Mismatch between IUCN range maps and species interactions data illustrated using the Serengeti food web

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Abstract: **Background.** Range maps are a useful tool to describe the spatial distribution of species. However, they need to be used with caution, as they essentially represent a rough approximation of a species' suitable habitats. When stacked together, the resulting communities in each grid cell may not always be realistic, especially when species interactions are taken into account. Here we show the extent of the mismatch between range maps, provided by the International Union for Conservation of Nature (IUCN), and species interactions data. More precisely, we show that local networks built from those stacked range maps often yield unrealistic communities, where species of higher trophic levels are completely disconnected from primary producers. **Methodology.** We used the well-described Serengeti food web of mammals and plants as our case study, and provide updated range maps for all predators by taking into account food-web structure. We then used occurrence data from the Global Biodiversity Information Facility (GBIF) to investigate where data is most lacking. **Results.** We found that most predator ranges comprised large areas without any overlapping distribution of their preys. However, many of these areas contained GBIF occurrences of the predator. **Conclusions.** Our results suggest that the mismatch between both data sources could be due either to the lack of information about ecological interactions or the geographical occurrence of preys. We finally discuss general guidelines to help identify defective data among distributions and interactions data, and we recommend this method as a valuable way to assess whether the occurrence data that are being used, even if incomplete, are ecologically accurate.

Introduction

Finding a species in a certain location is like finding an encrypted message that traveled through time. It carries the species' evolutionary history, migration patterns, as well as any direct and indirect effects generated by other species (some of which we may not even know exist). Ecologists have been trying to decode this message with progressively more powerful tools, from their field notes to highly complex computational algorithms. However, to succeed in this challenge it is important to have the right clues in hand. There are many ways we can be misled by data - or the lack of it: taxonomic errors, geographic inaccuracy, or sampling biases (Ladle and Hortal 2013; Hortal et al. 2015; Poisot et al. 2021). One way to identify - and potentially fix - these errors is to combine many different pieces of information about the occurrence of a species, so agreements and mismatches can emerge. Here we suggest jointly analyzing species occurrence (range maps and point occurrences) and ecological interactions to identify mismatches between datasets.

Interactions form complex networks that shape ecological structures and maintain the essential functions of ecosystems, such as seed dispersal, pollination, and biological control (Albrecht 2018; Fricke et al. 2022) that ultimately affect the composition, richness, and successional patterns of communities across biomes. Yet, the connection between occurrence and interaction data is a frequent debate in ecology (Blanchet, Cazelles, and Gravel 2020). For instance, macroecological models are often used with point or range occurrence data in order to investigate the dynamics of a species with its environment. However, these models do not account for ecological interactions, which might largely affect species distribution (Abrego et al., n.d.; Afkhami, McIntyre, and Strauss 2014; Araújo, Marcondes-Machado, and Costa 2014; Godsoe et al. 2017; Godsoe and Harmon 2012). Some researchers argue that occurrence data can also capture real-time interactions (Roy et al. 2016; Ryan et al. 2018), and, because of that, it would not be necessary to include ecological interaction dynamics in macroecological models. On the other hand, many mechanistic simulation models in ecology have considered the effect of competition and facilitation in range shifts, whilst the use of trophic interactions in this context remains insufficient (Cabral, Valente, and Hartig 2017).

A significant challenge in this debate is the quality and quantity of species distribution and ecological data (Boakes et al. 2010; Ronquillo et al. 2020; Meyer, Weigelt, and Kreft 2016) - a gap that can lead to erroneous conclusions in macroecological research (Hortal et al. 2008). Amongst the geographical data available are the range maps provided by the International Union for the Conservation of Nature (IUCN). Such maps consist of simplified polygons, often created as alpha or convex hulls around known species locations, refined by expert knowledge about the species (2021). These maps can be used in macroecological inferences in the lack of more precise information (Fourcade 2016; Alhajeri and Fourcade 2019), but it has been recommended that they are used with caution since they tend to underestimate the distribution of species that are not well-known (Herkt, Skidmore, and Fahr 2017), do not represent spatial variation in species occurrence and abundance (Dallas, Pironon, and Santini 2020), and can include inadequate areas within the estimated range. Another source of species distribution information is the Global Biodiversity Information Facility (GBIF), which is an online repository of georeferenced observational records that come from various sources, including community science programs, museum collections, and long-term monitoring schemes. A great source of bias in these datasets is the irregular sampling effort, with more occurrences originating from attractive and accessible areas and observation of charismatic species (Alhajeri and Fourcade 2019). As for ecological data, a complete assessment is difficult and is aggravated by biased sampling methods and data aggregation (Poisot et al. 2020; Hortal et al. 2015). Nevertheless, we have witnessed an increase in the availability of biodiversity data in the last decades, including those collected through community science projects (Callaghan et al. 2019; Pocock et al. 2015) and dedicated databases, such as Mangal (Poisot et al. 2016). This provides an opportunity to merge species distribution and ecological interaction data to improve our predictions of where a species may be found across large spatial scales (e.g., continental and global).

In this context, we elaborate a method that allows us to refine distribution data (more precisely range maps) based on interaction data, considering the basic assumption that predators can only be present in regions where they are connected to at least one herbivore - and thus indirectly connected to primary producers. We used a Serengeti food web dataset (Baskerville et al. 2011) (which comprises carnivores, herbivores, and plants from Tanzania) to demonstrate how a mismatch between occurrence and interaction data can highlight significant uncertainty areas in IUCN range maps. Finally, we add the GBIF occurrence points for the Serengeti species to the investigation, discuss the mechanisms that can lead to the lack of agreement between data, and build from that a vision for the next steps, reinforcing the importance of geographically explicit interaction data.

Methods

Organisms cannot persist unless they are directly or indirectly connected to a primary producer within their associated food web (Power 1992). Therefore, the range of a predator (omnivore or carnivore) depends on the overlapping ranges of its preys. If sections of a predator's range does not overlap with at least one of its prey it will become disconnected from primary producers, and therefore we would not expect the predator to occur in this area. This mismatch can be the result of different mechanisms, like the overestimation of the predator's range, taxonomic errors, or the lack of information about trophic links. Thus, given that herbivores are the main connection between plant resources (directly limited by environmental conditions) and predators (Dobson 2009; Scott et al. 2018), here we adjusted the ranges of predators based on a simple rule: we removed any part of a predator's range that did not intersect with the range of at least one prey herbivore species. So, unless the range of the predator overlapped with at least one prey item, which in turn is directly connected to a primary producer (plants), we removed that section of the predator's range. Finally, we calculated the difference in range size between the original IUCN ranges and those adjusted based on species interaction data.

Data

We investigated the mismatch between savannah species ranges and interactions in Africa (fig. 1). These ecosystems host a range of different species, including the well-characterized predator-prey dynamics between iconic predators (e.g., lions, hyenas, and leopards) and large herbivores (e.g., antelopes, wildebeests, and zebras), as well as a range of herbivorous and carnivorous small mammals. The Serengeti ecosystem has been extensively studied and its food web is one of the most complete we have to date, including primary producers identified to the species level. Here we focus on six groups of herbivores and carnivores from the Serengeti Food Web Data Set (Baskerville et al. 2011). These species exhibit direct antagonistic (predator-prey) interactions with one another and are commonly found across savannah ecosystems on the African continent (McNaughton 1992). Plants in the network were included indirectly in our analyses as we do not expect the primary producers to significantly influence the range of herbivores for several reasons. Firstly, many savannah plants are functionally similar (i.e., grasses, trees and shrubs) and cooccur across the same habitats (Baskerville et al. 2011). Secondly, herbivores in the network are broadly generalists feeding on a wide range of different plants across habitats. Indeed, out of 129 plants in our dataset, herbivores ($n = 23$) had a mean out degree (mean number of preys) of around 22 ($std = 17.5$). There is also an absence of global range maps for many plant species (Daru 2020), which prevents their direct inclusion in our analysis. Therefore, we assume that plants consumed by herbivores are present across their ranges, and as such the ranges of herbivores are not expected to be significantly constrained by the availability of food plants.

From the wider ecological network presented in Baskerville (2011), we sampled interaction data for herbivores and carnivores. This subnetwork contained 32 taxa (23 herbivores and 9 carnivores) and 84 interactions and had a connectance of 0.08. Although self-loops are informative, we removed these interactions to allow for the original IUCN ranges of predators with cannibalistic interactions to be adjusted. We treated this overall network as a metaweb since it *should* contain all potential species interactions between mammalian taxa occurring across savannah ecosystems such as the Serengeti.

We compiled IUCN range maps for the 32 species included in the metaweb from the Spatial Data Download portal (www.iucnredlist.org/resources/spatial-data-download), which we rasterized at 10 arc-minute resolution ($\sim$19 km^2 at the equator). We then combined interaction data from the metaweb and cooccurrence data generated from species ranges to create networks for each raster pixel. This generated a total of 84,244 pixel-level networks. These networks describe potential predation, not actual interactions: the former is derived information from the metaweb, and the latter is contingent on the presence of herbivores.

Range overlap measurement

We calculated the geographical overlap, i.e. the extent to which interacting predator and prey species co-occurred across their ranges, as $a/(a+c)$, where a is the number of pixels where predator and prey cooccur and c is the number of pixels where only the focal species occur. This index of geographical overlap can be calculated with prey or predators as the focal species. Values vary between 0 and 1, with values closer to 1 indicating that there is a large overlap in the ranges of the two species and values closer to 0 indicating low cooccurrence across their ranges. For each predator species, we calculated its generality to understand whether the level of trophic specialization (i.e., number of prey items per predator) affects the extent to which the ranges of the species were altered. One would assume that predators with a greater number of prey taxa (i.e., a higher generality) are less likely to have significant changes in their range as it is more likely that at least one prey species is present across most of their range.

Validation

For each species in the dataset we collated point observation data from GBIF (www.gbif.org), and condensed these data into pixels representing presence or absence of the focal taxon. These data were used to validate the range adjustments made based on species interactions (see the previous section). To do so, we calculated the proportion of GBIF presence pixels occurring within both the original and adjusted species ranges. We then compared these proportions for the predators to verify if the range adjustments removed locations with GBIF observations, hence likely true habitats.

Results

Mammal species found in the Serengeti food web are widespread in Africa, especially in grasslands and savannahs (first panel of fig. 1). However, most local networks (83.2%) built using the original IUCN range maps had at least one mammal species without a path to a primary producer (second panel of fig. 1). On average, local food webs had almost the third of their mammal species (mean = 30.5%, median = 14.3%) disconnected from basal species. In addition, many networks (16.6%) only had disconnected mammals; these networks however all had a very low number of mammal species, specifically between 1 and 4 (from a total of 32). As expected, the proportion of carnivores with a path to a primary producer was conditional on the total number of mammal species in each local network (third panel of fig. 1).

[Figure 1 about here.]

Specialized predators lose more range

[Figure 2 about here.]

Predators with fewer prey lose more range with our method (fig. 2). For instance, both *Leptailurus serval* and *Canis mesomelas* have only one prey in the Serengeti food web (tbl. 1), each of them with a very small range compared to those of their predator. This discrepancy between range sizes promotes significant range loss. On the other hand, predators of the genus *Panthera* are some of the most connected species, and they also lose the least proportion of their ranges. This mismatch between predators and preys can also be a result of taxonomic disagreement between the geographical and ecological data. Although *Canis aureus* has the same number of prey as *Caracal caracal*, none of the prey taxa of the former occurs inside its original range (tbl. 1), which results in complete range loss.

[Figure 3 about here.]

There was high variation in the overlap of predator and prey ranges (fig. 3). The high density of points on the left-hand side of fig. 3 indicates that most preys have small ranges in comparison to those of the set of carnivores in the networks, resulting in either low overlap between both ranges (bottom) or high overlap of ranges because much of that of the prey is within predators' range (top). The top-right side of the plot encompasses situations where the ranges of both predator and prey are similar and overlapping, while the bottom-right part of the plot represents a situation where the range of the predator is smaller than that of its prey and much of it occurs within the preys' range. For example, *Panthera pardus* had many preys occurring inside its range, with highly variable levels of overlap (tbl. 1). In general, species exhibited more consistent values of prey-predator overlap, than predator-prey overlap – indicated by the spread of points along the x-axis, yet more restricted variation on the y-axis (fig. 3). There was also no overall relationship between the two metrics, or for any predator species.

Table 1: List of species analyzed, their out and in degrees, total original range size (in pixels), and proportion of their ranges occupied by their preys and predators (values between 0 and 1). Species are sorted according to the groups identified by Baskerville et al. (2011). Notice how some species are isolated in the network (*Loxodonta africana*) and how *Canis aureus*'s range does not overlap with any of its preys.

Species	Number of preys	Number of predators	Total range size	Proportion of range occupied by preys	Proportion of range occupied by predators
Large carnivores					
Acinonyx jubatus	8	1	15540	0.560	0.670
Crocuta crocuta	12	1	43307	0.848	0.252
Lycaon pictus	14	0	3873	0.916	-
Panthera leo	18	0	11384	0.934	-
Panthera pardus	22	0	68137	0.766	-
Small carnivores					
Canis aureus	4	1	7358	0.000	0.780
Canis mesomelas	1	1	19872	0.190	0.995
Caracal caracal	4	0	47243	0.832	-
Leptailurus serval	1	1	38856	0.011	0.979
Small herbivores					
Damaliscus lunatus	0	4	5567	-	1
Hippopotamus amphibius	0	0	3695	-	-

Species	Number of preys	Number of predators	Total range size	Proportion of range occupied by preys	Proportion of range occupied by predators
Kobus ellipsiprymnus	0	4	26705	-	1
Ourebia ourebi	0	5	22380	-	1
Pedetes capensis	0	2	11901	-	1
Phacochoerus africanus	0	5	29963	-	0.999
Redunca redunca	0	5	17465	-	1
Rhabdomys pumilio	0	5	465	-	0.998
Tragelaphus oryx	0	2	20852	-	0.991
Tragelaphus scriptus	0	3	36011	-	0.984
Large grazers					
Aepyceros melampus	0	5	10579	-	1
Alcelaphus buselaphus	0	4	20761	-	1
Connochaetes taurinus	0	6	9650	-	1
Equus quagga	0	5	7070	-	1
Eudorcas thomsonii	0	6	463	-	1
Nanger granti	0	6	2303	-	1
Hyraxes					
Heterohyrax brucei	0	1	17728	-	0.972
Procavia capensis	0	1	47697	-	0.647
Others					
Giraffa camelopardalis	0	1	5418	-	0.470
Loxodonta africana	0	0	9654	-	-
Madoqua kirkii	0	7	4002	-	1

Species	Number of preys	Number of predators	Total range size	Proportion of range occupied by preys	Proportion of range occupied by predators
Papio anubis	0	1	23171	-	0.938
Syncerus caffer	0	1	25223	-	0.250

Validation with GBIF occurrences

The proportion of GBIF pixels (pixels with at least one GBIF occurrence) falling in the IUCN ranges varied from low to high depending on the species (fig. 4, left). The lowest proportions occurred for species with small ranges (such as *Lycaon pictus*), although some species with small ranges showed high overlap. Species with median and large ranges had high proportions of occurrences falling into their IUCN range. Predators and preys displayed similar overlap variations. While no species had all of its GBIF occurrences within its IUCN range, one species had this proportion equal to zero, *Canis aureus*, which is also the only species whose range is not covered by any of its preys. This result reinforces the concern raised in the literature on the use of IUCN range maps for species that are not well known (Herkt, Skidmore, and Fahr 2017), demonstrating how small range species are likely to have their distribution underestimated in the IUCN database. Additionally, the fact that *Canis aureus* had none of its GBIF pixels overlapping with IUCN maps suggests a taxonomic mismatch between both databases, which we explore in the Discussion section.

The proportion of GBIF pixels in updated ranges can only be equal to or lower than that of the original ranges, as our analysis removes pixels from the original range and does not add new ones. Rather, the absence of a difference between the two types of ranges indicates that no pixels with GBIF observations, hence likely true habitats, were removed by our analysis. Here this proportion was mostly similar to that of the original IUCN ranges for most predator species (fig. 4). Four species showed no difference in proportion while three species showed only small differences (proportions of 0.01 to 0.05). On the other hand, two species, *Canis* *mesomelas*, and *Leptailurus serval* showed very high differences, with overlaps lower by 0.548 and 0.871 respectively. For *Leptailurus serval*, none of the GBIF observations occurred in the updated range. These two species are also the only predators with a single prey in our metaweb. Our results delineate how a mismatch between GBIF and IUCN databases differ greatly with small changes in herbivore species ranges, and it is somewhat positively related to range size for predator species. Moreover, we show that accounting for interactions does not necessarily aggravates this dissimilarity, but it is relevant for species with little ecological information or specialists.

[Figure 4 about here.]

Discussion

The jackal is a widespread taxon in northern Africa, Europe, and Australasia, generally well adapted to local conditions due to its largely varied diet (Tsunoda and Saito 2020; Krofel et al. 2021). Because of that, we expected that the *Canis* species in our dataset would be the ones losing the least amount of range, with a higher value of the proportion of GBIF pixels within their IUCN range maps. However, the taxonomy of this group is a matter of intense discussion, as molecular and morphological data seem to disagree in the clustering of species and subspecies (Krofel et al. 2021; Stoyanov 2020). This debate is indeed reflected in our analysis: the GBIF identification of the golden jackal is incompatible with the one used by IUCN, each of them mapping its distribution in completely different places. This led to a complete exclusion of *Canis aureus* from its original range in our analysis, despite the fact that this species has four documented preys in our metaweb. This example illustrates how the taxonomic, geographical and ecological data can be used to validate one another.

Here we show that when ecological interaction data (predator-prey interactions within food webs) are used to refine species range maps, there are significant reductions in the IUCN range size of predatory organisms. Despite showing the potential importance of accounting for species interactions when estimating the range of a species, it remains unclear the extent to which the patterns observed represent ecological processes or a lack of data. In the following sections, we discuss the implications of our findings, in terms of species range maps, interaction data, and the next steps required to enhance understanding of species distributions using information on ecological networks.

Connectivity, diversity and range preservation

In the Serengeti food web there is a positive relationship between the out degrees of predators and the size of their ranges (tbl. 1). In addition, our results show that there is a negative relationship between the relative loss of predators' ranges and their number of preys (fig. 2), reinforcing the idea that generalist species can preserve their distributions longer while losing interactions. The factors limiting the geographical range of a species in a community can vary with connectivity and richness (Svenning et al. 2014). Younger communities may be more affected by environmental limitations because they are dominated by generalist species, while older metacommunities are probably affected in different ways in the center of the distribution, at the edge of ranges, and in sink and source communities (Svenning et al. 2014; Godsoe et al. 2017; Cazelles et al. 2016; Bullock et al. 2000). Additionally, it is likely that species with larger ranges of distribution and those that are more generalists would co-occur with a greater number of other species (Dáttilo et al. 2020), while dispersal capacity of competitive species modulate their aggregation in space and the effect of interactions on their range limits (Godsoe et al. 2017).

Geographical mismatch and data availability

The geographical mismatch between predators and preys has ecological consequences such as loss of ecosystem functioning and extinction of populations (Anderson et al. 2016; Dáttilo and Rico-Gray 2018; Pringle et al. 2016; Young et al. 2013). Climate change is one of the causes of this, leading, for instance, to the decrease of plant populations due to the lack of pollination (Bullock et al. 2000; Afkhami, McIntyre, and Strauss 2014; Godsoe et al. 2017). However, this mismatch can also be purely informational. When the distribution of predators and preys does not superpose, it can mean we lack information about the distribution of either species or about their interactions (e.g., predators may be feeding on different species than the ones in our dataset outside the Serengeti ecosystem). Here we addressed part of this problem by comparing the IUCN range maps with GBIF occurrences, which helped us clarify what is the shortfall for each species.

The lack of superposition between IUCN range maps and GBIF occurrences suggests that we certainly do miss geographical information about the distribution of a certain species, but it is not an indicator of the completeness of the information about ecological interactions. However, if both GBIF and IUCN occurrences tend to superpose and still the species is locally removed, this indicates we don't have information about all its interactions. The combination of this rationale with our method of updating range maps based on ecological interactions allows us to have a clearer idea of which information we are missing. For example, the lion (*Panthera leo*) was one of the species with the smallest difference between the original and the updated ranges (fig. 2), but 59.5% of the GBIF occurrences for this species fell outside the IUCN range (fig. 4). In this particular case, the IUCN maps seem to agree with species interaction data. However, the disagreement between the IUCN and the GBIF databases is concerning and suggests that the IUCN maps might underestimate the lion's distribution. On the other hand, *Leptailurus serval* and *Canis mesomelas* are two of the three species that lose the higher proportion of range due to the lack of paths to a herbivore (fig. 2), but are also some of the species with the higher proportion of GBIF occurrences inside IUCN range maps (fig. 4). This indicates that the information we are missing for these two species is related to either the occurrence of an interaction or the presence of interacting species. To illustrate that, we mapped the GBIF data for the prey of *Leptailurus serval*, with a mobility buffer around each point (fig. 5). When considering GBIF data, approximately 53% of the prey's occurrences are within the portion of the serval's range that was lost. With the buffer area, this corresponds to 13% of the lost range. This means that by adding GBIF information, we would reduce the loss of range (or information) for the predator by 13% since its distribution is conditional on the occurrence of its preys.

[Figure 5 about here.]

Finally, the extreme case of *Canis aureus* illustrates a lack of both geographical and ecological information: none of its GBIF occurrences and none of its preys occur inside its IUCN range.

We believe, therefore, that the validation of species distribution based on ecological interaction is a relevant method that can further fill in information gaps. Nevertheless, it is imperative that more geographically explicit data about ecological networks and interactions become available. This would help clarify when cooccurrences can be translated into interactions and help the development of more advanced validation methods for occurrence data.

Next steps

Here we demonstrated how we can detect uncertainty in species distribution data using ecological interactions. Knowing where questionable occurrence data are can be crucial in ecological modelling (Hortal 2008; Ladle and Hortal 2013), and accounting for these errors can improve model outputs by diminishing the error propagation (Draper 1995). For instance, we believe this is a way to account for ecological interactions in habitat suitability models without making the models more complex, but making sure (not assuming) that the input data - the species occurrence - actually accounts for ecological interactions. It is important to notice, however, that the quality and usefulness of this method are highly correlated with the amount and quality of data available about species' occurrences **and** interactions. With this paper we hope to add to the collective effort to decode the encrypted message that is the occurrence of a species in space and time. A promising avenue that adds to our method is the prediction of networks and interactions in large scales (Strydom et al. 2021), for they can add valuable information about ecological interactions where they are missing. Additionally, in order to achieve a robust modelling framework towards actual species distribution models we should invest in efforts to collect and combine open data on species occurrence and interactions, especially because we may be losing ecological interactions at least as fast as we are losing species (Valiente-Banuet et al. 2015).

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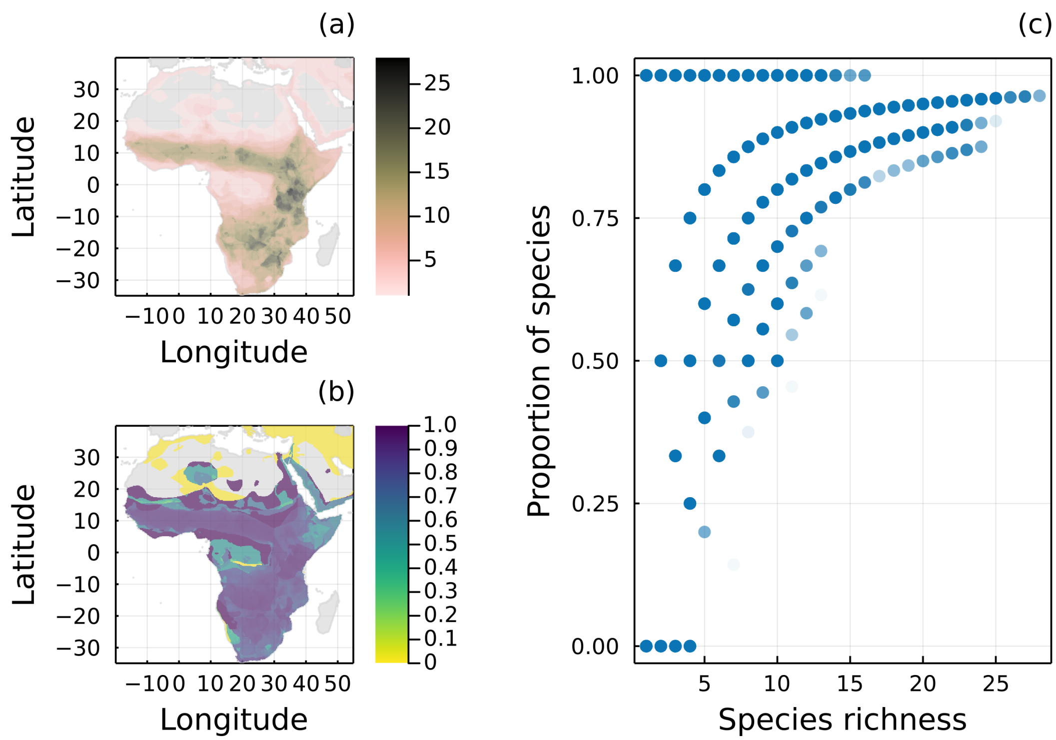

Figure 1: (a) Spatial distribution of species richness according to the original IUCN range maps of all 32 mammal species of the Serengeti food web. (b) Proportion of mammal species remaining in each local network (i.e., each pixel) after removing all species without a path to a primary producer. (c) Proportion of mammal species remaining in each local network as a function of the number of species given by the original IUCN range maps.

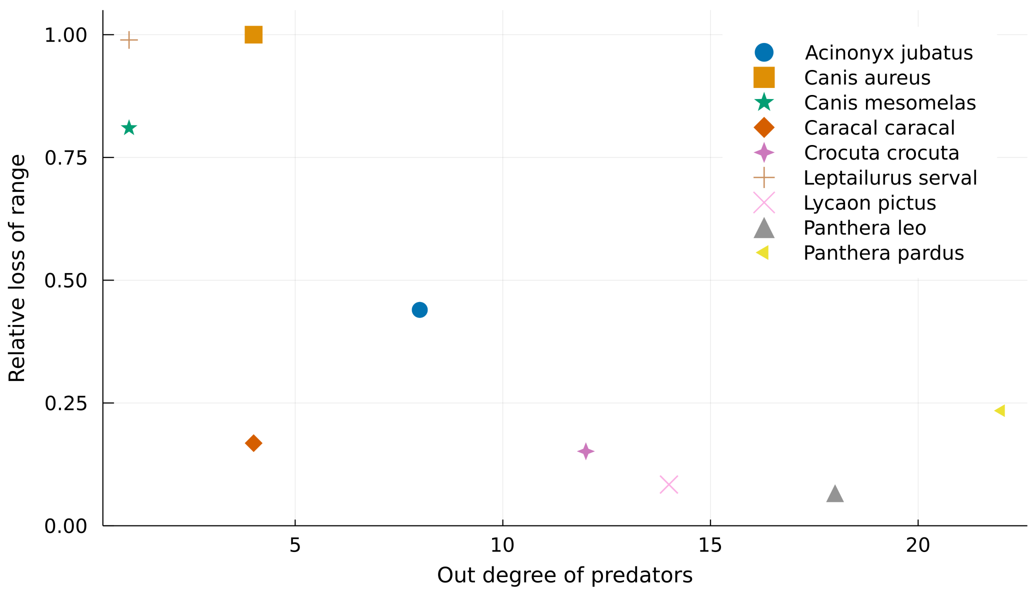

Figure 2: Negative relationship between the out degree of predator species and their relative range loss. More specialized predators lose a higher proportion of their ranges due to mismatches with the ranges of their preys.

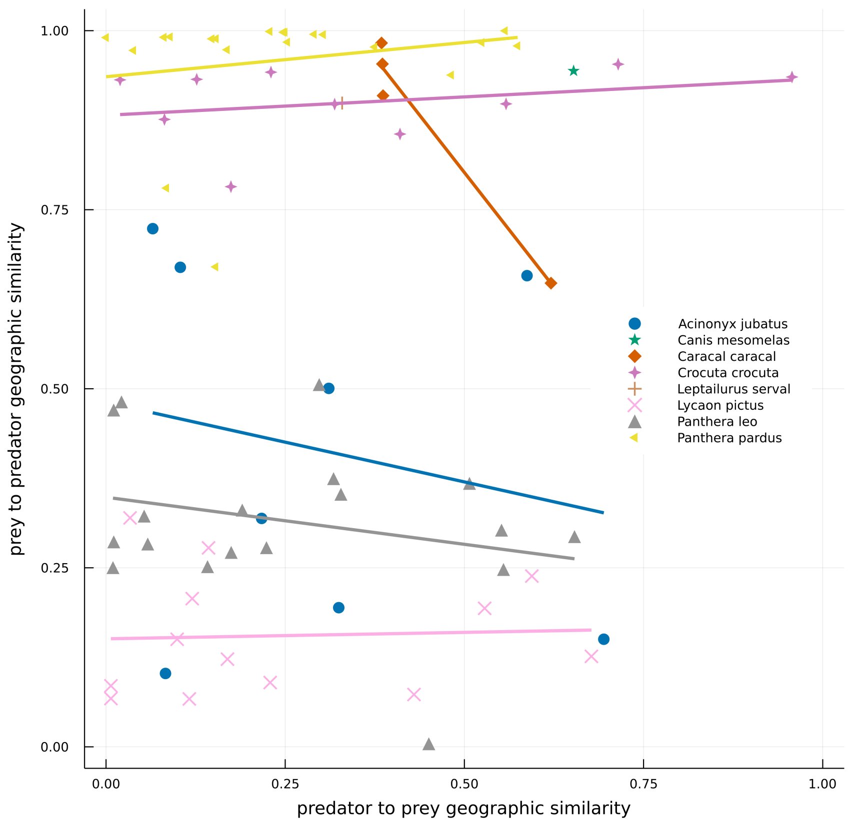

Figure 3: Geographical similarity between the original IUCN range maps of predators and preys. Dots represent predator-prey pairs, with different symbols corresponding to different predators. For a given pair of species, the number c of pixels where the focal species is present but not the other and the number a of pixels where the predator and prey cooccur, were calculated. Geographic similarities were given by $a/(a+c)$, with the predator being the focal species in the predator to prey similarity (x-axis), while the prey is the focal one in the prey to predator similarity (y-axis). One of the predators, *Canis aureus*, is not represented in the image because it is an extreme case (where all its range is suppressed by the absence of preys) and it would make the interpretation of the data more difficult.

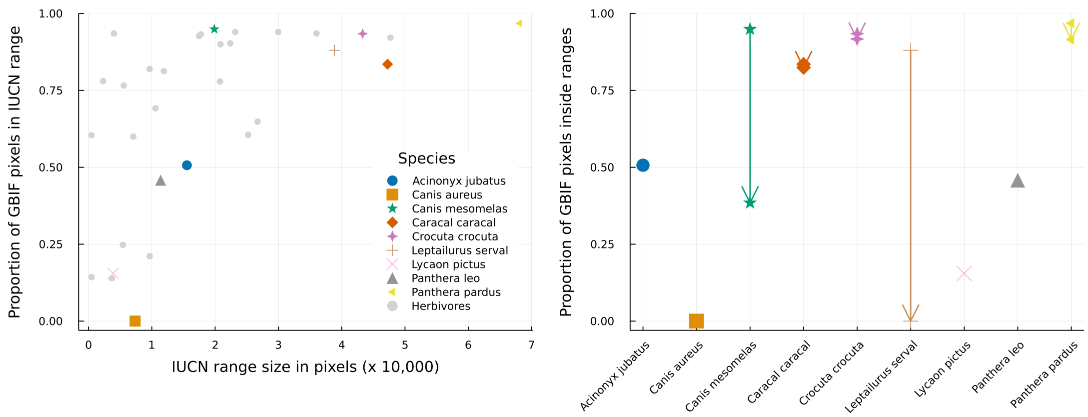

Figure 4: Left panel: Distribution of the proportion of GBIF pixels (pixels with at least one occurrence in GBIF) falling into the IUCN range for different range sizes. Right panel: Differences between the proportion of GBIF pixels falling into the IUCN and the updated ranges for every predator species. Arrows go from the proportion inside the original range to the proportion inside the updated range, which can only be equal or lower. Overlapping markers indicate no difference between the types of layers. Species markers are the same on both figures, with predators presented in distinct colored markers and all herbivores grouped in a single grey marker. Pixels represent a resolution of 10 arc-minutes.

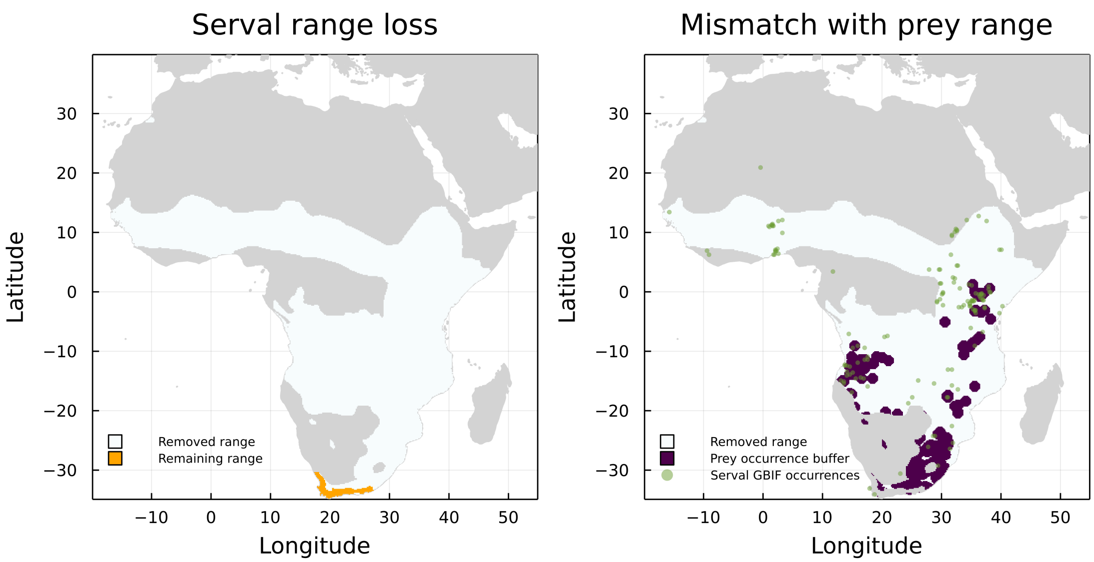

Figure 5: Mismatch between serval's range loss and GBIF occurrence of its prey. The left panel shows the reduction of serval's range when we consider the IUCN data on its prey. On the right panel, we added GBIF data on both serval and its prey, with a buffer for the prey to account for species mobility.