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Research Letters

Are threatened species important for glueing interaction networks together?

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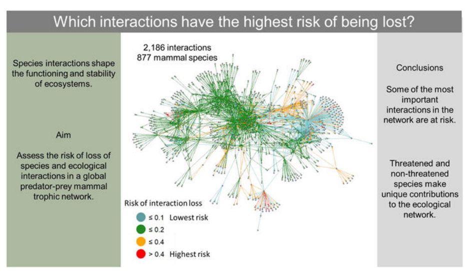
HIGHLIGHTS

- Ecological interactions shape the functioning and stability of ecosystems.
- We assessed the vulnerability of species and their interactions in a mammal network.
- The most important interactions in the network are, at least, partially at risk.
- Threatened and non-threatened species make unique contributions to the ecological network.

GRAPHICAL ABSTRACT



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ABSTRACT

Biotic interactions are a critical element for the functioning and the stability of ecosystems, yet anthropogenic pressures can significantly disrupt these networks of interacting species. While species-focused conservation is central to most conservation policy, it is also vital to identify the interactions at risk and the ones that play a disproportionate role in glueing communities together. Here we assess the importance of species for ecological network integrity and the risk of loss of interactions that is brought by species loss in a global predator-prey network comprising 877 mammal species. We calculated the importance of species and their interactions using network centrality analyses. The risk of loss of interactions was determined by quantifying the extinction risk of each pair of interacting species. Additionally, we examined whether specific traits or phylogenetic history influenced both extinction risk and species importance. We found that extinction risk is unrelated to species' importance in the network. We also showed that the most important interactions are at least partially at risk of being lost. Moreover, important and threatened species showed higher ecological distinctiveness, but similar low evolutionary distinctiveness. We emphasise that conservation strategies should consider the contributions of both threatened and non-threatened species to ecological networks, acknowledging the vital roles they play for ecosystem stability and function.

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Introduction

Species are interwoven into complex webs of interactions, where each species plays a unique ecological role, contributing to the network's collective stability (Montoya et al., 2006). Communities of interacting species, however, are simultaneously threatened by a plethora of perturbations (Doherty et al., 2023). Understanding the risk of interaction loss and species loss can help us maintain the integrity and functioning of ecosystems. Indeed, the extinction of biotic interactions disrupts ecological networks and can have repercussive and often unnoticed consequences on whole ecosystems (e.g., cascading effects, Zipkin et al., 2020), including losses of ecological functions (Jordano, 2016) and services (Civantos et al., 2012).

Although understanding the potential consequences of biodiversity loss continues to be an urgent societal goal, the main approach used to tackle the current biodiversity crisis is to quantify species richness and their extinction risk. This can lead to misinformed conservation policy and outcomes (Oliveira et al., 2020) because it ignores other facets of biodiversity that account for evolutionary and ecological differences among species, which represent how species respond to the environment (Jarzyna and Jetz, 2016). In this sense, species interactions are key to understanding biodiversity organisation within communities, and predicting ecosystem stability and resistance to different components of environmental change (Montoya et al., 2006; Lurgi et al., 2012), and important ecosystem functions, such as primary production, pest control or pollination (Montoya et al., 2003; Thompson et al., 2012). Yet, our ability to predict the vulnerability of ecological interactions is very limited.

The susceptibility of network interactions to change is contingent upon the nature of the agent of change in question (Aizen et al., 2012). For example, climate change can cause distributional and phenological mismatches, altering species interactions (Araújo and Luoto, 2007; Cahill et al., 2013). Changes in species interactions are an important cause of documented population declines and extinctions related to climate change (Cahill et al., 2013). Therefore, predicting the potential disappearance or risk of interaction loss could avoid the collapse of ecological communities (Jordano, 2016). Overall, understanding and conserving biotic interactions is essential for the well-being of both the species and the broader ecosystems they inhabit.

Here we aim to assess the risk of the loss of species and ecological interactions in a global predator-prey mammal trophic network through the following objectives: 1) Determine which species are the most important within the mammal trophic network and asses their extinction risk; 2) Determine which are the most important interactions and how threatened these interactions are; and 3) Assess whether the level of importance of species is associated with specific ecological traits or phylogenetic history (i.e., ecological and evolutionary distinctiveness, range size).

Methods

Data

We used the database of >17,000 unique predator-prey global mammal interactions compiled by (Fricke et al., 2022) and selected only binary predator-prey interactions, excluding interactions within the same species (e.g., cannibalism; n = 29). Each species was assigned to a threat status according to the IUCN red list (IUCN, 2023). We excluded species qualified as data deficient by the IUCN as their level of threat is uncertain. The resulting database contained 2186 interactions from 877 mammal species (834 prey and 96 predator species; with some species being classified both as prey and predator) ranging from body masses between 0.002 and 4500 kg.

Importance and risk of species loss

We calculated centrality metrics to determine which nodes (species) are more important within the mammals' ecological network. Specifically, we calculated the Integrated Value of Influence (IVI) index for each species using the R package *influential* (Salavaty et al., 2020). This index integrates the most relevant and commonly used network centrality measures (degree centrality, ClusterRank, neighbourhood connectivity, local *H* index, betweenness centrality, and collective influence). The IVI index ranges from 1 (least important) to 100 (most important), and the nodes with the highest IVI index have the potential to cause the highest impact (disruption) on the entire network (Salavaty et al., 2020).

Subsequently, to assess if the most important species are at higher risk of extinction, we performed an ANOVA to evaluate whether significant differences existed in the IVI index across all five categories of threat (LC, NT, VU, EN, CR). We also assessed if any differences arose when comparing non-threatened (LC and NT) versus threatened species combined (VU, EN, and CR).

Importance and risk of interaction loss

To assess the importance of each interaction (link) within the network, we obtained a measure of betweenness centrality for each interaction called edge betweenness (Girvan and Newman, 2002). This measure describes the frequency with which a link acts as a bridge along the shortest path between two nodes in the network. For example, if a network contains species that are only connected by a few edges, then all shortest paths between different species would go along one of these few edges. Thus, the edges connecting species will have a high edge betweenness. As such, this metric identifies the interactions that can significantly affect the overall connectivity of the network in case of disruption (Girvan and Newman, 2002; Csárdi et al., 2023). We calculated the "importance of the interaction" metric for each of the 2186 pairwise interactions using the 'edge betweenness' function from the R package igraph (Csárdi et al., 2023).

We obtained the risk of interaction loss using the threat status of each of the two species taking part in each of the 2186 specific interactions. The movement among IUCN categories (e.g., the change from LC to NT, from NT to VU, etc.) can reflect a constant change in probability of extinction (e.g., by factor 2, as presented by (Isaac et al., 2007), or a nonlinear relationship (e.g. as presented by Redding and Mooers (Redding and Mooers, 2006) or the IUCN itself). However, both, the constant and nonlinear change, reflect similar probabilities of extinction of the interaction between two species. Hence, we used the parameters inferred from (Isaac et al., 2007) by (Mooers et al., 2008), and the probability of each species defined by the IUCN category used was:

$\text{Prob(ext)}_{CR} = 0.4$ in 100 years; $\text{Prob(ext)}_{EN} = 0.2$ in 100 years; $\text{Prob(ext)}_{vu} = 0.1$ in 100 years; $\text{Prob(ext)}_{NT} = 0.05$ in 100 years; $\text{Prob(ext)}_{LC} = 0.025$ in 100 years.

We then calculated the probability of extinction of interactions based on the probability of extinction of each species involved in the interaction. That is, in order to maintain an interaction, the survival of both species involved in the interaction needs to be guaranteed. Therefore, the probability of extinction of the interaction between species A and species B corresponds to the union of the probability of extinction of species A and the probability of extinction of species B (equation 1). Importantly, by using this probability of the union, we assume that the probability of extinction of a species is independent of the probability of extinction of the other species (see also Williams and Araújo, 2000, 2002). Although this may not always be true, it is impossible for us to know the dependencies of these probabilities of extinctions.

We calculated the probability of extinction of each interaction as follows:

P (extinction of the interaction) = [P (extinction sp. A) + P (extinction sp. B)] - [P (extinction sp. A) * P (extinction sp. B)] (equation 1)

The probability of extinction of the interaction was calculated for each of the 2186 interactions and was considered the "risk of interaction loss". Instead of using these probabilities directly in the subsequent statistical analyses, we categorised the extinction risk into levels –similar to the approach used for IUCN species-level categorisation– to analyse differences in the mean importance of the interactions. To do this, we performed an ANOVA to compare the means of our "importance of the interaction" metric across the different categories of the "risk of interaction loss". Categories of the "risk of interaction loss" go from 0.04 (lowest risk) to 0.52 (highest risk of interaction loss; see Table S1 for all categories).

Importance and risk of species loss and ecological traits

Finally, we assessed whether the level of importance or threat of a species is associated with ecological distinctiveness (EcoD), evolutionary distinctiveness (EvoD), or range size (square kilometres). We obtained EcoD data from (Cooke et al., 2020). EcoD summarises a species' form, function and ecological strategy (using six traits) and quantifies how uncommon the traits of a given species are compared to all other species globally. Thus, EcoD summarises the ecological irreplaceability of each species (Cooke et al., 2020). EvoD is the amount of unique evolutionary history each species has and was obtained from (https://www.edgeofexistence.org/; accessed September 2022). Finally, we obtained the range size area of each species from (Pillay et al., 2022).

We then performed individual linear regressions to assess the relationship between the degree of importance of species (response variable: IVI index) and EcoD, EvoD and range size. We also performed individual ANOVAs to assess whether EcoD, EvoD and range area differed across species' risk of extinction (i.e., threatened and non-threatened categories).

Results

Important and threatened species

The mammal network has more non-threatened species (n = 727) than threatened species (n = 150). The threat status category of the 877 species was distributed as follows: 666 are least concern (LC), 61 are near threatened (NT), 79 are vulnerable (VU), 53 are endangered (EN) and 18 are critically endangered (CR).

The average IVI index did not significantly differ across the five categories of threat (ANOVA test, $F_{4,882} = 0.02$, $p = 0.86$; Fig. S1). Also,

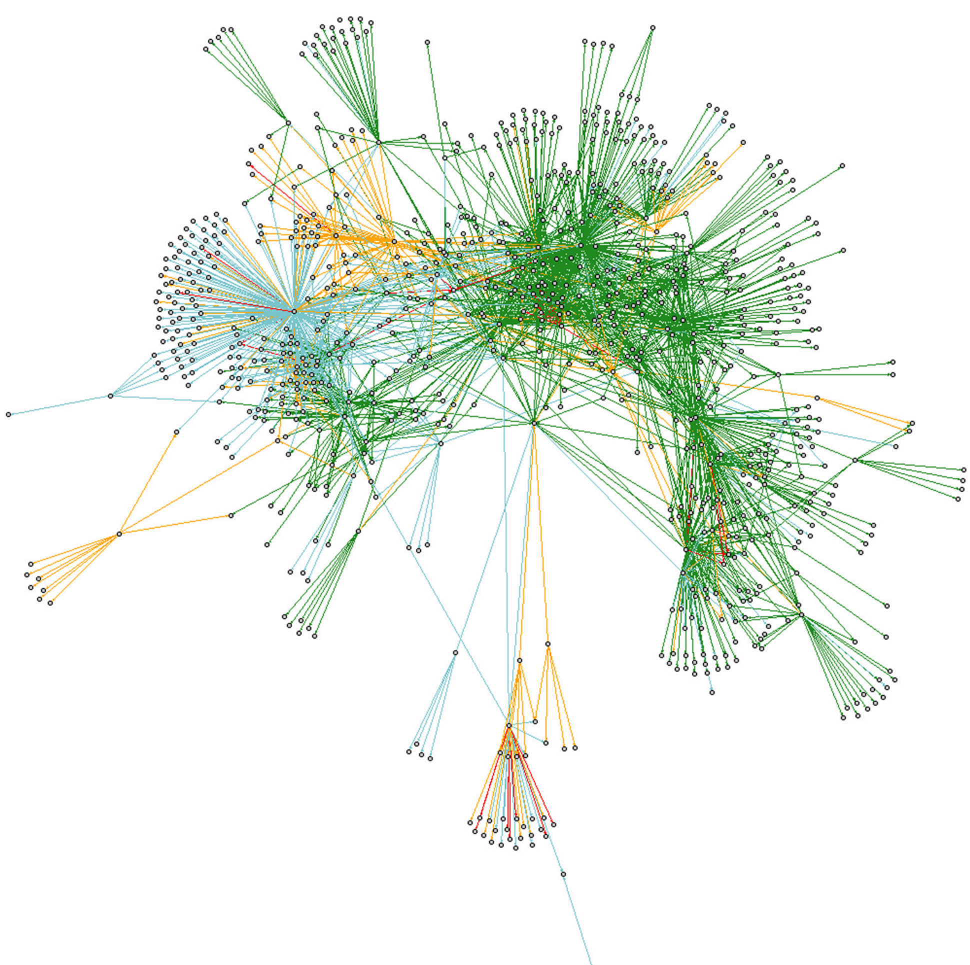

Fig. 1. Risk of mammals' interaction losses. Nodes are individual species, links are interactions. Risk of interaction loss goes from 0.04 (lowest risk) to 0.52 (highest risk of interaction loss), and coloured links represent the risk of interaction loss: green (interaction between two non-threatened species; level of risk ≤ 0.1), blue (interaction between one VU species and one VU or non-threatened species; level of risk ≤ 0.2), orange (interaction between one EN species and one EN or VU or non-threatened species; level of risk ≤ 0.4), red (interaction between one CR species and one species from any category of threat; level of risk > 0.4). Non-threatened = least concern or near threatened; VU = vulnerable, EN = endangered, CR = critically endangered.

threatened and non-threatened species showed similar levels of importance ($F_{1,885} = 0.15$, $p = 0.69$), with the mean IVI index being 1.94 and 1.75 for threatened and non-threatened species, respectively. Regarding the threat status of the most important species, we found that three out of the ten most important species (with the highest IVI index) are threatened with extinction (2 VU, 1 EN), and seven out of the 40 most important species are threatened with extinction (4 VU, 3 EN), with no CR species within the 50 most important species (Fig. S2).

Important and threatened interactions

The majority of interactions (60.3%; n = 1331) take place among species belonging to the same threat status. Most of the interactions have a risk of loss below 0.1 (66.9%; n = 1476), meaning that most interactions occur across non-threatened prey and non-threatened predators (green links in Fig. 1). Additionally, 26.7% of the interactions have at least one threatened prey or predator (n = 585; some blue, orange and red links in Fig. 1), and some interactions have both, threatened prey and predator (n = 150; belonging to 17 predator and 100 prey species). If considering only prey and predators that are either EN or CR, then the number of interactions is 15 comprising 6 predator and 12 prey species. Threatened predators interact mainly (77.2% of interactions) with non-threatened prey and the rest with threatened prey. This means that almost a quarter of the diet of threatened predators within our studied network is associated with threatened species. Although, their diet very likely relies also on species not included in this study.

We found no relationship between the importance of the interaction and the risk of interaction loss ($F_{1,2184} = 2.32$, $p = 0.12$). Yet, most individual interactions have a low score of betweenness (<35), regardless of the level of risk of interaction loss (Fig. S3). The highest value of edge betweenness (edge betweenness = 7,594.25) was found among an interaction with the lowest risk of interaction loss (LC-LC interaction; Fig. S3), yet the LC-VU interaction had the highest mean betweenness score (Table S1), suggesting that the most important interactions are at least partially at risk of being lost.

Importance and risk of species loss and ecological traits

The IVI index was positively related to the degree of EcoD of species (t_{885} value = 8.42, $p < 0.001$; Fig. 2A) and range area (t_{885} value = 15, $p < 0.001$; Fig. 2C), but we found no significant relation between the IVI index and the EvoD of species (t_{885} value = −1.30, $p = 0.19$; Fig. 2B).

Regarding the threat status, we found that threatened species had a significantly higher degree of EcoD compared to non-threatened species ($F_{1,885} = 35.23$, $p < 0.001$; Fig. 2D), but similar EvoD ($F_{1,885} = 2.40$, $p = 0.12$; Fig. 2E). As expected, threatened species occupy smaller geographical areas compared to non-threatened species ($F_{1,885} = 27.45$, $p < 0.001$; Fig. 2F).

Discussion

Our study explores the relationship between the levels of importance and threat of species and their interactions within the global predator-prey mammal network. Both threatened and non-threatened species and their interactions wielded similar levels of importance within the mammal network. Thus, while protecting threatened species is vital to prevent accelerating extinctions, disregarding non-threatened species would neglect their significant contributions to ecological network integrity and maintaining ecosystem resilience (Baker et al., 2019). Further, besides focusing on species richness and threat status, facets such as ecological distinctiveness provide invaluable aspects to consider when tackling conservation prioritisation.

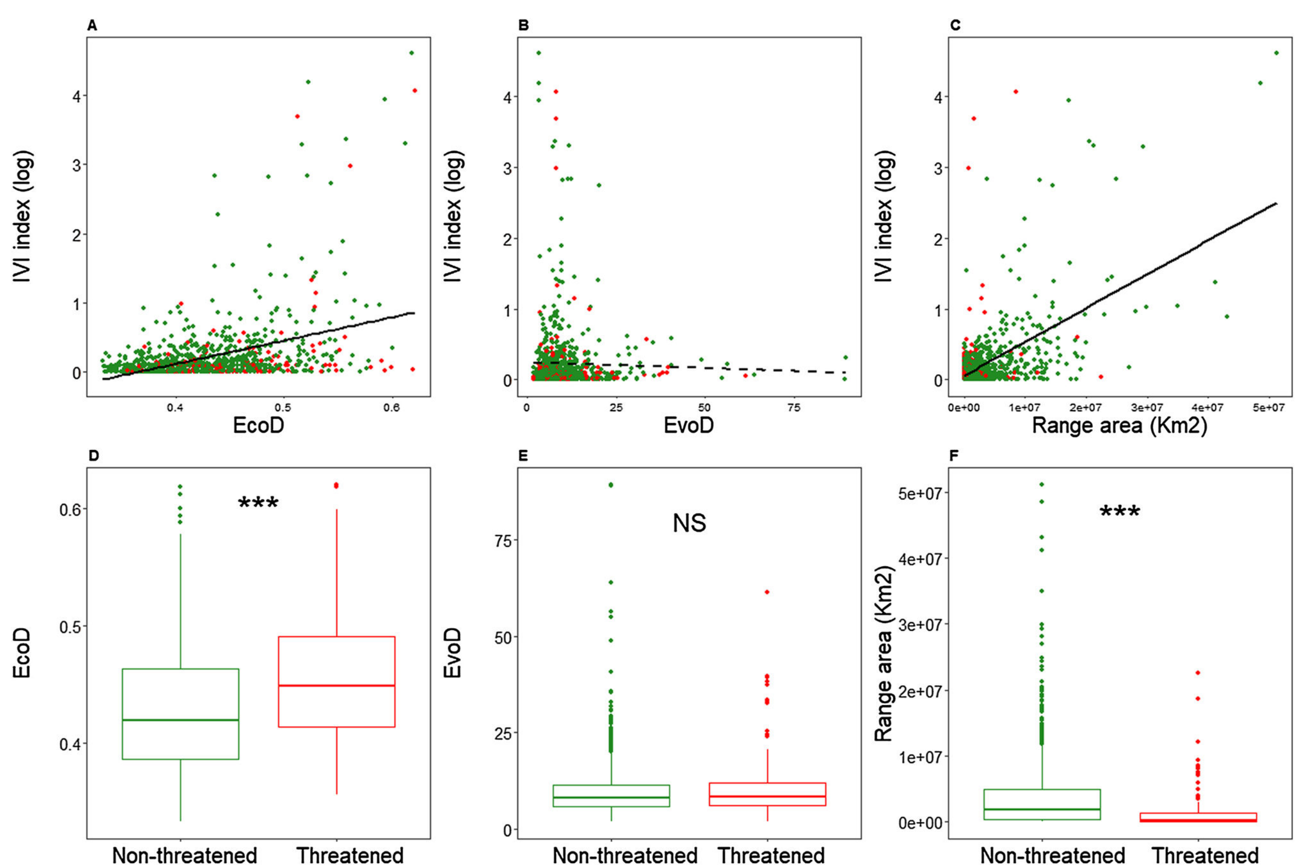

Fig. 2. Relationship between ecological distinctiveness (EcoD), evolutionary distinctiveness (EvoD), range area (square km) with IVI index and threatened category. Green dots represent non-threatened species, and red dots represent threatened species. Solid black lines and asterisks represent significant differences ($p < 0.001$).

Of special interest is that the most important species within the network (with the highest IVI index) are predators (e.g., *Canis lupus* (grey wolf), *Vulpes vulpes* (red fox), *Panthera pardus* (leopard), *Canis latrans* (coyote), *Panthera leo* (lion), *Lynx lynx* (bobcat), *Puma concolor* (puma), *Felis silvestris* (European wildcat), *Panthera tigris* (tiger), *Ursus arctos* (brown bear)), and their disappearance would have a disproportionately large impact on their ecosystems relative to their abundance. Similarly, despite limited data on other types of ecological networks, studies on plant-frugivore interactions have shown that some of the most important bird species (i.e., contributed most to network organisation) were categorised as "higher risk of extinction" (Vidal et al., 2014). This supports our idea that ongoing extinctions may significantly affect current ecological networks (Vidal et al., 2014). Gaining insights into how extinction risks affect various types of ecological interactions is essential for addressing gaps in our understanding, and for predicting the consequences of global changes for ecosystem stability and functionality.

We found that the level of importance of a species within the network was positively related to its ecological distinctiveness. Species with high levels of ecological distinctiveness, displaying distinctively unique roles or functions within the system, are disproportionately represented in IUCN threatened categories (Loiseau et al., 2020). Furthermore, such species are expected to contribute to the resilience of ecosystems by helping support and maintain an array of processes and functions (Hector and Bagchi, 2007). Thus, the imminent extinction of ecologically unique species (three of the top 10 most important species are threatened) may represent a disproportionate loss of ecological function. Losing the most ecologically distinct species may have manifold, more diverse consequences for the ecosystem than losing species that are redundant (i.e., have similar combinations of traits, thus lower ecological distinctiveness) (Villéger et al., 2010; Monnet et al., 2014). Moreover, ecologically distinct species may decline even if there is an increase in community taxonomic diversity (Villéger et al., 2010; Monnet et al., 2014). Several non-threatened species were also highly ecologically distinct species (Fig. 2A), emphasising that both threatened and non-threatened species make unique contributions to ecological diversity and can play critical roles in ecosystems across the globe (Cooke et al., 2020).

We found that the interactions with the highest degree of importance are, at least, partially at risk (involving one threatened and one non-threatened species). Therefore, our focus should extend beyond a species' conservation status to include the species it interacts with. For example, conserving the threatened Iberian lynx (*Lynx pardinus*) is inextricably related to the conservation of the non-threatened, yet declining rabbit (*Oryctolagus cuniculus*), which serves as its main prey (Fordham et al., 2013). Conservation prioritisation strategies for rewilding also consider the presence of a broad array of herbivores or carnivore species, which are essential for the re-establishment and maintenance of critical ecosystem processes, regardless of their conservation status (Araújo and Alagador, 2024). These examples illustrate a point that is emphasised by our findings: to effectively conserve biodiversity, one needs to extend beyond analysis of threat, and consider the critical roles of species within ecosystems. Indeed, within the mammal ecological network, the interactions between LC-LC species are the second most important. Notably, 12% (737 species) of all 5973 mammal species are categorised as non-threatened by the IUCN, but have declining populations (e.g., *Leopardus pardalis*, ranked at number 24 in the IVI index). Considering declines in abundance of non-threatened species is of particular interest as the decline in abundance of a species may bring the loss of ecological interactions well before the actual disappearance of that species (Valiente-Banuet et al., 2015). As such, declines in abundance, even for non-threatened species, could cause cascading effects (García-Callejas et al., 2019), the extinction of ecological interactions, secondary extinctions, and the disruption of ecosystem functioning (Baker et al., 2019).

The threat of species and ecological interactions will not diminish until we tackle the drivers of biodiversity loss. For example, human population density and land-use intensification can lower proportions of both apex and basal species, potentially causing cascading effects (Botella et al., 2024) and altering the structure of food webs in predictable ways (Mestre et al., 2022). Indeed, human pressures have already caused a simplification of the architecture of mammal food webs across several regions worldwide (Mendoza and Araújo, 2019), likely inducing changes to ecosystem functions, services, stability and resilience (Botella et al., 2024). A comprehensive conservation strategy should consider both threatened and non-threatened species' contributions to ecological networks, acknowledging that their ecological traits and evolutionary history influence ecosystem stability and functionality. Protecting species solely based on their threat status overlooks the concealed attributes of species and the loss of ecological or phylogenetically distinct species could undermine the integrity of evolutionary and ecological processes and functions.

CRediT authorship contribution statement

Conceptualization: PG, NG, JDGT, MBA, VAGB; Data curation: PG; Formal analysis: PG; Methodology: PG, VAGB; Visualization: PG; Writing – original draft: PG; Writing – review & editing. PG, NG, JDGT, FM, MBA, VAGB.

Declaration of competing interest

MBA is an Advisory Board for PECON and was not involved in the editorial review or the decision to publish this article.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.pecon.2024.11.003.

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