

# Should small-ranged species always be prioritised for conservation?

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# Abstract

Alarming trend in biodiversity decline has been observed due to anthropogenic drivers, reinforcing the need to identify priority species for conservation. We discuss the prioritisation of species with small distribution sizes for conservation through two often-neglected perspectives: exposure to human-driven threats and importance to biodiversity. To evaluate species exposure, we estimated the amount of human pressure they encounter within their distribution ranges. To estimate their distinctive contributions to ecosystem functions and services, we calculated decreases in phylogenetic diversity after sequential species exclusion. We found that small-ranged species are not the most exposed to human-driven threats, as phylogenetic diversity is not always more affected by the loss of small-ranged species when compared to broad-ranged species. We propose conservation strategies to cope better with small-ranged species' vulnerability and to identify species with higher conservation needs. Under species high exposure to human-driven threats, conservation initiatives would benefit from distinguishing the causes of small range size. Conservation efforts on species whose distribution is mostly limited by abiotic suitability could focus on ecosystem management, while a focus on species management could be more adequate for species whose distribution is mostly limited by the accessibility. We also discuss the use of a response–effect framework to improve our capacity to identify species more negatively impacted by human-driven threats and with more distinctive effects on ecosystem processes. Small-ranged species should be prioritised for conservation when a negative correlation between species' ability to cope with environmental change and the distinctiveness of their effects on ecosystem processes is found.

## Introduction

Alarming trends in global biodiversity declines are known to be directly related to five anthropogenic drivers of biodiversity loss: land use change, direct exploitation, climate change, pollution, and invasive alien species (Díaz et al. 2019; Jaureguiberry et al. 2022). Maintaining biodiversity is of utmost importance due to its role in supporting ecosystem functions and services (Johnson et al. 2017; Díaz et al. 2019). However, this is not a trivial task given that species within different biomes and ecosystems are not affected to the same extent by above-mentioned human-driven threats (Bellard et al. 2022). The vulnerability of species to these threats largely depends on extrinsic and intrinsic factors to species, such as their exposure and how they cope with environmental changes (Dawson et al. 2011). Another challenge is that available resources for conservation initiatives are critically limited, making efforts to identify priority species for conservation a necessary practice (Cullen 2013).

It is widely agreed that species with smaller distribution range sizes must be prioritised for conservation (e.g. Broennimann et al. 2006; Saupe et al. 2015; Kraus et al. 2023). Smaller distribution ranges are seen as the result of a narrow niche breadth or an optimum related to uncommon set of resources and conditions in the landscape, combined with a lower capacity or time to disperse across disjunct patches where its optimum is found (Gaston 1996; Slatyer et al. 2013). That is, small-ranged species would have a low tolerance to environmental changes and are unlikely to track new suitable locations if their current

occurrence sites become unsuitable (i.e. higher sensitivity and lower adaptive capacity to environmental variability *sensu* Dawson et al. 2011). The corollary is that, when compared with broad-ranged species, small-ranged species are more vulnerable to environmental changes. However, this reasoning is true if, and only if, exposure of small-ranged species to human-driven threats exceeds their capacity to cope with environmental change if persisting in situ (Dawson et al. 2011). Yet, the exposure of small-ranged species to human-driven threats is poorly understood due to the focus of studies on other components of species vulnerability.

Another important line of reasoning is that the loss of small-ranged species may be more critical for biodiversity, as they may offer distinctive responses to environmental challenges and their contributions to ecosystem functions and services which are irreplaceable. For example, species with a distinctive evolutionary history (i.e. belonging to a species-poor clade in a phylogenetic tree) are expected to have evolved traits that confer them responses and effects on the environment that no other species have (Faith 1992; Winter et al. 2013; Cardillo 2023). This would increase the contribution of such species to local and regional phylogenetic and functional diversity when compared to species with higher phylogenetic and functional redundancy. The loss of these species may lead to the irreversible loss of particular ecosystem functions and represent a hazard to the stability of ecosystems, or of any ecological contexts they are found (i.e. the ability of a system to retain its function and structure in the face of perturbations; Van Meerbeek et al. 2021). To the best of our knowledge, no studies have investigated the importance of small-ranged species to biodiversity from the perspective of distinctive contributions to ecosystem functions and services. Recognizing possible distinctive contributions to biodiversity can significantly help to prioritise species for more efficient conservation strategies.

Desiccation-tolerant vascular plants (DT plants) are an opportune model system for discussing the conservation priority of small-ranged species since they are found in diverse clades in tracheophytes phylogeny and many species have a small range size. DT plants form a paraphyletic group of plants with the rare ability (among vascular plants) to lose up to 95% of their cellular water content and resume their metabolic activity when rehydrated (Oliver et al. 2000; Marks et al. 2021). Despite converging to tolerate desiccation (but see Bondi et al. 2023), DT plants form a very diverse group of plants concerning ecological and geographical aspects. While some species show a wider geographical occurrence and broader tolerance to environmental constraints (e.g. some DT ferns such as *Asplenium trichomanes* L., Polypodiaceae, which thrives in urban environments), many species display a more restricted distribution and narrower ecological niches (e.g. some DT seed plants such as *Barbacenia purpurea* Hook., Velloziaceae, which are only found in rock outcrops; Porembski 2021; Bondi et al. 2024). Besides, DT plants are greatly neglected for conservation (Porembski 2021), making studies that enable our capacity to identify species with higher needs for conservation timely and necessary.

In this study, we used DT plants to challenge the simplistic narrative that small-ranged species should be prioritised for conservation. For that, we evaluated the exposure of small-ranged species to human-driven threats and estimated their importance to the diversity scores in their ecological contexts from a phylogenetic perspective (please see Fig. S1 for more details). We tested the hypothesis that (i) small-

ranged species are more exposed to human-driven threats than broad-ranged species, and that (ii) phylogenetic diversity is more affected by the loss of small-ranged species than broad-ranged species. For that, we used occurrence records from all known DT plants and calculated their (a) distribution area as a proxy for their geographical range size. Then, we determined (b) the magnitude of human pressure within their distribution ranges to estimate exposure to human-driven threats. At last, we (c) simulated sequential species exclusion, from small-ranged to broad-ranged species, to quantify decreases in phylogenetic diversity in the global biomes they are found in to estimate their importance to biodiversity in their ecological contexts.

## Methods

### Distribution range sizes

In this study, we used the most updated global list of DT plants, provided by Bondi et al. (2024). In this list, 337 species, in which mature leaves were proven desiccation tolerant by existing literature, were ensembled using Tropicos taxonomic backbone (Tropicos.org 2023). In all our approaches, we split species into three major taxonomic groups: lycophytes, ferns, and seed plants (according to PPG I 2016). For each species we obtained occurrence records from botanical collections, sourced from three databases: (i) GBIF – Global Biodiversity Information Facility (GBIF.org 2023; Table S1), (ii) Tropicos, and (iii) Species Link (speciesLink network 2023). We removed duplicate, erroneous, or uncertain records using information from Plants of the World Online (POWO 2023). For occurrence records lacking geographical coordinates, we assigned the coordinates of the centroid of the closest municipality for the provided locality. To account for uneven sampling bias, we reduced multiple records for the same species within a 1 km radius to a single occurrence. This radius was chosen under the assumption that most species populations grow on isolated inselbergs, which are rock outcrops with island-like characteristics (Porembski 2021).

We used the resulting occurrence records to estimate the species distribution range sizes by calculating the area (in km<sup>2</sup>) of each species' distribution hypothesis. Lower values of distribution area denote smaller distribution range sizes. To generate the species' distribution hypothesis, we consider the 50% consensus from the species distribution model outputs of two distinct modelling approaches (Fig. 1, but see Fig. S2 for more details). Ideally, the first approach used was the Inverse Distance Weighted interpolation technique (IDW), which models the species distribution considering only the spatial arrangement of known occurrence points. The second approach applied was the Maximum Entropy technique (MaxEnt; Phillips et al. 2004), in which we model the species distribution considering the species' climatic niche. Here, we calibrated the MaxEnt models for each species using bioclimatic variables retrieved from Chelsa v2.1 database (Karger et al. 2017). To avoid overfitting, we selected the bioclimatic variables (out of the original 19; Table S2) that were not collinear (variation inflation factor < 10) and whose relative contribution, determined by a jackknife test, was higher than 5%. This was performed for each species individually.

To evaluate the accuracy of both modelling approaches, we calculated the Area Under the Receiver Operating Characteristic Curve (AUC) and True Skill Statistics (TSS) using k-fold cross-validation ( $k = 5$ ) with 100, 1000, or 10000 random background points, depending if the presence points were  $< 100$ , between 100 and 300, or  $> 300$  respectively (Barbet-Massin et al. 2012). Then, we ensembled five random cross-validation routines in which at least 50% consensus was reached between models that scored at least 0.8 and 0.6 for AUC and TSS, respectively. Lastly, the species distribution hypotheses were generated based on thresholds that optimized sensitivity and specificity (i.e. minimum omission rates for true positives and true negatives). The models were built using a spatial resolution of  $2^{\circ}30'' \times 2^{\circ}30''$ , extending the area  $5^{\circ}$  beyond the outermost occurrence points for each species.

The MaxEnt technique was chosen because of its capacity to predict suitable areas of occurrence for species with high reliability, even when sample sizes are small (Elith et al. 2011; Hernandez et al. 2006; Wisz et al. 2008; Yackulic et al. 2013). The IDW method was selected because it is a spatially-based approach that serves as an alternative to (and sometimes outperforms) niche-based models, like MaxEnt (Diniz-Filho et al. 2003; Pearson and Dawson 2003; Bahn and McGill 2007). When species occurrence records were lower than 5 points, we did not perform the above-described modelling approaches. Instead, we conducted the circular area approach with a buffer radius of 50 km ( $Ca_{50}$ ), as described by Hijmans and Spooner (2001). This method was chosen because it allows us to estimate the distribution range size of all DT plants, without neglecting rare or undersampled species in our analyses.

## Exposure of small-ranged species to human-driven threats

To estimate the exposure of species to human-driven threats, we quantified the magnitude of human pressure to which species are subjected within their distribution range. For that, we calculated the mean of the extracted grid values from the global map of human pressure (Bowler et al. 2020) in which the species is predicted to occur, according to our distribution hypotheses' boundaries. Although we recognise that the importance of threats to biodiversity is context-dependent (Bellard et al. 2022), we chose this approach because Bowler et al. (2020) attempted to encompass the main drivers of biodiversity change in a global scale and in a comparable manner. In their study, Bowler et al. (2020) used ranked values from 16 variables related to the 5 main anthropogenic drivers of biodiversity loss (land use change, direct exploitation, climate change, pollution, and invasive alien species; Díaz et al. 2019; Bellard et al. 2022; Jaureguiberry et al. 2022) to assess the cumulative human pressure as the additive resultant of human use, human population density, climate change, pollution, and alien potential (please note that land use change and direct exploitation are together depicted by human use). A higher cumulative human pressure would describe a higher exposure of species to human-driven threats. We evaluated the species' mean cumulative human pressure as a function of their distribution area in order to identify increases or decreases in species exposure to human-driven threats as a function of species distribution range size. After testing its assumptions, we conducted linear regression models for lycophytes and ferns, log-transforming species distribution area to satisfy the model assumptions. In

parallel, we ran a generalized least squares regression to angiosperms, log-transforming both variables. The generalized least squares method was chosen to allow heteroscedasticity among model residuals.

## Importance of small-ranged species to biodiversity

To estimate the importance of small-ranged species to diversity scores in their ecological contexts, we simulated sequential extinctions of species and quantified the decreases in phylogenetic diversity. Taking into account the spatial scale of this study, we used 14 WWF (Table S3) major terrestrial biomes to represent species ecological contexts under the assumption that biomes form a set of vegetation types associated with similar climatic conditions, which would contribute for their sharing taxonomic groups and vegetation physiognomy (Olson et al. 2001; Coutinho 2006). First, we assembled a list of DT plants found in each major biome. Then, we excluded one species at a time, from small-ranged to broad-ranged species, calculating the alpha phylogenetic diversity after each exclusion round. The sequential extinction of species proceeded until two species were left. Since phylogenetic diversity is sensitive to species richness, we compared the small-to-broad-ranged species extinction curves with null models for each major biome, in which species were randomly excluded in each exclusion round and the phylogenetic diversity was calculated. We repeated the random species extinction curves 99 times and calculated the mean phylogenetic diversity values for each exclusion round to construct the null models.

We then plotted the phylogenetic diversity as a function of sequential exclusion rounds, calculating the AUC for all species extinction curves. The AUC was used to compare the small-to-broad-ranged species extinction curves with the random species extinction curves. Lower AUC values for small-to-broad-ranged species extinction curves denote a higher decrease in phylogenetic diversity after the exclusion of small-ranged species than expected by chance. That is because a high decrease in phylogenetic diversity after the exclusion of small-ranged species causes the extinction curves to show a concave shape at initial exclusion rounds, decreasing the AUC values. Consequently, small-ranged species can be expected to have a greater importance to phylogenetic diversity. The opposite is also true. A low decrease in phylogenetic diversity after the exclusion of small-ranged species causes extinction curves to exhibit a convex shape at initial exclusion rounds, increasing the AUC values. Thus, lower AUC values for small-to-broad-ranged species extinction curves depict the existence of some degree of phylogenetic redundancy found by small-ranged species in a given biome. Due to the high number of polytomies for lycophytes used in this study, this taxonomic group was not considered for the exclusion simulations. The simulation of sequential species extinctions was only performed for biomes in which more than 10 species were reported.

We used the total branch length of the resulting phylogenetic trees to estimate the phylogenetic diversity (Faith 1992; Cardoso et al. 2015) and the phylogenetic hypothesis provided by Jin and Qian (2019) to construct every phylogenetic tree. We chose phylogenetic diversity to estimate the importance of small-ranged species to the diversity scores under the assumption that closely related species are expected to assemble ecologically rather than distantly related ones (Faith 1992; Winter et al. 2013; Cardillo 2023). In this way, this metric is also supposed to describe how distinct are species regarding their responses to

environmental challenges and how distinctive are their contributions to ecosystem functions and services, besides the evolutionary potential in the given ecological context.

All modelling routines, statistical analyses, and graphical representations were conducted in R software (R Core Team 2024; Table S4).

## Results

Species varied in 4 orders of magnitude in relation to their distribution range size (Table S5). While *Micraira spinifera* (Poaceae), an endemic species from Australia, exhibited the smallest distribution range size (1273 km<sup>2</sup>), the widespread *Microchloa indica* (Poaceae) showed the biggest distribution area (15839389 km<sup>2</sup>). We did not include *Tripogon polyanthus* (Poaceae) in our analyses because no valid occurrence points could be found for this species.

## Exposure to human-driven threats

Three species showed no human pressure within their occurrence ranges: the South American species *Blossfeldia liliputana* (Cactaceae) and *Barbaceniopsis humahuquensis* (Velloziaceae), and the African species *Xerophyta eglandulosa* (Velloziaceae). In contrast, the species *Oropetium roxburghianum* (Poaceae), native from India and West Himalaya (POWO, 2023), showed the highest score of mean human pressure among all DT plants (5.42 ± 0.029).

A significant relationship between species distribution range size and exposure to human-driven threats was just existent for lycophytes, where broad-ranged species are more exposed to human pressures (Table 1; Fig. 2). We did not find any trend relating to small-ranged ferns and seed plants with higher or lower exposure to direct and indirect effects of human activities.

Table 1  
Summary of the relationship between species distribution range size and exposure to human-driven threats (including land use change, direct exploitation, climate change, pollution, and invasive alien species). Species were grouped in lycophytes, ferns, and seed plants. While linear models were conducted for lycophytes and ferns, generalized least squares were conducted to seed plants.

|             | Intercept | slope  | F/t-statistics | p-value |
|-------------|-----------|--------|----------------|---------|
| Lycophytes  | -0.478    | 0.362  | 4.370          | 0.0002  |
| Ferns       | 4.720     | -0.001 | -0.020         | 0.9840  |
| Seed plants | 0.009     | -0.143 | 0.213          | 0.8311  |

## Importance of small-ranged species to biodiversity

We found species in all global major biomes, except for Mangrove. Tropical and subtropical moist broadleaf forests was the biome with highest DT plants species richness (240 species). Among species, 19 species were endemic from a biome. While *Borya inopinata* (Boryaceae), *Craterostigma lanceolatum* (Linderniaceae), *Lindernia monroi* (Linderniaceae), *Micraira lazaridis* (Poaceae), *Micraira multinervia* (Poaceae), *Micraira spinifera* (Poaceae), *Micraira tenuis* (Poaceae), *Micraira viscidula* (Poaceae), and *Vellozia ciliata* (Velloziaceae) were endemic to Tropical and subtropical grasslands, savannas, and shrublands; *Oreocharis mileensis* (Gesneriaceae), *Eragrostiella brachyphylla* (Poaceae), *Loxogramme lanceolata* (Polypodiaceae), *Actiniopteris australis* (Pteridaceae), *Barbacenia fanniae* (Velloziaceae), *Xerophyta eglandulosa* (Velloziaceae), and *Xerophyta nandrasanae* (Velloziaceae) were endemic to Tropical and subtropical moist broadleaf forests; *Craterostigma wilmsii* (Linderniaceae) and *Xerophyta viscosa* (Velloziaceae) endemic to Montane grasslands and shrublands; and *Lindernia intrepidus* (Linderniaceae) endemic to Deserts and xeric shrublands. On the other hand, *Asplenium adiantum-nigrum* (Aspleniaceae) was recorded in all 13 biomes (excluding Mangrove).

The importance of small-ranged species to biodiversity varied depending on the major biome and taxonomic group. The small-to-broad-ranged species extinction curves yielded lower AUC values compared to random species extinction curves in nearly all biomes for ferns (9 out of 11 biomes; Table 2; Fig. 3a). Lower AUC curves in those biomes can be interpreted as a higher contribution of small-ranged species phylogenetic diversity. The opposite pattern was found for seed plants. Small-to-broad-ranged species extinction curves exhibited higher AUC values than random species extinction curves in most biomes (6 out of 8 biomes; Table 2; Fig. 3b), which suggests a higher phylogenetic redundancy of small-ranged seed plants.

Table 2

Area under the curve (AUC) for species extinction curves in which species were sequentially excluded from small-ranged to broad-ranged species (small-ranged) and for species extinction curves in which species were randomly excluded (null models). The species extinction curves consisted of changes in phylogenetic diversity as a function of sequential species exclusion. This procedure was repeated for each major terrestrial biome, and species were grouped as ferns and seed plants. TM - Tropical and subtropical moist broadleaf forests; TD - Tropical and subtropical dry broadleaf forests; TC - Tropical and subtropical coniferous forests; MB - Temperate broadleaf and mixed forests; MC - Temperate coniferous forests; BF - Boreal forests/taiga; TS - Tropical and subtropical grasslands, savannas, and shrublands; MS - Temperate grasslands, savannas, and shrublands; FS - Flooded grasslands and savannas; MG - Montane grasslands and shrublands; TU – Tundra; MF - Mediterranean forests, woodlands, and scrub or sclerophyll forests; DX - Deserts and xeric shrublands; MA – Mangrove.

| Ferns  |                  |                |               | Seed plants      |                |               |
|--------|------------------|----------------|---------------|------------------|----------------|---------------|
| Biomes | Species richness | AUC            | AUC           | Species richness | AUC            | AUC           |
|        |                  | (small-ranged) | (null models) |                  | (small-ranged) | (null models) |
| TM     | 130              | 5554           | 5659          | 110              | 6833           | 6070          |
| TD     | 108              | 5729           | 5715          | 36               | 5810           | 5670          |
| TC     | 64               | 5620           | 5695          | 8                | 6927           | 5082          |
| MB     | 58               | 4743           | 5497          | 18               | 5558           | 5623          |
| MC     | 51               | 5375           | 5401          | 9                | 6083           | 5997          |
| BF     | 9                | 3765           | 5219          | -                | -              | -             |
| TS     | 109              | 5589           | 5727          | 104              | 6900           | 6104          |
| MS     | 67               | 4933           | 5491          | 5                | 5537           | 5096          |
| FS     | 87               | 5583           | 5764          | 32               | 6337           | 6081          |
| MG     | 118              | 5352           | 5657          | 50               | 6478           | 5955          |
| TU     | 8                | 4463           | 5202          | -                | -              | -             |
| MF     | 60               | 5000           | 5519          | 14               | 4836           | 6418          |
| DX     | 135              | 5448           | 5598          | 55               | 6727           | 6264          |
| MA     | 0                | -              | -             | 0                | -              | -             |

## Discussion

Our findings do not support the view that small-ranged species should always be prioritised for conservation. We found that small-ranged species are not more exposed to human-driven threats than broad-ranged species. Since species exposure to threats is an important component of species vulnerability to environmental change (Dawson et al. 2011), our view is that species range size alone is

insufficient evidence to prioritise species for conservation. This perception agrees with existing conservation initiatives that recommend multiple lines of evidence to judge species threatened with extinction (e.g. IUCN's criteria B; IUCN Standards and Petitions Committee 2024). It does not mean that attention to the conservation of small-ranged species is unjustifiable, especially if we accept the premise that these species have a lower ability to cope with changes when compared to broad-ranged species (i.e. high sensitivity and low adaptive capacity to environmental changes). We first suggest that scientists and policymakers critically evaluate the sensitivity and adaptive capacity of small-ranged species to environmental change, while their exposure to changes is closely monitored. In case of increased vulnerability (i.e. higher exposure to human-driven threats), we believe that conservation strategies would benefit from distinguishing the causes of the species' small distribution range size. If the species distribution is mostly limited by abiotic suitability, species would be more sensitive to changes and conservation efforts could mainly focus on the ecosystem. If the species distribution is mostly limited by the accessibility to suitable habitats, species would have lower adaptive capacity and conservation efforts could mainly focus on the species' populations. By adopting such reasoning, we believe conservation efforts are likely to be more efficient because they would be based on the species' conservation needs.

Phylogenetic diversity is not always more affected by the loss of small-ranged species when compared to the loss of broad-ranged species. While small-ranged ferns showed a higher contribution to phylogenetic diversity in most biomes, the loss of small-ranged seed plants had a reduced impact on the phylogenetic diversity of most biomes. Thus, the species distribution range size alone is not enough evidence for conservation strategies that seek to prioritise species with distinctive contributions to ecosystem functions and services. We believe that conservation strategies would benefit from a more straightforward functional approach that integrates the response of species to environmental changes and their distinctive effects on the ecosystem. For instance, a negative correlation between species' ability to cope with environmental change and the distinctiveness of their effects on ecosystem processes would allow us to identify species that are, at the same time, more negatively affected by human-driven threats and have distinctive contributions to ecosystem functions and services. This would allow us to identify, for example, situations in which small-ranged species should be prioritised for conservation, when they are the species most affected by environmental changes.

### **Understanding the causes of small distribution range size is essential to ensure more efficient conservation strategies**

Our results did not support our hypothesis that small-ranged species are more exposed to human-driven treatments than broad-ranged species. Instead, in the only major taxonomic group in which a significant correlation was found (lycophytes), species with a broader distribution range were more exposed to human-driven threats than species with a smaller distribution range. Yet, it could still be argued that small-ranged species are a good starting point for more refined species conservation assessments. Small-ranged species are expected to have small population sizes (Brown 1984; Lawton 1993; Johnson 1998), which places them close to critical abundance thresholds to maintain viable populations (due to

the Allee effect; Stephens et al. 1999; Chen and Hui 2009). This can be considered enough reason to consider small-ranged species in conservation initiatives. Besides, due to their higher sensitivity and lower adaptive capacity, even minor changes in environmental conditions could exceed small-ranged species' capacity to cope with changes. Under low exposure to human-driven threats, small-ranged species should be closely monitored. However, under higher exposure, we believe that disentangling the causes for small distribution range sizes could help us to better understand their sensitivity and adaptive capacity to human-driven changes and to tailor more efficient conservation strategies. We base our reasoning on two widely accepted conceptual frameworks, as explained below.

The first is the BAM (B – biotic, A – abiotic, M – movement or accessibility) framework from Soberón and Peterson (2005) for understanding species' geographical distribution as a result of the interplay of different processes. Soberón and Peterson (2005) employ a Venn diagram composed of the abovementioned 3 elements (B, A, and M) to show that the stable occurrence of a species is only observed in locations that are abiotically and biotically suitable and spatially accessible. That is, the intersection area between B, A, and M would represent the actual distribution of species, while the intersection between only B and A would describe suitable areas for the species occurrence but not accessible (please see Fig. 1 from Soberón and Peterson, 2005). The second is the vulnerability framework of Dawson et al. (2011) for understanding species vulnerability to environmental changes through its different components. Dawson et al. (2011) show that a species is only found vulnerable to environmental changes if it is exposed, sensitive, and has a low adaptive capacity to cope with changes. According to the authors, conservation efforts must vary from minimal interventions with low-level monitoring to direct, targeted, and intensive interventions as species are more exposed (and have more barriers to dispersal), and exhibit higher sensitivity and lower adaptive capacity (please see Fig. 3 from Dawson et al. 2011).

Neglecting the importance of biotic interactions for now, the distribution of a small-ranged species can be caused by factors limiting their abiotic suitability and/or the accessibility to suitable habitats (Fig. 4). Species are limited by abiotic suitability when they exhibit a narrow niche breadth or when suitable abiotic conditions are rare across the landscape (Soberón and Peterson 2005). Alternatively, a species is limited by the accessibility to suitable habitats when it fails to disperse to suitable locations or when the evolutionary time was not sufficient to allow the species to spread across the space (Soberón and Peterson 2005). This distinction leads to different interpretations of species vulnerability. If the species is mostly constrained by abiotic suitability, it can be expected to be more sensitive to changes. If the species is mostly constrained by its dispersal limitation, it can be expected to have a lower adaptive capacity and be more likely to encounter barriers to dispersal owing to habitat fragmentation. We argue that, if policymakers are aware of the main causes of species' small range size (and therefore whether small-ranged species are mostly vulnerable by their sensitivity or adaptive capacity), we could draw more efficient conservation strategies because they would be based on the species conservation needs.

Conservation efforts on any small-ranged species mostly constrained by abiotic suitability could mainly focus on the ecosystem to secure prevailing conditions as close as possible to their original states or to

ensure that species will be able to find new suitable areas for occurrence via their natural dispersal mechanisms (e.g. habitat and landscape management). The challenges to preserve prevailing conditions vary according to the anthropogenic driver in question. For example, protection areas could be more effective in reducing exposure to land use change than in preventing the negative effects of climate change (Díaz et al. 2019; although they contribute to reducing further shifts in climate; Duncanson et al. 2023). To mitigate the negative effects of climate change on species mostly constrained by abiotic suitability, scientists and policymakers should consider the connectivity between protection areas (e.g. Dobrowski et al. 2021), since these species are (in theory) able to track new suitable habitats and new suitable areas might arise in currently unsuitable locations (e.g. Franklin et al. 2016, Ohlemüller et al. 2008).

On the other hand, conservation actions on species mostly constrained by their dispersal limitation could thoroughly consider active interventions focused on the species' populations to ensure that species will be able to find new suitable areas for occurrence (e.g. assisted migration or translocation). A priori, species mostly constrained by their dispersal limitation are less sensitive to environmental changes. So, such interventions are mostly necessary if we cannot reverse or reduce the environmental changes. It is noteworthy to mention that studies are still necessary, not only to effectively identify areas suitable but not accessible (e.g. Elliott et al. 2024), as to also to better understand the impact of the intentional introduction of species in new ecological contexts (e.g. measuring the effect of interactions on the response of other species in the presence of new arrivals; Dehling and Stouffer 2018). For instance, the biotic component, despite being often neglected (Rosado et al. 2016), is also a determinant of species occurrence (Soberón and Peterson 2005) and can determine the success of conservation initiatives.

Some other aspects must be considered by scientists and policymakers. First, the vulnerability of species might change with the context. If small-ranged species have a lower ability to cope with changes (i.e. high sensitivity and low adaptive capacity to environmental changes) and are similarly exposed to them, we can expect them to be more vulnerable than coexisting broad-ranged species in a local context. Second, it is likely that small-ranged species are constrained by both abiotic suitability and dispersal limitation (Gaston 1996). In this case, more attention to changes in exposure is necessary to anticipate possible extirpations (and extinctions) of species that already have high sensitivity and low adaptive capacity to changes. Third, the pace of environmental changes might be higher than the time needed for a species to move (Dawson et al. 2011). This is even more special when we consider the increasing fragmentation of habitats worldwide (Andrén 1997; Collingham and Huntley 2000). That means that even small-ranged species that have not been historically constrained by dispersal limitation are likely to show lower adaptive capacity in the face of changes. Finally, scientists and policymakers must keep in mind that global drivers of biodiversity loss might interact synergistically, which can amplify their impacts (Bowler et al. 2020; Bellard et al. 2022; Jaureguiberry et al. 2022). This makes conservation assessments more challenging and reinforces the need to move beyond simplistic conservation strategies (Bellard et al. 2022).

## **The integration of species' responses to environmental changes and their distinctive effects on the ecosystem can improve conservation strategies**

Our results did not support the hypothesis that phylogenetic diversity is more affected by the loss of small-ranged species than broad-ranged species. Thus, based on the perspective that species with distinctive contributions to ecosystem functions and services are of utmost concern for conservation, we infer that small-ranged species may not necessarily be prioritised for conservation. This view is corroborated by our results that small-ranged species are not necessarily more exposed to human-driven changes. Yet, small-ranged species may, at the same time, be found vulnerable to human-driven threats and have distinctive contributions to ecosystem functions and services. It is crucial that scientists and policymakers are aware of such occasions. Understanding species' phylogenetic relationships is useful for identifying distinct evolutionary pathways that can lead to distinctive ways species respond to and affect their environment (Faith 1992 Winter et al. 2013). However, it has limited use for evaluating possible correlations between species' responses to environmental changes and their effects on the ecosystem. We believe that a functional approach is more adequate to integrate aspects of species vulnerability and their influence on ecosystem processes. We use a trait-based response-effect framework to support our view, as explained below.

Suding et al. (2008) proposed a framework to improve our capacity to predict how species respond to environmental changes and how changes in a community can affect ecosystem functioning. In this framework, species in a community are grouped in *response groups*, based on their similar responses to the environment, and *effect groups*, based on their similar contributions to ecosystem function. Species from the same response group are supposed to be affected by environmental changes in a similar way. If species from this response group are also clustered in the same effect group, environmental changes that promote the loss of these species would also lead to the loss of the ecosystem functions supported by them (Suding et al. 2008). For example, a set of species in a community are grouped together in the same response group and in the same effect group. A human-driven threat that leads to the exclusion of the response group they belong to might also result in the complete loss of function the effect group they belong to can provide. Situations such as the previous example would be more critical to the community if the ability of species to cope with environmental change is negatively correlated with the strength of species' effects on ecosystem processes. For instance, a community would be more negatively affected by human-driven threats if the species from the response group with the lower ability to cope with environmental changes were also the ones with a higher contribution to ecosystem functions and services (please see Fig. 2 from Suding et al. 2008).

In their framework, Suding et al. (2008) propose the use of species abundance to estimate the strength of species' effects on ecosystem processes (due to the mass-ratio hypothesis; Grime 1998). However, small-ranged species are likely to have small abundances (Brown 1984; Lawton, 1993). At the same time that smaller abundances can increase small-ranged species extinction risks (Johnson 1998), it would also decrease the strength of their effects on ecosystem processes. Thus, we propose a small alteration to the trait-based response-effect framework. Instead of discussing the strength of species' effects on

ecosystem processes, we believe we should focus on the distinctive contributions to ecosystem functions and services to better understand the importance of small-ranged species. Here, for simplification, we assume that all species in a community are subject to roughly the same magnitude of environmental change, although small-ranged species would be more negatively affected by human-driven threats (i.e. small-ranged species would be grouped in the same response group, with more negative responses to changes). Then, a negative correlation between species' ability to cope with environmental change and the distinctiveness of their effect on ecosystem processes would depict situations in which the loss of small-ranged species would be more critical to the community (Fig. 5).

Using our adapted response–effect framework, scientists and policymakers would also be able to identify situations in which small-ranged species are not necessarily the ones to be prioritised for conservation. For example, if species' ability to cope with environmental change increases as the distinctiveness of their effects increase (i.e. positive correlation between response and effect), small-ranged species might be found functionally redundant in the community (i.e. their contributions can be performed by other species; Buisson et al. 2013). It does not mean that they are dispensable, as species are hardly redundant in every aspect and functional redundancy promotes greater resilience to disturbances and higher stability in ecological functions (Walker 1995; Biggs et al. 2020). Yet, scientists and policymakers might opt for the prioritisation of species with lower functional redundancy because their extinction would represent a complete loss of important ecosystem functions and services (Walker 1995). Alternatively, the absence of correlation between species' ability to cope with environmental change and distinctiveness of their contribution to ecosystem processes might indicate that species distribution range size is not a good indicator of species prioritisation for conservation. In this case, some small-ranged species might show a more distinctive contribution to ecosystem functions and services, while others might be found functionally redundant. Yet, it is to test the assumption of lower ability of small-ranged to cope with environmental change, as whether small-ranged species are to be grouped in the same response group or not.

We also suggest disentangling “distinctive contributions” in a functional diversity context. Species can show a distinctive contribution to ecosystem processes by diverging from average contributions to ecosystem function (depicted by functional originality) or by diverging from other species' contributions in the community (described by functional uniqueness; please see Fig. 1 from Buisson et al. 2013; Pavoine et al. 2017). For example, in a community where soil retention by species' root systems is low, a species can be distinct by exhibiting a high soil retention (functionally original) or by showing soil retention levels that no other species in the community have (functionally unique). In both situations, a higher diversity of ecosystem functions and services is achieved, but from different mechanisms. For instance, functional originality is likely to be related to phylogenetic distinctiveness (i.e. isolation level of clades in a phylogenetic tree) and can describe species that enlarge the functional space of a community (Buisson et al. 2013; Pavoine et al. 2017). On the other hand, functional uniqueness can be a better metric to evaluate species' functional redundancy in a community (Buisson et al. 2013). We should not discard the possibility of a species having both original and unique contributions to

ecosystem processes (Buisson et al. 2013), as it should be interpreted as complementary lines of evidence for the conservation of species.

In our study, we showed that small-ranged ferns from most biomes originate from distinct phylogenetic clades. However, in our study design, we cannot infer whether the contribution of these species to ecosystem processes in these biomes is either or both original and unique. We believe such questions could be answered when applying our adapted response–effect framework. It is also noteworthy to mention that, as highlighted by Suding et al. (2008), scientists and policymakers must be aware of the many factors that might reduce the predictability of this framework. Factors such as emergent properties, ecosystem feedbacks, and time lags in the effects of environmental changes on the community should also be considered for more efficient conservation strategies.

## Declarations

## Author Contribution

T. G. and L. B. conceived the idea and wrote the manuscript; L. B. and B. P.-M. collected and analyzed the data. All authors contributed critically to the drafts and gave final approval for publication.

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## Data Availability

Data is provided within the manuscript or supplementary information files.

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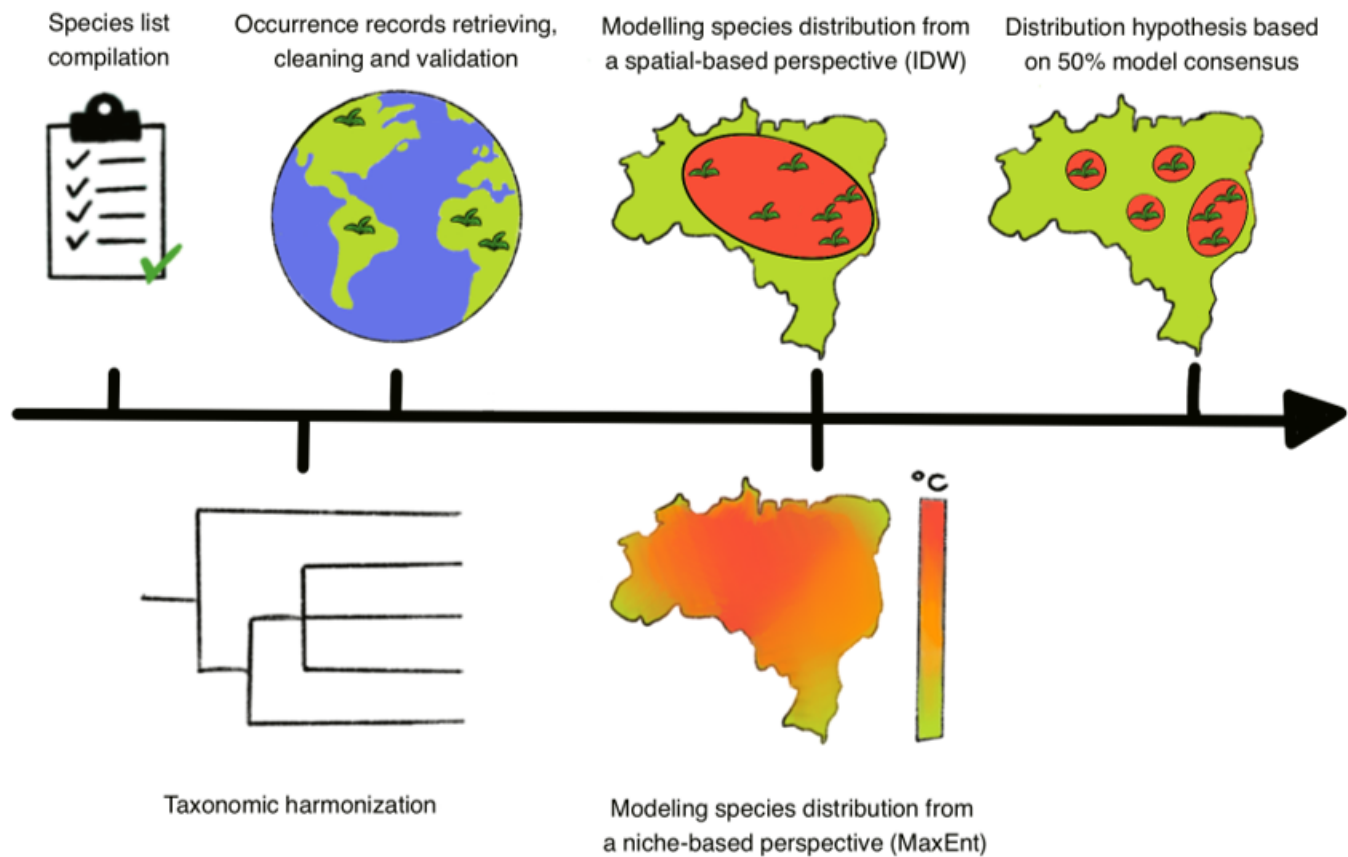
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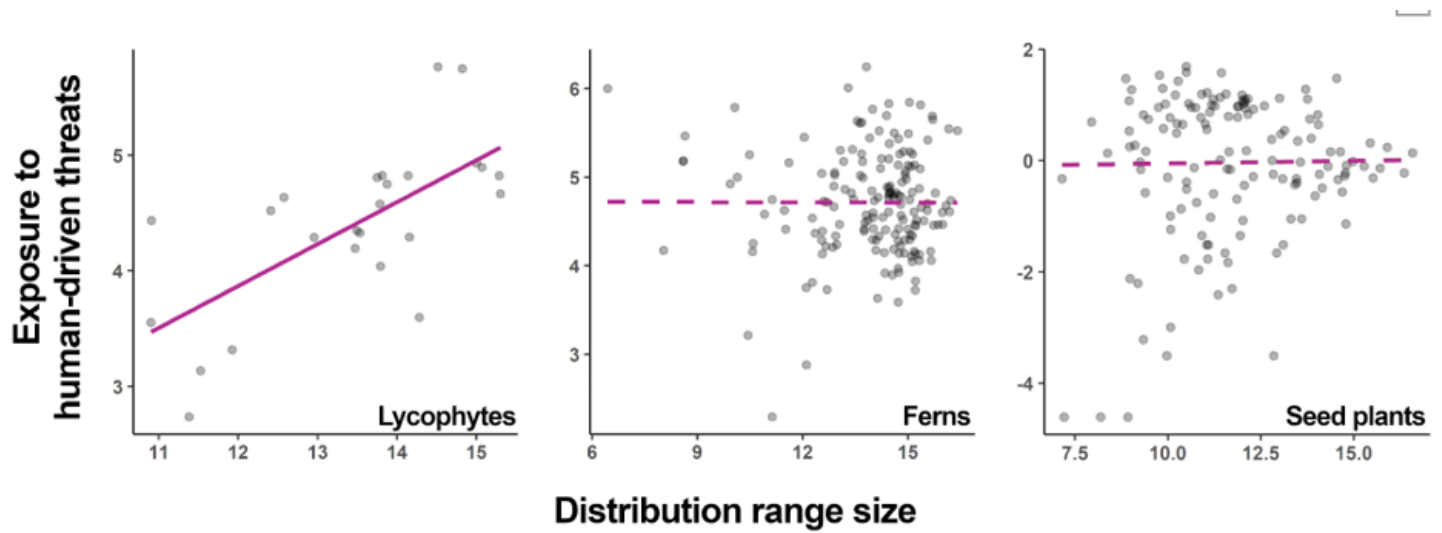
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## Figures



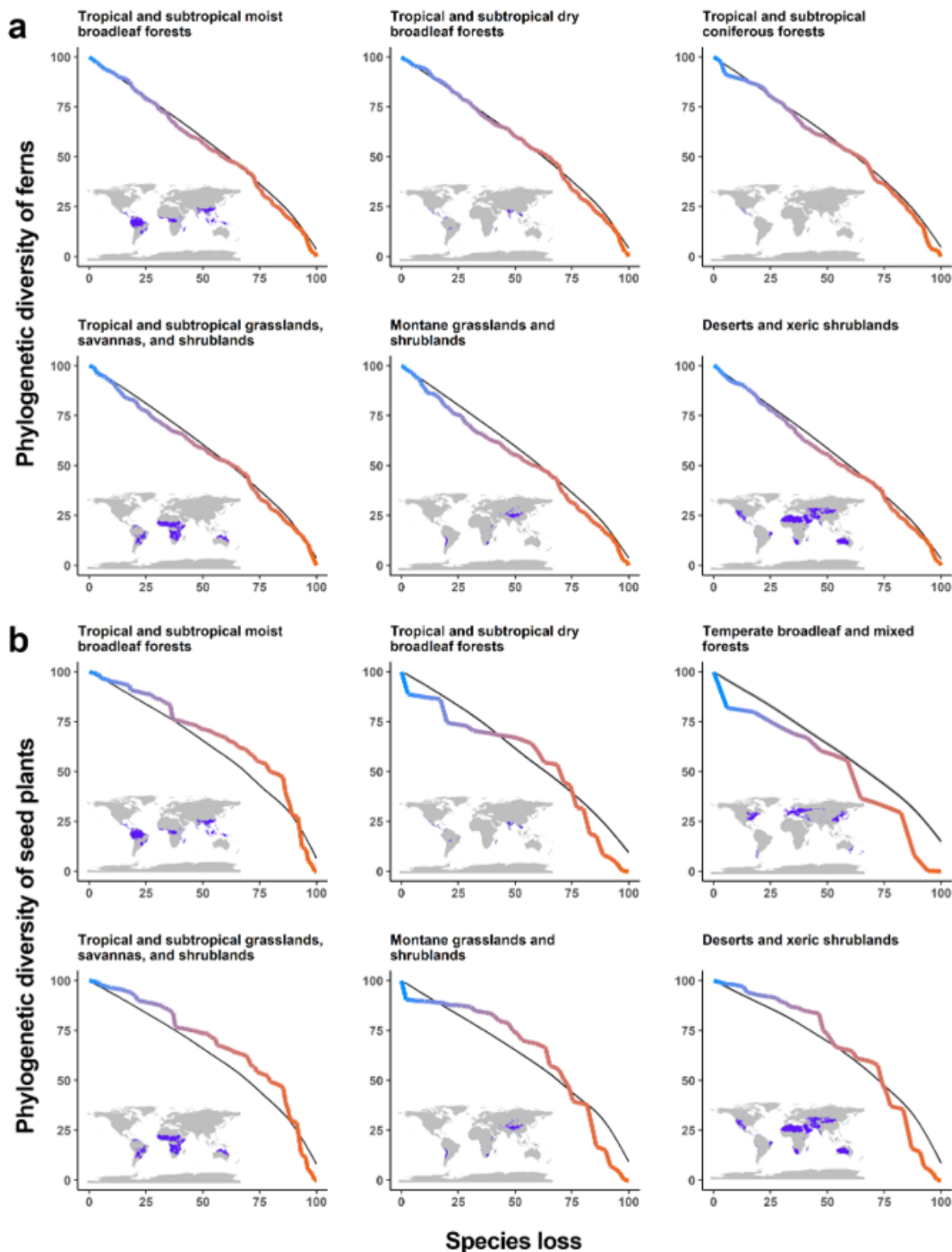
**Figure 1**

Methodological workflow to obtain species distribution hypotheses, used to calculate species distribution range size. IDW and MaxEnt stand for the Inverse Distance Weighted interpolation technique and the Maximum Entropy techniques.



**Figure 2**

Exposure of species to human-driven threats (including land use change, direct exploitation, climate change, pollution, and invasive alien species) as a function of species distribution range size. Species were grouped as lycophytes, ferns, and seed plants, and values for species distribution range size were log-transformed to all species. Exposure values were log-transformed only to angiosperms in order to reduce the variability of residuals for this group of species. Solid lines represent significant and dashed lines non-significant relationships.



**Figure 3**

Changes in phylogenetic diversity as a function of sequential species exclusion (species loss) in the six richest biomes in (a) ferns and (b) seed plant species. Colourful curves denote species extinction curves in which species were sequentially excluded from small-ranged to broad-ranged species, while black curves represent null models in which species were randomly excluded. Both variables were standardized to the same magnitude of variation.

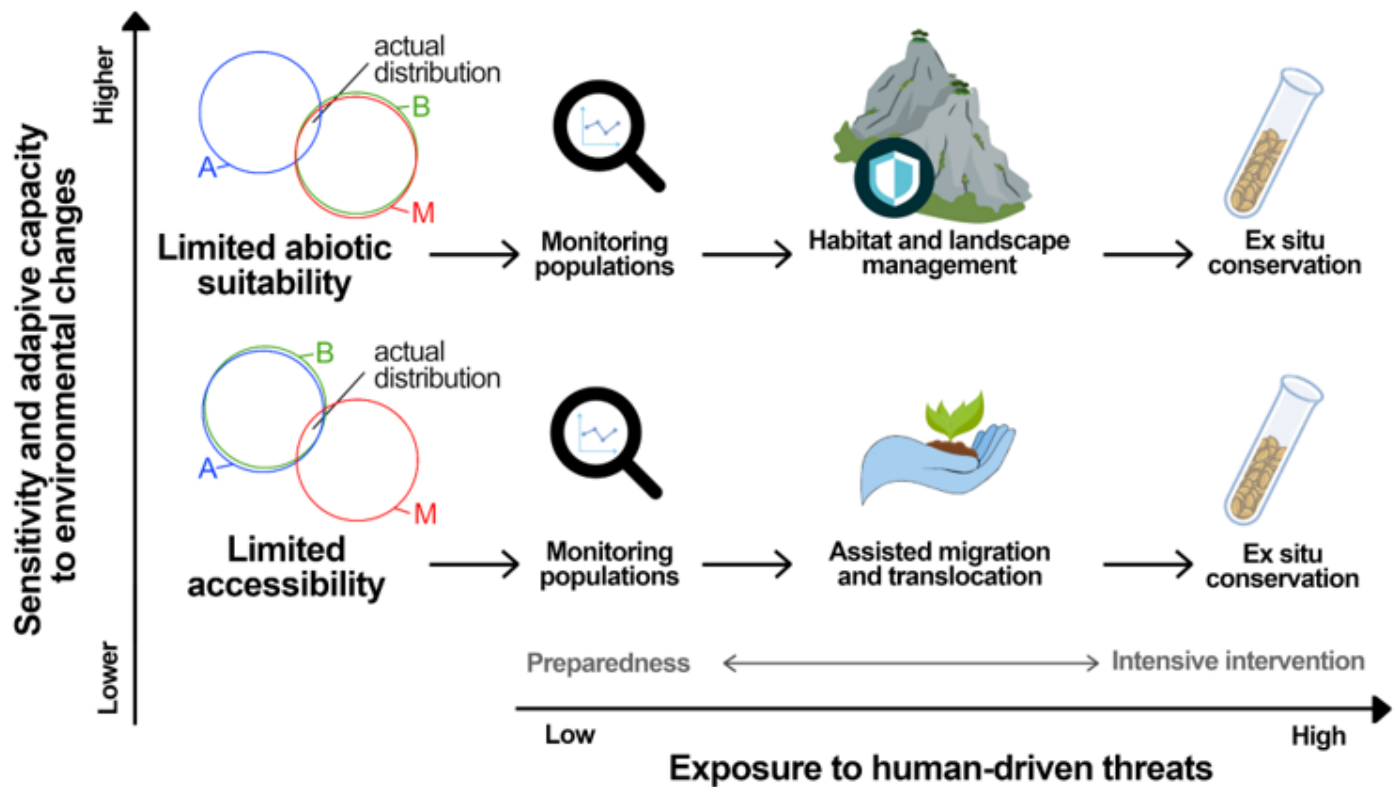
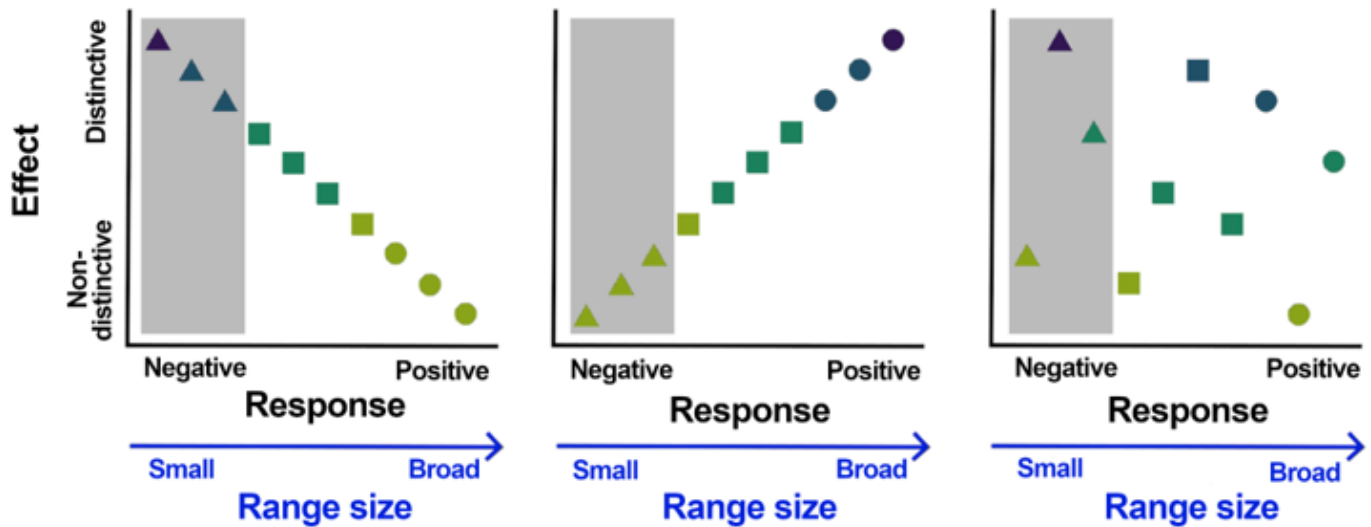


Figure 4

Alternative conservation strategies for small-ranged species based on the BAM (B – biotic, A – abiotic, M – movement or accessibility) framework from Soberón and Peterson (2005) and the vulnerability framework from Dawson et al. (2011). Under low exposure to human-driven threats, small-ranged species should be monitored due to their higher sensitivity and lower adaptive capacity when compared to broad-ranged species. Under higher exposure to changes, more intensive interventions must take into account the causes of species' small distribution range size. If the species distribution is mostly limited by abiotic suitability, we could assume that the species is more sensitive to changes but has a higher adaptive capacity. For such species, we recommend conservation efforts focused on the ecosystem, such as habitat and landscape management. If the species distribution is mostly limited by the accessibility to suitable habitats, we could assume that the species has a lower adaptive capacity but is less sensitive to changes. For such species, we recommend conservation efforts focused on the species, such as assisted migration and translocation.



**Figure 5**

Adapted trait-based response-effect framework from Suding et al. (2008) to identify priority species for conservation according to their response and distinctive effect on ecosystem processes. Shapes denote response groups, while colours depict effect groups. The grey rectangles represent species with a higher risk of local extinction due to their negative responses to human-driven threats. Here, we assume that small-ranged species are more negatively impacted by human-driven threats and are clustered in the response group. Then, small-ranged species should be prioritised for conservation when a negative correlation between species' ability to cope with environmental change and the distinctiveness of their effects on ecosystem processes is found. Alternatively, small-ranged species are not necessarily the ones to be prioritised for conservation if a positive or non-significant correlation between species' ability to cope with environmental change and the distinctiveness of their effects on ecosystem processes is found. That is because, under the perspective that species with distinctive contributions to ecosystem functions and services are of utmost concern for conservation, small-ranged species might be functionally redundant in the community.

## Supplementary Files

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