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Identifying functionally distinctive and threatened species

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Author contributions

Sandrine Pavoine: Conceptualization, Methodology, Software, Formal analysis, Writing-Original draft preparation, Visualization. **Carlo Ricotta:** Writing-Reviewing and Editing.

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Highlights

- Loss of species with distinctive functional traits may weaken ecosystems.
- Threatened species with atypical traits that could soon disappear must be listed.
- We show how to obtain a unique measure that allows identifying these species.
- This is done while considering different viewpoints on functional distinctiveness.
- This approach could help formalize conservation policies on ecological diversity.

Abstract

Functional traits determine species' responses to environmental change and/or determine species' effects on ecosystem functions. When species with distinctive functional traits are threatened, there is a risk that ecosystem properties are also threatened. This is because functionally distinctive species may be those that have irreplaceable roles in an ecosystem and/or those that would be able to survive unusual environmental disturbances. To include functional distinctiveness as a criterion in conservation strategies, we need formal quantification of species' degree of distinctiveness while incorporating extinction risk. Based on previously developed quantitative methods, we develop a framework that links different metrics of functional distinctiveness and accounts for all species' extinction probabilities. Our framework is particularly relevant at the local scale, where species extinctions impact

ecosystem functioning and where conservation policies are developed. As a case study, we thus applied our framework to the mammals of Indian dry forests known to be threatened with a drastic decrease in functional diversity and identified top-priority species as the threatened, most functionally distinctive species. We notably highlight that although some of the top-priority species we identified are charismatic and targeted by conservation actions, others are not. On the basis of this case study, we note that less charismatic, less known species that may be key for ecosystems could be revealed by applying our framework to a range of ecosystems and taxa.

Keywords: average dissimilarity, conservation priorities, extinction probability, trait-based diversity, ecological strategies

1. Introduction

Traits can reflect a species' ecological strategies and its function in its ecosystem (Cooke et al., 2020). Traits considered functional may indeed represent species' morphological, physiological, phenological or behavioral features (e.g., Carmona et al., 2021) that determine the effect a species has on its ecosystem properties ("effect traits", e.g., Lavorel and Garnier, 2002; Gorczynski et al., 2021). Studies of the ecological impacts that species extinction may have in the near future on ecosystems (e.g., Fritz and Purvis, 2010; Toussaint et al., 2021) mostly focus on such effect traits. The other facet of functional traits is the species' sensitivity or response to environmental changes ("response traits"). Species that have distinctive response-trait values and redundant effect traits may ensure the stability of ecosystem functioning if their distinctive response traits allow them to cope better than other species with some specific environmental change (response-trait diversity as insurance, Loreau et al., 2001). Redundancy in response trait values within a species assemblage would, in contrast, lead to high extinction risk and a drastic decline in effect trait diversity in the case of environmental disturbance. Overall, functionally distinctive species contributing to ecological diversity are generally expected to contribute disproportionately to local-scale ecosystem functions (Cooke et al., 2020).

The disproportionate loss of functionally distinctive species may thus increase the risk that a system collapses compared to random extinction (e.g., Flynn et al., 2009). Measuring to what degree a species is functionally distinctive allows the identification of species with irreplaceable ecological strategies (Cooke et al., 2020). Then, determining those functionally distinctive species that are threatened with extinction could alert conservation actors to consider these species in their programs. Functional distinctiveness can be measured using a variety of methods based on either a single trait or multiple traits. For example, with a quantitative trait, Redding et al. (2010) used the absolute distance from the average or median score for a trait as an index of distinctiveness. With a categorical trait, they used the frequency of species that share the same category as the target species as an index of ordinariness (i.e., this frequency decreases with the target species' distinctiveness).

When several traits are considered, however, those simple measurements are not used. Instead, species-to-species functional dissimilarities are first calculated, which has the advantage of allowing the consideration of any type and any number of traits when comparing species (e.g., Pavoine et al., 2009). The functional dissimilarity is calculated between two

species, while functional distinctiveness represents how distinctive a species is compared to a whole set of species. Once functional dissimilarities have been calculated, the functional distinctiveness of a focal species can be measured by using the set of functional dissimilarities between the focal species and all other species. The most commonly used indices of functional distinctiveness are the average functional dissimilarity to other species and the minimum functional dissimilarity to another species. These two indices may, however, lead to distinct priority settings (e.g., Cooke et al., 2020). Indeed, a species may be functionally distant, on average, from all other species but functionally similar to one of them (Kosman et al., 2019). The mathematical index used (e.g., average versus minimum dissimilarity) is thus likely to influence the conclusions on which species are most functionally distinctive and thus the decisions in terms of conservation priority. Pavoine and Ricotta (2021) thus developed a generalized index that has these two most commonly used indices of functional distinctiveness as special cases. By varying a parameter of the generalized index, distinctiveness measurement varies from the distance to the most functionally similar species, through classical average dissimilarity to other species, to the maximum dissimilarity with another species. From this generalized index, it is thus possible to identify the definition(s) of functional distinctiveness (from the distance to the most functionally similar species, through classical average dissimilarity to other species, to the maximum dissimilarity with another species) according to which a species ranks among the most distinctive. Here, we extend this approach to allow for the consideration of species extinction probabilities in functional distinctiveness. As functional distinctiveness expresses the rarity of a species' functional characteristics, a basic principle for the functional distinctiveness of a given species is that it increases with the extinction probability of the species that share functional aspects with it and it decreases with the extinction probability of the species that have distinct functional characteristics from it. Species with high extinction probability in the near future and high current functional distinctiveness are thus those that are most expected to lead to drastic decline in functional diversity. Our extended framework allows the identification of those species that are of conservation interest according to a large range of possibilities to measure functional distinctiveness from the distance to the most to the distance to the least functionally similar species.

As an illustration, we analyzed the functional distinctiveness of mammals in the dry forests of India. Most analyses of functional distinctiveness have been performed globally (at the world scale), while local analyses may be the most impactful for three reasons (Toussaint

et al., 2021). First, most conservation policies are defined at a local, country level within nations (see also, e.g., Brodie et al., 2021). Second, as countries host distinct types of ecosystems and faunas, small scales are those where the impacts of extinction on ecosystem functioning can be studied (see also, e.g., Carmona et al., 2021). Third, a species may be functionally distinctive in a country, possibly fulfilling a critical role in its ecosystem, while its trait values could be more frequent elsewhere so that it would not have been considered functionally distinctive at a global scale. We chose to focus on the Indo-Malay realm because it exhibits high functional diversity in vertebrates and is susceptible to drastic loss in functional diversity in the near future (Fritz and Purvis, 2010; Toussaint et al., 2021); the most drastic loss of all realms if currently threatened mammal species were driven extinct (Toussaint et al., 2021). Within the Indo-Malay realm, India and the forest biome exhibit the highest number of threatened species (Redford et al., 2011). In this context, the mammals of the Indian dry forests, with high species richness and functional diversity, appeared to us as a relevant group to analyze for our illustration. We measured the functional distinctiveness of each mammal species in the dry forests of India, while analyzing the influence of extinction probabilities and that of trait selection on this measurement.

2. Methods

We start here with an index of functional distinctiveness named ${}^{\alpha}Deq_j^*$ (Pavoine and Ricotta, 2021) that relies on functional dissimilarities among species. Then, we add information on species extinction risk to this index to respect the principle that the functional distinctiveness of a given species increases with the extinction probability of the species that share functional aspects with it while it decreases with the extinction probability of the species that have distinct functional characteristics from it (see Appendix A for an illustration).

Consider an assemblage of N species. Let d_{ij} be the functional dissimilarity between species i and j . Consider that the N species are ordered from the most similar to the most dissimilar species to j . The species that is most similar to j is j itself ($d_{jj} = 0$); we denote c , the c^{th} species most functionally similar to j and pose $c = 0$ for species j itself. c thus varies from 0 to $N-1$. Note that the framework is still valid if there are ties in the d_{ij} values and the species that have even functional dissimilarities to j can be ordered in any way without changing the

value of ${}^\alpha Deq_j^*$. ${}^\alpha Deq_j^*$ is a parametric index of functional distinctiveness, where the parameter α varies from $-\infty$ to $+\infty$. Compared to the Pavoine and Ricotta (2021) formulation of ${}^\alpha Deq_j^*$, we reformulate ${}^\alpha Deq_j^*$ as follows (see Appendix A for the original formula):

$${}^\alpha Deq_j^* = \sum_{c=1}^{N-1} d_{cj} \left(\frac{(c+1)^{\alpha-1} - (c)^{\alpha-1}}{N^{\alpha-1} - 1} \right) \quad (1)$$

Considering the limit of ${}^\alpha Deq_j^*$ when α tends to 1, we pose ${}^1 Deq_j^* = \sum_{c=1}^{N-1} d_{cj} (\log_N (c + 1) - \log_N (c))$.

Our new formulation of index ${}^\alpha Deq_j^*$ explicitly highlights that parameter α controls the importance given to species with close trait values compared to those with distant trait values in the calculation of functional distinctiveness. With Eq. 1, ${}^\alpha Deq_j^*$ is revealed to be the weighted mean of the functional dissimilarities between species j and all other species with weights equal to

$${}^\alpha \pi_c = \frac{(c+1)^{\alpha-1} - (c)^{\alpha-1}}{N^{\alpha-1} - 1} \quad (2)$$

knowing that $\sum_{c=1}^{N-1} {}^\alpha \pi_c = 1$ (Appendix A). The case $\alpha = 2$ is the only case for which species' weights are even (${}^\alpha \pi_c = 1/(N-1)$): ${}^2 Deq_j^*$ is the average functional dissimilarity to other species. When $\alpha < 2$, ${}^\alpha Deq_j^*$ places more weight on a species' minimum dissimilarity as species weights increase from the species most functionally dissimilar to the species least functionally dissimilar to j . The lower α is, the steeper the increase in weights, so that when α tends to $-\infty$, ${}^\alpha Deq_j^*$ tends to $\min_i(d_{ij})$, which is the minimum functional dissimilarity to another species. Conversely, with $\alpha > 2$, ${}^\alpha Deq_j^*$ places more weight on a species' maximum dissimilarity as species weights increase from the species least functionally dissimilar to the species most functionally dissimilar to j . The higher α is, the steeper the increase in weights, so that when α tends to $+\infty$, ${}^\alpha Deq_j^*$ tends to $\max_i(d_{ij})$, which is the maximum functional

dissimilarity to another species (Appendix B in Pavoine and Ricotta, 2021) (see Fig. 1 for a theoretical example). Our reformulation of ${}^\alpha Deq_j^*$ thus allows an easier interpretation of the values taken by this index.

The main novelty of our work is the consideration of species extinction probabilities by the inclusion, in Eq. 1, of their complements, the survival probabilities: Note ε_i the extinction probability of species i ; then its survival probability σ_i (= probability of no extinction) can be calculated as $\sigma_i = 1 - \varepsilon_i$. As in Pavoine and Ricotta's (2022) framework on evolutionary distinctiveness, here, for functional distinctiveness, we consider that the target species j is safe, and we replace N with N_j , the sum of the survival probabilities of all species (i.e., $N_j = \sum_{c=1}^{N-1} \sigma_{c|j} + 1$), and c with $N_{c-1|j}$, the sum of the survival probability of species j and of the $c-1$ other species that are the most functionally similar to species j (i.e., for $c = 1$, $N_{c-1|j} = 1$, survival probability of species j , and for $c > 1$, $N_{c-1|j} = \sum_{k=1}^{c-1} \sigma_{k|j} + 1$) (Fig. 1). This yields:

$${}^\alpha f_j = \sum_{c=1}^{N-1} d_{cj} \left(\frac{(N_{c|j})^{\alpha-1} - (N_{c-1|j})^{\alpha-1}}{N_j^{\alpha-1} - 1} \right) \quad (3)$$

${}^\alpha f_j$ is a weighted mean. In Eq. 3, the functional dissimilarity between j and the c^{th} species most functionally similar to j is indeed weighted by

$${}^\alpha \rho_c = \frac{(N_{c|j})^{\alpha-1} - (N_{c-1|j})^{\alpha-1}}{N_j^{\alpha-1} - 1} \quad (4)$$

with ${}^2\rho_c = \sigma_c / \sum_{c=1}^{N-1} \sigma_c$. The ${}^\alpha f_j$ values will thus depart from the ${}^\alpha Deq_j^*$ values if the ${}^\alpha \rho_c$ weights that account for species extinction probabilities (Eq. 4) depart from the ${}^\alpha \pi_c$ weights that omit species extinction probabilities (Eq. 2). For example in the theoretical data of Fig. 1 and considering negative α values, species A is more than twice more distinctive when extinction probabilities are included (${}^\alpha f_j$) than when they are omitted (${}^\alpha Deq_j^*$). Indeed, the

species whose functional characteristics are most similar to those of A (species D) being highly threatened, the weight associated to it in Eq. 4 decreased compared to that obtained with Eq. 2. As a consequence, the weighted dissimilarity to other species measured by ${}^{\alpha}f$ for species A is higher to that measured by ${}^{\alpha}Deq_j^*$ (Fig. 1).

3. Case study

3.1. Data

We considered all mammal species listed in the International Union for the Conservation of Nature Red List (IUCN, 2023) as extant (resident) in the dry forests of India. This amounted to 101 species. We considered six traits: body mass (g), diet (percentage of consumption across plant, invertebrate and vertebrate food items), foraging stratum (with three possibilities: ground level including aquatic foraging, arboreal and scansorial), activity cycle (nominal trait with three levels: 1=nocturnal only, 2=crepuscular or cathemeral, 3=diurnal only), habitat breadth (number of distinct suitable level 1 IUCN habitats from 1 to 7), use of freshwater habitat (with two possibilities, yes or no) (data obtained from Soria et al., 2021, except activity cycle for *Nesokia indica* and *Tetracerus quadricornis* obtained from Sridhara and Tripathi, 2005 and Meghwal et al., 2018). Adult body mass data were cube-root transformed before analysis. This transformation led to a linear relationship between body mass and body size (Appendix B; Fig. B.1.) and avoided the spurious assumption that the biological impact of a given difference in body mass would be the same between two small species as between two large species (Fritz and Purvis, 2010). We did not use body size, as some values were missing for this trait. Contrary to Fritz and Purvis (2010) and Cooke et al. (2020), we did not log-transform body mass, as this would have led to a bell-shaped distribution with a drastic undervaluation for the distinctiveness of large mammals. For each species, we also collected data on their generation length (obtained from Pacifici et al., 2013; completed by data available in Soria et al. (2021) and IUCN (2023); see details in Appendix B) and their IUCN category from least concern (LC), through near threatened (NT), vulnerable (VU) and endangered (EN) to critically endangered (CR) (IUCN, 2023). We considered global IUCN assessments, except for the lion, which is mostly known for its African populations, but whose Indian population is endangered. The IUCN category of *Belomys pearsonii* was unknown due to insufficient data. Removing this species from our

analysis would equate to considering it extinct. As a pessimistic, although less pessimistic than extinction, scenario we considered it as critically endangered.

3.2. Analysis

We used Pavoine et al.'s (2009) mixed-variables coefficient of distance to calculate functional distances from all functional traits listed above. The mixed-variables coefficient of distance first applies a dissimilarity coefficient to each trait and then calculates the final functional dissimilarity between two species as the mean of the dissimilarities over all traits. The mean can be weighted, and we used de Bello et al. (2021) weights that ensure traits contribute evenly to the final distance (constant Pearson correlation between the functional distance obtained with a single trait and the final distance). Correlations between traits were nevertheless low (dissimilarity-based correlations in $[-0.13, 0.27]$, the highest being between body mass and freshwater use). The underlying dissimilarity coefficients were the Manhattan metric for quantitative and ordinal traits, the Gower (1971) metric for nominal traits, and the Orloci (1967) chord distance for the diet expressed in terms of percentage of use.

We obtained extinction probabilities within the next 100 years with the model of Andermann et al. (2021; Crit E EX mode) that considers each species' conservation status (IUCN category), chances of conservation status changes (with mammals as a reference group), and generation length. Three criteria (A = reduction in population size; C = declining population size with low or extremely fluctuating number of mature individuals; and E = probability of extinction in the wild) used by IUCN (2023) to classify species into the categories VU, EN and CR consider generation length. Criterion E, directly linked to extinction probability, relies on generation length, as follows: for species in category EN, extinction probability of at least 0.2 within 20 years or five generation lengths (max. 100 years), whichever is longer; and for species in category CR, extinction probability of at least 0.5 within 10 years or three generation lengths (max. 100 years), whichever is longer. Considering generation lengths to translate IUCN categories into extinction probabilities is thus critical. Nevertheless, to evaluate the dependence of our conclusions on the Andermann et al. model, we also considered the pessimistic model of Mooers et al. (2008). This pessimistic model attributes an extinction probability within 100 years for each IUCN category as follows: 0.2 for LC species, 0.4 for NT, 0.8 for VU, 0.9 for EN and 0.99 for CR species.

The functional distances allowed the calculation of the functional distinctiveness first by index ${}^{\alpha}Deq^*$, which omits extinction probabilities, and then by ${}^{\alpha}f$, which includes extinction probabilities. To help explain the observed similarities and differences between the values of ${}^{\alpha}Deq^*$ and ${}^{\alpha}f$, we calculated the degree of similarity between each functional trait and the extinction probabilities by the squared cosine (i.e., Pearson correlation for quantitative traits and the quantitative levels of the diet trait and correlation ratio for nominal traits) (function `mixedVarSim` of package `ClustOfVar`, Chavent, 2017). Indeed, any correlation between the extinction probabilities and the functional traits would increase the chance that values of ${}^{\alpha}f$ are different from those of ${}^{\alpha}Deq^*$ (see, e.g., Appendix A). For example, if the trait values of a target species are shared with many species, the target species will not be considered distinctive by ${}^{\alpha}Deq^*$. However if species that are functionally similar to the target one are highly threatened while more dissimilar species are safe, then the target species would appear distinctive according to ${}^{\alpha}f$.

We identified the 10 most distinctive species according to ${}^{\alpha}Deq^*$ and ${}^{\alpha}f$ for each value of α we considered. We considered these species as top-distinctive and evaluated the dependence of the list of top-distinctive species on the selected traits by excluding each trait one-by-one. We next underlined threatened species among the top-distinctive species (see Violle et al., 2007, for the use of comparable methodological steps in the identification of scarce species with distinct traits). Then, we analyzed the distinctiveness ranks of all other threatened species (species classified as VU, EN or CR). For all calculations, we considered α varying from -10 to 10 with a step of 0.1.

4. Results

4.1. Considering extinction probabilities to calculate functional distinctiveness

Although the raw values of ${}^{\alpha}f$ and ${}^{\alpha}Deq^*$ were different, the selection of ${}^{\alpha}f$ over ${}^{\alpha}Deq^*$ to consider extinction probabilities hardly affected the ranking from highly distinctive to lowly distinctive species (Spearman rank correlations varied in the range [0.9928, 0.9995] with the Andermann et al. model of extinction probabilities and in [0.9747, 0.9944] with the pessimistic model). However, top-ranks were affected: the list of the 10 most functionally

distinct species varied depending on whether we considered extinction probabilities (with ${}^{\alpha}f$) or not (with ${}^{\alpha}Deq^*$) (Fig. 2a). The leopard *Panthera pardus* was notably highlighted by ${}^{\alpha}f$ as top-distinctive (with both models of extinction probability), although it was not indicated by ${}^{\alpha}Deq^*$. The gibbon *Hoolock hoolock* was highlighted as top-distinctive by ${}^{\alpha}f$ with the pessimistic model, although it was not classified top-distinctive with the Andermann et al. model or with the index ${}^{\alpha}Deq^*$. Conversely, the rusty-spotted cat *Prionailurus rubiginosus* identified as top-distinctive by ${}^{\alpha}Deq^*$ was no longer among the most distinctive when the extinction probabilities of its relatives were considered (in ${}^{\alpha}f$, Fig. 2a). Some species were top-distinctive when high weight was put toward the minimum functional dissimilarity in the distinctiveness index (for low values of α in ${}^{\alpha}Deq^*$ and ${}^{\alpha}f$; e.g., *Melursus ursinus*), others when low weight was put toward the minimum functional dissimilarity (for high α values; e.g., *Prionailurus viverrinus*), and others regardless of the weight (for all α values; *Rucervus eldii*, *Elephas maximus*, *Neofelis nebulosa* and *Bos gaurus*). *Bubalee arnee* and *Rhinoceros unicornis* were also top-distinctive for all values of α , but only when the pessimistic model of extinction probabilities was used. The list of the 10 most distinctive species was thus dependent on the distinctiveness index, the model of extinction probability and the value for parameter α . For example, the widely used simple average functional dissimilarity to all species ($={}^2Deq^*$) would have highlighted *R. unicornis*, *B. arnee*, *R. eldii*, *E. maximus*, *P. viverrinus*, *B. gaurus*, *Lutra lutra*, *N. nebulosa*, *Pardofelis marmorata*, and *Moschiola indica* as the 1st to 10th most distinctive species, respectively (Fig. 2a). In contrast, considering a low value for α (e.g., -10) and the pessimistic model of extinction would highlight *R. eldii*, *E. maximus*, *M. indica*, *B. gaurus*, *N. nebulosa*, *R. unicornis*, *Paradoxurus hermaphroditus*, *Martes flavigula*, *P. marmorata* and *M. ursinus* as the 1st to 10th most distinctive species, respectively (Fig. 2a).

4.2. Influence of trait selection on functional distinctiveness

We observed that by modifying the set of selected traits, the list of top-distinctive species could be drastically changed, with up to 37% of the species list modified (Fig. 2b). In particular, the distinctiveness of the Eurasian otter *L. lutra*, the fishing cat *P. viverrinus*, the Indian chevrotain *M. indica* and Eld's deer *R. eldii* is driven by their use of freshwater habitat. That of the honey badger *Mellivora capensis* is dependent on the fact that all traits are considered, as removing traits one by one (except diet) excludes this species from the list of

top-distinctive species. The Asian elephant *E. maximus* and gaur *B. gaurus* were excluded from the top-distinctive species as soon as body mass was discarded. This was not the case, however, for other large species, such as the wild water buffalo (*B. arnee*) and the greater one-horned rhino (*R. unicornis*), as these two species remained top-distinctive regardless of the set of traits we considered. Apart from *B. arnee* and *R. unicornis*, only the clouded leopard *N. nebulosa* remained in the top list regardless of the trait set considered: all indices and trait combinations identified *B. arnee*, *R. unicornis* and *N. nebulosa* as top-distinctive. Depending on the set of traits considered, four threatened species could be included on the list of top-distinctive species. These are the pangolins *Manis pentadactyla* and *Manis crassicaudata*, the macaque *Macaca leonina* and the lion *Panthera leo* (Fig. 2b).

4.3. Extinction probability of top-distinctive species

Correlations were low between the Andermann et al. extinction probabilities and species traits in our case study (Fig. 3). However, we observed a relatively strong association of high pessimistic extinction probabilities with high body masses (Fig. 3). This association corresponded to a Pearson correlation of 0.49 between cube-root transformed body mass and the pessimistic extinction probability. The correlation between the extinction probability (ϵ) and the distinctiveness (${}^{\alpha}f$) of a species was higher with the pessimistic model (0.37 ± 0.04) than with the Andermann et al. model (0.14 ± 0.05). However, none of the top-distinctive species were classified as CR by IUCN (Fig. 2a). More than half of them were nevertheless threatened, being VU or EN. In particular, all species underlined as top-distinctive according to all values of α we considered in ${}^{\alpha}Deq^*$ and ${}^{\alpha}f$ were threatened (Fig. 2). According to ${}^{\alpha}Deq^*$, these are *B. gaurus*, *E. maximus*, *N. nebulosa* and *R. eldii*. Accounting for extinction probabilities with ${}^{\alpha}f$, these four species were also top-distinctive regardless of α in addition to the rhino *R. unicornis* under the pessimistic model of extinction probability.

4.4. Distinctiveness of other threatened species

Although none of the top-distinctive species were classified CR by IUCN, some threatened species, including a CR species (the Chinese pangolin *M. pentadactyla*), had one of the 25% highest distinctiveness values for at least one value of the α parameter for ${}^{\alpha}f$ (Fig. 4). These are the northern pig-tailed macaque *M. leonina*, the lion *P. leo*, the flying squirrels *Biswamoyopterus biswasi* and *B. pearsonii*, and the pangolins *M. crassicaudata* and *M.*

pentadactyla. The two pangolin species, the lion, and the Sambar deer *Rusa unicolor* had one of the top 50% most distinctive values for all values of the α parameter we considered in $^{\alpha}f$. The tiger *Panthera tigris* was also among the 50% most distinctive species regardless of α but under the pessimistic model of extinction probability only. The other threatened species had relatively low functional distinctiveness.

5. Discussion

We adapted a parametric framework for the measurement of functional distinctiveness to account for the extinction probabilities of species. We applied this framework to detect threatened most functionally distinctive mammals in the dry forests of India. Here, we discuss the definition of functional distinctiveness in terms of available, selected data and in terms of the measurement formula. We also discuss the potential consequences that functional distinctiveness may have as a tool for conservation policies using the example of mammals in Indian dry forests as a case study.

5.1. Functional distinctiveness depends on the selection of traits and a model of extinction risk

The first step when studying functionally distinctive and threatened species is to select relevant traits. This selection could indeed influence conservation priorities that rely on functional distinctiveness, as illustrated by our case study. Among the currently available information on species traits, organism size (body length and mass) is one of the major axes of functional space (Carmona et al., 2021). It is included in most, if not all, analyses of functional or ecological distinctiveness (e.g., Leitão et al., 2016; Cooke et al., 2020; Carmona et al., 2021; Burner et al., 2022). Considering body size in distinctiveness measurement places an emphasis on large species because they are less numerous than small species and, in vertebrate groups, are often associated with an increased risk of extinction (Toussaint et al., 2021). In scientific studies, threatened large mammals, however, already receive more attention than nonthreatened species, which themselves receive more attention than threatened small mammals (Trimble and van Aarde, 2010). At least in this group, considering body mass when measuring functional distinctiveness could thus tend to highlight species that are

already considered by conservation policies. Indeed, when we excluded body mass from the selected traits, two of the largest species (*E. maximus* and *B. gaurus*) were no longer among the 10 most distinctive species. However, other large species remained (*B. arnee*, *R. unicornis*), indicating that being large is not the sole reason for their top-distinctiveness. In addition, even when considering body mass, large species were not the sole species identified in our case study as the most functionally distinctive by our framework. Small-sized (e.g., Grey slender loris *Loris lydekkerianus*) and medium-sized (e.g., western hoolock gibbon *H. hoolock*, clouded leopard *N. nebulosa* and to a lesser extent the pangolins) species were also top-distinctive.

Trait selection depends on the taxonomic group, spatial scale and habitat considered. In our case study, we considered body mass and information on trophic ecology, behavior (activity cycle) and habitat preferences, for which we did not have to impute data. Previous studies on functional distinctiveness often included several traits across four categories: morphology, trophic ecology (feeding), reproduction, behavior and habitat preferences (e.g., Cooke et al., 2020; Soares et al., 2021; Trindade-Santos et al., 2022). Apart from body mass, we did not include morphometric traits, as it is still unclear whether species with odd morphologies have rare ecological roles (Redding et al., 2010). This might depend on the group and on the morphometrical traits considered (e.g., seed dispersal in birds linked to beak shape or type of consumed items linked to the shape of fish teeth). In contrast to other studies (e.g., Cooke et al., 2020; Carmona et al., 2021; Toussaint et al., 2021; Burner et al., 2022), we did not include life history traits linked to reproduction. Reproductive traits could be qualified as effect traits by considering, for instance, that they influence food availability (e.g., for prey) (Luck et al., 2012) and the level of pressure on other organisms (e.g., for predators). However, reproductive traits could be more directly linked to the persistence strategies of species and could thus be more directly viewed as response traits (Toussaint et al., 2021). Additionally, reproduction was partially included in our model of extinction probabilities via the consideration of generation length.

In addition to functional traits, our approach considered each species' extinction probability. Our case study illustrated the sensitivity of our approach to the way species extinction probabilities are quantified. This sensitivity is shared with all current approaches that aim to detect threatened and functionally or phylogenetically distinctive species. This is both an advantage as it shows that the approaches efficiently consider extinction probabilities and a limitation as access to precise estimates of local extinction probabilities relying on

models in population genetics and population dynamics are not yet available for such a large set of species as all mammals found in a rich region. At large scales, models of extinction probabilities thus rely on the IUCN red list. Global and regional IUCN assessments may be different; for example, the lion *P. leo* is evaluated globally as vulnerable (IUCN, 2023) but endangered in India (*P. leo spp. persica*, IUCN 2023). However, although regional definitions of the IUCN categories of extinction risk have started to be published (IUCN, 2023), they are limited to a few geographic areas and taxonomic groups and were not available for all species in our case study. In addition, there are currently no identified consensus models of species extinction probability at regional and global scales, and all have a large degree of uncertainty (e.g., Mooers et al., 2008; Andermann et al., 2021). The model of Andermann et al. (2021) that we selected conforms to the IUCN definition of the extinction probabilities interpreted with regard to the generation length. It also accounts for known IUCN category changes in the past to predict the future probability of category change, providing a unique extinction probability for each species. However, it does not yet discriminate between changes due to increased knowledge on the species and actual modification of the state of its populations. In contrast, the pessimistic model assigns an arbitrary single extinction probability to all species that share the same IUCN conservation status (Mooers et al., 2008). Overall, there is thus a critical need for research on the regional estimates of extinction probabilities, the country-size scale at which most conservation policies are defined.

5.2. Choosing a single viewpoint on functional distinctiveness influences conservation priorities

The second step when studying functionally distinctive and threatened species is to select a relevant formula to quantify to what degree a species is functionally distinctive and threatened. This quantitative measurement will then serve to rank species from the most to the least functionally distinctive and threatened. Choosing a formula means choosing precisely what we want to conserve in priority.

For example, according to Kosman et al. (2019), "a species might be, on average, quite distant from most species but functionally similar to one other species. The conservation priority for such a species might be lower than that of a species with the same average distance to other species, but that is also consistently different from all other species (i.e., a species without a close neighbor in functional space)". Looking at various values of α , our

framework allows navigating among different definitions of species' distinctiveness, from the minimum to the maximum functional dissimilarity to another species, while accounting (index $^{\alpha}f$) or not ($^{\alpha}Deq^*$) for species' extinction probabilities. High values of α highlight species at the edges of the trait space, with extreme trait values. Protecting them could help to maintain a broad range of ecological strategies (Cooke et al., 2020). At a global level, Carmona et al. (2021) observed that threatened mammals indeed tend to be close to the boundaries of trait distributions. Low values of α highlight species that have no functionally close species and that could thus have unique, irreplaceable ecological strategies (Cooke et al., 2020). "Functional outliers" (Violle et al., 2017) could thus be defined as the species that are top-distinctive regardless of α , as they are at the border of the "functional space" and far from all others. In our case study, the clouded leopard *N. nebulosa* is notably underlined as a top functional outlier, as it remained top-distinctive regardless of the distinctiveness index used, the parameter α chosen, the extinction model used and the set of traits considered.

Similar to others (e.g., Carmona et al., 2021) and consistent with the rich literature on phylogenetic distinctiveness (e.g., Redding and Mooers, 2006; Isaac et al., 2007; Steel et al., 2007), a species' functional distinctiveness could be multiplied by its extinction probability to obtain a synthetic index (index $^{\alpha}f_j'$) that could be used as a criterion in conservation policies. However, such a multiplicative index is a compromise between a species' extinction probability and distinctiveness. In the absence of a strong correlation between extinction probability and distinctiveness, the highest values for such synthetic indices could thus be obtained either for highly distinctive species with a low to moderate extinction probability or for highly threatened species with low to moderate distinctiveness. Such a multiplicative index could be dominated by the influence of extinction probability over distinctiveness if, as likely in many taxonomic groups, variability in extinction risk is higher than that in distinctiveness. To avoid the difficult step of defining a synthetic index, we followed here Violle et al.'s (2017) suggestion of distinguishing species into four categories: those that are dominant (or not threatened) and have indistinct traits, those that are scarce (or threatened) and have indistinct traits, those that are dominant and have distinct traits, and those that are scarce and have distinct traits. A more drastic proposition (e.g., Kosman et al., 2019) is to admit that distinctive species are worth increased consideration in conservation practices even if they are currently widespread and not threatened. For example, in our case study, the state of near threatened species identified as top-distinctive in Indian dry forests under both Andermann et al. and the pessimistic models of extinction (marbled cat *P. marmorata* and

Eurasian otter *L. lutra*) could be further surveyed, and actions developed to avoid these species becoming threatened. Current policies include hunting prohibition and partial occurrences in a protected area for the marbled cat (IUCN, 2023). Although monitoring programs do exist and conservation actions are numerous for the Eurasian otter, the conservation gain for this species is estimated to have been low thus far (IUCN, 2023).

5.3. Fundability of conservation actions for functionally distinctive and threatened species

Conservation actions exist for most species that we identified as distinctive and threatened in Indian dry forests. They significantly contributed to the preservation of these species but were not sufficient to avoid drastic declines in their populations in the last few decades. Conservation actions often mainly consist of occurrence in a protected area (IUCN, 2023). For example, the Indian rhinoceros (*R. unicornis*) experienced drastic loss of its distribution range outside protected areas (Pacifci et al., 2020). Protected areas may be the last chance for these species. However, such areas have restricted ranges (with animal persecution still occurring via illegal trade, especially on the borders) and are often disconnected and isolated (absence of corridors). Our case study thus illustrates that enhanced conservation actions are still necessary for threatened functionally distinctive species (regionally and globally) to avoid extinction in the coming decades.

Conservation initiatives that consider distinctiveness as an important criterion are still rare. Launched in 2007 (Isaac et al., 2007), the "edge of existence" (EDGE) initiative nevertheless collects one-time and monthly donations by the public to support actions for the preservation of evolutionarily distinctive and threatened species in many countries around the world. Similar to what is done by the EDGE initiative, other initiatives could identify species that are threatened and functionally distinctive but have not or have rarely attracted the attention of conservation initiatives. Indeed, discrepancies between functional and evolutionary distinctiveness have been observed (e.g., Cooke et al., 2020). In addition, in contrast to the analysis of evolutionary distinctiveness, which is currently global, the study of functional distinctiveness could be carried out, as in our case study, more locally within countries and within habitat types, to more directly characterize the impact the loss of a species could have on ecosystem functioning. As conservation actions currently mostly rely on individual donations, the feasibility of such an approach would depend on the motivation

of the general public to preserve threatened functionally distinctive species. This motivation will have to be evaluated in a wide range of taxonomic groups.

Cooke et al. (2020) found that ecologically distinctive mammal species tend to be charismatic species. Additionally, the most charismatic species for the public tend to be large-size species with high (threatened) IUCN scores (Macdonald et al., 2015), especially mammals (Albert et al., 2018), and many of them have populations in India: the tiger (*P. tigris*), the lion (*P. leo*), the elephant (including *E. maximus*), the leopard (*P. pardus*), the rhino (including *R. unicornis*) and the gray wolf (*Canis lupus*). The fact that a species is charismatic can motivate the general public to fund conservation actions (Albert et al., 2018; Courchamp et al., 2018). However, despite conservation actions, many charismatic species are still declining (Courchamp et al., 2018; IUCN, 2023).

Even within charismatic taxonomic groups, such as mammals, the feasibility of conservation campaigns that target noncharismatic species still has to be determined. For example, pangolins have been highlighted in our data set as threatened species with relatively high functional distinctiveness in Indian dry forests. Pangolin species are well known by conservation actors to be poached, being the species most heavily trafficked to extinction among wild mammals. Despite this, they only recently attracted the interest of the media because the pangolin has been, without concrete evidence, claimed to be an intermediate host of SARS-CoV-2 at the origin of the COVID-19 pandemic (Heighton and Gaubert, 2021), an increased interest that could, however, lead to a negative public perception of the interest in preserving pangolins (Choo et al., 2022).

5.5 Conclusion

Herein, we modified a parametric framework of functional distinctiveness to account for species' extinction probabilities so that the functional distinctiveness of a given species increases with the extinction probability of the species that share functional aspects with it and decreases with the extinction probability of the species that have distinct functional characteristics from it. We showed that, in this framework, functional distinctiveness is simply measured as a weighted mean of functional differences with other species. The weights in the weighted mean allow navigating through different definitions of functional distinctiveness from the minimum to the maximum functional difference from another species

while accounting for species' extinction risks. Applying this framework to a variety of taxa, habitats and realms will likely both reinforce the support for the conservation of large carnivores and herbivores with distinctive functions and reveal less charismatic, less well-known threatened species with distinct functional traits and ecological strategies that have key roles in their ecosystems. There is thus a need to study the feasibility of such an approach on understudied species and taxonomic groups for which functional traits may be available at regional levels rather than at a global level. We hope our framework will support studies on functional distinctiveness by incorporating species extinction probabilities. We also hope it will contribute to the inclusion of functional distinctiveness as one of the criteria that should be considered when prioritizing species within countries for conservation.

The following are the supplementary data related to this article.

Appendix A. Additional information on methods.

Appendix B. Supplementary analyses performed on the mammals of Indian dry forests.

Appendix C. Data set.

Appendix D. R function.

Appendix E. R script.

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Figure legends

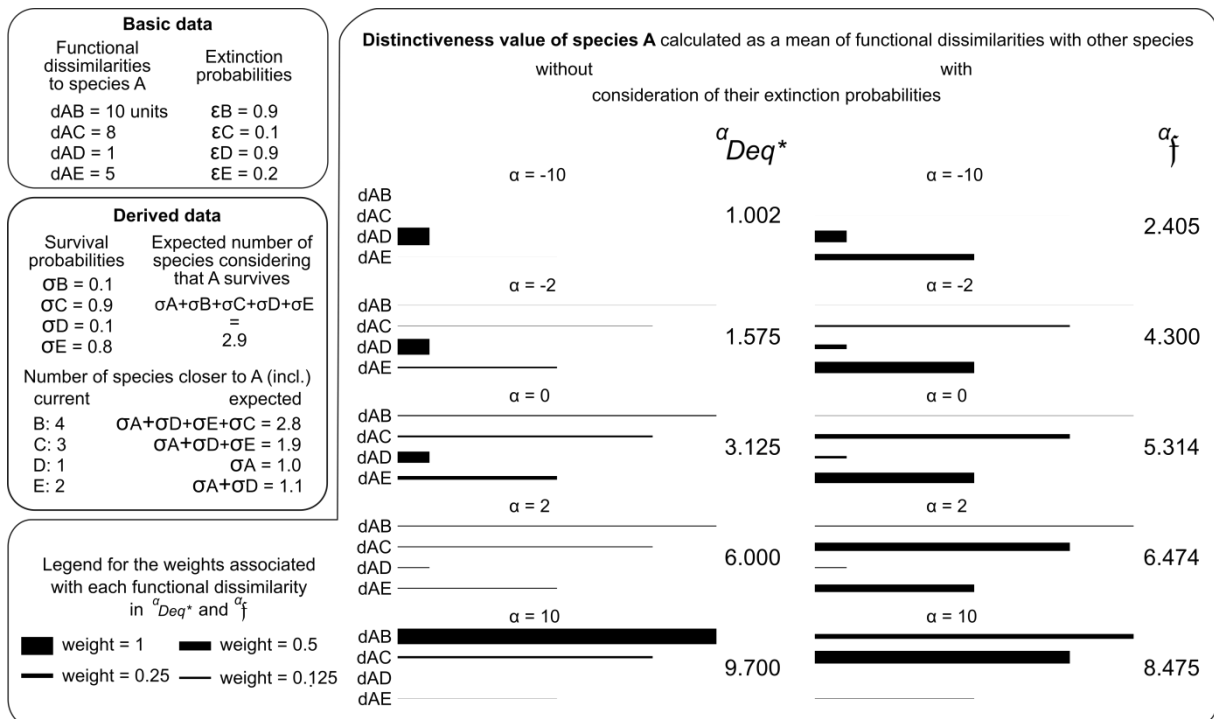


Fig. 1. Theoretical example of the calculation of functional distinctiveness as a mean of functional dissimilarities with other species. Basic data specify the functional dissimilarities (d) and extinction probabilities (ϵ). The derived data specify, for each species, its survival probability ($\sigma = 1 - \epsilon$) and its order of proximity with species A (number of current species closer to A). The derived data also provide the total expected number of species and the expected number of species that are functionally closer to A (including A) than the specified species, both calculated considering that species A survives ($\sigma_A = 1$). In the largest box on the calculation of the distinctiveness of A, the length of a segment represents a value of functional dissimilarity as specified in the basic data. The thickness of a segment represents the weight used in α_{Deq}^* and α_f , both being weighted means of functional dissimilarities. The absence of a segment means that the weight is negligible ($\ll 0.001$) so that the corresponding functional dissimilarity hardly influences the distinctiveness value. For each index (α_{Deq}^* and α_f), distinctiveness values are given for 5 values of their parameter α , and they are rounded to 3 decimal places.

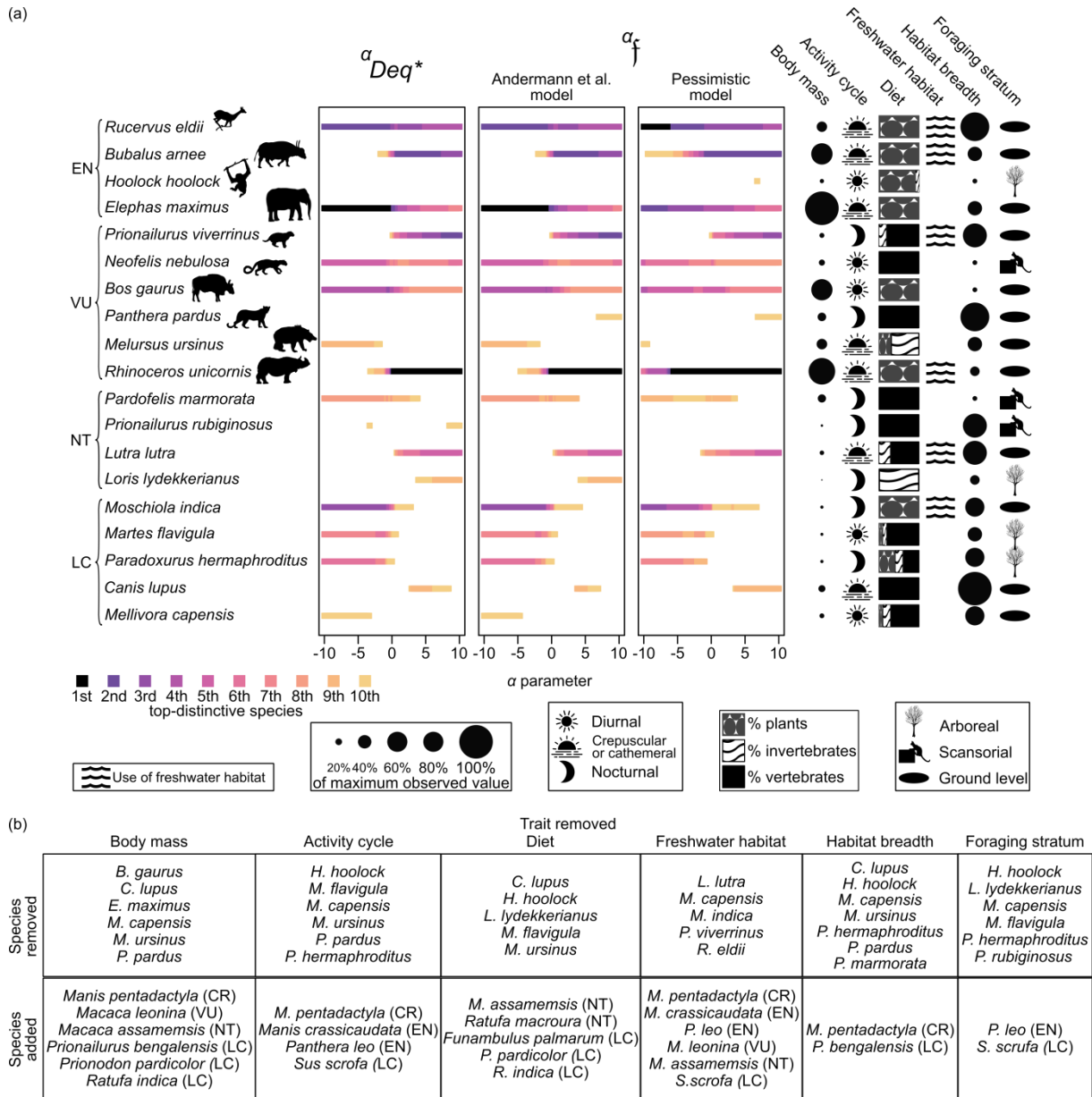


Fig. 2. Top-distinctive species. (a) Rates of distinctiveness, IUCN category and traits of top-distinctive species. All species listed were ranked among the top-10 highest in terms of ${}^{\alpha}Deq^*$ or ${}^{\alpha}f$ distinctiveness values for at least one α value that we considered. Silhouettes are displayed for those species that are threatened as vulnerable (VU) or endangered (EN). Species are organized by IUCN category from least concern (LC), through near threatened (NT) and VU, to EN. Within each category, they are organized from the lowest (bottom) to the highest (top) extinction probability according to the Andermann et al. model. Their ranks from the 1st most distinctive to the 10th most distinctive are highlighted by squares from dark to light tone. (b) Changes that would occur in the list of 10 most distinctive species (according to ${}^{\alpha}Deq^*$ and ${}^{\alpha}f$) if a trait were excluded from the calculation of functional dissimilarities

between species. The table indicates the species that were no longer among the 10 most distinctive ("species removed") and those that integrated the list of 10 most distinctive species when the specified trait was excluded. The IUCN status of those species that could integrate the list of 10 most distinctive species are provided from LC to critically endangered (CR).

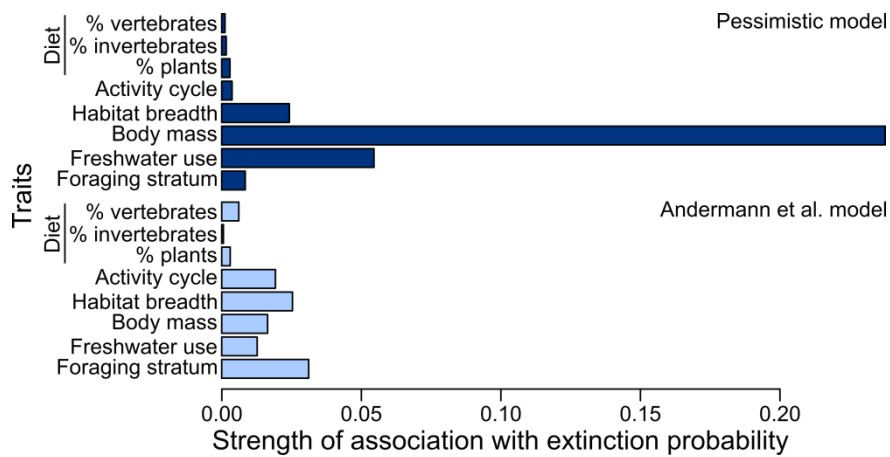


Fig. 3. Strength of association between each trait and the extinction probabilities. Association, as measured by squared Pearson correlation or correlation ratio depending on the trait type, varies between 0 (no association) and 1 (maximum association). Dark bars were obtained with the pessimistic model of extinction probability, and light bars were obtained with the Andermann et al. model.

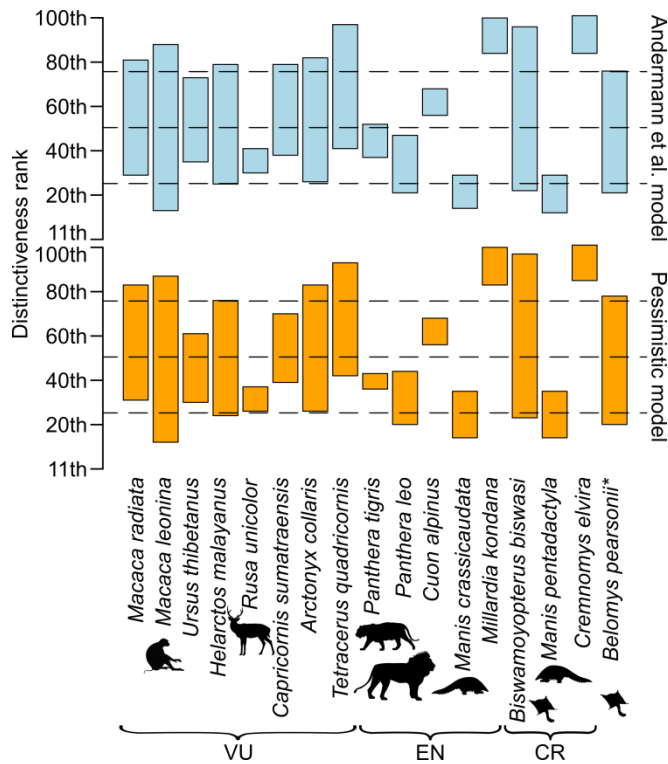


Fig. 4. Distinctiveness ranks of threatened species that were not classified among the top-distinctive species in Fig. 3. Ranks are provided for αf with both models of extinction as indicated on the right side of the bar plots. As these species were not identified as top-distinctive, ranks are given from the 11th most to the least (101th) distinctive species: the lower the rank, the higher the distinctiveness. For each species, a box indicates the range of variation between the minimum and maximum observed ranks. Dashed lines indicate the limits of the 25% top-distinctiveness (up to the 25th rank), 50% top-distinctiveness (up to the 50th rank), and 75% top-distinctiveness (up to 75th rank) values. IUCN status is provided below species names (**B. pearsonii* has unknown IUCN status).