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

Gracielle T. Higino [1]   Francis Banville [2,3,4]   Gabriel Dansereau [2,4]   Norma R. Forero-Muñoz [2,4]

Fredric M. Windsor [5]   Timothée Poisot [2,4]

[1] Biodiversity Research Centre, University of British Columbia   [2] Université de Montréal   [3] Université de Sherbrooke   [4] Quebec Centre for Biodiversity Science   [5] School of Natural and Environmental Sciences, Newcastle University

Correspondance to:

Gracielle T. Higino — graciellehigino@gmail.com

Timothée Poisot — timothee.poisot@umontreal.ca

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 (e.g., due to updates in the taxonomy of a species), geographic inaccuracy (e.g., approximate coordinates or lack of documentation about their accuracy), or sampling biases (e.g. data clustered near roads or research centers) (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. Although previous studies have combined different types of occurrence data to measure the accuracy of datasets (Hurlbert and Jetz 2007; Hurlbert and White 2005; Ficetola et al. 2014), none have used different types of information so far (i.e., ecological characteristics other than geographical distribution). Here we suggest jointly analysing 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; Wisz et al. 2013). 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, although it has been demonstrated that they might largely affect species distribution (Abrego et al. 2021; Afkhami, McIntyre, and Strauss 2014; Araújo, Marcondes-Machado, and Costa 2014; Godsoe et al. 2017; Godsoe and Harmon 2012; Gotelli, Graves, and Rahbek 2010; Wisz et al. 2013). Some researchers argue that occurrence data can

also capture real-time interactions (see Roy et al. 2016; Ryan et al. 2018), and, because of that,
it would not be necessary to include ecological interaction dynamics in macroecological mod-
els. On the other hand, many mechanistic simulation models in ecology have considered the
effect of competition and facilitation in range shifts. For example, Gotelli *et al.* (2010) demon-
strate how conspecific attraction might be the main factor driving the distribution of migratory
birds; Afkhami *et al.* (2014) explores how mutualistic fungal endophytes are responsible or
expanding the range of native grass; many other examples are discussed in Wisz *et al.* (2013).
Although interactions across trophic levels are demonstrated to determine species range (Wisz
et al. 2013), the use of these interactions in mechanistic simulation models in macroecology
remains insufficient (as discussed in Cabral, Valente, and Hartig 2017).

A significant challenge in this debate is the quality and quantity of species distribution and eco-
logical 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 (IUCN Red List Technical Working Group 2019). These maps can be used in macroeco-
logical 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 under-
estimate the distribution of species that are not well-known (Herkt, Skidmore, and Fahr 2017)
(especially at fine scale resolutions; Hurlbert and Jetz (2007); Hurlbert and White (2005)), 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 on-
line 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 originat-
ing 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). Never-theless, 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 oppor-tunity 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).

It has been demonstrated that the agreement between range maps and point data varies geograph-ically (Hurlbert and Jetz 2007; Hurlbert and White 2005; Ficetola et al. 2014). Adding ecolog-ical interaction data to this comparison might help to elucidate where these (dis)agreements are more likely to be true and which dataset better represent the actual distribution of species. 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 mis-match 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 misestimation of both the predator's and the preys'

ranges (Ladle and Hortal 2013; Rondinini et al. 2006), taxonomic errors (Isaac, Mallet, and

Mace 2004; Ladle and Hortal 2013), or the lack of information about trophic links (i.e., the

lack of connection between the ranges of a predator and a primary producer may be due a third

species we don't know is connected to both). 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 net-

work 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

114 species (Daru 2020), which prevents their direct inclusion in our analysis. Therefore, we as-

115 sume that plants consumed by herbivores are present across their ranges, and as such the ranges

116 of herbivores are not expected to be significantly constrained by the availability of food plants.

117 From the wider ecological network presented in Baskerville (2011), we sampled interaction data

118 for herbivores and carnivores. This subnetwork contained 32 taxa (23 herbivores and 9 carni-

119 vores) and 84 interactions and had a connectance of 0.08. Although self-loops are informative,

120 we removed these interactions to allow for the original IUCN ranges of predators with canni-

121 balistic interactions to be adjusted. We treated this overall network as a metaweb since it *should*

122 contain all potential species interactions between mammalian taxa occurring across savannah

123 ecosystems such as the Serengeti.

124 We compiled IUCN range maps for the 32 species included in the metaweb from the Spatial Data

125 Download portal (www.iucnredlist.org/resources/spatial-data-download), which we rasterized

126 at 10 arc-minute resolution (~18 km at the equator). We restricted the rasters a spatial extent

127 comprised between latitudes 35°S and 40°N and longitudes 20°W and 55°E. We then combined

128 interaction data from the metaweb and cooccurrence data generated from species ranges to create

129 networks for each raster pixel. This generated a total of 84,244 pixel-level networks. These

130 networks describe potential predation, not actual interactions: the former is derived information

131 from the metaweb, and the latter is contingent on the presence of herbivores.

Range overlap measurement

133 We calculated the geographical overlap, i.e. the extent to which interacting predator and prey

134 species co-occurred across their ranges, as $a/(a + c)$, where a is the number of pixels where

135 predator and prey cooccur and c is the number of pixels where only the focal species occur.

136 This index of geographical overlap can be calculated with prey or predators as the focal species.

137 Values vary between 0 and 1, with values closer to 1 indicating that there is a large overlap in

138 the ranges of the two species and values closer to 0 indicating low cooccurrence across their

139 ranges. For each predator species, we calculated its generality to understand whether the level

140 of trophic specialization (i.e., number of prey items per predator) affects the extent to which the

141 ranges of the species were altered. One would assume that predators with a greater number of

142 prey taxa (i.e., a higher generality) are less likely to have significant changes in their range as it

143 is more likely that at least one prey species is present across most of their range.

Validation

145 For each species in the dataset we collated point observation data from GBIF (www.gbif.org).

146 We restricted our queries to the data with spatial coordinates and which were inside the spatial

147 extent of our rasters. We did not use continental or date filters to retrieve as much data as possible.

148 However, a few observations were localized in the ocean near latitude 0° and longitude 0°. We

149 assumed these were errors and removed all observations falling in the extent between latitudes

150 2°S and 2°N and longitudes 2°W and 2°E to keep only mainland sites.

151 We then converted the occurrence data into raster format by determining which pixels had a

152 least one GBIF occurrence. This allowed us to remove the effect of repeated sampling in some

153 locations. These data were used to validate the range adjustments made based on species in-

154 teractions (see beginning of Methods section). To do so, we calculated the proportion of GBIF

155 presence pixels occurring within both the original IUCN species range and the adjusted one. We

156 then compared these proportions for the predators to verify if the range adjustments removed

157 locations with GBIF observations, hence likely true habitats.

Software

159 We performed all analyses using *Julia* v1.7.2 (Bezanson et al. 2017). We used the packages

160 `SimpleSDMLayers.jl` (Dansereau and Poisot 2021) to manipulate the raster layers, `EcologicalNetworks.jl`

161 (Poisot et al. 2019) to construct and manipulate the interaction networks, and `GBIF.jl` (Dansereau

162 and Poisot 2021) to retrieve the species occurrences from GBIF. We also used *GDAL* (GDAL/OGR

163 contributors 2021) to rasterize the IUCN range maps (initially available as shapefiles from the

164 Spatial Data Download portal). All the scripts required to reproduce the analyses are available

165 at https://doi.org/10.5281/zenodo.6842861.

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 a 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 analysed, 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	-

Species	Number of preys	Number of predators	Total range size	Proportion of range occupied by preys	Proportion of range occupied by predators
Leptailurus serval	1	1	38856	0.011	0.979
Small herbivores					
Damaliscus lunatus	0	4	5567	-	1
Hippopotamus amphibius	0	0	3695	-	-
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

Species	Number of preys	Number of predators	Total range size	Proportion of range occupied by preys	Proportion of range occupied by predators
Others					
Giraffa camelopardalis	0	1	5418	-	0.470
Loxodonta africana	0	0	9654	-	-
Madoqua kirkii	0	7	4002	-	1
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 within the IUCN ranges varied from low to high depending on the species (fig. 4, left). The lowest proportions occurred for species with small ranges. Amongst herbivores, *Rhabdomys pumilio* has a proportion of 22.6% of its presence pixels within its IUCN range, while predators have this proportion above 55% (such as *Lycaon pictus*, with 55.1%, and *Canis aureus*, with 56.2%). Nevertheless, some species with smaller ranges showed high data overlap (such as *Canis mesomelas*, with 94.9%, and many herbivores). Overall, predators and preys displayed similar overlap variations, and species with median and large ranges had higher proportions of occurrences falling into their IUCN range.

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). Two species showed no difference in proportion while four species showed only

small differences (*Crocuta crocuta* lost 1.3% of the original data overlap; *Acinonyx jubatus* lost 1.9%; *Panthera pardus* lost 8.8%; and *Caracal caracal* lost 12.3%). On the other hand, three species, *Canis aureus*, *Canis mesomelas*, and *Leptailurus serval* showed very high differences, with overlaps lowered by 100%, 57.4%, and 100% respectively. These last two species are also the only predators with a single prey in our metaweb. *Canis aureus* has four preys, but it has one of the smallest ranges in IUCN, which 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 such a conspicuous mismatch between both the original and updated IUCN range maps, and between GBIF and IUCN data, may indicate a taxonomic incongruency between the three databases used here, which we explore in the Discussion section. 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 probably influenced our results: with originally only 56.2% of the GBIF pixels of the golden jackal (*Canis aureus*) overlapping with the IUCN data, we suspect that many of the GBIF occurrences refer to other *Canis* species,

and that its taxonomic identification in the network database is probably outdated. 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.

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. Here, we showed that there is a negative relationship between the relative loss of predators' ranges and their number of preys, 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 this 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 no difference between the original and the updated ranges, but 40.7% of the GBIF occurrences for this species fell outside its 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, 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 42% of the prey's occurrences are within the portion of the serval's range that was lost. With the buffer area, this corresponds to 15% of the lost range. This means that by adding GBIF information,

299 we would reduce the loss of range (or information) for the predator by 15% since its distribution

300 is conditional on the occurrence of its preys.

301   [Figure 5 about here.]

302 Finally, the extreme case of *Canis aureus* illustrates a lack of both geographical and ecological

303 information: only half of its GBIF presence pixels and none of its preys occur inside its IUCN

304 range. We believe, therefore, that the validation of species distribution based on ecological inter-

305 action is a relevant method that can further fill in information gaps. Nevertheless, it is imperative

306 that more geographically explicit data about ecological networks and interactions become avail-

307 able. This would help clarify when cooccurrences can be translated into interactions (Windsor

308 et al. 2022) and help the development of more advanced validation methods for occurrence data.

309 **Next steps**

310 Here we demonstrated how we can detect uncertainty in species distribution data using ecolog-

311 ical interactions. Knowing where questionable occurrence data are can be crucial in ecological

312 modelling (Hortal 2008; Ladle and Hortal 2013), and accounting for these errors can improve

313 model outputs by diminishing the error propagation (Draper 1995). For instance, we believe

314 this is a way to account for ecological interactions in habitat suitability models without making

315 the models more complex, but by making sure (not assuming) that the input data - the species

316 occurrence - actually accounts for ecological interactions. It is important to notice, however,

317 that the quality and usefulness of this method are highly correlated with the amount and quality

318 of data available about species' occurrences **and** interactions. With this paper, we hope to add

319 to the collective effort to decode the encrypted message that is the occurrence of a species in

320 space and time. A promising avenue that adds to our method is the prediction of networks and

321 interactions in large scales (Strydom et al. 2021; Windsor et al. 2022), for they can add valu-

322 able information about ecological interactions where they are missing. Additionally, in order to

323 achieve a robust modelling framework towards actual species distribution models we should in-

324 vest in efforts to collect and combine open data on species occurrence and interactions (Windsor

et al. 2022), especially because we may be losing ecological interactions at least as fast as we are losing species (Valiente-Banuet et al. 2015).

Acknowledgements

We acknowledge that this study was conducted on land within the traditional unceded territory of the Saint Lawrence Iroquoian, Anishinabewaki, Mohawk, Huron-Wendat, and Omàmiwinini-wak nations. We thank the editor and reviewer for their thoughtful comments, which considerably improved this manuscript.

References

Abrego, Nerea, Tomas Roslin, Tea Huotari, Yinqiu Ji, Niels Martin Schmidt, Jiaxin Wang, Douglas W. Yu, and Otso Ovaskainen. 2021. "Accounting for Species Interactions Is Necessary for Predicting How Arctic Arthropod Communities Respond to Climate Change." *Ecography* 44 (6): 885–96. https://doi.org/10.1111/ecog.05547.

Afkhami, Michelle E., Patrick J. McIntyre, and Sharon Y. Strauss. 2014. "Mutualist-Mediated Effects on Species' Range Limits Across Large Geographic Scales." *Ecology Letters* 17 (10): 1265–73. https://doi.org/10.1111/ele.12332.

Albrecht, Jörg. 2018. "Plant and Animal Functional Diversity Drive Mutualistic Network Assembly Across an Elevational Gradient." *NATURE COMMUNICATIONS*, 10.

Alhajeri, Bader H, and Yoan Fourcade. 2019. "High Correlation Between Species-Level Environmental Data Estimates Extracted from IUCN Expert Range Maps and from GBIF Occurrence Data." *Journal of Biogeography*, 13. https://doi.org/10.1111/jbi.13619.

Anderson, T. Michael, Staci White, Bryant Davis, Rob Erhardt, Meredith Palmer, Alexandra Swanson, Margaret Kosmala, and Craig Packer. 2016. "The Spatial Distribution of African Savannah Herbivores: Species Associations and Habitat Occupancy in a Landscape Context." *Philosophical Transactions of the Royal Society B: Biological Sciences* 371 (1703): 20150314. https://doi.org/10.1098/rstb.2015.0314.

Araújo, Carlos B. de, Luiz Octavio Marcondes-Machado, and Gabriel C. Costa. 2014. "The Importance of Biotic Interactions in Species Distribution Models: A Test of the Eltonian Noise Hypothesis Using Parrots." *Journal of Biogeography* 41 (3): 513–23. https://doi.org/10.1111/jbi.12234.

Baskerville, Edward B., Andy P. Dobson, Trevor Bedford, Stefano Allesina, T. Michael Anderson, and Mercedes Pascual. 2011. "Spatial Guilds in the Serengeti Food Web Revealed by a Bayesian Group Model." *PLOS Computational Biology* 7 (12): e1002321. https://doi.org/10.1371/journal.pcbi.1002321.

Bezanson, Jeff, Alan Edelman, Stefan Karpinski, and Viral B. Shah. 2017. "Julia: A Fresh Approach to Numerical Computing." *SIAM Review* 59 (1): 65–98. https://doi.org/10.1137/141000671.

Blanchet, F. Guillaume, Kevin Cazelles, and Dominique Gravel. 2020. "Co-Occurrence Is Not Evidence of Ecological Interactions." *Ecology Letters* 23 (7): 1050–63. https://doi.org/10.1111/ele.13525.

Boakes, Elizabeth H., Philip J. K. McGowan, Richard A. Fuller, Ding Chang-qing, Natalie E. Clark, Kim O'Connor, and Georgina M. Mace. 2010. "Distorted Views of Biodiversity: Spatial and Temporal Bias in Species Occurrence Data." *PLOS Biology* 8 (6): e1000385. https://doi.org/10.1371/journal.pbio.1000385.

Bullock, James M., Rebecca J. Edwards, Peter D. Carey, and Rob J. Rose. 2000. "Geographical Separation of Two Ulex Species at Three Spatial Scales: Does Competition Limit Species' Ranges?" *Ecography* 23 (2): 257–71. https://doi.org/10.1111/j.1600-0587.2000.tb00281.x.

Cabral, Juliano Sarmento, Luis Valente, and Florian Hartig. 2017. "Mechanistic Simulation Models in Macroecology and Biogeography: State-of-Art and Prospects." *Ecography* 40 (2): 267–80. https://doi.org/10.1111/ecog.02480.

Callaghan, Corey T., Jodi J. L. Rowley, William K. Cornwell, Alistair G. B. Poore, and Richard E. Major. 2019. "Improving Big Citizen Science Data: Moving Beyond Haphazard Sampling." *PLOS Biology* 17 (6): e3000357. https://doi.org/10.1371/journal.pbio.

3000357.

Cazelles, Kévin, Nicolas Mouquet, David Mouillot, and Dominique Gravel. 2016. "On the Integration of Biotic Interaction and Environmental Constraints at the Biogeographical Scale." *Ecography* 39 (10): 921–31. https://doi.org/10.1111/ecog.01714.

Dallas, Tad, Samuel Pironon, and Luca Santini. 2020. "The Abundant-Centre Is Not All That Abundant: A Comment to Osorio-Olvera Et Al. 2020," 2020.02.27.968586. https://doi.org/10.1101/2020.02.27.968586.

Dansereau, Gabriel, and Timothée Poisot. 2021. "SimpleSDMLayers.jl and GBIF.jl: A Framework for Species Distribution Modeling in Julia." *Journal of Open Source Software* 6 (57): 2872. https://doi.org/10.21105/joss.02872.

Daru, Barnabas H. 2020. "GreenMaps: A Tool for Addressing the Wallacean Shortfall in the Global Distribution of Plants." *bioRxiv*, 2020.02.21.960161. https://doi.org/10.1101/2020.02.21.960161.

Dáttilo, Wesley, Nathalia Barrozo-Chávez, Andrés Lira-Noriega, Roger Guevara, Fabricio Villalobos, Diego Santiago-Alarcon, Frederico Siqueira Neves, Thiago Izzo, and Sérvio Pontes Ribeiro. 2020. "Species-Level Drivers of Mammalian Ectoparasite Faunas." *Journal of Animal Ecology* 89 (8): 1754–65. https://doi.org/10.1111/1365-2656.13216.

Dáttilo, Wesley, and Victor Rico-Gray, eds. 2018. *Ecological Networks in the Tropics: An Integrative Overview of Species Interactions from Some of the Most Species-Rich Habitats on Earth*. 1st ed. 2018. Cham: Springer International Publishing : Imprint: Springer. https://doi.org/10.1007/978-3-319-68228-0.

Dobson, Andy. 2009. "Food-Web Structure and Ecosystem Services: Insights from the Serengeti." *Philosophical Transactions of the Royal Society B: Biological Sciences* 364 (1524): 1665–82. https://doi.org/10.1098/rstb.2008.0287.

Draper, D. 1995. "Assessment and Propagation of Model Uncertainty." *Journal of the Royal Statistical Society Series B-Statistical Methodology* 57 (1): 45–97. https://doi.org/10.1111/j.2517-6161.1995.tb02015.x.

Ficetola, Gentile Francesco, Carlo Rondinini, Anna Bonardi, Vineet Katariya, Emilio Padoa-Schioppa, and Ariadne Angulo. 2014. "An Evaluation of the Robustness of Global Amphibian Range Maps." *Journal of Biogeography* 41 (2): 211–21. https://doi.org/10.1111/jbi.12206.

Fourcade, Yoan. 2016. "Comparing Species Distributions Modelled from Occurrence Data and from Expert-Based Range Maps. Implication for Predicting Range Shifts with Climate Change." *Ecological Informatics* 36: 8–14. https://doi.org/10.1016/j.ecoinf.2016.09.002.

Fricke, Evan C., Alejandro Ordonez, Haldre S. Rogers, and Jens-Christian Svenning. 2022. "The Effects of Defaunation on Plants' Capacity to Track Climate Change." *Science*. https://doi.org/10.1126/science.abk3510.

GDAL/OGR contributors. 2021. *GDAL/OGR Geospatial Data Abstraction Software Library*. Manual. Open Source Geospatial Foundation.

Godsoe, William, and Luke J. Harmon. 2012. "How Do Species Interactions Affect Species Distribution Models?" *Ecography* 35 (9): 811–20. https://doi.org/10.1111/j.1600-0587.2011.07103.x.

Godsoe, William, Jill Jankowski, Robert D. Holt, and Dominique Gravel. 2017. "Integrating Biogeography with Contemporary Niche Theory." *Trends in Ecology and Evolution* 32 (7): 488–99. https://doi.org/10.1016/j.tree.2017.03.008.

Gotelli, Nicholas J., Gary R. Graves, and Carsten Rahbek. 2010. "Macroecological Signals of Species Interactions in the Danish Avifauna." *Proceedings of the National Academy of Sciences* 107 (11): 5030–35. https://doi.org/10.1073/pnas.0914089107.

Herkt, K. Matthias B., Andrew K. Skidmore, and Jakob Fahr. 2017. "Macroecological Conclusions Based on IUCN Expert Maps: A Call for Caution." *Global Ecology and Biogeography* 26 (8): 930–41. https://doi.org/10.1111/geb.12601.

Hortal, Joaquín. 2008. "Uncertainty and the Measurement of Terrestrial Biodiversity Gradients." *Journal of Biogeography* 35 (8): 1335–36. https://doi.org/10.1111/j.1365-2699.2008.01955.x.

Hortal, Joaquín, Francesco de Bello, José Alexandre F. Diniz-Filho, Thomas M. Lewinsohn, Jorge M. Lobo, and Richard J. Ladle. 2015. "Seven Shortfalls That Beset Large-Scale Knowledge of Biodiversity." *Annual Review of Ecology, Evolution, and Systematics* 46 (1): 523–49. https://doi.org/10.1146/annurev-ecolsys-112414-054400.

Hortal, Joaquín, Alberto Jiménez-Valverde, José F. Gómez, Jorge M. Lobo, and Andrés Baselga. 2008. "Historical Bias in Biodiversity Inventories Affects the Observed Environmental Niche of the Species." *Oikos* 117 (6): 847–58. https://doi.org/10.1111/j.0030-1299.2008.16434.x.

Hurlbert, Allen H., and Walter Jetz. 2007. "Species Richness, Hotspots, and the Scale Dependence of Range Maps in Ecology and Conservation." *Proceedings of the National Academy of Sciences* 104 (33): 13384–89. https://doi.org/10.1073/pnas.0704469104.

Hurlbert, Allen H., and Ethan P. White. 2005. "Disparity Between Range Map- and Survey-Based Analyses of Species Richness: Patterns, Processes and Implications." *Ecology Letters* 8 (3): 319–27. https://doi.org/10.1111/j.1461-0248.2005.00726.x.

Isaac, Nick J. B., James Mallet, and Georgina M. Mace. 2004. "Taxonomic Inflation: Its Influence on Macroecology and Conservation." *Trends in Ecology & Evolution* 19 (9): 464–69. https://doi.org/10.1016/j.tree.2004.06.004.

IUCN Red List Technical Working Group. 2019. "Mapping Standards and Data Quality for IUCN Red List Spatial Data." Prepared by the Standards and Petitions Working Group of the IUCN SSC Red ....

Krofel, M., J. Hatlauf, W. Bogdanowicz, L. a. D. Campbell, R. Godinho, Y. V. Jhala, A. C. Kitchener, et al. 2021. "Towards Resolving Taxonomic Uncertainties in Wolf, Dog and Jackal Lineages of Africa, Eurasia and Australasia." *Journal of Zoology* n/a (n/a): 1–14. https://doi.org/10.1111/jzo.12946.

Ladle, Richard, and Joaquín Hortal. 2013. "Mapping Species Distributions: Living with Uncertainty." *Frontiers of Biogeography* 5 (1): 4–6.

McNaughton, S. J. 1992. "The Propagation of Disturbance in Savannas Through Food Webs." *Journal of Vegetation Science* 3 (3): 301–14. https://doi.org/10.2307/3235755.

Meyer, Carsten, Patrick Weigelt, and Holger Kreft. 2016. "Multidimensional Biases, Gaps and Uncertainties in Global Plant Occurrence Information." *Ecology Letters* 19 (8): 992–1006. https://doi.org/10.1111/ele.12624.

Pocock, Michael J. O., Helen E. Roy, Chris D. Preston, and David B. Roy. 2015. "The Biological Records Centre: A Pioneer of Citizen Science." *Biological Journal of the Linnean Society* 115 (3): 475–93. https://doi.org/10.1111/bij.12548.

Poisot, Timothée, Benjamin Baiser, Jennifer A Dunne, Sonia Kéfi, François Massol, Nicolas Mouquet, Tamara N Romanuk, Daniel B Stouffer, Spencer A Wood, and Dominique Gravel. 2016. "Mangal - Making Ecological Network Analysis Simple." *Ecography* 39 (4): 384–90.

Poisot, Timothée, Gabriel Bergeron, Kevin Cazelles, Tad Dallas, Dominique Gravel, Andrew MacDonald, Benjamin Mercier, Clément Violet, and Steve Vissault. 2021. "Global Knowledge Gaps in Species Interaction Networks Data." *Journal of Biogeography* 48 (7): 1552–63. https://doi.org/10.1111/jbi.14127.

Poisot, Timothée, Gabriel Bergeron, Kevin Cazelles, Tad Dallas, Dominique Gravel, Andrew Macdonald, Benjamin Mercier, Clément Violet, and Steve Vissault. 2020. "Environmental Biases in the Study of Ecological Networks at the Planetary Scale." *bioRxiv*, 2020.01.27.921429. https://doi.org/10.1101/2020.01.27.921429.

Poisot, Timothée, Zachary Bélisle, Laura Hoebeke, Michiel Stock, and Piotr Szefer. 2019. "EcologicalNetworks.jl: Analysing Ecological Networks of Species Interactions." *Ecography* 42 (11): 1850–61. https://doi.org/10.1111/ecog.04310.

Power, Mary E. 1992. "Top-Down and Bottom-Up Forces in Food Webs: Do Plants Have Primacy." *Ecology* 73 (3): 733–46. https://doi.org/10.2307/1940153.

Pringle, Robert M., Kirsten M. Prior, Todd M. Palmer, Truman P. Young, and Jacob R. Goheen. 2016. "Large Herbivores Promote Habitat Specialization and Beta Diversity of African Savanna Trees." *Ecology* 97 (10): 2640–57. https://doi.org/10.1002/ecy.1522.

Rondinini, Carlo, Kerrie A. Wilson, Luigi Boitani, Hedley Grantham, and Hugh P. Possingham. 2006. "Tradeoffs of Different Types of Species Occurrence Data for Use in Systematic Conservation Planning." *Ecology Letters* 9 (10): 1136–45. https://doi.org/10.1111/

489   j.1461-0248.2006.00970.x.

490   Ronquillo, Cristina, Fernanda Alves-Martins, Vicente Mazimpaka, Thadeu Sobral-Souza, Bruno
491   Vilela-Silva, Nagore G. Medina, and Joaquín Hortal. 2020. "Assessing Spatial and Tempo-
492   ral Biases and Gaps in the Publicly Available Distributional Information of Iberian Mosses."
493   *Biodiversity Data Journal* 8: e53474. https://doi.org/10.3897/BDJ.8.e53474.

494   Roy, Helen E., Elizabeth Baxter, Aoine Saunders, and Michael J. O. Pocock. 2016. "Focal
495   Plant Observations as a Standardised Method for Pollinator Monitoring: Opportunities and
496   Limitations for Mass Participation Citizen Science." *PLOS ONE* 11 (3): e0150794. https:
497   //doi.org/10.1371/journal.pone.0150794.

498   Ryan, S. F., N. L. Adamson, A. Aktipis, L. K. Andersen, R. Austin, L. Barnes, M. R. Beasley,
499   et al. 2018. "The Role of Citizen Science in Addressing Grand Challenges in Food and
500   Agriculture Research." *Proceedings of the Royal Society B: Biological Sciences* 285 (1891).
501   https://doi.org/10.1098/rspb.2018.1977.

502   Scott, Abigail L., Paul H. York, Clare Duncan, Peter I. Macreadie, Rod M. Connolly, Megan T.
503   Ellis, Jessie C. Jarvis, Kristin I. Jinks, Helene Marsh, and Michael A. Rasheed. 2018. "The
504   Role of Herbivory in Structuring Tropical Seagrass Ecosystem Service Delivery." *Frontiers
505   in Plant Science* 9: 127. https://doi.org/10.3389/fpls.2018.00127.

506   Stoyanov, S. 2020. "Cranial Variability and Differentiation Among Golden Jackals (Canis Au-
507   reus) in Europe, Asia Minor and Africa." *ZooKeys*. https://doi.org/10.3897/zookeys.
508   917.39449.

509   Strydom, Tanya, Michael D. Catchen, Francis Banville, Dominique Caron, Gabriel Dansereau,
510   Philippe Desjardins-Proulx, Norma R. Forero-Muñoz, et al. 2021. "A Roadmap Towards
511   Predicting Species Interaction Networks (across Space and Time)." *Philosophical Trans-
512   actions of the Royal Society B: Biological Sciences* 376 (1837): 20210063. https://doi.
513   org/10.1098/rstb.2021.0063.

514   Svenning, Jens Christian, Dominique Gravel, Robert D. Holt, Frank M. Schurr, Wilfried Thuiller,
515   Tamara Münkemüller, Katja H. Schiffers, et al. 2014. "The Influence of Interspecific In-
516   teractions on Species Range Expansion Rates." *Ecography* 37 (12): 1198–1209. https:

517   //doi.org/10.1111/j.1600-0587.2013.00574.x.

518 Tsunoda, Hiroshi, and Masayuki U. Saito. 2020. "Variations in the Trophic Niches of the Golden

519   Jackal Canis Aureus Across the Eurasian Continent Associated with Biogeographic and An-

520   thropogenic Factors." *Journal of Vertebrate Biology* 69 (4): 20056.1. https://doi.org/

521   10.25225/jvb.20056.

522 Valiente-Banuet, Alfonso, Marcelo A. Aizen, Julio M. Alcántara, Juan Arroyo, Andrea Cocucci,

523   Mauro Galetti, María B. García, et al. 2015. "Beyond Species Loss: The Extinction of

524   Ecological Interactions in a Changing World." Edited by Marc Johnson. *Functional Ecology*

525   29 (3): 299–307. https://doi.org/10.1111/1365-2435.12356.

526 Windsor, Fredric M., Johan van den Hoogen, Thomas W. Crowther, and Darren M. Evans. 2022.

527   "Using Ecological Networks to Answer Questions in Global Biogeography and Ecology."

528   *Journal of Biogeography* n/a (n/a). https://doi.org/10.1111/jbi.14447.

529 Wisz, Mary Susanne, Julien Pottier, W Daniel Kissling, Loïc Pellissier, Jonathan Lenoir, Chris-

530   tian F Damgaard, Carsten F Dormann, et al. 2013. "The Role of Biotic Interactions in

531   Shaping Distributions and Realised Assemblages of Species: Implications for Species Dis-

532   tribution Modelling." *Biological Reviews of the Cambridge Philosophical Society* 88 (1):

533   15–30. https://doi.org/10.1111/j.1469-185X.2012.00235.x.

534 Young, Hillary S., Douglas J. McCauley, Kristofer M. Helgen, Jacob R. Goheen, Erik Otárola-

535   Castillo, Todd M. Palmer, Robert M. Pringle, Truman P. Young, and Rodolfo Dirzo. 2013.

536   "Effects of Mammalian Herbivore Declines on Plant Communities: Observations and Ex-

537   periments in an A Frican Savanna." Edited by Luis Santamaria. *Journal of Ecology* 101 (4):

538   1030–41. https://doi.org/10.1111/1365-2745.12096.

Figure 1

Geographical distribution of species richness and removal of predators.

(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.

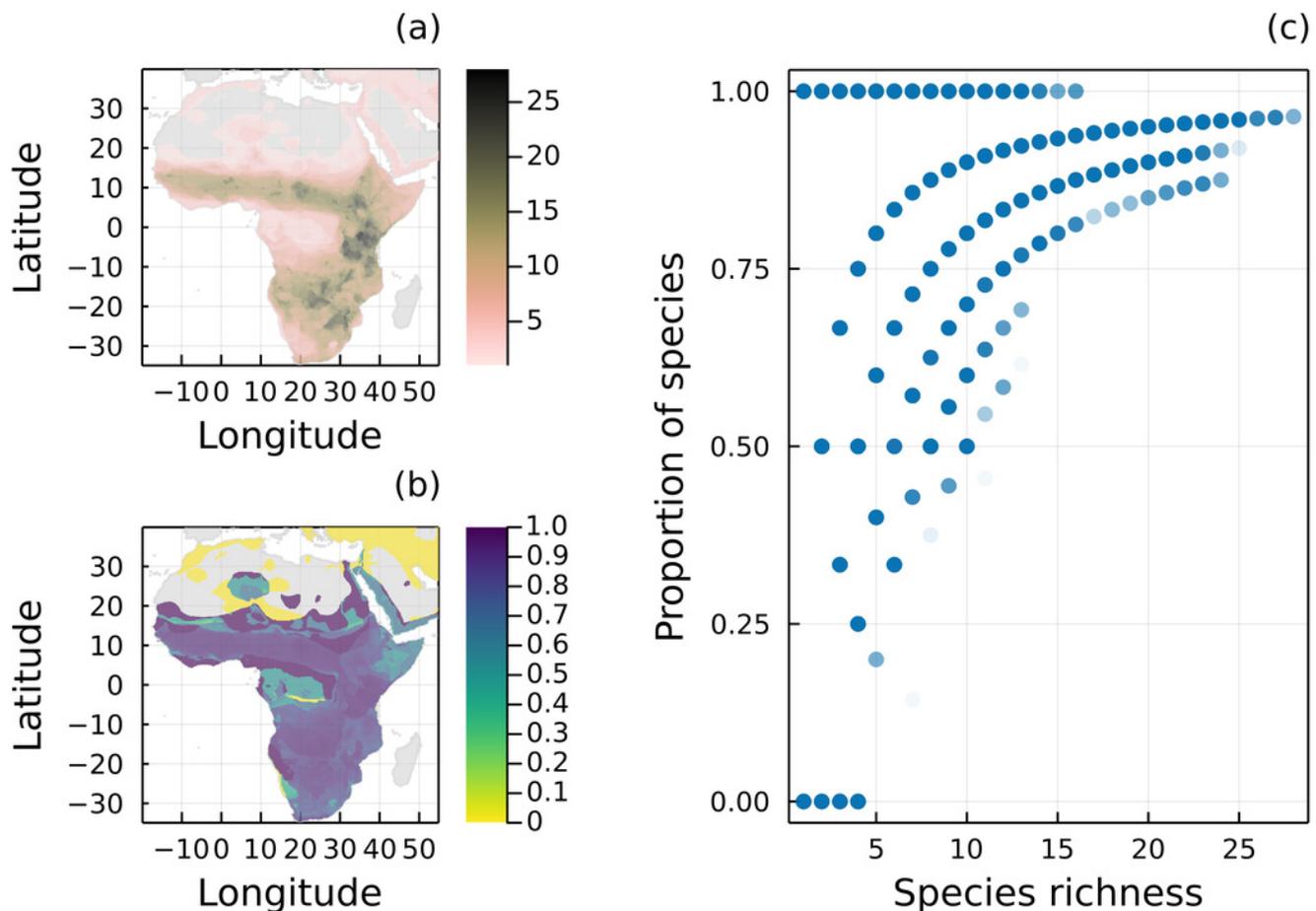



Figure 2

Relationship between the number of preys of each predator and their relative range loss.

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.

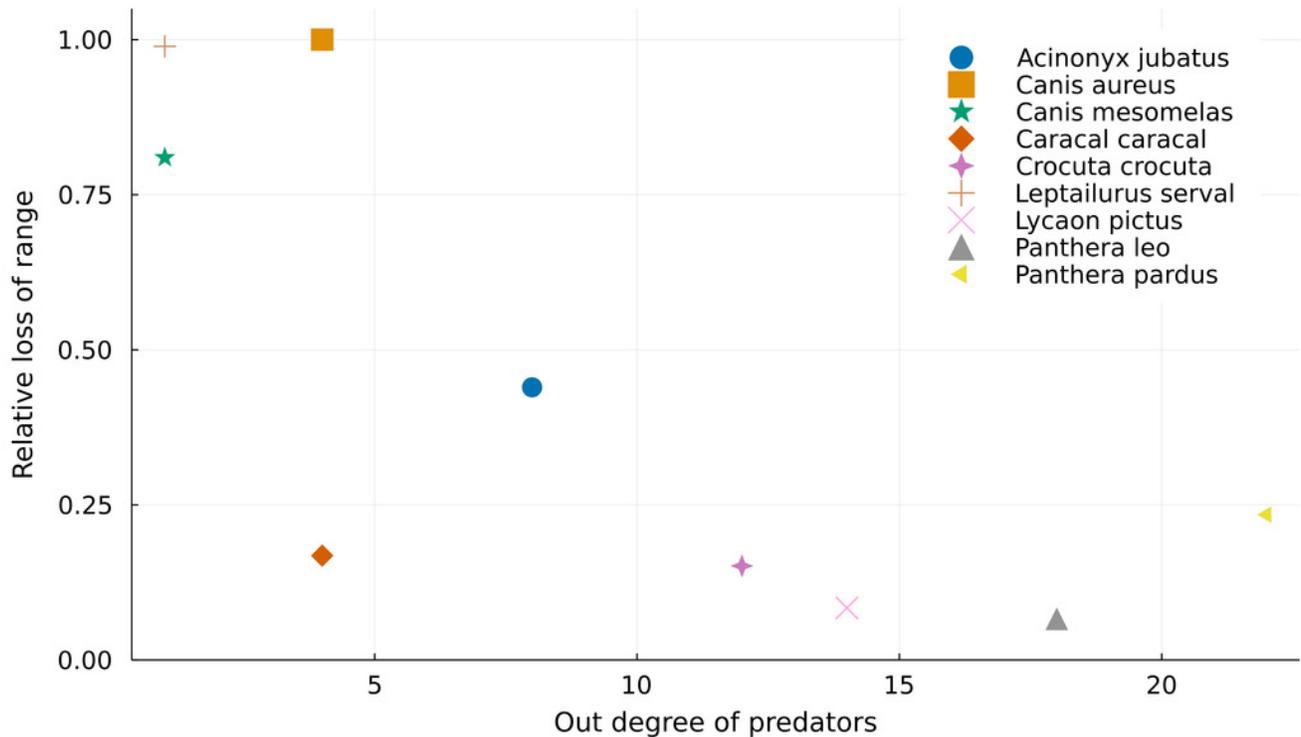



Figure 3

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.

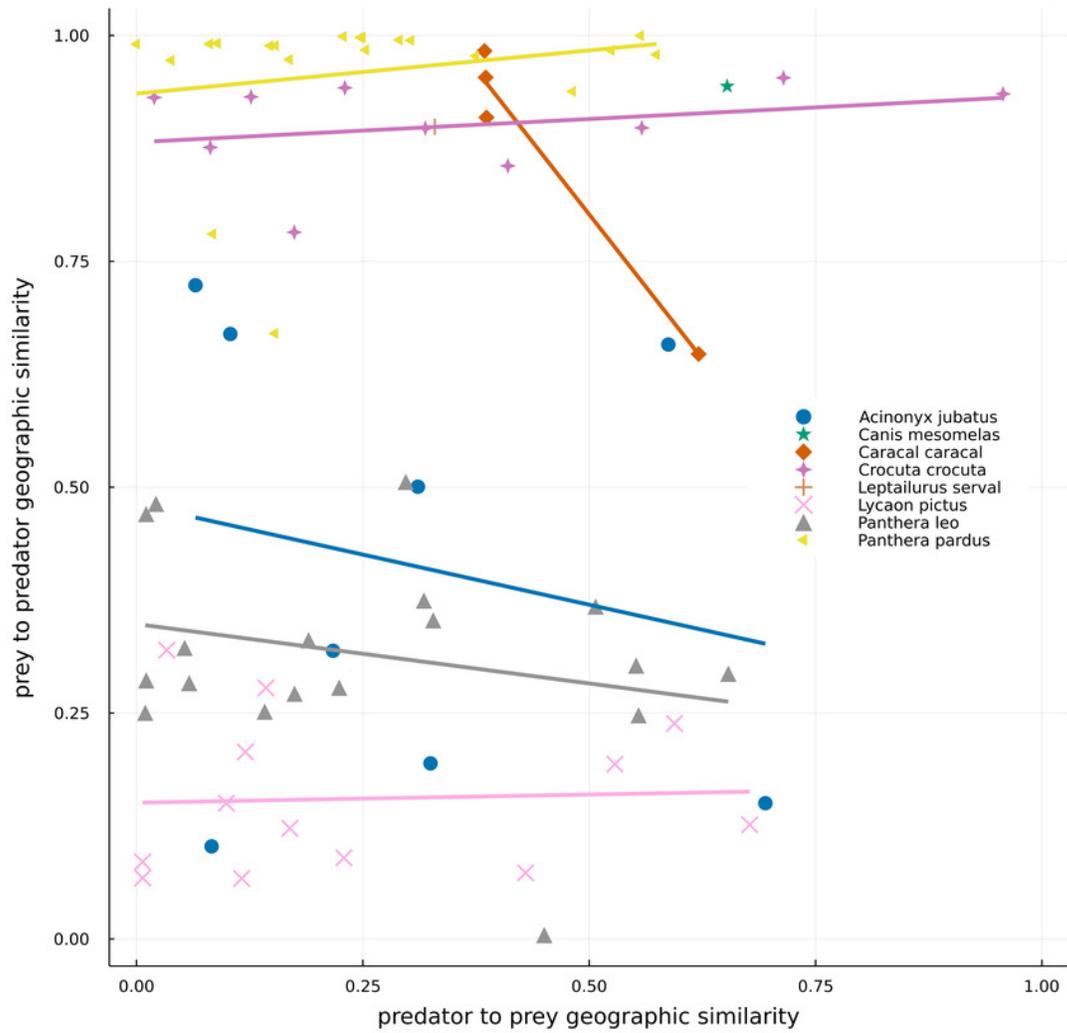



Figure 4

Distribution of GBIF and IUCN mismatch between different range sizes.

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.

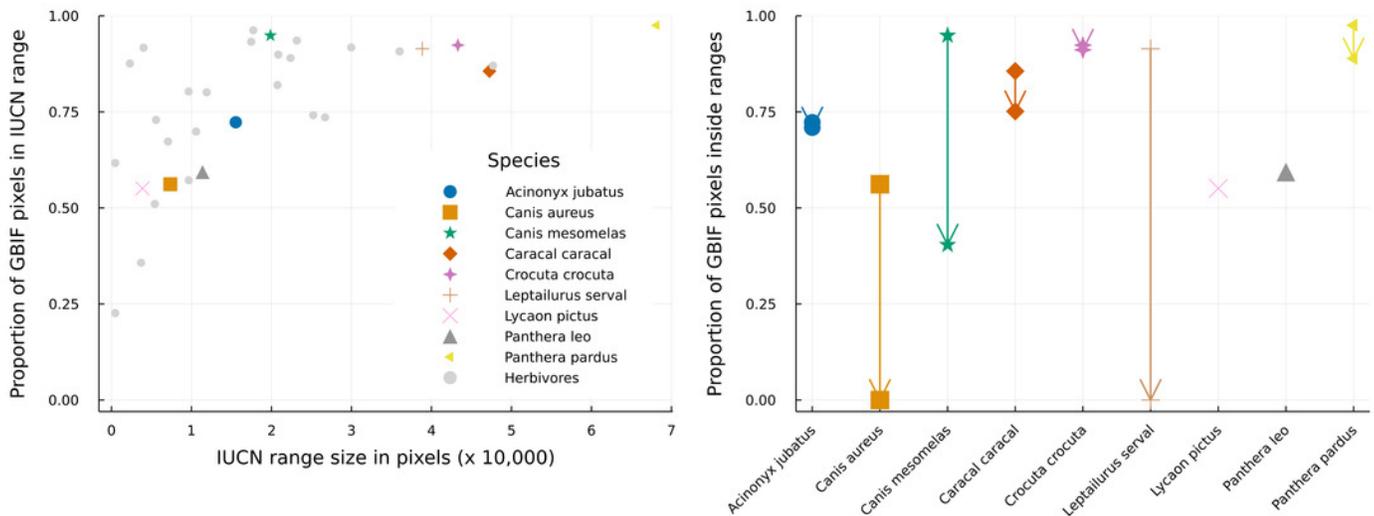
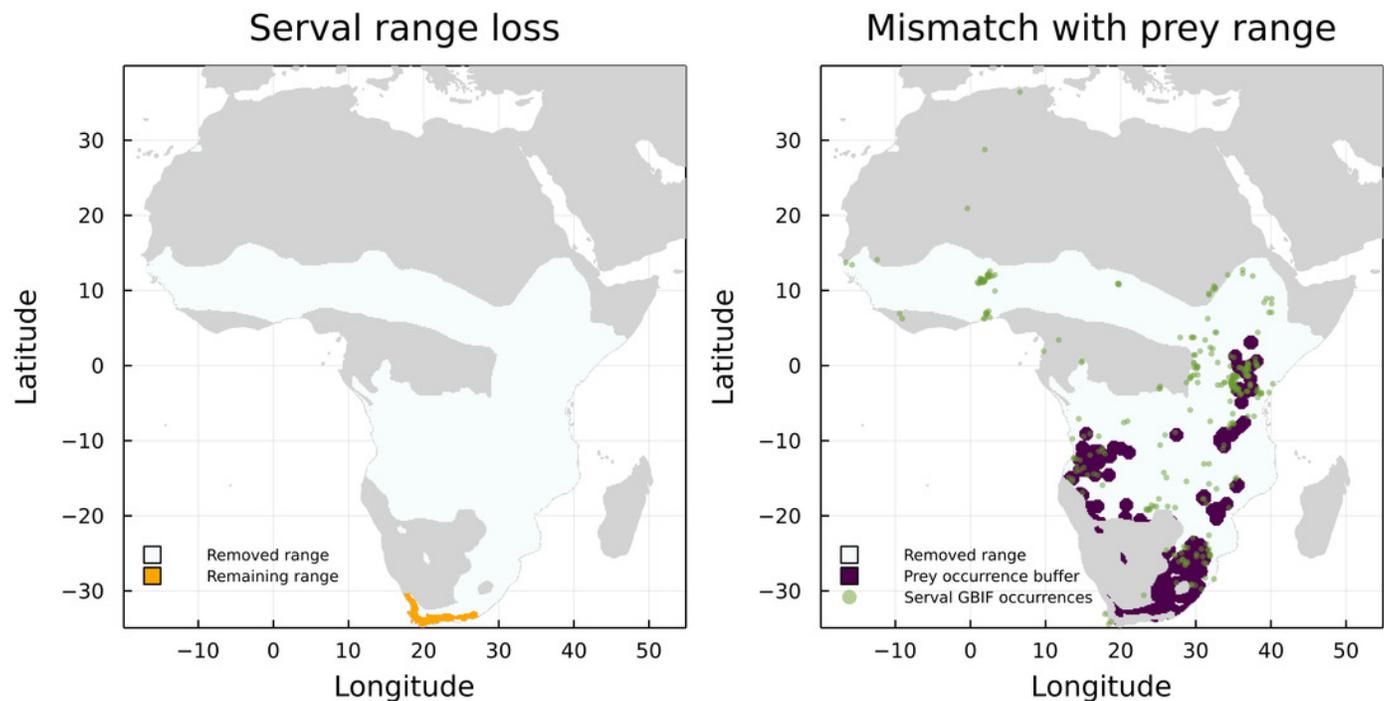



Figure 5

Comparison between the serval's IUCN range loss and its mismatch with GBIF data.

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.

List of species in the network, their ranges, degrees and overlap with prey's ranges.

List of species analysed, 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	-	-
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
Papio anubis	0	1	23171	-	0.938
Syncerus caffer	0	1	25223	-	0.250