of priority areas for multiple facets of biodiversity (Brum et al., 2017; Pollock, Thuiller, & Jetz, 2017; Strecker, Olden, Whittier, & Paukert, 2011).

We used Core Area Zonation (CAZ) as the cell removal rules in Zonation, which ranks the cells across the landscape based on the most important occurrence of a feature, and hence could identify core areas of features in biodiversity-poor areas (Moilanen et al., 2014).

We also incorporated connectivity considerations by using the Boundary Length Penalty (BLP) to produce more compact reserve solutions (Moilanen & Wintle, 2007). We ran three separate analyses to identify priorities for three different biodiversity facets: a species-level analysis (taxonomic prioritisation); an analysis based on phylogenetic groups (phylogenetic prioritisation); and an analysis based on functional groups (functional prioritisation). Further technical details are provided in Appendix S2.

Biodiversity features for spatial prioritisation

We used individual species as the biodiversity features for the spatial prioritisation based on taxonomic diversity. We performed area-weighted resampling to scale up the habitat suitability maps from the original 300 m resolution to 1 km. We used a resolution of 1 km as a compromise between computational time and relevance for conservation management on the island. We weighted 14 species endemic to Sumatra twice as much as the non-endemic species to represent the higher global value of their conservation on the island. We also

performed a sensitivity analysis on alternative weighting of endemic species, but the results showed no substantial differences (see Appendix S4).

For spatial prioritisation based on phylogenetic diversity, we defined phylogenetic groups following the framework developed by Strecker et al. (2011) and Brum et al. (2017). We used the mammalian phylogenetic supertree created by Bininda-Emonds et al. (2007) and updated by Fritz et al. (2009) to create a phylogenetic distance matrix among 181 mammal species in Sumatra, after excluding three species which were not available in the mammalian super-tree. We then performed principal coordinate analysis (PCoA) on the phylogenetic distance matrix and selected the first 16 eigenvectors which explained >1% of total variation. These eigenvectors altogether accounted for 69% of the total variation. Each eigenvector was split into 10% quantiles (see Appendix S4 for the sensitivity test), and then converted into binary variables. Our quantiles were wider than those used in Brum et al. (2017) because we had fewer number of species in Sumatra. To represent phylogenetic groups in spatial maps, we created a binary matrix of species \times phylogenetic group. Area-weighted habitat suitability maps at 1 km resolution were reclassified into binary maps with a threshold of 0.05 (this threshold reduces the risk of introducing commission errors without penalising species with narrow habitat distributions), and then were converted into grid \times species matrix. Finally, we multiplied the two matrices to obtain grid \times phylogenetic groups matrix, in which a grid cell contained the number of species belonging to a particular phylogenetic group. We then generated spatial maps of phylogenetic group distribution from this matrix.

We mapped mammalian functional traits with similar procedure with phylogeny-based prioritisation, using life-history traits as opposed to phylogenetic eigenvectors. We selected five life history and ecological categories, represented by nine traits: adult body mass, maximum longevity, reproductive speed (weaning age, gestation length), reproduction output (neonate body mass, litter size and litters per year) and resource use (trophic level and

habitat breadth). We used the global dataset for terrestrial mammal traits compiled by Pacifici et al. (2013) and Di Marco & Santini (2015) from various sources, such as PanTHERIA (Jones et al., 2009) and AnAge (Tacutu et al., 2013). We assigned the presence/absence of each level of categorical traits in a binary matrix of species \times trait. We split continuous traits into 10% quantiles, and we assigned presence/absence of each same-size trait level to species. Next, we multiplied the grid \times species matrix with species \times trait matrix. We converted the resulting matrix of grid \times trait into spatial maps of functional trait levels. The detailed procedure of data preparation is provided in Appendix S2.

We ran the prioritisation analysis separately using species' habitat suitability maps as inputs in taxonomy-based prioritisation, phylogenetic group maps in phylogeny-based prioritisation and levels of functional traits in trait-based prioritisation. We then extracted the top 5%, 10%, 17% and 25% of priority areas for each prioritisation scenarios and overlaid them with the extent of suitable habitat of the charismatic megafauna species. We measured the surrogacy potential of charismatic megafauna as the proportion of priority areas across Sumatra that overlapped with the extent of suitable habitat of the species under consideration. In addition, we also calculated the surrogacy potentials of other mammal species in Sumatra to compare the performance of the four charismatic megafauna species with that of other species.

Results

Surrogacy for terrestrial mammal species

Among the four charismatic megafauna species, the tiger had the highest spatial overlap with other mammal species, representing a mean of 52% (SD = 27%) of the extent of suitable habitat of other Sumatran mammals (Fig. 2). The representation levels for other charismatic species were much lower: 18% for the elephant (SD = 12%), 9% for the orangutan (SD =

11%), and 2% for the rhinoceros (SD = 2%). Only two species had a high spatial overlap with the elephant (i.e., 93% for the lesser large-footed myotis *Myotis hasseltii* and 85% for the big-eared horseshoe bat *Rhinolopus macrotis*). Likewise, only two species had a high spatial overlap with the orangutan (i.e., 81% for the big-eared horseshoe bat and 71% for the pen-tailed treeshrew *Ptilocercus lowii*).

Most of the suitable habitat for orangutan and rhinoceros overlapped with the tiger, but only 41% of the elephant's extent of suitable habitat overlapped with the tiger's. The suitable habitat for tiger overlapped substantially (52%) with the critically endangered Sunda pangolin *Manis javanica*. Of the 12 endangered species (Fig. 2), only one was underrepresented by the tiger, i.e., the hairy-nosed otter *Lutra sumatrana*, with representation level of 12%. The other 11 endangered species were well represented by the tiger with the overlap between their range and tiger range ranging from 40% to 89%. Combining the four surrogate species only improved the representation levels by a mean of 5% (SD = 6%, range = 0–12%) compared to the performance of the tiger alone.

Surrogacy for priority areas based on multiple facets of biodiversity

We discovered substantial spatial mismatches among the areas identified under taxonomic, phylogenetic and functional diversity prioritisation scenarios (Fig. 3). When looking at the top 5% priority areas for each biodiversity facets, which altogether encompassed an area of 21,595 km², we found an overlap of only 3,227 km² (15%) across the three facets. Priority areas shared among the three prioritisation scenarios mostly occurred in highlands of northern Sumatra and western mountain ranges. In taxonomy-based prioritisation, the priority areas were more spread out across the island, including central lowland and eastern coasts. The spatial solution for prioritisation based on phylogenetic groups was more clumped in the western half of the island. Priority areas for conserving functional traits were more congruent

to phylogeny-based (20% overlap) than taxonomy-based prioritisation (17% overlap).

In general, most of the extent of suitable habitat of the charismatic species was of high conservation priority (Fig. 4). The orangutan and rhinoceros covered areas in Sumatra with relatively higher conservation priority ranks than the tiger and elephant. Among the four, elephant had the most variability in representing conservation priorities, e.g., for taxonomic prioritisation, $IQRelephant = 0.44$, $IQRtiger = 0.23$, $IQRorangutan = 0.10$, $IQRrhinoceros = 0.05$ (complete summary statistics in Appendix S4).

While most of the suitable habitats for the orangutan and rhinoceros overlapped with areas of high conservation priority, these only accounted for small areal amounts of top priority areas, given the restricted distribution of these species (Fig. 5). The tiger's suitable habitat had the highest areal coverage of priority areas for the three biodiversity facets, and it represented phylogenetic priorities particularly well. Elephant, having approximately half of tiger's suitable habitat, represented less than half of the amount of priority areas covered by the tiger. Combining all charismatic species improved the representation of priority areas, but only by a small amount compared to the tiger (Fig. 5). We also identified priority areas that were not covered by any of the four charismatic species' distributions, e.g., for the top 5% priority areas, 28% (taxonomy-based priority), 8% (phylogeny-based) and 18% (trait-based) were outside the extent of suitable habitat of the charismatic species.

Evaluation on the potential of the other 180 mammal species in Sumatra in representing priority areas revealed that the extent of suitable habitat was a good predictor of surrogacy potential (Fig. 6). However, species with similar size of suitable habitat represented varying proportions of priority areas. The tiger had a higher surrogacy potential compared to most other species with similar size of suitable habitat. The elephant, on the opposite, had an underperforming surrogacy potential than was predicted by its size of suitable habitat.

Discussion

The role of the charismatic megafauna in Sumatra as biodiversity surrogates

We used recently developed techniques to evaluate the conservation effectiveness of using charismatic megafauna as surrogates for taxonomic, phylogenetic and functional diversity of Sumatran mammals. We found that Sumatran tiger had the highest surrogacy potential because most of the co-occurring mammals were well represented within its distribution, and it covered high amounts of priority areas for the three biodiversity facets (taxonomic, phylogenetic and functional diversity). This is related to its relatively large distribution compared to the other charismatic species in Sumatra. However, the tiger also had higher surrogacy potential than predicted based on its distribution size alone. This supports the finding from a previous study that large predators have important surrogate roles for other mammals (Thornton et al., 2016).

The Sumatran elephant had the second highest potential as a surrogate species in Sumatra in terms of the representation of co-occurring species. However, it covered a lower proportion of priority areas than expected by its range size because it did not occur in most of western mountain ranges where most of the priority areas were found. The orangutan and rhinoceros represented relatively lower amounts of total priority areas, which matched with their restricted distribution range. However, almost the entire ranges of these two species encompassed top-ranked priority areas. This implies allocating conservation resources to protect areas within the range of the orangutan and the rhino would result in a high contribution to the protection of broader biodiversity, but this strategy alone will likely be insufficient for Sumatran biodiversity given the restricted distribution of the two species.

The combination of spatial prioritisation and surrogacy analysis allowed us to identify areas within the charismatic species' habitats with high and low conservation priorities. The choice of flagship species depends on the broad conservation goals of the people developing

the marketing campaign and the preferences of their target audiences, so our analysis should not be used to prioritise conservation effort between flagships. Instead, we propose the use of spatial conservation prioritisation techniques to identify areas within the ranges of charismatic megafauna species that also provide benefits to the broader biodiversity.

Considering that charismatic megafauna did not represent the whole extent of identified priority areas, even with all species combined, our results suggest that conservation managers and policy makers in Sumatra should protect important areas for biodiversity that occur outside the range of charismatic species. Our findings agree with previous work suggesting that targeting charismatic megafauna in conservation is not enough to achieve broader biodiversity conservation targets, yet the benefit of their protection can be improved by using well-surveyed taxonomic groups and habitat types (Di Minin & Moilanen, 2014).

Habitat suitability models used in this study are a more accurate depiction of species distributions compared to geographic ranges (IUCN range maps) because unsuitable habitats have been excluded from the distribution (Rondinini, Wilson, Boitani, Grantham, & Possingham, 2006). However, suitable habitat is not necessarily translated into species presence, as species may be extirpated from its suitable habitat due to human-caused disturbances. This issue can be addressed by performing habitat suitability model validation for all species considered in the study or developing inductive species distribution models as input features for future study. This, however, requires collecting occurrence data for all considered species, which are not currently available. In this study, we only considered mammalian diversity due to data availability along all biodiversity facets. Future work is still necessary to incorporate other vertebrate, invertebrate and plant taxa in spatial conservation planning (Di Marco et al., 2017). Moreover, while our study was only aimed at identifying important areas for biodiversity (and how these relate to charismatic species), there are other factors that needs to be considered to maximise the conservation effectiveness of selected

priority areas, such as the presence of threatening processes and the cost of undertaking conservation actions.

What should we conserve? Integrating the conservation of charismatic species and the multiple facets of biodiversity

Charismatic species have been the focus of many conservation organisations, both to allocate funding and define priorities for actions. While it is important to reduce extinction risks faced by the endangered charismatic species, there are also many threatened non-charismatic species that play vital ecosystem functions or are evolutionary distinct, but often receive little protection (Isaac, Turvey, Collen, Waterman, & Baillie, 2007). Simply assuming that protecting the habitats of charismatic megafauna species will also provide co-benefits to the rest of biodiversity can lead to the extinction of understudied species.

The use of taxonomic diversity alone for identifying conservation priorities has been questioned and regarded as inadequate because it fails to represent distinctiveness among species (Vane-Wright, Humphries, & Williams, 1991). Of the top 5% priority areas in Sumatra, we found that only 15% (3,227 km²) was spatially congruent among the taxonomic, phylogenetic and functional diversity, while a total of nearly 13,000 km² would be required to represent top priority areas under all biodiversity facets. This implies that the use of only one biodiversity facet in conservation planning could result in the failure to maintain the other aspects. Species are the products of evolutionary and ecological processes (Bøhn & Amundsen, 2004), and species-focused conservation strategies may be insufficient to guarantee the protection of evolutionary history and the maintenance of ecosystem functioning.

Selecting a wide-ranging charismatic species to delineate protected areas of high biodiversity importance could be an effective strategy for protecting broader biodiversity.

However, protecting the entire distribution of a threatened charismatic species is challenging and cost-inefficient. Therefore, we suggest prioritising the protection of wide-ranging charismatic species' habitats that also give the highest contribution to other biodiversity elements. Although our results suggested that combining the four charismatic species only slightly increase the spatial representation of priority areas, based on a marketing perspective, campaigns that create a 'flagship fleet' by using all four species may appeal to a broader target audience, and so increase potential funding and support (Veríssimo et al., 2014).

We also suggest it is important to follow a complementary approach, integrating as a goal both the protection of charismatic species and the protection of areas of high biodiversity importance outside the distribution of these species. Our results showed that even protecting an area as small as 1,734–5,949 km² outside the distribution of the four charismatic species would result in a much more complete coverage of top priority areas for the conservation of the taxonomic, phylogenetic and functional diversity of Sumatran mammals. Choosing new flagship species or flagship fleet from overlooked species list to promote the new protected area systems and raise funds (Smith et al., 2012) can be a winning strategy for this purpose. This needs a more thorough assessment, which includes deciding the target audience and formulating the marketing strategy (Verissimo et al., 2011).

We chose Sumatra as our case study area because it hosts some of the highest global concentrations of terrestrial and threatened mammals, and the distribution of charismatic species is a key driver of conservation action there. This is especially relevant within a region (i.e., Southeast Asia) that is today receiving proportionally less attention from international conservation journals than it used to in past decades (Di Marco et al., 2017). Biodiversity co-occurring with charismatic species may benefit from protected area establishment and law

enforcement efforts, such as patrolling to safeguard the protected areas from illegal activities (Linkie et al., 2015). Therefore, our recommendation is also relevant in regions beyond Sumatra where (i) the conservation of charismatic megafauna is prominent and (ii) protected areas are enforced by means that exclude any harmful illegal activities. While charismatic megafauna are primarily protected for the sake of these species, conservation decision-makers should also consider broader benefits for other aspects of biodiversity in conservation planning as we face increasing rate of species extinction worldwide. Our study revealed a framework to plan conservation strategies in which the protection of charismatic megafauna benefits broader aspects of biodiversity; we showed the ‘umbrella’ effectiveness of different charismatic species, and identified important biodiversity areas outside the distribution of charismatic species using spatial prioritisation techniques.

While it is ideal to protect all aspects of biodiversity, implementing systematic conservation planning is challenging, especially in developing countries where the growth rate of human population is high, land tenure conflicts are prominent and wildlife habitats are fragmented. Based on our findings, we provide several recommendations for conservation managers in Sumatra that may help advancing more efficient conservation of mammals on the island:

1. Enforcement of protected area management in places where there is high overlap between taxonomic, phylogenetic and functional diversity, such as Leuser Landscape and Bukit Barisan Mountain Ranges, especially where the three facets of biodiversity also overlap with the habitat of charismatic megafauna species.
2. Expansion of current protected areas or establishment of new protected areas to cover unprotected top priority areas identified in this study by using the Sumatran “big four” to raise funds and gain political and public support. If the priority areas are outside the habitat of the “big four”, new flagship species/fleet should be identified

3. Collation and digitisation of species occurrence records of all taxa to enable more robust species distribution modelling and spatial conservation planning.

Authors' Contributions

M.C.S. conceived the ideas, and M.C.S, M.D.M., and S.K. designed the study. M.D.M. and

C.R. developed and provided the global habitat suitability models for terrestrial mammals.

M.C.S. and M.D.M. analysed the data. M.C.S. led the writing, and all authors contributed in the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

We thank A. Reside for the advice in using Zonation; Bob Smith, an anonymous reviewer

and the Editor for constructive comments on the manuscript. We thank the Indonesian

Endowment Fund for Education (LPDP) of the Ministry of Finance for funding to MCS. SK

was supported by the Australian Research Council.

Supporting Information

List of mammal species in Sumatra (Appendix S1), data preparation for prioritisation analysis

(Appendix S2), representation of native terrestrial mammal species (Appendix S3) and

sensitivity tests and other results of spatial prioritisation analysis (Appendix S4) are available

online.

Data Accessibility

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.6n0b28n>

(Sibarani, Di Marco, Rondinini, & Kark, 2019).

References

- Andelman, S. J., & Fagan, W. F. (2000). Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? *Proceedings of the National Academy of Science*, 97(11), 5954–5959. doi:10.1073/pnas.100126797
- Badan Pusat Statistik. (2012). Indonesian population based on provinces 1971, 1980, 1990, 1995, 2000, and 2010. Retrieved January 30, 2018, from www.bps.go.id
- Bininda-Emonds, O. R. P., Cardillo, M., Jones, K. E., Macphee, R. D. E., Beck, R. M. D., Grenyer, R., ... Purvis, A. (2007). The delayed rise of present-day mammals. *Nature*, 446(7135), 507–512. doi:10.1038/nature05634
- Bøhn, T., & Amundsen, P.-A. (2004). Ecological interactions and evolution: forgotten parts of biodiversity? *BioScience*, 54(9), 804–805. doi:10.1641/0006-3568(2004)054[0804:EIAEFP]2.0.CO;2
- Bottrill, M. C., Joseph, L. N., Carwardine, J., Bode, M., Cook, C., Game, E. T., ... Possingham, H. P. (2008). Is conservation triage just smart decision making? *Trends in Ecology and Evolution*, 23(12), 649–654. doi:10.1016/j.tree.2008.07.007
- Brum, F. T., Graham, C. H., Costa, G. C., Hedges, S. B., Penone, C., Radeloff, V. C., ... Davidson, A. D. (2017). Global priorities for conservation across multiple dimensions of mammalian diversity. *Proceedings of the National Academy of Sciences*, 114(29), 7641–7646. doi:10.1073/pnas.1706461114
- Caro, T. M. (2010). *Conservation by proxy: indicator, umbrella, keystone, flagship, and other surrogate species*. Washington: Island Press.
- Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecology Letters*, 13(8), 1030–1040. doi:10.1111/j.1461-0248.2010.01493.x

- Di Marco, M., Chapman, S., Althor, G., Kearney, S., Besancon, C., Butt, N., ... Watson, J. E. M. (2017). Changing trends and persisting biases in three decades of conservation science. *Global Ecology and Conservation*, *10*, 32–42. doi:10.1016/j.gecco.2017.01.008
- Di Marco, M., & Santini, L. (2015). Human pressures predict species' geographic range size better than biological traits. *Global Change Biology*, *21*(6), 2169–2178. doi:10.1111/gcb.12834
- Di Minin, E., & Moilanen, A. (2014). Improving the surrogacy effectiveness of charismatic megafauna with well-surveyed taxonomic groups and habitat types. *Journal of Applied Ecology*, *51*(2), 281–288. doi:10.1111/1365-2664.12203
- Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, *61*(1), 1–10. doi:10.1016/0006-3207(92)91201-3
- Fritz, S. A., Bininda-Emonds, O. R. P., & Purvis, A. (2009). Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecology Letters*, *12*(6), 538–549. doi:10.1111/j.1461-0248.2009.01307.x
- GADM. (2009). Global administrative areas version 1.0. Retrieved February 2, 2018, from www.gadm.org
- Hijmans, R. J., & van Etten, J. (2012). raster: Geographic analysis and modeling with raster data. R package version 2.0-12.
- Isaac, N. J. B., Turvey, S. T., Collen, B., Waterman, C., & Baillie, J. E. M. (2007). Mammals on the EDGE: Conservation priorities based on threat and phylogeny. *PLoS ONE*, *2*(3), e296. doi:10.1371/journal.pone.0000296
- IUCN. (2016). The IUCN Red List of Threatened Species. Version 2016-1. Retrieved July 15, 2017, from <http://www.iucnredlist.org>
- Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., ... Purvis, A. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of

extant and recently extinct mammals. *Ecology*, 90(9), 2648. doi:10.1890/08-1494.1

Joseph, L. N., Maloney, R. F., & Possingham, H. P. (2009). Optimal allocation of resources among threatened species: a project prioritization protocol. *Conservation Biology*, 23(2), 328–338. doi:10.1111/j.1523-1739.2008.01124.x

Li, B. V., & Pimm, S. L. (2016). China's endemic vertebrates sheltering under the protective umbrella of the giant panda. *Conservation Biology*, 30(2), 329–339. doi:10.1111/cobi.12618

Linkie, M., Martyr, D. J., Harihar, A., Risdianto, D., Nugraha, R. T., Maryati, ... Wong, W.-M. (2015). Safeguarding Sumatran tigers: evaluating effectiveness of law enforcement patrols and local informant networks. *Journal of Applied Ecology*, 52(4), 851–860. doi:10.1111/1365-2664.12461

Margono, B. A., Turubanova, S., Zhuravleva, I., Potapov, P., & Tyukavina, A. (2012). Mapping and monitoring deforestation and forest degradation in Sumatra (Indonesia) using Landsat time series data sets from 1990 to 2010. *Environmental Research Letters*, 7(3), 034010. doi:10.1088/1748-9326/7/3/034010

Mazel, F., Guilhaumon, F., Mouquet, N., Devictor, V., Gravel, D., Renaud, J., ... Thuiller, W. (2014). Multifaceted diversity-area relationships reveal global hotspots of mammalian species, trait and lineage diversity. *Global Ecology and Biogeography*, 23(8), 836–847. doi:10.1111/geb.12158

Ministry of Forestry of the Republic of Indonesia. (2007). Strategy and action plan for the conservation of rhinos in Indonesia. Retrieved October 15, 2017, from http://www.rhinosourcecenter.com/pdf_files/134/1347679274.pdf

Moilanen, A., Franco, A. M. A., Early, R. I., Fox, R., Wintle, B., & Thomas, C. D. (2005). Prioritising multiple use landscapes for conservation: methods for large multi species planning problems. *Proceedings of the Royal Society of London, Series B: Biological*

Sciences, 272(1575), 1885–1891. doi:10.1098/rspb.2005.3164

Moilanen, A., Kujala, H., & Leathwick, J. R. (2009). The Zonation framework and software for conservation prioritization. In A. Moilanen, K. A. Wilson, & H. P. Possingham (Eds.), *Spatial conservation prioritization: quantitative methods & computational tools* (pp. 196–210). Oxford: Oxford University Press.

Moilanen, A., Pouzols, F. M., Meller, L., Veach, V., Arponen, A., Leppänen, J., & Kujala, H. (2014). *Spatial conservation planning methods and software ZONATION. User Manual*. Helsinki: C-BIG Conservation Biology Informatics Group, University of Helsinki.

Moilanen, A., & Wintle, B. A. (2007). The boundary-quality penalty: a quantitative method for approximating species responses to fragmentation in reserve selection. *Conservation Biology*, 21(2), 355–364. doi:10.1111/j.1523-1739.2006.00625.x

Nater, A., Mattle-Greminger, M. P., Nurcahyo, A., Nowak, M. G., de Manuel, M., Desai, T., ... Krützen, M. (2017). Morphometric, behavioral, and genomic evidence for a new orangutan species. *Current Biology*, 27(22), 3487–3498.e10. doi:10.1016/j.cub.2017.09.047

Pacifici, M., Santini, L., Di Marco, M., Baisero, D., Francucci, L., Grottolo Marasini, G., ... Rondinini, C. (2013). Generation length for mammals. *Nature Conservation*, 5(November), 89–94. doi:10.3897/natureconservation.5.5734

Pebesma, E. J., & Bivand, R. S. (2005). Classes and methods for spatial data in R: the sp package. *R News*, 5(2), 9–13.

Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: back to basics and looking forward. *Ecology Letters*, 9(6), 741–758. doi:10.1111/j.1461-0248.2006.00924.x

PHKA. (2015). Pembangunan area perlindungan intensif (Intensive Protection Zone) di Taman Nasional Bukit Barisan Selatan sebagai upaya peningkatan populasi badak Sumatera. Dirjen PHKA, Ministry of Forestry, Republic of Indonesia.

Pollock, L. J., Thuiller, W., & Jetz, W. (2017). Large conservation gains possible for global biodiversity facets. *Nature*, *546*(7656), 141–144. doi:10.1038/nature22368

R Development Core Team. (2008). R: A language and environment for statistical computing. Retrieved September 15, 2017, from <http://www.r-project.org>

Roberge, J.-M., & Angelstam, P. (2004). Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology*, *18*(1), 76–85. doi:10.1111/j.1523-1739.2004.00450.x

Rondinini, C., Di Marco, M., Chiozza, F., Santulli, G., Baisero, D., Visconti, P., ... Boitani, L. (2011). Global habitat suitability models of terrestrial mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 2633–2641. doi:10.1098/rstb.2011.0113

Rondinini, C., Wilson, K. A., Boitani, L., Grantham, H., & Possingham, H. P. (2006). Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecology Letters*, *9*(10), 1136–1145. doi:10.1111/j.1461-0248.2006.00970.x

Sibarani, M. C., Di Marco, M., Rondinini, C., & Kark, S. (2019). Data from: Measuring the surrogacy potential of charismatic megafauna species across taxonomic, phylogenetic and functional diversity on a megadiverse island. Dryad Digital Repository. doi:10.5061/dryad.6n0b28n

Smith, R. J., Veríssimo, D., Isaac, N. J. B., & Jones, K. E. (2012). Identifying Cinderella species: uncovering mammals with conservation flagship appeal. *Conservation Letters*, *5*(3), 205–212. doi:10.1111/j.1755-263X.2012.00229.x

Soehartono, T., Susilo, H. D., Andayani, N., Utami Atmoko, S. S., Sihite, J., Saleh, C., & Sutrisno, A. (2007). Strategi dan rencana aksi konservasi orangutan Indonesia 2007-2017. *Kehutanan, Indonesia*. Department of Forestry, Republic of Indonesia.

Soehartono, T., Susilo, H. D., Sitompul, A. F., Gunaryadi, D., Purastuti, E. M., Azmi, W., ...

Stremme, C. (2007). Strategi dan rencana aksi konservasi gajah sumatera dan gajah kalimantan 2007-2017. Department of Forestry, Republic of Indonesia.

Soehartono, T., Wibisono, H. T., Sunarto, Martyr, D., Susilo, H. D., Maddox, T., & Priatna, D. (2007). Strategi dan rencana aksi konservasi harimau sumatera (2007-2017). Department of Forestry, Republic of Indonesia.

Strecker, A. L., Olden, J. D., Whittier, J. B., & Paukert, C. P. (2011). Defining conservation priorities for freshwater fishes according to taxonomic, functional, and phylogenetic diversity. *Ecological Applications*, *21*(8), 3002–3013. doi:10.1890/11-0599.1

Tacutu, R., Craig, T., Budovsky, A., Wuttke, D., Lehmann, G., Taranukha, D., ... De Magalhães, J. P. (2013). Human Ageing Genomic Resources: integrated databases and tools for the biology and genetics of ageing. *Nucleic Acids Research*, *41*(D1), 1027–1033. doi:10.1093/nar/gks1155

Thornton, D., Zeller, K., Rondinini, C., Boitani, L., Kevin, C., Burdette, C., ... Quigley, H. (2016). Assessing the umbrella value of a range-wide conservation network for jaguars (*Panthera onca*). *Ecological Applications*, *26*(4), 1112–1124. doi:10.1890/15-0602

Vane-Wright, R. I., Humphries, C. J., & Williams, P. H. (1991). What to protect? Systematics and the agony of choice. *Biological Conservation*, *55*(3), 235–254. doi:10.1016/0006-3207(91)90030-D

Veríssimo, D., Fraser, I., Girão, W., Campos, A. A., Smith, R. J., & Macmillan, D. C. (2014). Evaluating conservation flagships and flagship fleets. *Conservation Letters*, *7*(3), 263–270. doi:10.1111/conl.12070

Verissimo, D., MacMillan, D. C., & Smith, R. J. (2011). Toward a systematic approach for identifying conservation flagships. *Conservation Letters*, *4*(1), 1–8. doi:10.1111/j.1755-263X.2010.00151.x

Williams, P. H., Burgess, N. D., & Rahbek, C. (2000). Flagship species, ecological complementarity and conserving the diversity of mammals and birds in sub-Saharan Africa. *Animal Conservation*, 3(3), 249–260. doi:10.1017/S1367943000000974

Figures

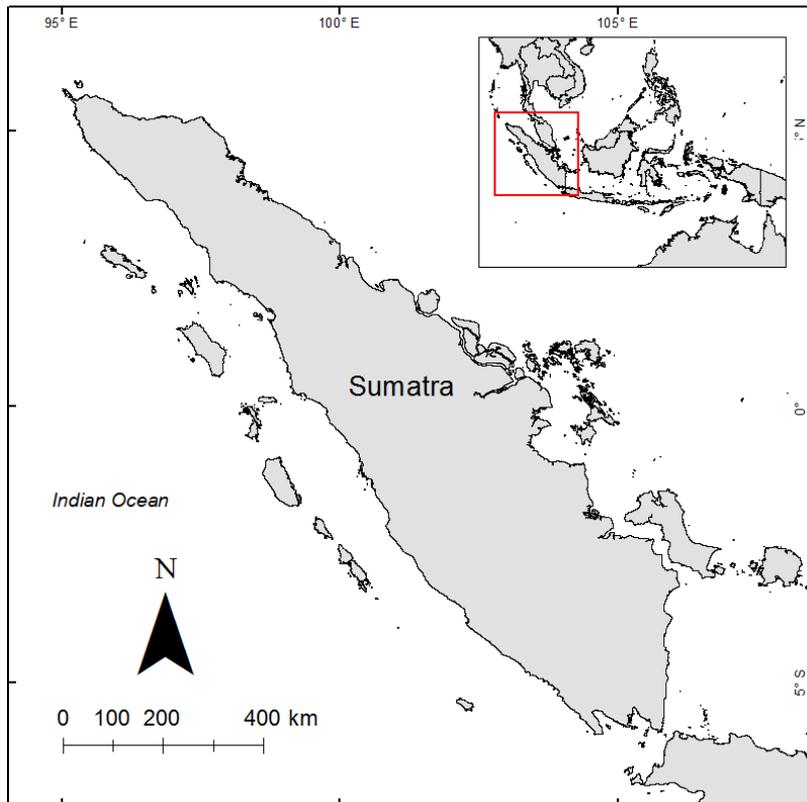


Figure 1. Map of the study region, Sumatra Island. Small insert map shows the location of the island in Indonesia.

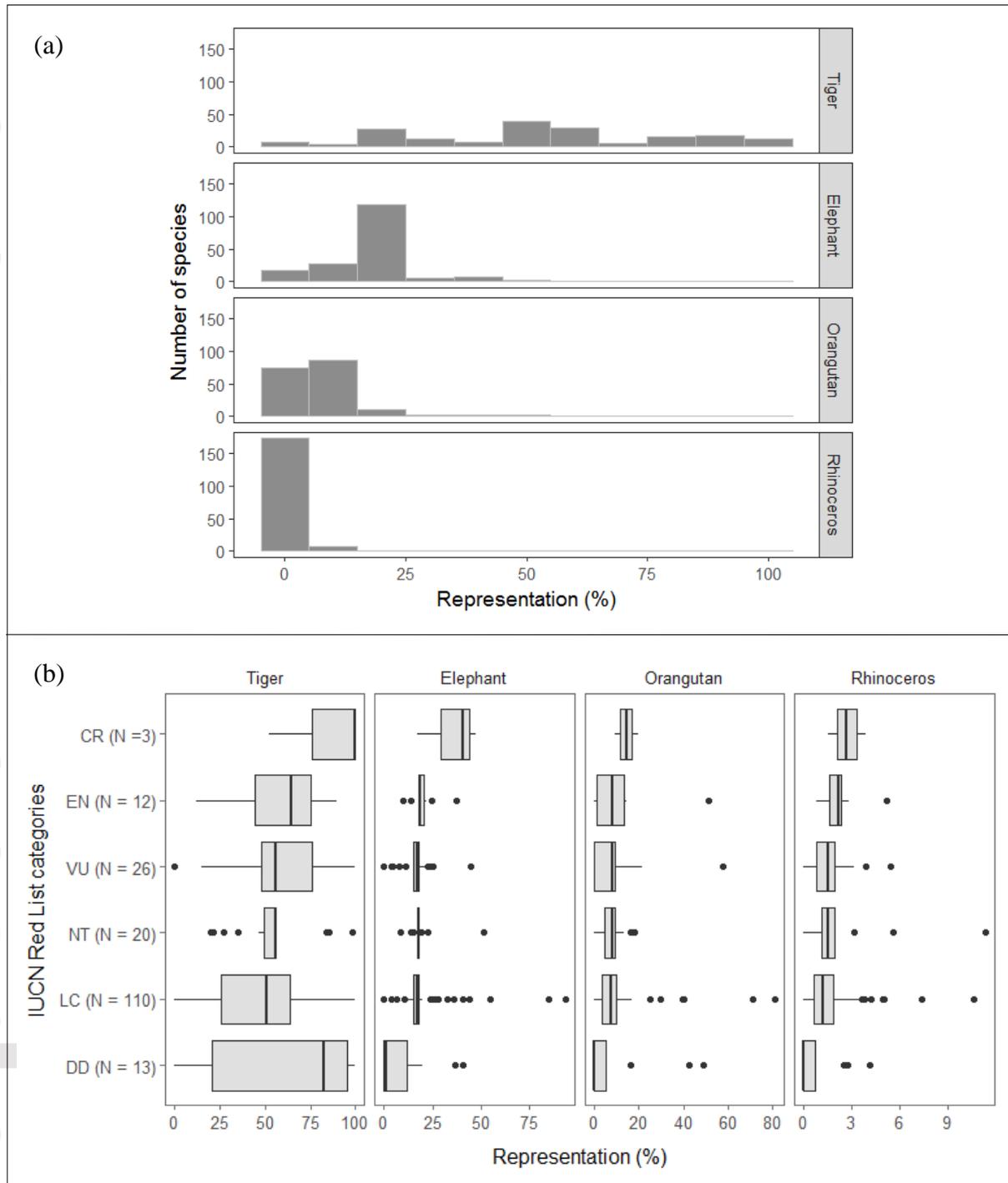


Figure 2. The representation of the co-occurring mammal species within the suitable habitat of charismatic megafauna: (a) overall and (b) categorised according to their IUCN Red List categories. DD: Data Deficient; LC: Least Concern; NT: Near Threatened; VU: Vulnerable; EN: Endangered; CR: Critically Endangered. Note that the scales of y-axis of (b) are different across the four charismatic megafauna species.

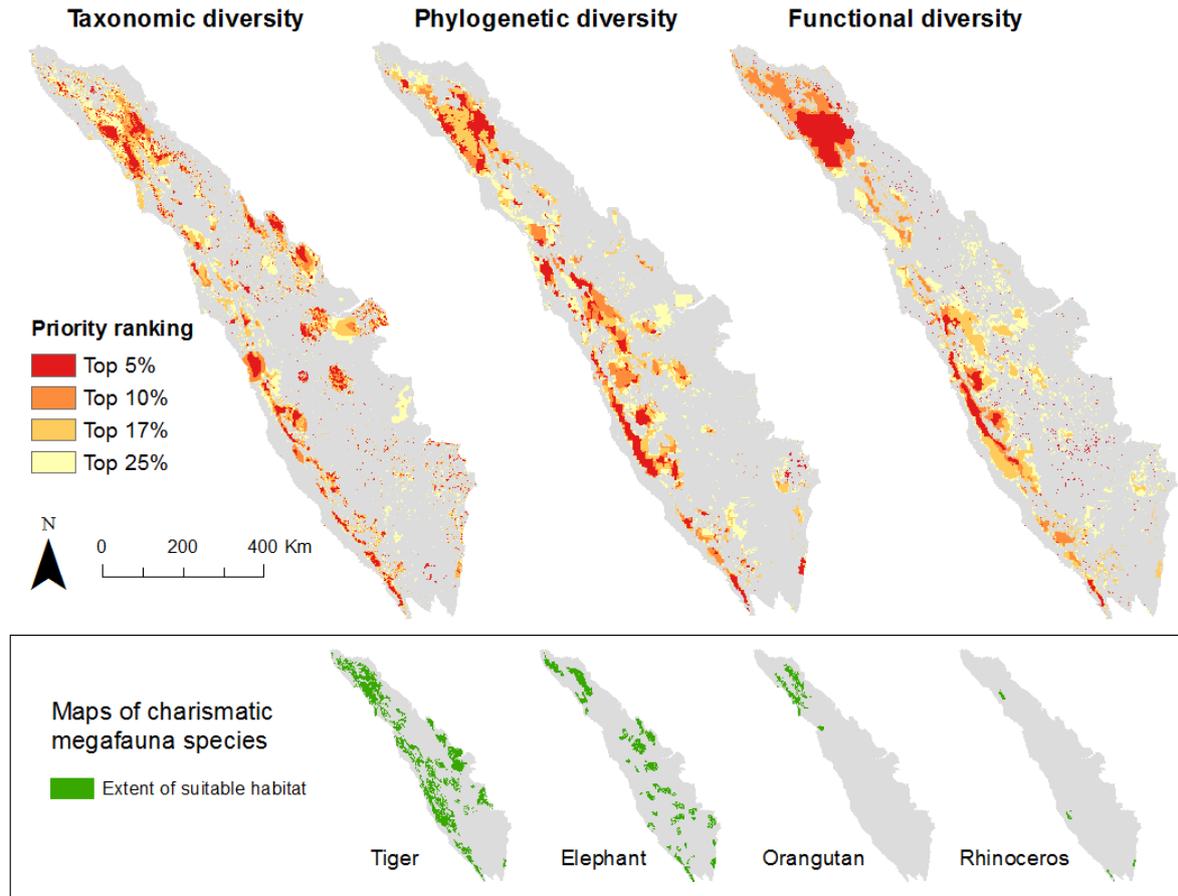


Figure 3. Priority conservation areas in Sumatra based on multiple facets of biodiversity. The top maps report the spatial prioritisation results, reporting the ranking of conservation priority throughout the landscape (with 0 meaning lowest importance and 1 meaning highest importance). We categorised high priority areas into four groups of nested priority rankings: Top 5% (values of > 0.95), top 10% (>0.90), top 17% (>0.83) and top 25% (>0.75). The inset maps report the spatial distribution of charismatic megafauna species.

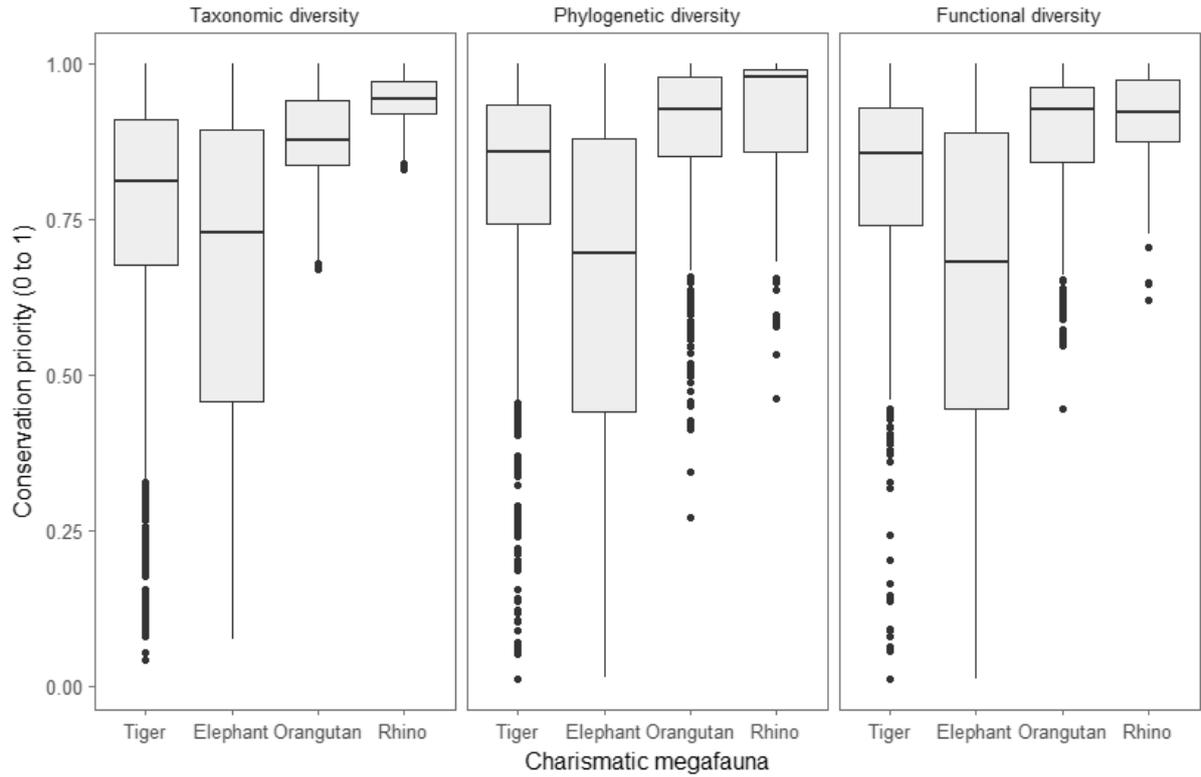


Figure 4. Boxplots showing the variation of conservation priority ranks within the extent of suitable habitat of charismatic megafauna species. The y-axis represents the conservation priority ranks that were computed based on iterative cell removal process of Zonation, ranging from 0 (lowest priority) to 1 (highest priority).

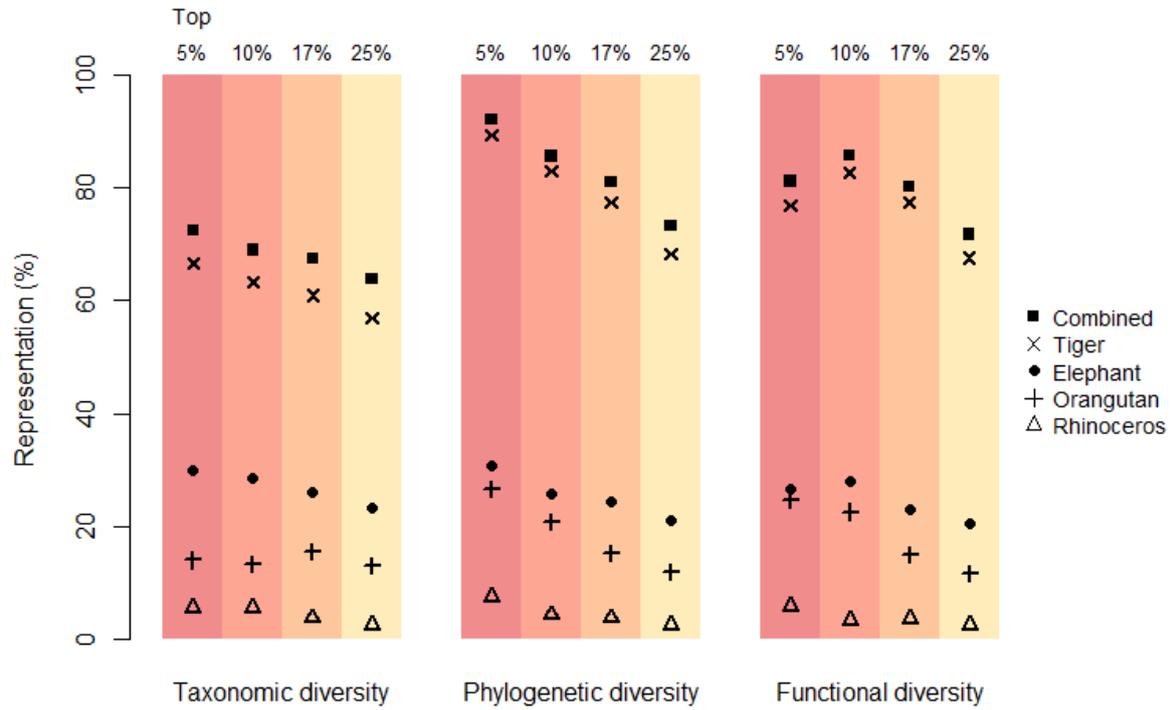


Figure 5. Representation of top priority areas within the extent of suitable habitat of charismatic species. A decrease in priority corresponds with increasing size of areas that need to be protected. For example, the top 25% priority area refers to 25% of the size of the entire landscape and the highest 25% of priority scores from Zonation algorithm. Therefore, a greater size of protected area is less represented within the extent of suitable habitat of the four charismatic megafauna.

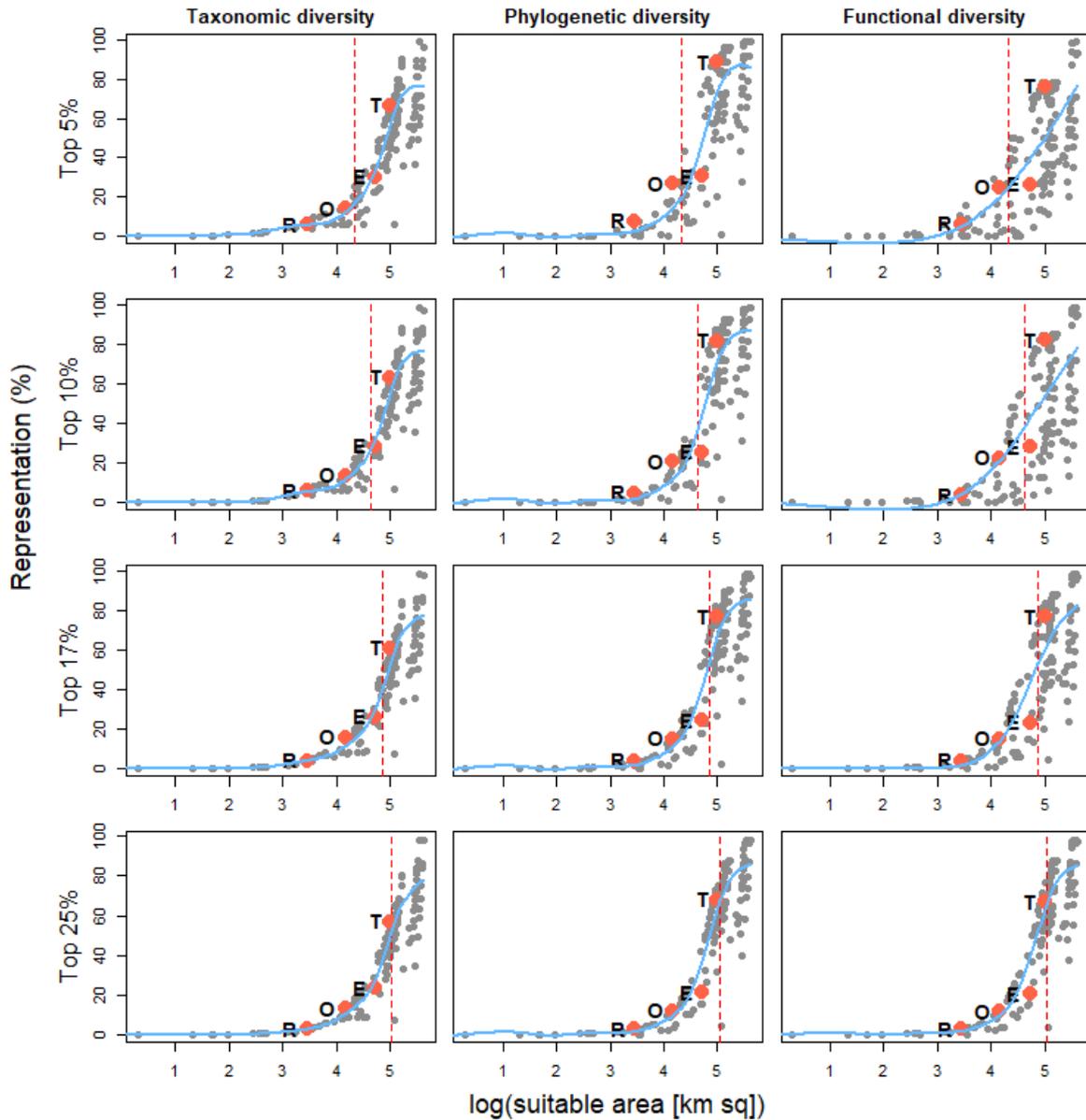


Figure 6. The representation of top 5% priority areas (a), top 10% priority areas (b), top 17% priority areas (c), and top 25% priority areas (d) within the suitable habitat of charismatic megafauna relative to their extent of suitable habitat. Letters in the plot indicate the charismatic megafauna species: T = tiger, E = Asian elephant, O = Sumatran orangutan, R = Sumatran rhinoceros. Grey points indicate the other mammal species in Sumatra (180 species). Blue lines represent fitted values of priority area representation based on generalised additive models.