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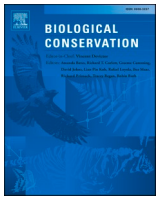
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Selecting umbrella species as mammal biodiversity indicators in tropical forest

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ABSTRACT

Conservation managers often monitor umbrella species as indicators of broader biodiversity patterns, but this assumption is seldom evaluated due to lack of survey data and objective umbrella criteria. We evaluated the performance of eight candidate umbrella species in representing broader patterns of mammal biodiversity in Sumatra, Indonesia, using a comprehensive camera trap dataset from the island's largest remaining tropical rainforest. We employed an occupancy modeling framework to quantify the association between species-level occupancy and four community-level biodiversity parameters while accounting for imperfect detection. Sambar deer and clouded leopard were consistently ranked the top umbrellas. Areas where these species were prevalent were associated with higher levels of community occupancy, species richness, functional and phylogenetic diversity. Sumatran tiger and rhino were among the lower ranked umbrellas, and inadequately represented other biodiversity parameters despite being the main subjects of monitoring. Our results demonstrate that the occurrence status of charismatic species commonly regarded as umbrellas does not necessarily represent broader patterns of biodiversity. Species that are frequently overlooked by conservation decision-making may better represent overall mammal diversity. We advocate utilizing umbrella fleets with multiple species monitored to better represent biodiversity patterns, and encourage broader application of our data-driven framework to assess umbrella species performance.

1. Introduction

Safeguarding biodiversity is an overarching conservation goal, but in reality, limited resources place constraints on the scale and extent of species protection (Allan et al., 2019; Sitas et al., 2009). Threats to biodiversity are especially profound in tropical regions where human activities have led to a contraction of terrestrial mammal distributions by >40 % since the 1990s (Gallego-Zamorano et al., 2020). To overcome this issue, conservation managers often focus on umbrella species, assuming that prioritizing, protecting, and monitoring a single (e.g. Drever et al., 2019; Thornton et al., 2016) or small number of species (e.g. Maslo et al., 2016; Steenweg et al., 2023) will benefit other co-occurring taxa. In monitoring programs, umbrella species are often used as proxies for broader patterns of biodiversity without the need to acquire and analyze data for the entire community (Caro, 2010). The use of umbrella species in this way, if proven representative, should lead to efficiencies and cost savings in ecological monitoring and conservation programs.

The umbrella concept assumes the presence of certain species – usually wide-ranging ones with large area requirements – is co-distributed with other taxa (Caro, 2010). Despite being a fundamental tool in wildlife monitoring, the reliability of the umbrella species approach is uncertain since there is limited quantitative evaluation of species performance to reflect overall patterns of biodiversity (Steenweg et al., 2023; Thornton et al., 2016). For example, large-bodied charismatic species (generally mammals) are typically selected as umbrellas based on public interest or their capacity to generate conservation funding, rather than an underlying correlation between their distributions and those of other taxa (Caro, 2010; Di Minin and Moilanen, 2014; McGowan et al., 2020). Moreover, umbrella species assessment is often

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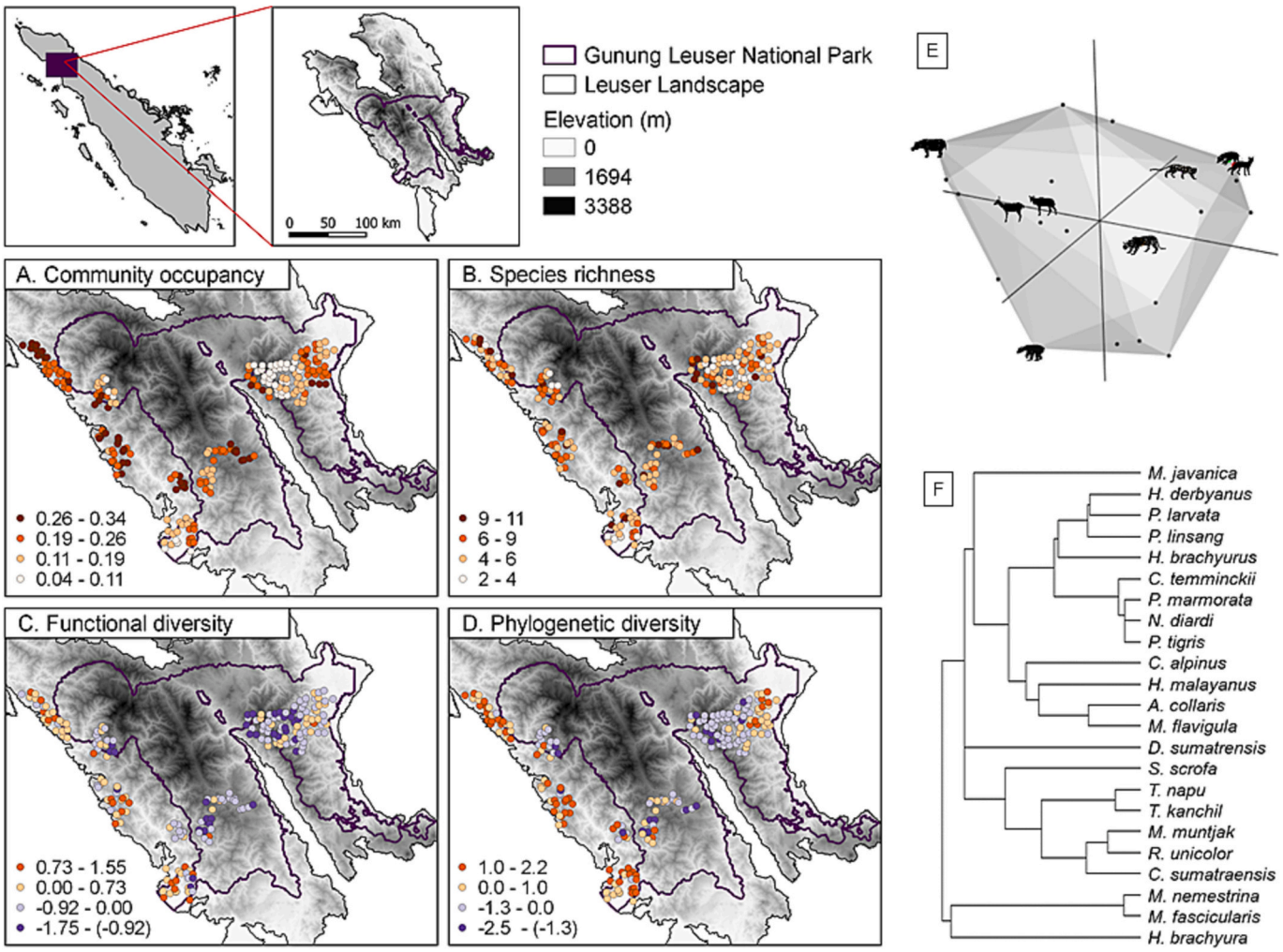


Fig. 1. (A-D) Distribution of mammal biodiversity parameter values across 212 camera sites in Leuser Ecosystem, Sumatra. Values in legends are divided into four categories based on their quartiles. The upper quartile represents the top 25 % values. Negative values of FD and PD (light-deep purple) indicates functional and phylogenetic clustering. (E) Trait space occupied by mammal species in Leuser. Grey areas represent the first three axes used to calculate functional diversity metric. Species positions represented by black points while umbrella species illustrated by icons. (F) Phylogenetic tree (unweighted by detection-corrected matrix) informing the relationship between species in the community.

hampered by insufficient data due to the high cost of monitoring programs in terms of data acquisition and analysis, as well as difficulties in evaluating the status of cryptic and elusive species (Wearn and Glover-Kapfer, 2019). This is exacerbated by approaches that generate data for single or selected species, while ignoring the broader wildlife community (Chaudhary et al., 2022; Lindenmayer and Likens, 2011).

An additional constraint to identifying umbrella species is that most assessments focus on a single biodiversity parameter such as species richness – i.e. the number of species in the community (Drever et al., 2019; Thornton et al., 2016). However, richness can be a misleading biodiversity parameter because it does not account for species identity or distinguish between native and non-native species. Other important biodiversity parameters, such as functional and phylogenetic diversity, are often overlooked (Jarzyna and Jetz, 2016). Functional diversity (FD) informs wildlife community functional uniqueness and trait distribution patterns (Laliberte and Legendre, 2010), while phylogenetic diversity (PD) accounts for community evolutionary history and relationship patterns (Winter et al., 2013). These parameters have important roles in the biological community e.g. the loss of species with important ecological roles can trigger cascading ecological impacts and the extinction of evolutionarily-distinct species extirpates millions of years of evolutionary information (Brum et al., 2017). Measures of functional or phylogenetic diversity are increasingly used to account for the community resilience towards environmental change and anthropogenic disturbances (Gorczynski et al., 2021; Penjor et al., 2022) and to inform conservation priorities (Brum et al., 2017; Rapacciuolo et al., 2019). Yet they are rarely considered in conservation decision making at local level.

Few umbrella evaluations have explicitly accounted for imperfect detection (e.g. Mortelliti et al., 2022; Steenweg et al., 2023), which can cause substantial bias in biodiversity parameter estimates (Laliberte and Legendre, 2010; Si et al., 2018). Advances in monitoring and statistical methods can overcome some of detectability limitations associated with identifying appropriate umbrella species. For example, remotely-operated technologies such as camera traps can generate data on multiple species, including elusive and cryptic species that inhabit tropical forest ecosystem (Wearn and Glover-Kapfer, 2019).

The proliferation of hierarchical multi-species models provides a robust analytical framework to characterize the occupancy status of individual species and entire communities while accounting for detection bias (Dorazio and Royle, 2005; MacKenzie et al., 2018). Species occupancy is more useful for conservation management than presence/absence or distribution range as it can inform where individuals occur in suboptimal environments on the edge of their fundamental niche (i.e. the environmental conditions in which a species is able to survive and reproduce) (MacKenzie et al., 2018). These models also produce

improved precision of species-specific effects for rare or elusive species, effectively allowing more explicit consideration of underrepresented taxa in conservation management (Dorazio and Royle, 2005; Pacifici et al., 2014).

We assessed the performance of eight candidate umbrella species to represent multiple facets of biodiversity (community occupancy, species richness, functional diversity, and phylogenetic diversity) in a tropical rainforest mammal community while accounting for imperfect detection. In particular, we were interested in whether the occupancy of commonly used umbrella species e.g. charismatic megafauna like tiger and rhinoceros followed the broad patterns of mammal biodiversity, or whether they are better represented by other taxa. To answer this objective, first, we applied an occupancy modeling framework to inform species and community-level occurrence and species richness. Second, we calculated detection-corrected estimates of functional and phylogenetic diversity. Finally, we tested the strengths and patterns of association between umbrella species occupancy and four community-level biodiversity parameters. Our case-study is based on an camera trapping campaign undertaken in an extensive tropical forest in Sumatra, Indonesia, with focus on mammals since they are frequently promoted as umbrellas and the target of conservation programs.

2. Methods

2.1. Study system

We undertook our evaluation in the Leuser Ecosystem, a 25,000 km^2 tract of contiguous tropical forest in northern Sumatra (Fig. 1A). The area comprises a mosaic of peat swamp, lowland, hill, sub-montane, and montane forest. While 75 % of the landscape (18,673 km^2) is designated for conservation – including the Gunung Leuser National Park (8282 km^2), a UNESCO World Heritage Site – the remaining forest experiences some encroachment from agricultural expansion, road development, and human settlements (Sloan et al., 2018).

2.2. Biodiversity monitoring

To obtain detection/non-detection data for the mammal community, we conducted two systematic camera trap surveys: one in the West of Leuser (multiple clusters; 132 sites; May 2016–August 2017) and another survey in the East Leuser (a single cluster; 84 sites; June 2017–March 2018). Four camera trap models were utilized: Panthera V4 and V5, Reconyx HC500, and Bushnell NatureView 119440. After removing malfunctioned cameras from the dataset, we retrieved information from 212 camera trap sites (west = 128; east = 84), stratified across the four dominant forest types of the region: montane (>1800 m; 41 locations), sub-montane (1000–1800 m; 63 sites), hill (300–1000 m; 58 sites), and lowland forest (0–300 m; 50 sites). Camera sites were distributed across an elevational range of 19–2754 m asl (mean = 1008 m asl) and separated by a mean distance of 2 km (range: 0.9–5.3 km). At each site, a pair of cameras was deployed in parallel on forest trails or clearings approximately 0.5 m off the ground. On average, cameras were deployed for 85 consecutive trap nights per site (range: 10–230 nights), yielding a total survey effort of 18,102 nights.

2.3. Analytical framework

We calculated four biodiversity parameters derived from an occupancy modeling framework to explicitly account for detection bias: community occupancy and species richness derived from the occupancy model, along with the detection-corrected measures of functional and phylogenetic diversity.

a. Occupancy modeling

We employed Bayesian hierarchical multi-species occupancy models with data augmentation (Dorazio et al., 2006; Kery and Royle, 2016) to estimate community-level occupancy (i.e. the weighted average of all species occupancy estimates based on number of species detections), species-specific occupancy, and species richness. We combined detection data from West and East Leuser study areas and collapsed species-specific detection histories into sampling occasions of five camera trap nights to reduce over-dispersion and increase independence between temporal occasions (MacKenzie et al., 2018). To fulfill the assumption of demographic closure, we limited the data period to 90 days, resulting in a maximum of 18 sampling occasions per site (range: 3–18 occasions). We excluded species that could not be reliably detected using our survey methods (i.e. highly arboreal species like Sumatran orangutan, Thomas' langur, and black giant squirrel; $N = 3$) and domestic taxa (i.e. domestic dog). Small-bodied mammals (<1 kg body mass; e.g., rats and squirrels) were also excluded as most were difficult to reliably identify to species level. We considered only mammal species that were detected in at least five sampling occasions due to difficulties differentiating between ecological and observational processes when species detections are very low. This selection process resulted in a community of 23 medium-large mammals (Appendix S1).

To identify the environmental factors underpinning mammal occurrence, we extracted six spatial covariates (30 m resolution) in each camera trap site based on their reported influence on medium-large mammal occupancy elsewhere in Southeast Asia (Deere et al., 2020; detail of covariate selection in Appendix S2). We characterized the topographic complexity of our study area using elevation and elevation-derived Terrain Ruggedness Index (TRI) data obtained from the Shuttle Radar Topographic Mission (SRTM) (Rabus et al., 2003). To account for the extent and quality of forest habitat we quantified proportional forest cover (MoEF, 2018) and aboveground biomass (t ha^{-1}; Santoro and Cartus, 2021) respectively. To assess proximity to key environmental resources we calculated Euclidean distance to the nearest water body (meter; BIG RI, 2021). To explore sensitivity to human pressure, we calculated accessibility (i.e. travel time from human settlements in seconds) derived from a travel time cost surface model that account for the influence of roads, rivers, land cover, and elevation (Deere et al., 2020; Frakes et al., 2015).

We built a hierarchical multi-species occupancy model with the selected covariates with the following form (Appendix S3 for detailed model):

$$\begin{aligned}\text{logit}(\psi_{i,j}) =& \alpha_{0i} + \alpha_{1i}TRI_j + \alpha_{2i}TRI^2{}_j + \alpha_{3i}Elevation_j + \alpha_{4i}Elevation^2{}_j \\ &+ \alpha_{5i}Forest_Cover_j + \alpha_{6i}Biomass_j + \alpha_{7i}Distance_to_Water_{j\,j} \\ &+ \alpha_{8i}Accesibility_j + \alpha_{9i}Accesibility^2{}_j + \varepsilon_i Survey_Block_j\end{aligned}$$

$$\text{logit}\left(p_{i,j,k}\right) = \beta_{0i} + \beta_{1i}Camera_Type_j + \beta_{2i}Elevation_j + \beta_{3i}Trap_Effort_j$$

We modeled the occupancy ($\psi_{i,j}$) and detection probabilities ($p_{i,j,k}$) of species i at site j across temporal replicates k on the logit scale with species-specific random intercepts (α_0, β_0) and slopes (α_{1-9}, β_{1-2}). Species-specific responses were drawn as random effects from community-level distributions in both occupancy and detection models with estimable hyper-parameters that represent community trends. We modeled the influence of TRI, elevation, and accessibility on species occurrence using quadratic terms to account for non-linear responses. The occupancy model also incorporated a spatial random effect term (ε) to account for clustered sampling due to the blocked survey areas (East and West Leuser). Detection probability accounted for the influence of the camera trap model, elevation representing associated changes in forest type, and trapping effort (total trap nights) in each site.

Occupancy models were specified within a Bayesian framework using JAGS (Just Another Gibbs Sampler) via R package jagsUI (v1.5.1; Kellner, 2019). We ran three parallel Markov chains with 100,000 iterations where we removed 50,000 iterations as burn-in, and the remaining iterations were thinned by 50. Model performance was evaluated using Gelman-Rubin statistics and Bayesian p-values (Gelman

et al., 1996) which showed a good fit (Appendix S4). Estimates of species-specific occupancy of candidate umbrella species along with community occupancy and species richness in each camera trap site were extracted from model output.

b. Functional and phylogenetic diversity

To account for imperfect detection when quantifying functional and phylogenetic diversity we incorporated the detection-corrected occurrence matrix following the approach of Penjor et al. (2022). Throughout, we express diversity estimates at the camera trap site-level.

Functional diversity (FD) was expressed using the functional dispersal (FDis) metric, which represents the distribution of species in multidimensional trait space weighted by their true site-level occurrence (z-value) (Gorczynski et al., 2021). Functional dispersal calculates the average distance to a community centroid in trait space with distance to common species contributing more to the metric than rare species (Laliberte and Legendre, 2010). We collated trait data for conservation priority mammal species from the PanTHERIA database (Jones et al., 2009). Species were classified based on six traits: activity patterns (cathemeral, diurnal, nocturnal), diet (herbivore, carnivore, omnivore), habitat breadth (number of habitats where species lives), body mass (kg), litter size, and life span (maximum adult age; year).

For phylogenetic diversity (PD) we calculated the Mean Pairwise Distance (MPD) that represents phylogenetic distance among all pairs of species in the community (Kembel et al., 2010). We integrated species true occurrence estimates and based the calculations on phylogenetic profiles from the mammalian phylogenetic super tree. As trait and phylogenetic data for Sumatra endemic *Arctonyx hoevenii* (e.g. habitat breadth, body mass, litter size, life span) were not available, we used data from its closely related *Arctonyx collaris*.

We accounted for the influence of species richness on FDis and MPD metrics by comparing the observed mammal community in each site with 1000 null communities generated from the pool of all species in the study system using the "tip shuffling" null model approach (Penjor et al., 2022). Abundance-weighted standardized effect sizes or *ses* ($\frac{\mu\text{observed}-\mu\text{expected}}{\sigma\text{expected}}$) were computed using "richness" algorithm that randomizes community data matrix abundances while maintains species richness within samples (Kembel et al., 2010) for both metrics. Positive values of the Standardized Effect Size Functional Dispersal (sesFDis) indicate functional overdispersion (i.e. co-occurring species inhabit different trait niches) and positive Standardized Effect Size Mean Pairwise Distance (sesMPD) suggests phylogenetic overdispersion (i.e. larger phylogenetic distance between co-occurring species), while negative values indicate functional or phylogenetic clustering relative to null communities (Kembel et al., 2010; Penjor et al., 2022). All calculations were performed in the "FD" R package (v.1.0–12; Laliberté et al., 2014) and "Picante" R package (v.1.8.2; Kembel et al., 2010).

2.4. Umbrella species performance evaluation

We evaluated umbrella performance in a community of 23 medium-large mammals. Of the species in this community, only two (Sumatran tiger and rhinoceros) are actually monitored in the park. We selected a further six taxa from the community as candidate umbrellas based on five criteria by Seddon and Leech (2008): 1) well-known natural history and ecology, 2) large home range size, 3) management needs benefit other species in the study system, 4) moderate sensitivity to human disturbance, and 5) easily sampled or observed (detailed criteria see Appendix S5). All 23 species were evaluated against each criterion relative to other species in the community using a score of 1–3 (e.g., 3 = large home range (beyond 67th percentile), 2 = medium, 1 = small (below 33rd percentile), with the maximum score across the five criteria being 15). Eight species received a total score ≥ 10, and were selected as candidate umbrella species: Sumatran hog badger (*Arctonyx hoevenii*), mountain serow (*Capricornis sumatraensis*), dhole (*Cuon alpinus*), Sumatran rhinoceros (*Dicerorhinus sumatranus*), sun bear (*Helarctos malayanus*), Sunda clouded leopard (*Neofelis diardi*), Sumatran tiger (*Panthera tigris sumatrae*), and sambar deer (*Rusa unicolor*).

To evaluate how well umbrella species occupancy were associated with biodiversity parameters, we calculated dependence between these two variables using Bayesian linear regression in JAGS via R package jagsUI with model code adapted from Joseph (2013) and Kery and Royle (2016). This approach accounts for estimation uncertainty in both response and predictor variables to propagate error associated with model-derived biodiversity estimates (Joseph, 2013). Throughout, uncertainty was expressed using site-level standard deviations (SD) of the posterior distribution associated with species occupancy and biodiversity parameters derived from the occupancy framework.

We fitted a regression model with linear and quadratic terms for umbrella candidate occupancy to predict biodiversity parameters with following form:

$$Biodiversity_i = \beta_{0i} + \beta_1 SpeciesOccupancy_i + \beta_2 SpeciesOccupancy^2{}_i + eps.site_i$$

where $Biodiversity_i$ is the mammal biodiversity parameter estimates at camera site i, β_0 is the intercept parameter, and β_{1-2} are the species occupancy predictor effects influencing mammal biodiversity across sites. We added a site-level random effect (*eps.site*) to account for spatial autocorrelation in biodiversity parameter estimates (Moran's I observed mean = 1.03; expected mean = −0.005; p-value ≤0.00; Appendix S6).

We ran three parallel Markov chains with 50,000 iterations where we removed the first 25,000 iterations as burn-in, and the remaining iterations were thinned by 25. We tested model performance using the Gelman-Rubin convergence diagnostic (Gelman et al., 1996), which indicated good convergence. The strength and directionality of the relationships between species occupancy values and the other biodiversity parameters were determined from the β_1 coefficient (linear predictor), and the shape of the relationship (e.g. linear or quadratic) was inferred from the β_2 coefficient (quadratic term) and visual inspection of regression plots. We then ranked species based on their umbrella performance for each biodiversity parameter according to the β_1 coefficient values.

3. Results

3.1. Biodiversity and umbrella occupancy patterns

Overall mammal community occupancy (mean 0.19; range 0.04–0.34) was highest at low to medium elevation areas (Fig. 1A). To a lesser extent, mammal occurence tended to be higher in moderately rugged forest areas with larger tree biomass that were close to water sources and relatively easy to access, particularly in lowland habitats (Appendix S7–S8). Species richness (average of six species per site; range 2–11) was distributed evenly across elevations (Fig. 1B).

Functional diversity across the study area indicated overall trait clustering relative to null communities (mean sesFDis −0.20; range −1.75-1.55). Functional clustering occurred in 130 camera sites and was mostly found at higher elevations, while the majority of functional overdispersion (82 sites) was distributed in lowland areas (Fig. 1C). Phylogenetic diversity indicated a more phylogenetic overdispersion than expected by chance (mean sesMPD 0.16; range − 2.50-2.20). Similar with FD, PD distribution showed strong elevational gradients with net clustering (98 sites) at high elevation and overdispersion (114 sites) at low elevation (Fig. 1D).

Species-specific occupancy estimates were influenced by different combinations of predictors, in particular elevational gradients, depending on species ecology (Appendix S9). The occupancy of the eight umbrella candidate species varied across the landscape with some species restricted to high-elevation areas (e.g. hog badger), lowland (e.g. sambar deer), while others were more widespread (Appendix S10).

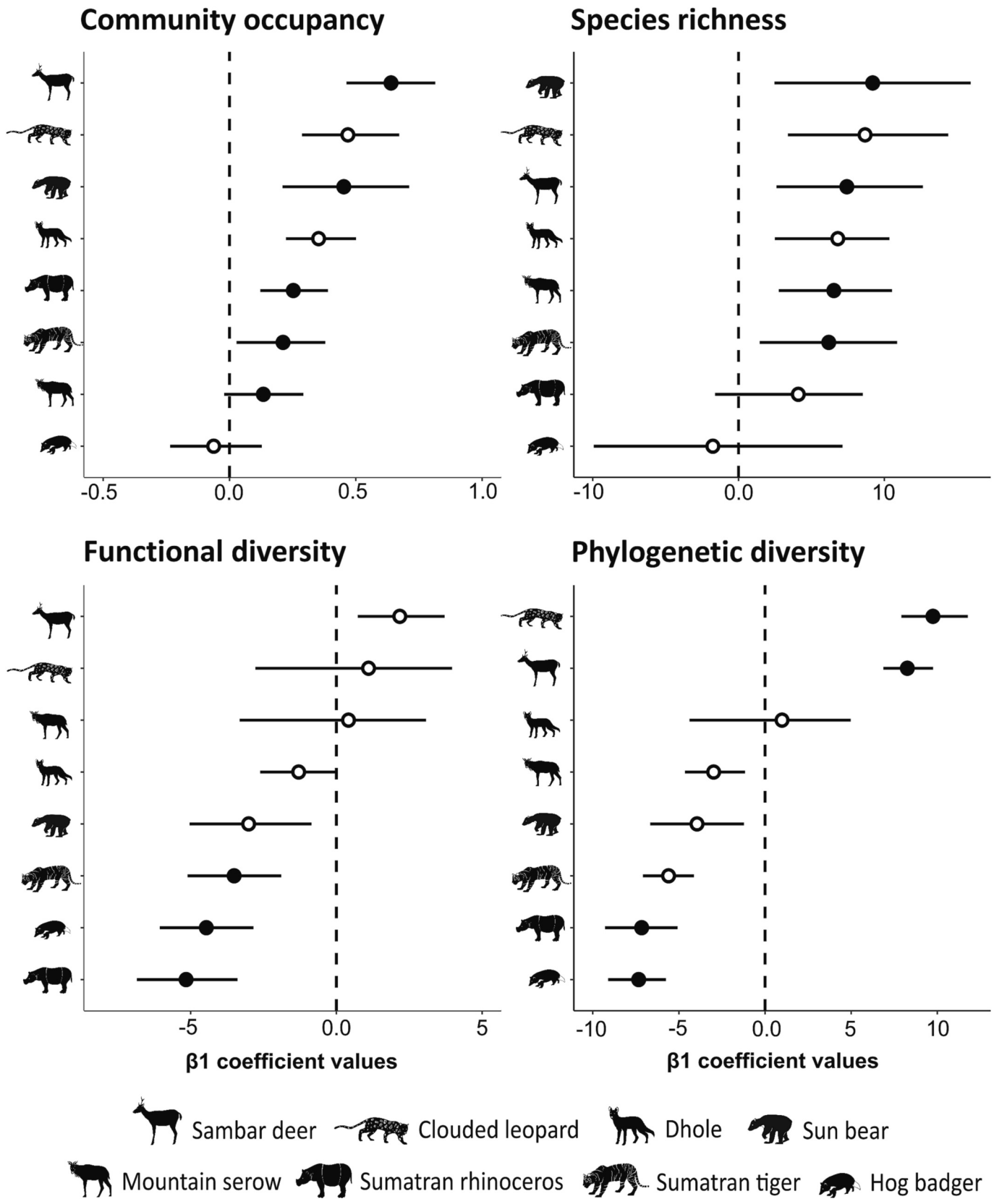


Fig. 2. Umbrella species performance ranking across four biodiversity parameters in medium-large mammal community. Closed circle points represent beta coefficient value of linear predictor (β_1). White circle points indicate significant quadratic relationship. Error bars represent 95 % Bayesian credible intervals of the coefficient estimates.

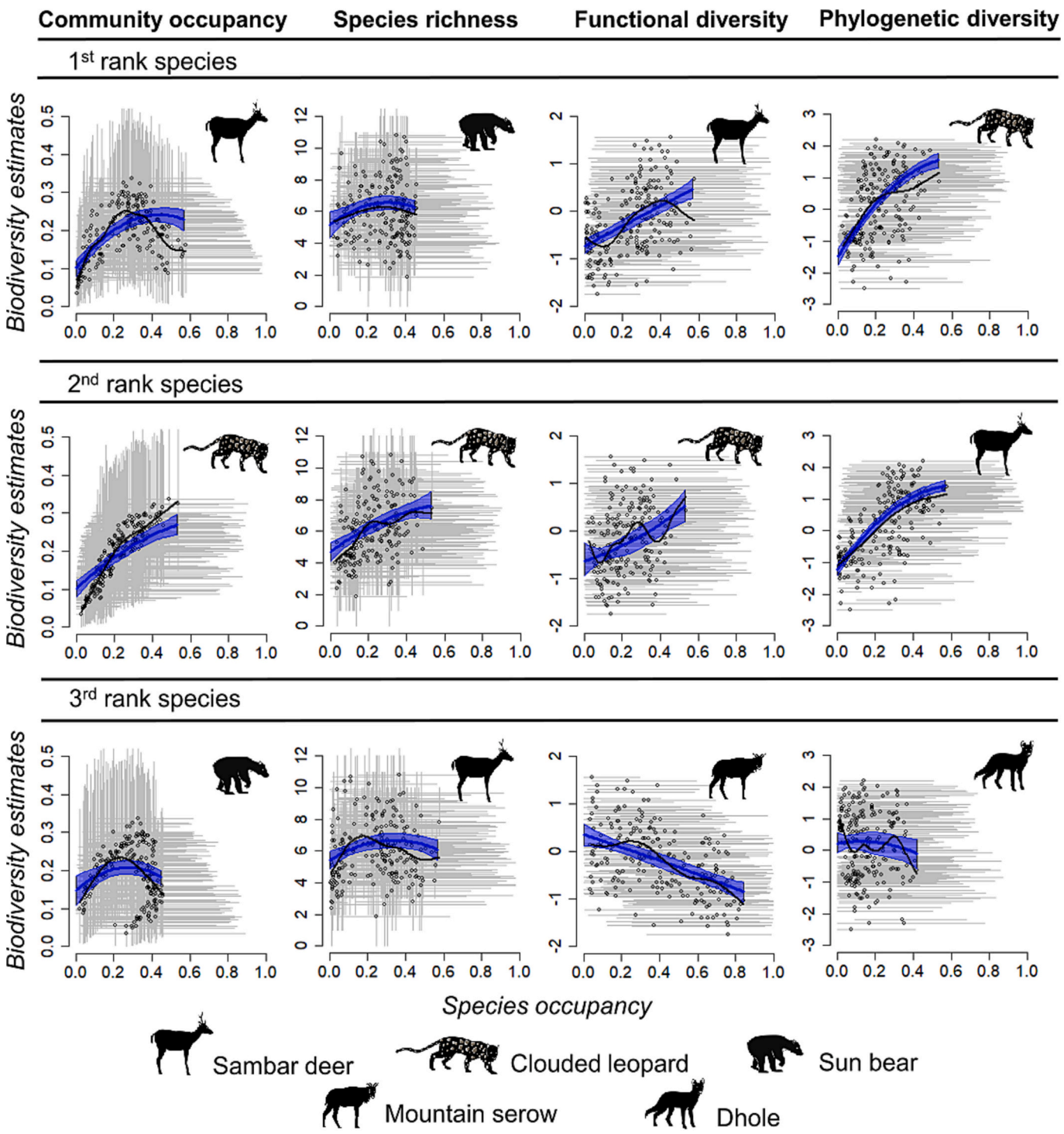


Fig. 3. Relationships between occupancy of the top three umbrella species with four biodiversity parameters. Points and thin grey lines inform point estimates of relationship with 95 % Bayesian credible intervals (BCIs) of response (vertical lines; for biodiversity parameters with uncertainty estimates) and predictor (horizontal lines) variables. Black line represents a spline smooth regression line. Blue line indicates the quadratic regression line that accounts for uncertainty in both response and predictor variables with 95 % BCI of the predictions represented by blue area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Umbrella species performance

Among the eight candidate species, sambar deer exhibited strong potential as an umbrella species, showing the strongest association with two of the four biodiversity parameters (Fig. 2, Appendix S11). Clouded leopard best represented phylogenetic diversity and was identified as the second highest ranking umbrella species for other biodiversity parameters. Only sambar deer and clouded leopard had significant positive association with community phylogenetic diversity.

Sun bear was identified as the best umbrella for species richness although its association strength was similar with other species from the 2nd to 6th rank. Mountain serow and dhole both ranked third as umbrella species for functional and phylogenetic diversity, but their associations were weak and showed negative trends (Fig. 3).

Table 1
Top umbrella performers based on this study evaluation and their qualification for meeting umbrella species criteria as proposed by Seddon and Leech (2008). Sumatran serow and dhole were excluded as they showed negative association with functional and phylogenetic diversity.

Umbrella criteria			
Natural history & ecology well known (number of scientific publications in Indonesia; relative to other species in community)	Well studied species (3 articles)	Well studied species (6 articles)	Well studied species (5 articles)
Large home range size (relative to other species in community)	Large (15 km^2)	Large (51 km^2)	Large (20.6 km^2)
Management needs benefit other species (in Gunung Leuser National Park)	Management concern (tiger prey)	Management concern (large carnivore)	Management concern (large carnivore)
Moderate sensitivity to human disturbance (forest specialist)	Moderate	Moderate	High
Easily sampled or observed (reliable species signs or easily identified in camera trap photographs)	Easy (reliable signs; easily identified in photographs)	Moderate (signs hard to detect; easily identified in photographs)	Easy (reliable signs; easily identified in photographs)
Co-occurrence with biodiversity parameters (evaluated in this study)	Community occupancy Species richness Functional diversity Phylogenetic diversity	Community occupancy Species richness Functional diversity Phylogenetic diversity	Community occupancy Species richness

Some species occupancy and biodiversity parameter relationships were non-linear (Fig. 3), implying that there was a limit to which higher occupancy could reliably predict higher values of biodiversity parameters. Nevertheless, visual inspection of these relationships showed that the top two umbrella species (sambar deer and clouded leopard) exhibited notable positive associations with biodiversity.

4. Discussion

Conservation managers often monitor umbrella species expecting them to represent broader patterns of biodiversity, but this underlying assumption has rarely been evaluated (Sibarani et al., 2019; Steenweg et al., 2023). Camera trap surveys provide detection data for multiple species simultaneously, but valuable information on species occupancy status, community-level biodiversity patterns, and the interconnecting relationships between them are often unavailable in the Global South due to funding priorities placed on single species and limited capacity to analyze biodiversity data (Chaudhary et al., 2022). Using a comprehensive camera trap dataset to quantitatively assess umbrella species performance, we demonstrate that charismatic species typically selected as conservation umbrellas (e.g. Sumatran tiger and rhinoceros) are in fact poor representatives of community-level patterns of biological diversity. Our results highlight that taxa frequently overlooked by conservation decision-making may better represent overall diversity, which alligns with the conclusion drawn in other landscape (Penjor et al., 2024).

Three of the eight candidate species stood out as high-performing umbrellas for mammal biodiversity: sambar deer, clouded leopard, and sun bear. While sun bear performed best as umbrella for species richness, other species (2nd to 6th ranks) also demonstrated similar performances indicating several potential umbrellas for richness. Sambar and clouded leopard were consistently highly ranked across all four biodiversity parameters. Their habitat preference in forest lowlands aligns with areas where higher biodiversity occurs as evidenced by their umbrella performance. Furthermore, those three umbrellas fulfilled most of the five umbrella species criteria by Seddon and Leech (2008) i. e. they have large home range (>10 km^2) relative to other species in the community, sensitive to human disturbance, and can be reliably detected through camera traps or sign identifications (Table 1). They also received considerable conservation attention as large carnivore and herbivore taxa, albeit less than their sympatric megafauna species.

4.1. Limited umbrella performance of Sumatran charismatic

High conservation value species such as Sumatran tiger and rhinoceros poorly represented broader mammal community, despite scoring well as umbrella candidates (Appendix S5). We acknowledge that both species are highly threatened and there is a possibility that their occurrence did not coincide with mammal biodiversity because they have been actively hunted throughout their range, which is particularly the case for the Sumatran rhinoceros (Pusparini et al., 2015; Putra, 2014). The pressure could shape the localized distribution (e.g. relatively few occurrences in lowland forest; Appendix S10) and lower detection for these species, although the current hunting pressure is lower due to the active protection in Leuser. It is worth noting that hunting also impacts other species indiscriminately especially snare hunting, although the scale might be in lesser extent (Harrison et al., 2016).

An island-wide assessment by Sibarani et al. (2019) reported tigers as the top umbrella for mammal biodiversity among four charismatic Sumatran species: orangutan, rhinoceros, and elephant using expert-driven habitat-suitability models from a global study (Rondinini et al., 2011). This discrepancy in umbrella performance with our more localized study in Leuser highlights the potential limitations of global biodiversity datasets and expert opinion to inform finer-scale species distribution patterns (Merow et al., 2017; Rondinini et al., 2011; Sibarani et al., 2019). Our appraisal, based on primary biodiversity data, shows that tigers occupy medium to high elevation habitats (e.g. hill and sub-mountain forest). Regardless of its large home range, these areas do not overlap with forest lowlands that tend to harbor higher diversity of other mammal taxa. Thus, we recommend caution in outlining monitoring priorities based on secondary data sources (e.g. IUCN red list species range) if primary data is available, as evidenced here in the case of tigers.

While our study implies tiger and rhinoceros did not perform well as umbrella species, species-based conservation programs in Sumatra disproportionately focus on these taxa. Between 2017 and 2019 an estimated USD 4.5 million was invested in the conservation of four charismatic megafauna (Sumatran rhinoceros, tiger, elephant, and orangutan) through Debt-for-Nature swaps, surpassing the total investment for landscape-based conservation programs (USD ~3.3 million) across the island (KEHATI, 2019). Focusing conservation actions on single-species, and in particular the charismatic ones, inevitably leads to management decisions solely based on focal species ecology and threats (Chaudhary et al., 2022; Lindenmayer and Likens, 2011).

4.2. Integrating umbrella species into wildlife monitoring

Cost-effective monitoring programs that cover a wide range of species are needed to support managers in their efforts to evaluate the impact of anthropogenic disturbances and conservation interventions (Caro, 2010; Mortelliti et al., 2022). Surveying entire ecological communities (mammals or cross-taxa) offers a more holistic picture of biodiversity patterns, but it demands significant amounts of time,

expertise, and resources, which are typically in scarce supply in tropical countries. While camera traps are a powerful tool for capturing multi-species data, implementing surveys at scales appropriate to conservation management (e.g. across the whole landscape) can be logistically challenging, thus limiting our capacity to make reliable inferences about rare or threatened species due to insufficient data (Wearn and Glover-Kapfer, 2019; Zipkin and Saunders, 2018). Our study evaluated the robustness of umbrella species performance and provides an alternative to community studies when there are limited resources by focusing the scope of assessment to a few representative species.

While no single species can represent all facets of biological diversity, identifying species with habitat preferences that reflect important areas for other wildlife is imperative for protected area managers so they can optimize monitoring under restricted budgets. As some species are more representative of particular aspects of biodiversity than others, we advocate the adoption of an 'umbrella fleet', which integrates multiple top umbrella species to benefit the overarching purpose of conserving biodiversity and the ecosystem (Lambeck, 1997). The fleet approach ensures the protection of crucial aspects of biological diversity that might be overlooked by prioritizing the needs of single taxa and can be integrated into current species-based programs. For example, sambar deer and clouded leopard are highly complementary umbrella species owing to their different ecological niches (i.e. herbivore vs carnivore; semi-arboreal vs terrestrial). A coupled monitoring approach based on these species would likely be more representative of a greater breadth of species than one focused on other taxa. This strategy also supports the inclusion of multiple facets of biodiversity as strategies focusing on species distribution and richness are not sufficient to ensure the protection of ecological functions and evolutionary history in an ecosystem (Sattler et al., 2014; Sibarani et al., 2019). Shown by our result, the sun bear performed well as umbrella for species richness and community occupancy, but did not capture functional or phylogenetic diversity at all. Thus, prioritizing monitoring or management based on sun bear alone could compromise these facets of biodiversity.

In the context of tropical forest management in Sumatra, the presence of charismatic tiger and rhinoceros gathers much needed public support and funding for biodiversity monitoring and protection. Concurrently, implementing an umbrella fleet approach in the existing monitoring programs can assist in the identification of priority high biodiversity areas. Documenting the detection of umbrella species through current species monitoring programs and other activities such as ranger protection patrols enables efficient documentation of real-time information of their occurrence and anthropogenic pressures. For example, camera trapping and sign surveys targeting Sumatran tiger can inform the occurrence of its prey sambar deer and sympatric carnivores like sun bear (Allen et al., 2020; Widodo et al., 2022). Although not spatially overlapping with tigers, the relatively elusive clouded leopard is often detected by camera traps (Widodo et al., 2022). Combined with multispecies occupancy modeling, the generated occupancy estimates of these umbrella species can serve as indicative of the broader patterns of mammal biodiversity.

4.3. Future directions

We note some opportunities to improve future evaluation of umbrella species. First, evaluation of umbrella performance in different habitat types (e.g. disturbed forests, forest edge, or plantations) is needed to assess whether the occupancy of monitored species is indicative of biodiversity across a broader range of habitats. Second is the need to validate umbrella species performance for other taxonomic groups, should these data become available. Third, the opportunity to combine datasets from different surveys (i.e. camera trap and protection patrols) to inform species occupancy and biodiversity at larger spatio-temporal scale (Miller et al., 2019). The integrated framework then can be incorporated with our analytical framework to extract the occupancy status for each taxon, calculate overall cross-taxon biodiversity association, and evaluate the umbrella performance among individual taxa.

Our appraisal highlights the extent to which mammal species used in wildlife monitoring programs in conservation areas effectively represent the integrity of the overall community present. As the application of the umbrella species concept is context-specific – it depends on landscape, species community, and management goals (Lindenmayer and Likens, 2011; Seddon and Leech, 2008) – we encourage the adoption of our data-driven framework for broader applications. Finally, we advocate the integration of umbrella species with current conservation management practice to ensure the integrated and effective protection of biodiversity and ecosystems.

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CRediT authorship contribution statement

AR, NJD, JWB, and MJS conceived the ideas and designed the study; ER collected the data; AR and NJD analyzed the data; AR, NJD, and MJS led the writing of manuscript. All authors contributed to the drafts and gave final approval for publication.

Declaration of competing interest

The authors of this manuscript have no conflicts of interest to disclose.

Data availability

Example dataset and model codes associated with this manuscript can be accessed at https://github.com/Ardiantiono/Umbrella-species-assessment-Biological-Conservation.git.

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Appendix A. Supplementary data

Supplementary material to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110511.

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