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Combining extinction probability and functional or phylogenetic distinctiveness to define conservation priorities

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ABSTRACT

Given the current accelerating extinction rates, an increasing number of species-based conservation strategies have emerged because of the public interest in helping save particular species by funding rescue actions. Although public interest has focused mainly on well-studied, charismatic species, conservation scientists have developed tools to help prioritize species conservation from a more objective perspective, preserving ecosystem functioning and human well-being for future generations. For that purpose, species-centered biodiversity indicators that account not only for the extinction risk of a species but also for its evolutionary and/or functional distinctiveness have been developed. A species is considered irreplaceable and distinctive if it is isolated on the phylogenetic tree and/or if it has distinct traits, especially functional traits that determine the species' effects on ecosystems. The quantitative values representing extinction risk and distinctiveness of species have often been multiplied to define a quantitative conservation priority score. However, there is a plethora of ways to combine several conservation criteria into a single quantitative priority score, and the product of this multiplication is one such possibility. Each possible way of combining extinction risk and distinctiveness provides a different point of view on which of these should prevail to set conservation priorities. We set up an axiomatic framework on how a species' distinctiveness could be combined with its extinction risk via a tool used to define conservation priorities. By doing so, we show that further work is still needed to better communicate biodiversity indicators to the public and ensure an informed choice of indicators.

1. Introduction

Several conservation strategies have been developed in response to the global accelerating extinction rates and because of the rapid increase in extinction risk of many extant species (e.g., Pimm et al., 2014; Urban, 2015). Extinction risk has thus been considered early on as an obviously critical criterion for defining conservation priorities (e.g., Mace et al., 2007). In the past, most conservation strategies also considered the amount of endemism as a reason to prioritize the conservation of a particular area; for example, using the legal definition of the protection status established for an area or, more frequently, for parts of it. Conservation strategies used to focus first on the management of whole ecosystems before considering the management of single species (Mace et al., 2007). Species-based conservation strategies have emerged for several reasons (Mace et al., 2007): first, asking the general public for donations to manage an ecosystem is a concept that is harder to grasp than asking for help in saving a particular species; second, it is easier to assess the efficiency and eventual success of conservation efforts when they target a single species than when they target a whole ecosystem; and third, even ecosystem-based strategies often end up directing actions toward particular species since these are manageable components of ecosystems. In addition, several criteria have been considered in species-based strategies to complement extinction risk, including selecting a species that is charismatic (flagship species), a species that has such large habitat range and complex habitat requirements for survival that protecting it will protect many other species (umbrella species) or a species that has a disproportionate effect on its ecosystem (keystone species) (Mace et al., 2007; Barua, 2011).

Several suggestions have been made to emphasize the importance of keystone species (Simberloff, 1998). Indeed, the concept of keystone species involves a compromise between species-based and ecosystem-based strategies because it implies the identification and preservation of species with critical effects on ecosystems, those with disproportionate contributions to ecosystem functions relative to their abundance

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(Power et al., 1996). A more recent concept related to "keystone species" is that of "distinctive species". A species is distinctive if its biological characteristics are rare (Pavoine et al., 2017). Examples of distinctive species are those that are isolated on the phylogenetic tree (evolutionary distinctiveness; e.g., Crozier, 1992; Isaac et al., 2007; Redding and Mooers, 2006; Steel et al., 2007). Another aspect of distinctiveness addressed in the ecological literature is functional distinctiveness (e.g., Pavoine et al., 2017; Violle et al., 2017). Functionally distinctive species are those that have functional trait values far removed from those of other species (Mouillot et al., 2008; Pavoine et al., 2017). In this context, functional traits are often defined as effect traits that define a species' role in ecosystem functioning (Lavorel and Garnier, 2002). The functionally distinctive species strongly contribute to functional diversity relative to their abundance and are expected to disproportionately contribute to ecosystem functions. Scarce, functionally distinctive species are thus likely to be keystone species. In addition, due to the rarity of their biological characteristics, the loss of distinctive species is unlikely to be compensated for by the abundance of other species. Considering distinctiveness, the irreplaceability of the species is at stake (Isaac et al., 2007).

In the last three decades, distinctiveness has thus progressively emerged as a key ecological criterion for setting conservation priorities. Different approaches have been developed to identify species that are distinctive and threatened with extinction and to develop action plans to conserve those that receive insufficient attention from conservation actors (e.g., Gumbs et al., 2023b; Isaac et al., 2007). Once these species are identified, a second stage can be to check whether they could also serve as umbrella species or as locally supported flagship species, as is the case, for example, with the koala, Phascolarctos cinereus, in Australia (Yang and Pavoine, 2023). Conservationists that aimed to operationalize this strategy searched for combinations of two core criteria (extinction risk and distinctiveness) as unique quantitative indicators of conservation interest. The most common of these combinations has been to first define numerical, nonnegative indices of both extinction risk and distinctiveness and to calculate their product (e.g., Carmona et al., 2021; Isaac et al., 2007; Redding and Mooers, 2006; Steel et al., 2007). The product is then either considered directly or log-transformed (Gumbs et al., 2023b; Isaac et al., 2007).

Redding and Mooers (2006) first introduced an index of conservation interest that is the product between a value of extinction risk and a value of evolutionary distinctiveness. By considering that distinctiveness is the amount of evolutionary history embodied by a species, this product was used as an indicator of the amount of evolutionary history expected to be lost as a result of the extinction of a given species in the near future (Redding and Mooers, 2006). In the last decade, the related index that has been most popularized was the EDGE index (Isaac et al., 2007), where the product of evolutionary distinctiveness by extinction risk is log-transformed as follows: $EDGE = log(1 + ED) + GE \times log(2) = log((1 + ED)) + log(2) = l$ + ED)(2^{GE})), where 1 + ED is an index of distinctiveness and 2^{GE} is an index of extinction risk. This EDGE formula has been at the core of the EDGE of Existence programme, a charity program by the Zoological Society of London (www.edgeofexistence.org) aimed at raising funds for the preservation of evolutionarily distinct and globally endangered species. The EDGE statistic was used to "generate a list of species that are both evolutionarily distinct and globally endangered" (Isaac et al., 2007). It also inspired several complementary developments that integrate functional distinctiveness into the formula (e.g., Hidasi-Neto et al., 2015). As part of the EDGE2 framework, the EDGE of Existence programme recently adopted a new core index (EDGE2), (Gumbs et al., 2023b), that is a direct product of a value of extinction risk and a value of evolutionary distinctiveness. This core index developed by Gumbs et al. (2023b) represents the expected increase in evolutionary history safeguarded in the near future if conservation measures ensured the survival of a species compared with no measures at all.

Other approaches could be developed to combine two or more criteria for the definition of indicators of conservation interest (Mace

et al., 2007). Some approaches use the sum of quantitative scores assigned to species for a set of parameters, each of which reflects a reason to prioritize a species for conservation. For example, simply summing the scores of parameters and identifying species with the largest sum is a previously used approach (see, e.g., the Conservation Needs Assessment process developed by Amphibian Ark, Johnson et al., 2020, for the standardized use of summed values of distinctiveness, extinction risk, and other criteria such as socio-economic significance into a prioritization score). However, "there is an infinity of ways in which the scores could be combined: adding, multiplying, taking the product of the largest three values, and so forth" (Mace et al., 2007). Although the possibilities are infinite, we must be aware that each one defines a precise point of view on how species should be prioritized for conservation. For the product of distinctiveness and extinction risk, the implicit point of view can be defined as follows: if a species is not threatened, then there is no need to prioritize it for conservation (extinction risk = 0 leading to extinction risk \times distinctiveness = 0). If it is not distinctive, there is no need to prioritize it for conservation (distinctiveness = 0 leading to extinction risk \times distinctiveness = 0). If species were simply ranked from the highest (1st rate, top-priority species) to the lowest product of distinctiveness and extinction risk, there would be a risk, especially in taxonomic groups where distinctiveness and threat are uncorrelated, that species are classified as top priorities although they have moderate distinctiveness (because of their high extinction risk) or although they have moderate extinction risk (because of their high distinctiveness). A solution that was historically proposed by the EDGE of Existence programme to avoid that is to select species that not only have high EDGE values, but that are also threatened and have above average distinctiveness within the species group considered (Isaac et al., 2007). As part of the recent EDGE2 version of this program, alternative solutions were proposed including targeting threatened species that have above median EDGE2 value or considering different profiles of species such as threatened and distinctive species, nonthreatened but distinctive species, and species with sufficiently high extinction risk but borderline distinctiveness (Gumbs et al., 2023b).

Combining several criteria into a single quantitative score raises conceptual and mathematical issues related to how the score can be interpreted (e.g., Gouhier and Pillai, 2020). Here, building on these previous developments, we set up an axiomatic framework for how a species' distinctiveness could be combined with its extinction risk via a tool aimed at defining conservation priorities. More generally, the framework we have developed is not limited to evolutionary or functional distinctiveness, but it could serve as a basis for discussion in any scenario where two quantitative scores of irreplaceability and extinction risk need to be combined.

2. Methods

Let *D* be any distinctiveness index. Consider also ε , a measure of the extinction probability in [0,1]. We consider the following approaches that have been or could be developed to define an index of conservation interest for a species using solely its distinctiveness value and its extinction probability. We underline the conditions satisfied by each approach.

2.1. Current widely used approach

As underlined in the introduction, the current most frequently used approach that combines distinctiveness (*D*) and extinction probability (ε) is to use their product, which yields for any species *j*:

$$C_j = D_j \times \varepsilon_j \tag{1}$$

The interpretation of C_j value depends on the way D_j and ε_j are defined. For example, if D_j is considered to be the amount of diversity embodied by species j, then C_j can be viewed as an expected loss of diversity through the extinction of species j (e.g., Redding and Mooers,

2006). Alternatively, if D_j is measured as a probability that species j does not share any biological characteristics with the other species, then C_j would be viewed as the probability that species j is driven extinct shortly and that it was distinctive (provided these two events are independent). The conditions satisfied by this multiplicative C index (Eq. (1)) are as follows:

C1. The conservation interest of a species increases with its distinctiveness.

C2. The conservation interest of a species increases with its extinction probability.

C3. The conservation interest of a species is the highest if its distinctiveness **and** its extinction probability are maximized.

C4. The conservation interest of a species is the lowest if <u>either</u> its distinctiveness **or** its extinction probability are minimal.

In *C*, high values for the criteria of distinctiveness and extinction risk are both equally necessary to define a species of high conservation interest (Fig. 1; see also Fig. A1a in Appendix A).

2.2. Five alternatives

In this section, we consider that *D* is standardized so that it varies in [0, 1] (see Appendix A for discussion on this standardization). With this restriction on the definition of *D*, an index of ordinariness can be defined as O = 1 - D. This index represents how common a species' trait values are or how many close relatives a species has in the phylogeny. Similarly, the extinction probability of a species (ε) can be determined by its survival probability, defined as $\sigma = 1 - \varepsilon$. Additionally, we restrict the analysis to indices of conservation interest that vary between 0 and 1.

An alternative to Eq. (1) is

$$C_j^* = 1 - O_j \times \sigma_j \tag{2}$$

If O_j is measured as a probability that species *j* shares biological characteristics with the other species, then C_j^* can be viewed as the probability that species *j* either is driven extinct in the near future or that it is distinctive (provided these two events are independent). With C^* , being highly threatened or being distinctive are two independently but equally important criteria for a species to be of conservation interest. The conditions satisfied by this alternative C^* index (Eq. (2)) are C1 and C2, as defined above, in addition to:

C5. The conservation interest of a species is the highest if <u>either</u> its distinctiveness **or** its extinction probability are maximized.

C6. The conservation interest of a species is the lowest if its distinctiveness **and** extinction probability are both minimal.

In C^* (Eq. (2)), a high value for one of the two criteria of distinctiveness and extinction risk is sufficient to define that a species is of conservation interest (Fig. 1 and Fig. A1b in Appendix A). A property of Eq. (2) that Eq. (1) does not have is that the conservation interest for a species, as measured by Eq. (2), cannot be decreased by considering a species' own distinctiveness value compared to simply considering its extinction probability $(C_j^* \ge \varepsilon_j)$. Similarly, the conservation interest for a species cannot be decreased by considering a species' own extinction probability compared to simply considering its distinctiveness $(C_j^* \ge D_j)$. C^* can be equivalently formulated as $C_j^* = D_j + \varepsilon_j - D_j \times \varepsilon_j$, which shows that *C* and *C** have opposite behaviors. In *C*, there is a "penalty" in conservation interest for not being distinctive or not being highly threatened. In contrast, in *C**, being distinctive or threatened is a bonus for being considered of conservation interest. In addition to conditions 1, 2, 5 and 6, *C** thus also satisfies:

C7. The conservation interest of a species <u>cannot be lower than</u> <u>both its extinction probability and its distinctiveness</u> (i.e., conservation interest index $\geq \max(D, \varepsilon)$).

A compromise between C and C* would be the additive index

$$A_j = \frac{D_j + \varepsilon_j}{2} \tag{3}$$

A is the arithmetic mean of *D* and ε , while *C* is the square of the geometric mean. The meaning behind *A* is that each criterion of distinctiveness and extinction risk, used to define conservation priorities, fairly increases the conservation interest of a species, so that both distinctiveness and risk are required to reach high priority scores (Fig. 1). For example, if a species is highly distinctive (e.g., $D_j = 0.99$) but not threatened ($\varepsilon_j << 0.10$) or if it is highly threatened (e.g., $\varepsilon_j = 0.99$) but not distinctive ($D_j << 0.10$), then in both cases, only half of the criteria are fulfilled for conservation $A_j \approx 0.5$. Conservation interest as measured by *A* is a fair compromise between considering that the conservation interest of a species is its extinction probability and considering that it is its distinctiveness. The conservation interest index A_j defined by Eq. (3) increases linearly with both the species' extinction

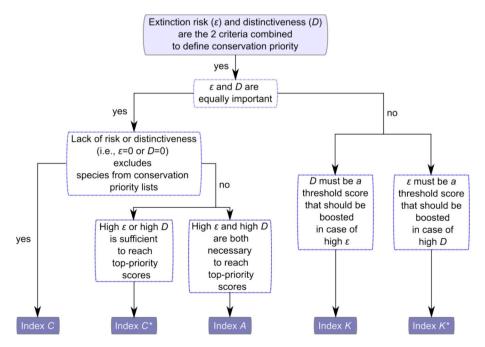


Fig. 1. Guide through the indices of conservation interest discussed in this paper (See section "2. Methods" for definitions of the indices).

probability and its distinctiveness (Fig. A1c in Appendix A). The conditions satisfied by A (Eq. (3)) are C1, C2, C3, and C6, as defined above, in addition to:

C8. The conservation interest of a species <u>cannot be lower than its</u> <u>lowest value between extinction probability and distinctiveness</u> (i. e., conservation interest index $\geq \min(D, \varepsilon)$).

The indices *C*, C^* , and *A* result from balanced consideration of a species' distinctiveness and its extinction probability. Alternative indices can be developed to provide asymmetric effects on a species' distinctiveness and extinction probability (Fig. 1) so that one of the two following conditions is satisfied:

C9. The conservation interest of a species cannot be lower than its distinctiveness.

C10. The conservation interest of a species cannot be lower than its extinction probability.

These alternative indices use a power function applied either to distinctiveness or to extinction probability. The first one is

$$K_i = D_i^{\sigma_j} \tag{4}$$

and satisfies conditions C1, C2, C5, C6 and C9.

The second one is

 $K_i^* = \varepsilon_i^{O_j} \tag{5}$

and satisfies conditions C1, C2, C5, C6 and C10.

 K_i can be viewed as an extended measure of distinctiveness that would take into account the extinction probability of species *j*, while usually the distinctiveness of a species is measured only in light of the extinction probabilities of other species. Indeed species j's own extinction risk increases the perceived rarity of its biological characteristics. K_i^* can be viewed as an informed assessment of the urgency of taking action to improve species j' situation. The urgency level is at least proportional to the extinction probability. For an ordinary species, the level of urgency will indeed be only driven by extinction risk. However, it can be more severe for irreplaceable species, as we may wish to act on irreplaceable species in priority, as early as possible before such species are driven to be critically endangered. For a given value of distinctiveness, the conservation interest indices K_i defined by Eq. (4) and K_i^* defined in Eq. (5) increase nonlinearly with the species' extinction probability (Fig. A1d,e in Appendix A). Note that when D_i and σ_i are zero, we consider $K_i = 1$ (the limit of function x^x when x tends to zero); similarly, O_i and ε_i equal zero leads to $K_i^* = 1$.

An alternative to developing quantitative indicators of conservation interest is to consider the relationship between a species' extinction probability and its distinctiveness using a two-dimensional graph and to split species into 4 groups with different levels of conservation interest (Fig. 2). This fifth alternative approach mimics Violle et al.'s (2017) analysis of the functional rarity of a species based on a two-dimensional graph of the relationship between a species' sparseness and its functional distinctiveness. The definition of groups requires that thresholds are defined on extinction probabilities (low versus high ε) and distinctiveness (low versus high D). For example, Isaac et al. (2007) suggested that a list of high-priority species could be defined as those that have above-average distinctiveness and that are also threatened according to the International Union for the Conservation of Nature (IUCN) Red List (IUCN, 2023). Alternatively, Trindade-Santos et al. (2022) suggested that the rarest species are those with one of the 25 % highest range restrictiveness levels and one of the 25 % highest distinctiveness values. Another simple arbitrary strategy would be to set the threshold at 0.5 (the middle of the interval of variation in both ε and D). However, the graphical analysis allows the consideration of distinct thresholds for D and ε ; see our case study below for another example.

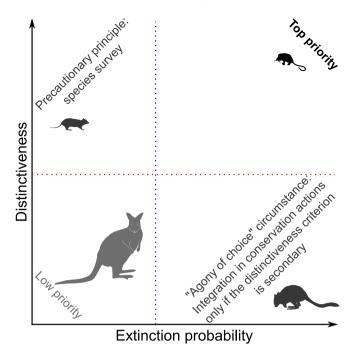


Fig. 2. Graphical approach to identifying top-priority species for conservation under the distinctiveness and extinction risk criteria. Broken lines define 4 groups with different combinations of low versus high distinctiveness and low versus high extinction probability. The positions of the broken lines here are arbitrary (see the case study for a concrete example). Silhouettes provide examples of Diprotodontia species in each of the four delimited groups: those of mountain pygmy possum *Burramys parvus* (threatened and distinctive), musky rat-kangaroo *Hypsiprymnodon moschatus* (distinctive but not threatened), bushtailed bettong *Bettongia penicillata* (threatened but not distinctive), and tammar wallaby *Macropus eugenii* (neither threatened nor distinctive).

2.3. Case study

We analyzed the conservation interest of diprotodont species referenced in the IUCN Red List (IUCN, 2023). Diprotodontia is one of the orders of marsupials that include koalas, kangaroos, wallabies, cuscuses, and possums. Yang and Pavoine (2023) collected phylogenetic data from Upham et al. (2019) for all 139 diprotodont species and calculated the probabilities of extinction within 100 years from the Andermann et al. (2021) model applied to the IUCN Red List status (IUCN, 2023). Diprotodont species were categorized on the IUCN Red List as of least concern (LC, 64 species), near threatened (NT, 23 species), vulnerable (VU, 23 species), endangered (EN, 14 species) or critically endangered (CR, 15 species). We used, as in Gumbs et al. (2023b) and Steel et al. (2007), the HEDGE ψ ' index to calculate the evolutionary distinctiveness of each species. We considered 1000 credible phylogenetic trees. For each species, we calculated the value taken by each numerical index of conservation interest applied to each phylogenetic tree and the extinction probabilities. We subsequently considered the mean of the resulting set of 1000 conservation-interest values. We identified, for each index of conservation interest, the 25 species with the highest mean values.

For the graphical approach, we considered for each species the mean of the distinctiveness values obtained from the 1000 phylogenetic trees and the extinction probabilities. We considered $1/\log_2(139)$ as a threshold for distinctiveness above which a species would be considered distinctive. This threshold corresponds to the length of any terminal branch in a phylogenetic tree if the tree had a unit height and was perfectly symmetric with regular bifurcations (speciation events) (Appendix A). For the extinction probabilities, we considered the mean between the highest extinction probability of a NT species and the lowest extinction probability of a VU species as a threshold between not-

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yet-threatened (ε < threshold) and threatened species (ε > threshold).

3. Results

The mountain pygmy possum *Burramys parvus* and leadbeater's possum *Gymnobelideus leadbeateri* were rated as the 1st and 2nd species of conservation interest according to all the numerical indices (Fig. 3). The two species even had outlying values for the *C* index compared to those of the other species. Indeed, these species were the only species with both high extinction probabilities and relatively high distinctiveness (Fig. 4). The 25 species with the highest values of conservation interest had various IUCN statuses except for those for which the *C* and *K** indices were used (Fig. 3): all the top 25 *K** species were threatened, and all the top 25 *C* species were threatened, except for one, the lemuroid ringtail possum *Hemibelideus lemuroides*.

Seven species were considered of top conservation priority according to the graphical approach (Fig. 4): two were CR (*B. parvus* and *G. leadbeateri*); the other five were VU (the bear cuscus *Ailurops ursinus*, the banded hare wallaby *Lagostrophus fasciatus*, the greater glider *Petauroides volans*, the koala *Phascolarctos cinereus*, and the long-footed potoroo *Potorous longipes*). Twenty species were considered distinctive but not threatened, among which the most distinctive were (in decreasing order) the Australian honey possum *T. rostratus*, the musky rat kangaroo *Hypsiprymnodon moschatus*, the feather-tailed possum *Distoechurus pennatus*, and the feathertail glider *Acrobates pygmaeus* for least concern species and the lemuroid ringtail possum *H. lemuroides* for near threatened species. Forty-five species were threatened but not distinctive (the most threatened of which was estimated to be the western ringtail possum *Pseudocheirus occidentalis*). Sixty-seven species were not threatened or distinctive.

Only three species were identified as of top priority for conservation by all the numerical indices and the graphical approach (Figs. 3, 4 and A.3 in Appendix A). These were *B. parvus, G. leadbeateri*, and *P. cinereus*. The other four species considered of top conservation priority according to the graphical approach were listed as top-25 according to at least one numerical index but not according to all: *A. ursinus* (by index *C*), *Lagostrophus fasciatus (C, A, K), P. volans* and *P. longipes (C, K)*. Among the 45 nondistinctive but threatened species, 12 were in the top-25 list according to all numerical indices of conservation interest (Fig. A.3, Appendix A): *Ailurops melanotis, Bettongia penicillata, Dendrolagus mayri*, *Dendrolagus pulcherrimus, Dendrolagus scottae, Dorcopsis atrata, Petaurus abidi, Phalanger matanim, Potorous gilbertii, Pseudocheirus occidentalis, Spilocuscus rufoniger*, and *Spilocuscus wilsoni*. In contrast, in the group of 20 distinctive but not threatened species, none were in the top-25 list of

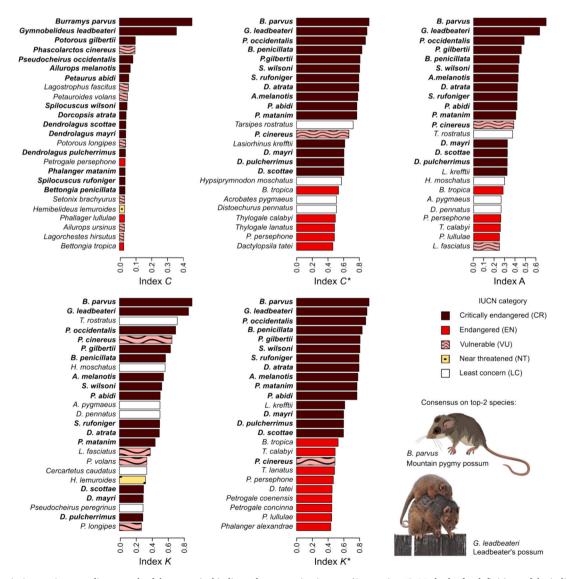


Fig. 3. Top-25 priority species according to each of the numerical indices of conservation interest (See section "2. Methods" for definitions of the indices). The name of species that have been classified in the top-25 priority list of all five indices have been bolded.

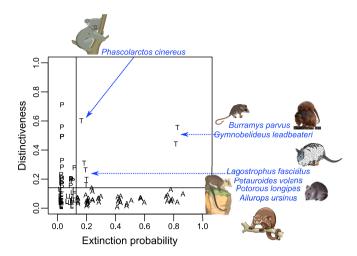


Fig. 4. Plot of species extinction probability (x-axis) and distinctiveness (yaxis). The plain lines indicate the two thresholds for the definition of the four groups of species (see Fig. 2). Species labeled "T" in the top right square defined by these two lines are considered of top priority; those in the bottom right square are threatened but not distinctive (labeled "A" for agony of choice); those in the top left square are distinctive but not threatened (labeled "P" for precautionary principle); and those labeled "L" in the bottom left square are considered of low priority. Latin names and silhouettes are provided for the topranked species.

all the numerical indices of conservation interest (Fig. A.3, Appendix A). However, seven of the species were in the top-25 for at least one of the numerical indices: A. pygmaeus (C^* , A, K), Cercartetus caudatus (K), D. pennatus (C^* , A, K), H. lemuroides (C, K), H. moschatus (C^* , A, K), Pseudocheirus peregrinus (K), and T. rostratus (C^* , A, K).

4. Discussion

4.1. A variety of distinctiveness indices

There are various methods for estimating extinction probabilities and distinctiveness. All of these methods are context-dependent, and their accuracy is dependent on data availability. The distinctiveness of a species depends on a reference set of species, and extinction probabilities can be defined at various spatial scales, from local to global extinction, and within various time windows. The extinction probability of a species increases with the time frame and decreases with the spatial scale from local to global. The link between distinctiveness and extinction risk might depend on these scales. While extinction risk and distinctiveness are rarely correlated at the global level, evolutionarily and functionally distinctive species are currently disproportionately affected locally by human-driven modifications of ecosystems. For example, local losses of evolutionarily and functionally distinctive species were observed in birds in agricultural (Frishkoff et al., 2014) and urbanized (Ibáñez-Álamo et al., 2017; Sol et al., 2017, 2020) sites and in amphibians due to the loss of native forests, especially by pastures and agroforestry plantations (Greenberg et al., 2018).

One of the differences between the two concepts lays in the perimeter of their definition. Compared to extinction probability, distinctiveness has multiple aspects as it can be measured for multiple dimensions of biodiversity. Each index of distinctiveness thus expresses only one of these aspects. The first decision to make when choosing an index of distinctiveness is whether to focus on evolutionary or functional aspects. For practical and theoretical reasons, policy makers who have to construct conservation strategies at the global scale could be more interested in evolutionary distinctiveness than in functional distinctiveness. Phylogenetic trees have been constructed for large taxonomic groups (e.g., Upham et al., 2019); however, while trait databases are expanding, few traits are well documented, and their relationship with ecosystem functions is still unclear. In addition, evolutionary distinctiveness has been associated with the benefits a species could bring in the future to human well-being (Faith et al., 2010). In contrast, policy makers who must design conservation strategies at the local scale (intracountry) may be interested in functional distinctiveness to preserve ecological processes and avoid the collapse of an identified ecosystem. If traits are phylogenetically conserved, then phylogeny may also be a reasonable proxy for functioning. On the other hand, if traits are related to short-term adaptive strategies, then traits and phylogeny tell quite different stories. In this latter case, instead of treating evolutionary distinctiveness and functional distinctiveness separately, Hidasi-Neto et al. (2015), in the EcoEDGE index, considered a fair mean of functional and evolutionary distinctiveness. However, this may complicate the index interpretation phase.

The second decision is to choose a mathematical formula to measure distinctiveness. A range of indices have now been developed to measure either evolutionary distinctiveness or functional distinctiveness. Although these have been developed in different contexts with different justifications, they can be positioned along a gradient that goes from a strong influence of the smallest (evolutionary or functional) dissimilarity to another species through a consideration of average dissimilarity (Redding et al., 2014) to a strong influence of the largest dissimilarity to another species (Pavoine and Ricotta, 2022, 2023). The index we used in the case study following Steel et al. (2007) and Gumbs et al. (2023b) is highly influenced by the smallest evolutionary dissimilarity to another species (Pavoine and Ricotta, 2022). Combining extinction risk and distinctiveness into a single quantitative index thus becomes an ultimate step that comes after numerous methodological stages that involve deciding among several alternatives and leads to the final values of extinction risk and distinctiveness for each species.

4.2. Distinctiveness as a necessary or sufficient criterion for conservation prioritization?

If extinction risk and distinctiveness were correlated, considering any one of these criteria would be sufficient to identify distinctive and threatened species. There are indeed case studies in which the most threatened species were found to be the most distinctive species; for example, interacting evolutionarily distinctive birds and plants within the Atlantic Forest tend to be threatened (Emer et al., 2019). In addition, the conservation status of many evolutionarily distinctive species has deteriorated, as is the case for distinctive mammals whose estimated global extinction risk increased according to the IUCN Red List assessment from 1996 to 2008 (Gumbs et al., 2023a). However, in many cases, and especially at the global level, the two criteria, extinction risk and distinctiveness, are currently uncorrelated (e.g., Funk and Burns, 2019; Morelli and Møller, 2018; Tonini et al., 2016).

The quantitative indices for conservation priority we introduced above represent different points of view on which criterion, between extinction risk and distinctiveness, takes priority over the other when deciding which species to preserve first. The indices C, C* and A treat extinction risk and distinctiveness equally, while indices K and K* treat extinction risk and distinctiveness asymmetrically. However, the greatest difference among these indices lies in their interpretation: whether each of the two criteria, extinction risk or distinctiveness, is considered necessary or sufficient to define a species as a conservation priority. For A and C, high conservation interest values can be obtained only if both extinction risk and distinctiveness are high, while for C^* , K and K^* , a common species that is highly threatened and a species of least concern that is highly distinctive would both have high conservation interest values. Thus, when using indices A or C, distinctiveness is considered a necessary but not sufficient criterion for a species to be defined as of high conservation interest. In contrast, when using C^* , K and K^* , this is a sufficient but not necessary criterion.

The variety of points of view expressed by the differences in indices

we considered above make us question the need for or, inversely, the detrimental effect of promoting an exclusive single approach to quantify conservation interest. The need to focus on a single approach may stem from the intrinsic limitations encountered when communicating them to a large public. Multiplying indicators may increase stakeholder confusion about their relative definitions. However, our developments above show that communication could be improved to justify the choice of an index among the potentially infinite number of alternative indices. Guiding the interpretation of each index that combines several criteria of conservation interest is also critical, as the use of such indices by government spokespeople, scientists, or NGOs is often interpreted by the public roughly, thanks to the index name, in light of everyday language (e.g., Barua, 2011).

Using all available indices of conservation interest and comparing them before setting priorities (e.g., Mace et al., 2007) could be a tempting approach to avoid choosing one formula over another. However, this approach would not ease the interpretation of indices. In addition, although we focused on a limited set of quantitative indices that combine extinction risk and distinctiveness, the possibilities of index development are actually infinite (e.g., Mace et al., 2007; Gouhier and Pillai, 2020). Comparing raw variables instead of different indices that combine them would thus be more parsimonious and less susceptible to incorrect interpretation. For example, by comparing different criteria (including threat and distinctiveness), the new EDGE2 framework (Gumbs et al., 2023b) allows practitioners to select sets of species based on their interests: not only those that are threatened and distinctive but also species that are nonthreatened but distinctive, species that are distinctive but without threat evaluation in the IUCN Red List, and species with sufficiently high extinction risk but borderline distinctiveness.

Compared to quantitative indices, the graphical approach that allows visualization of the values of extinction risk and distinctiveness of all species is less directive in setting conservation priorities but more informative than quantitative indices. Species that are both at high risk of extinction and highly distinctive can be easily identified on the graph (such as the mountain pygmy possum, leadbeater's possum, and koala in the case study). These may be considered top-priority species for conservation. Species that are at high risk of extinction but are not distinctive will not be considered by programs that focus on distinctive species. However, another group of species may be considered of second priority by these programs: that of nonthreatened highly distinctive species. In the context of evolutionary distinctiveness, these species were early highlighted by Steel et al. (2007) as important to consider when evaluating actions that might cause the extinction of species such as modifying or losing habitats. Faith (2015) then qualified them as 'loss-significant evolutionarily distinctive globally enduring' (LEDGE) species, and Gumbs et al. (2023b) grouped them in a watch list. Indeed, some of these species are near threatened (e.g., the lemuroid ringtail possum in the case study). Monitoring and preventive measures could be implemented for these species to prevent their condition from worsening. It is often less costly to take measures to prevent a species' condition from deteriorating than to act only when the species is in critical danger of extinction (Mace et al., 2007).

4.3. Reasons why the distinctiveness criterion may be critical for conservation

Conservation priority was once often considered equal to extinction risk, although extinction risk is actually only one aspect that could drive conservation prioritization—an aspect of urgency (Mace et al., 2007). While the analyses of distinctiveness were first mostly theoretical, evolutionary distinctiveness has been considered by the EDGE of Existence programme since 2007 (Isaac et al., 2007) and is now included as a criterion for conservation prioritization by The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2018) and as a complementary indicator by The Kunming-Montreal

Global Biodiversity Framework (GBF) (2030 under Goal A CBD/COP/ 15/L.26 and Target 4, www.cbd.int/gbf/targets/4/). Evolutionarily distinctive species are targeted by these global conservation initiatives because they could represent 'option values' for future benefits to humanity (Faith et al., 2010). This argument thus relies on the possibility of benefits that are yet to be discovered and documented, including promoting the health of ecosystems in the interest of human well-being (Faith et al., 2010). Evolutionarily distinctive species could have distinctive features, and humanity could benefit from future uses of these features (Faith et al., 2010). To reinforce this argument, some have checked whether evolutionarily distinctive species could currently and prominently provide benefits to humanity. For example, plant benefits relate to materials, fuels, human and nonhuman animal nutrition, medicines, poisons, and social and environmental aspects (Molina-Venegas, 2021). Molina-Venegas (2021) showed that extant multibeneficial plants that contribute to many types of benefits tend to have higher evolutionary distinctiveness than expected randomly. He identified a set of multiple beneficial and evolutionarily distinctive plants, including the endangered ginkgo (Ginkgo biloba, Ginkgoaceae) native to East Asia.

The concept of functional distinctiveness is more directly related to local ecosystem functioning and thus to the health of ecosystems. Its measurement could be infra-national instead of global (Pavoine and Ricotta, 2023). As the identification of keystone species with disproportionate roles in ecosystems is difficult (Power et al., 1996), identifying functionally distinctive species may be an easier way to evaluate the potential for a species to be irreplaceable and of importance to a community, provided that a sufficient set of traits can be documented for the species. In high-diversity communities, the loss of a previously threatened species will likely be compensated for by an increase in species that are functionally similar to it. However, if human activities drastically decrease the diversity of a community, a functionally distinctive species may have been thrust to be the last representative of its functional group and to play its keystone role (Power et al., 1996). Overall, the loss of functionally distinctive species may thus have dramatic effects on ecosystems.

The seemingly technical concept of keystone species is often poorly, if not incorrectly, defined in newspaper articles, where reporters often use cognitive shortcuts (Barua, 2011). The related concept of distinctiveness may be easier to communicate, as it points to species that are so different from others from a biological/ecological point of view that they are likely to be irreplaceable in ecosystem functions. The arguments based on benefits to human well-being and on benefits to the health of ecosystems may be easier to communicate to a large public than intrinsic ethical reasons for conservation (e.g., Faith et al., 2010). Land managers and policy makers could thus choose to protect species with disproportionately high community importance (Power et al., 1996) or with disproportionately high option value (Faith et al., 2010), among which are the distinctive species. This raises the question of developing useful indicators that integrate the concept of distinctiveness. The Secretariat for GBF target 4 identified the EDGE index. We showed here that EDGE relies on one of numerous possible ways to combine the extinction risk of a species with its distinctiveness to obtain a quantitative assessment of the species' conservation interest.

4.4. Directions for future research

Fifteen years ago, Sitas et al. (2009) wrote that "Species most likely to receive conservation attention are those which are well-studied, charismatic and that live in the developed world. Conservation status and evolutionary distinctiveness appear to have little importance in conservation decision-making at the global scale." Despite the consideration of evolutionary distinctiveness by the EDGE of Existence programme, the IPBES and the GBF are thus important steps (Gumbs et al., 2023a), from a practical view, conservation actions are often funded primarily by individual donations from the large public. Different people and organizations and different sectors in society can make different choices/recommendations when setting priorities (Mace et al., 2007). Thus, there is still a need to demonstrate the popularity of the distinctiveness criterion, that is, whether the large public would financially support conservation actions that first target distinctive species (Mace et al., 2007; Pavoine and Ricotta, 2022, 2023).

The discussion on how to apply two criteria to develop indicators of conservation interest may be extended to other types of criteria, such as sparseness and cultural importance. It may also be extended to any number of criteria, as a species may be a priority for conservation for more than two reasons (Mace et al., 2007). Other criteria include biological, ecological, economic, sociocultural aspects and practical issues (Mace et al., 2007). In addition, distinctiveness and extinction risk are aspects related to the rarity of a species. Other aspects include the number of individuals, the number of populations, the rarity of habitats and the size of the geographic range (Mace et al., 2007). These numerous variables are fundamentally different and can be compared via, for example, principal component analysis. Several ways of measuring distinctiveness could be used in this analysis, and methods such as principal component analysis could more efficiently determine according to which criteria a species should be prioritized for conservation (see also, Moffett et al., 2005).

The discussion regarding extinction risk and distinctiveness, as well as the methodologies suggested, could also be extended to any basic unit other than species, any unit for which we have good reasons to consider extinction or collapse risk and distinctiveness as criteria for conservation. Indeed, each conservation strategy is performed on a basic unit referred to as an element, and when several strategies can be implemented together, varying elements from one strategy to another ensures that a broad spectrum of biodiversity and ecological processes are targeted and preserved (e.g., Mace et al., 2007). These elements can include, for example, an infraspecific taxon, isolated populations of a species, OTUs for microorganisms, species assemblages in different locations of a region, or larger-scale ecosystems. In addition, measures of distinctiveness can be calculated for any type of element, and data can be collected to compare these elements (e.g., Pavoine et al., 2017). These can include trait data collected at the individual level to distinguish populations or species abundance and phylogenetic and average trait characteristics to contrast communities. Ecosystems can even be characterized by comparative sets of ecological, biophysical and/or environmental data when evaluating their distinctiveness. In addition, to overcome the difficulty of defining ecosystem boundaries, the IUCN started developing a Red List of Ecosystems (IUCN-CEM, 2023). The list estimates the health of an ecosystem considering reduction and restriction in geographic distribution, environmental degradation, disruption of biotic processes or interactions and the probability of imminent collapse. Identifying ecosystems that are both distinctive and threatened could thus be feasible. Theoretical developments to include the concept of distinctiveness in conservation strategies thus do exist. However, additional work is still needed to ensure well-informed choices among these developments and their correct interpretation by a large public.

CRediT authorship contribution statement

Sandrine Pavoine: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Conceptualization. **Carlo Ricotta:** Writing – review & editing, Methodology, Conceptualization.

Declaration of competing interest

We have no conflicts of interest to declare.

Data availability

Data and R scripts are available in Appendixes A-E.

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Appendixes A-E. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110657.

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