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ORIGINAL RESEARCH

Identifying remnant biodiversity hotspots in Southern Asia reveals disequilibrium in mammalian communities

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Abstract
Identification of highly biodiverse areas has become a crucial step in protecting species richness, especially considering the rapid collapse of biodiversity and the limited funds available to avert, far less to reverse, these trends. Therefore, we aimed to identify the most important areas for the conservation of specified mammalian groups in Southern Asia, a region rich in biodiversity hotspots threatened by increasing rates of habitat loss and other anthropogenic activities. To achieve this, we modelled the occupancy of ungulates and of small, medium and large carnivorans at 20 study sites across the region and identified hotspots of species richness. We analysed the variation of estimated space use between different species groups and ranked areas according to their predicted importance for mammalian species conservation. Our results reveal a significant positive correlation in the spatial utilization patterns of competitive carnivores, yet no correlation among carnivores and their prey species, suggesting that anthropogenic impacts in the region are constraining species to coexist in only the few remaining suitable areas, superseding interactions between species guilds. Although the rank of site importance varied amongst species groups, we were able to identify a consensus on sites that are crucial for the conservation of all groups considered. Most of these top-ranking sites were located in the peninsular region of Thailand. We argue that, of the areas assessed, these sites represent the most important refuges for species conservation in the region, and their protection is critical for the maintenance of the biodiversity in Southern Asia.

Keywords Carnivores · Habitat fragmentation · Landscape change · Occupancy · Species interactions · Ungulates

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Extended author information available on the last page of the article

Introduction

The conversion of natural landscapes into urban or agricultural lands represents the main threat to the conservation of biodiversity worldwide (Dirzo et al. 2014; IPBES 2019; Sala et al. 2000). With one-third of the world's land area being used for various forms of agriculture, coupled with the rapid growth of urban areas, protection of highly biodiverse regions has become an increasingly urgent global challenge (IPBES 2019). This is especially the case in Southern Asia, which encompasses some of the planet's most biologically diverse ecosystems and includes several biodiversity hotspots (Myers et al. 2000). Furthermore, this region faces the highest deforestation rates worldwide, with estimates suggesting that it could lose over half of its already greatly diminished forest cover and nearly 50% of its biodiversity within the next century (Clark et al. 2013; Hughes 2017a; Sodhi et al. 2010, 2004; Tan et al. 2022). Therefore, it is critical to identify and rank areas of high biodiversity value, to guide optimal conservation measures in this region (Margules et al. 2002).

Due to its high biodiversity and the acceleration of anthropogenic change, South and, especially, Southeast Asia have received increasing attention in ecological research and conservation applications in recent decades (Sodhi and Liow 2000; Steinmetz et al. 2006; Fisher et al. 2011; Brodie et al. 2023). However, much of that research has focused on single species and relatively small localities, limiting the capacity to extrapolate findings to identify areas important for the conservation of multiple species across the whole region (e.g., Johnson et al. 2006; Havmøller et al. 2016; Ratnayeke et al. 2018; Phumanee et al. 2021; Adhikari et al. 2022). To bridge this knowledge gap, Catullo et al. (2008) used species distribution ranges and developed habitat suitability maps of over one thousand mammal species found in the region. Using a gap analysis, they estimated species richness and identified highly biodiverse areas situated beyond protected areas. Based on these approaches, they identified areas of conservation hotspots. Subsequently, other studies have used similar approaches in the quest to identify significant areas for conservation within this region.

Hughes (2017b) modelled habitat suitability for several taxa, including 128 mammal species, using online repository data, to access species richness and demonstrated that most mammal species analysed had less than 30% of their range within protected areas, and the situation was even worse for the other analysed taxa. Finally, Macdonald et al. (2020) and Chiaverini et al. (2022) estimated species richness using camera trap data and conducted gap analysis by generating habitat suitability maps for terrestrial animals, including 74 and 57 mammals for mainland Southern Asia and the insular Sundaland, respectively. These studies found a mammal species richness pattern in the south and eastern portions of the mainland similar to the predictions of Catullo et al. (2008), but predicted a distinct pattern in the central and northwestern regions, as well as in the Sunda Islands.

These previously mentioned studies were based on comparing maps of predicted habitat suitability, rather than on actual spatial patterns of observed data. Therefore, although they provide valuable insights into biodiversity richness within the region, they do not confirm whether the modelled species can in fact be found in the areas predicted to be highly biodiverse. Given the similarity in the methods they used, the broad agreement of their results is not surprising. It is also noteworthy that none of these studies considered possible differences in habitat suitability between distinct mammalian taxa. Considering the ecological diversity among mammals, it is important to understand potential variations in their occurrence patterns. Still, as they account for imperfect detection of species, occupancy models can be a powerful tool to provide accurate estimates of occurrence and habitat use (Bailey et al. 2004), overcoming some limitations of previous studies that analysed spatial predictions from statistical models and providing new insights of occurrence rates of mammalian species.

Here, we aimed to quantify space use measures of carnivoran and ungulate species in Southern Asia and identify biodiversity rich areas for conservation. In order to do that, we utilized occupancy models that assess animals' space use within a landscape (*e.g*., the likelihood of areas being occupied). We tested three main hypotheses: (1) the space use of ungulates and large carnivorans would be positively correlated, as ungulates represent the main prey for large carnivorans (Wolf and Ripple 2016), making the occurrence of the prey a prerequisite for the survival of large carnivorans; (2) the space use of medium and large carnivorans would be negatively correlated, as large carnivorans tend to suppress smaller competitors as a consequence of intra-guild hostility (Prugh and Sivy 2020); (3) in a similar way, medium carnivorans would negatively affect the space use of small carnivorans (Prugh et al. 2009).

Methods

Camera trapping

We conducted systematic camera trap surveys between 2007 and 2022 across Southern Asia, including nine countries. The original focus of the sampling campaigns were mainly bigger felids (e.g., mainland clouded leopard, *Neofelis nebulosa* and Sunda clouded leopard, *N. diardi*, tiger, *Panthera tigris* and leopards, *P. pardus*), but several other species were captured by the cameras. All the species recorded by our camera traps were identified to the finest taxonomic level possible. Sampling occurred mainly in national parks and reserves, encompassing a broad altitudinal range and different ecotones. Cameras were placed in grids of different sizes with a distance of 1–2km between camera stations. Each station was composed of two cameras, placed ~40 cm above the ground, along trails and disused roads, where available, aiming to maximize detection success (Macdonald et al. 2018, 2019; Ash et al. 2021; Chiaverini et al. 2022).Trapping effort was determined based on the operational period of the camera traps, spanning from the initial image capture to the final image recorded before each camera trap was retrieved. In total, our dataset consisted of 5406 camera stations active over 280,075 trap nights.

Study area and landscape variables

Since our study sites were unevenly distributed, with some sites being clustered, while others were isolated, we aggregated the sites into regions to reduce heterogeneity and nonstationarity of species-environment relationships across broad environmental, geographic and sociological gradients (Legendre and Legendre 2012). To define an appropriate cluster distance characterizing data aggregation, we assembled geospatial data for a large set of biological, climatic, geomorphological, anthropogenic, economic and sociological variables (Supplementary Information, Table S1) that have been demonstrated to affect habitat space use in carnivoran and ungulate species (e.g., Rather et al. 2020; Liang et al. 2021; Niyogi et al. 2021; Penjor et al. 2021). For the variables that had temporally fluctuating data available, we collected yearly (from 2007 to 2021) and seasonal (May to October: rainy season in the mainland Southern Asia and dry season in the Sunda islands; November to April:

dry season in the mainland and rainy season in the islands) geospatial data, totalling 220 spatial layers, all projected at 250m resolution and processed with Google Earth Engine (Gorelick et al. 2017).

We extracted the value of all variables at the camera location and standardized their values. Variables were classified in two groups: ecological variables, including layers containing biological, climatic, anthropogenic and geomorphological data; and socio-economic, formed by a pixel-wise layer on Gross Domestic Product (GDP) (for more information on the variables, see Supplementary Information, Table S1). We calculated the pairwise geographic Euclidean distance between all camera stations. Similarly, we calculated pairwise socio-economic and ecological distances based on the standardized Euclidean distance in variable space between all camera stations using the variables described above. Subsequently, we calculated Mantel correlograms between the geographic and the ecological and socio-economic distances with the package Ecodist in R (Goslee and Urban 2007), to assess the range of geographical distance over which the ecological and socio-economic values are correlated. The analysis demonstrated that both the ecological and socio-economic values are correlated within 100km distance (Supplementary Information, Figure S1). Thus, we aggregated all camera stations located 100km or less apart from each other, resulting in a total of 20 study sites (Fig. 1). Henceforth, we will refer to the clustered camera stations based on these Mantel distances as study sites.

Space use occupancy modelling and studied species

Most occupancy models assume population closure (Emmet et al. 2021; Kendall et al. 2013; Rota et al. 2009). However, our dataset aggregates records from distinct locations and sampling periods. Thus, for mobile species, the independence between sites is likely violated. Therefore, we interpret occupancy as the probability of space use, which allows the relaxation of assumptions of closure and independence as long as the occupancy state of one site is independent of the occupancy of other sites (Mackenzie and Royle 2005).

For each study site, we generated a camera operational history matrix and a detection history matrix for individual species with the package camtrapR (Niedballa et al. 2016) in R. Detections were considered as binary data, detection (1) or non-detection (0) and sampling occasions were defined as 15-day periods to increase the probability of detections' independence. We modelled occupancy of all ungulate and carnivoran species that had at least 100 detections in the entire study region (Supplementary Information, Table S2). In order to access species' space use in each study site, we adopted a single-species, single-season occupancy model (MacKenzie et al. 2002) with no covariates using the R package unmarked (Fiske and Chandler 2011). We clustered ungulates into one group and divided carnivorans into three different groups: small, encompassing Herpestidae, Mustelidae, Prionodontidae and Viverridae families; medium, composed of the smaller Felidae (weighting less than 15kg) and one member of the Canidae (*Canis aureus*); and large carnivorans, composed of the bigger Felidae (weighting more than 15kg), the Ursidae family, and one Canidae (*Cuon alpinus*) (Supplementary Information, Table S3). For each species group, on each of our 20 study sites, we calculated two measures of space use: (1) the sum of within-group space use of all species, representing total richness across the group; and (2) the within-group mean, indicating average space use rate of each group (Fig. 1).

We ranked the importance of study sites for each species group separately, from the highest to the smallest value of the sum and mean of estimated space use. To understand how space use of species groups are related, we compared sites' rankings and performed

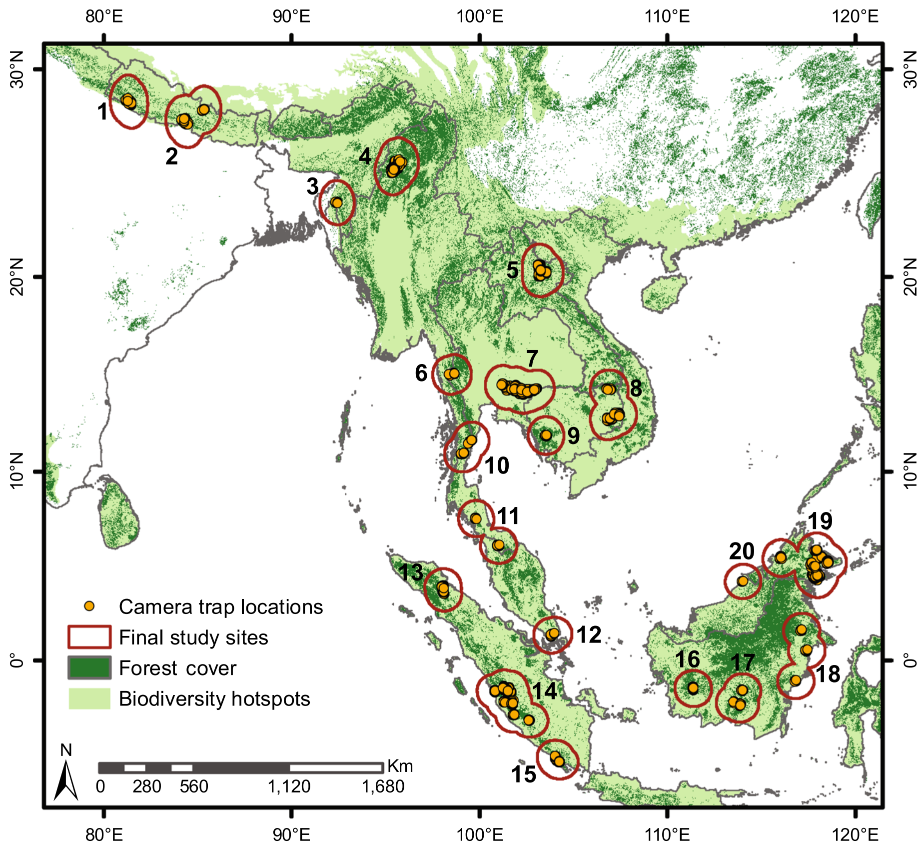

Fig. 1 Study sites determined based on the mantel correlograms. (1) Nepal North; (2) Nepal South; (3) India East; (4) Myanmar; (5) Laos; (6) Thailand Northwest; (7) Thailand Northeast; (8) Cambodia East; (9) Cambodia West; (10) Thailand Central; (11) Thailand South/Malaysia North; (12) Singapore; (13) Sumatra North; (14) Sumatra Central; (15) Sumatra South; (16) Kalimantan West; (17) Kalimantan Central; (18) Kalimantan East; (19) Sabah; (20) Sarawak. The shapefile of the biodiversity hotspots was obtained from the Critical Ecosystem Partnership Fund (CEPF)'s website (Hoffman et al. 2016). Data of remaining forest cover was obtained from Hansen et al. (2013) and shows the pixels that have at least 60% of forest cover within their area in 2022

a pairwise correlation among space use measures estimated for each site for all species groups. Finally, we also performed a two-way ANOVA test using species group and study site as covariates to understand what drives the difference in the estimated space use values.

Results

The total number of species modelled in each study site varied according to the number of species present in the site and model convergence. In total, we were able to model the space use of 53 species: 17 ungulates, 8 large, 6 medium and 22 small carnivorans (Supplementary Information, Table S2). We observed that sites with the highest ranking of space use sum and mean varied between species groups (Supplementary Information, Table S4), demonstrating that different areas hold varying levels of importance for the conservation of distinct species. This was expected, as for most species the space use values obtained varied greatly among sites (Supplementary Information, Table S5). However, we noted some tendencies. For example, the Thailand Northwest site was ranked as one of the five most important sites for all the species groups, while the sites Nepal South, Sumatra Central and Singapore were usually ranked as one of the five least important ones (Figs. 2, 3, Supplementary Information, Table S6 and Figure S2).

For medium carnivorans, we observed a high degree of consistency in the ranking of site importance between the sum and mean of space use values of species within this group (Pearson correlation $r=0.89$, $p<0.001$; Supplementary Information, Table S7), with four out of the five most and least important sites being identical for this species group. Specifically, Thailand Central, Thailand Northwest, Nepal North and Sumatra North occupied top positions for both space use measures, but Cambodia East and Thailand South/Malaysia North were only classified within the top five by either the sum or the mean, respectively (Supplementary Information, Table S4 and Figure S3). Although such consistency between sum and mean predictions was not found for small carnivorans and ungulates ($r=0.47$, $p<0.05$; Supplementary Information, Table S7), it was still possible to identify clear patterns in the most and least important sites for the two space use measures in both

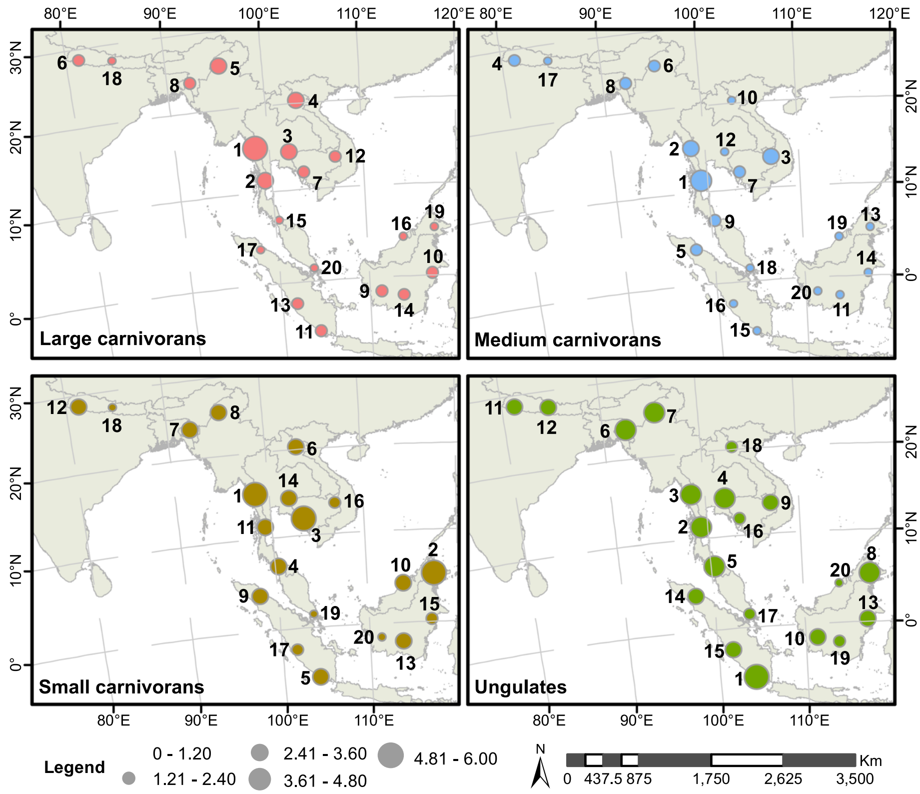

Fig. 2 Sum of the space use values estimated for the species of each group for each study site. Sites were ranked from the area with the highest (1) to the lowest sum (20). The size of the circles represents the value of the sum in each site. Distinct colours represent different species groups. Legend represents the range of space use sum values

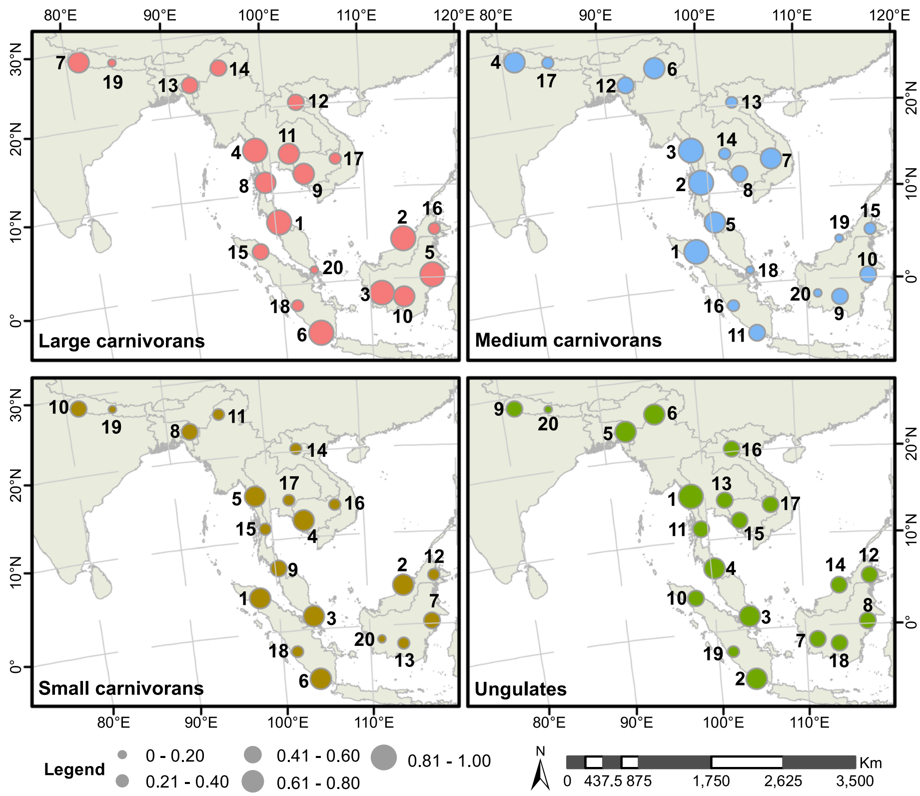

Fig. 3 Mean of the space use values estimated for the species of each group for each study site. Sites were ranked from the area with the highest (1) to the lowest mean (20). The size of the circles represents the value of the mean in each site. Distinct colours represent different species groups. Legend represents the range of space use mean values

species groups (Supplementary Information, Figure S3), with Thailand Northwest, Thailand South/Malaysia North and Sumatra South being among the most important sites for both. Singapore ranked highly for ungulates and small carnivorans but only based on the space use mean. India East, Thailand Central and Thailand Northeast were also on the top five for ungulates, while Sabah, Cambodia West, Sumatra North and Sarawak were important for small carnivorans, either according to the sum and/or the mean. Finally, the ranking of areas based on the two measures showed significant disparity for large carnivorans (non-significant correlation; Supplementary Information, Table S7 and Figure S3). This divergence was particularly evident in the case of Sarawak, which was selected as the second most important site according to the mean value but the fourth least important site according to the sum. Thailand Northwest stood out as the sole site highly ranked for both space use measures. Other sites, such as Thailand Central, Thailand Northeast, Laos and Myanmar classified in the top five by the sum, while Kalimantan West, Kalimantan East and Thailand South/Malaysia based on the mean.

Interestingly, the strongest correlation of space use estimates found between species groups was a positive relation between large and medium carnivorans (considering the sum of space use values: $r = 0.6$, $p < 0.05$), followed by ungulates and small carnivorans (considering the mean of space use values: $r=0.56$, $p<0.05$) and medium carnivorans and ungulates (considering the sum of space use values: $r=0.48$, $p<0.05$; Supplementary Information, Table S7). In addition, significant but positive weak correlations were found between medium carnivorans mean and small carnivorans sum, and large carnivorans sum and medium carnivorans mean (Supplementary Information, Table S7).

The ANOVA test demonstrated that, for the sum of the space use values, most of the variance is attributable to differences in species groups ($F=16.9$, $p<0.001$; Supplementary Information, Table 1) followed by variations among study sites ($F=3.42$, $p<0.001$; Supplementary Information, Table 1). Looking at the space use sum, medium and large carnivorans, and small carnivorans and ungulates are more similar to each other, with ungulates presenting the highest sum, followed by small, large and medium carnivorans (Fig. 4a). Still, Thailand Northwest is the most distinct study site, with the highest space use values, while Singapore had the lowest, followed by Sarawak and Kalimantan West (Fig. 4c). However, when looking at the mean of the estimated space use values, the analysis showed that only variations among study sites had a significant effect on species space use ($F=2.11$, $p<0.05$; Supplementary Information, Table 1). Notably, Thailand Northwest exhibited the highest mean space use values, followed by Sumatra North, while Nepal North, Singapore, Kalimantan West and Sumatra Central displayed the lowest ones (Fig. 4d). Surprisingly, large carnivorans presented the highest values of space use means in several sites, followed by ungulates, medium and small carnivorans. In fact, small carnivorans usually showed the smallest space use values according to the mean in most sites (Fig. 4; Supplementary Information, Table S4). In contrast, looking at the sum of the space use values, ungulates displayed the highest values, followed by small, large and then medium carnivorans (Fig. 4; Supplementary Information, Table S4).

Discussion

Species group interactions

Species interactions among mammalian guilds are vital for ecosystem functioning (Beschta & Ripple 2016; Morris et al. 2020; Roemer et al. 2009). However, anthropogenic activities can disrupt these natural interactions, leading to detrimental cascading effects through the entire environment (Dorresteijn et al. 2015; Shamoon et al. 2018; Atkins et al. 2019). Investigating the space use of distinct guilds and their interactions can, therefore, shed light on the responses of species guilds to intensive threats. However, existing work in the

Table 1 Two-way ANOVA test showing the degree of variation on the space use explained by species group and study sites, considering both space use mean and sum measures

		Df	Sum Sq	Mean Sq	F value	Pr(>F)
Space use sum	Species group	3	44.81	14.94	16.90	<0.001
	Study site	19	57.37	3.02	3.42	<0.001
	Residuals	57	50.38	0.88		
Space use mean	Species group	3	0.2	0.07	1.60	0.20
	Study site	19	1.67	0.09	2.11	0.02
	Residuals	57	2.38	0.04		

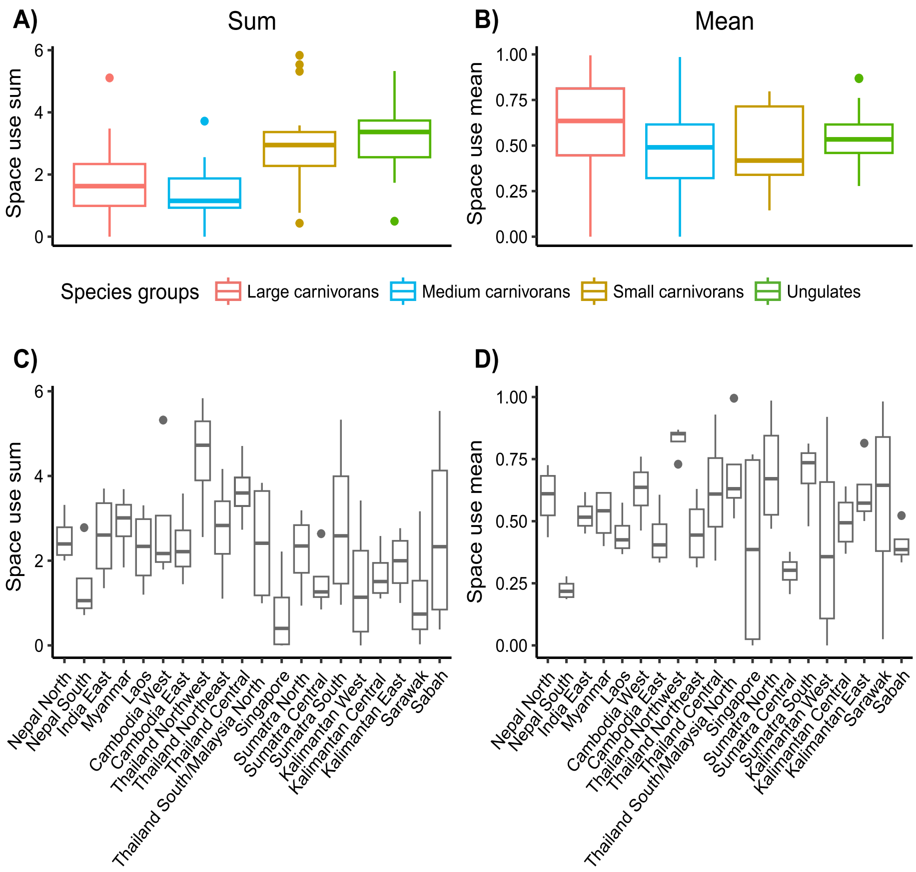

Fig. 4 Boxplot demonstrating the distribution of space use sum (**a**, **c**) and mean (**b**, **d**) by species group (**a**, **b**) and study sites (**c**, **d**)

region involving multi-landscape syntheses for wildlife using camera trap data predominately focuses on single species (Dunn et al. 2022; Carr et al. 2023; Honda et al. 2023) with relatively few multi-species papers or diversity (Amir et al. 2022; Brodie et al. 2023). Our analyses emphasize the possible consequences of habitat conversion and intensive poaching on species interactions in highly biodiverse areas throughout Southern Asia.

Contrary to our first hypothesis, the space use of ungulates and large carnivorans was not correlated. The occurrence and abundance of carnivorans is deeply influenced by the occurrence and abundance of their prey (Kamler et al. 2020; Karanth et al. 2004; Rasphone et al. 2022; Rostro-García et al. 2018). Therefore, this mismatch between predator and prey may be interpreted as a warning to the conservation of both species groups, consistent with prior warnings (Wolf & Ripple 2016). Although large carnivorans may adapt their diets accordingly to prey availability (Valeix et al. 2012; Ferretti et al. 2020), the high levels of poaching in several areas are depleting prey numbers drastically (Gray et al. 2021) and seem to be creating a disequilibrium (Storch et al. 2022) in these study sites to the extent that not even the space use sum of these two groups, which integrates all species in both trophic guilds, is correlated. This mismatch was also observed by

Gil-Sánchez and Sánchez-Cerdá (2023), who demonstrated that the number of areas in Southern Asia that have lost their megaherbivores is even greater than the number of areas that have lost their large predators, with only five small areas in Southern Asia still containing both their integral top predator and megaherbivore fauna. Still, it is imperative to consider that there may be a time-lag effect and, if so, carnivoran populations have not yet reached equilibrium with current prey assemblages and could crash further even without additional poaching.

Our second hypothesis was that large carnivorans would have a negative impact on medium carnivorans, resulting in a negative correlation in their space use. Intra-guild hostility often leads to the suppression of smaller sympatric carnivorans by larger ones (Chutipong et al. 2017; Newsome et al. 2017; Hearn et al. 2018; Prugh & Sivy 2020; Boron et al. 2023; Prugh et al. 2023). On the other hand, the decrease in population size or even local extinction of large carnivorans is thought to lead to mesopredator release, increasing the abundance of medium carnivorans (Prugh et al. 2009; Ripple et al. 2013; Mayhew et al. *in review*). These generalizations were the basis of our expectation that sites with lower space use of large carnivorans would have higher space use of medium carnivorans. However, the positive correlation we observed between large and medium carnivorans suggests that medium-large carnivorans might both avoid humans and thus show similar spatial distributions within and among landscapes (Luskin et al. 2017; Decœur et al. 2023; Hendry et al. 2023). Even though our study did not consider local spatial and temporal avoidance, which could partially explain these results, it is surprising to observe that medium carnivorans do not increase their space use when large carnivorans space use is lower. It seems that the effects of rapid recent defaunation, habitat loss and habitat fragmentation in the area are so great that they superseded the interaction of species (Valiente-Banuet et al. 2015; Mendoza & Araújo 2019; Rasphone et al. 2019; Boron et al. 2023), such that many species groups coexist only in the few remaining areas of suitable habitats. This disequilibrium between species guilds over the long term may increase competition, especially within small, isolated areas where they still exist, leading to local extinctions (Vucetich & Creel 1999; Tannerfeldt et al. 2002).

Likewise, regarding our third hypothesis, we predicted a negative correlation between medium and small carnivorans. However, the fact that they presented a positive correlation of space use was less unexpected. The members of the Herpestidae, Mustelidae, Prionodontidae and Viverridae families have very diverse diets and lifestyles, more so than medium carnivorans (Do Linh San et al. 2022), which could reduce competition, facilitating coexistence. However, this explanation alone would lead to their space use being independent, rather than positively correlated. Therefore, we posit that the low suitability of the surrounding areas must be constraining these species to the same sites. Similar to the pattern observed between large and medium-sized carnivorans, these results suggest that the dominant driver of species composition may be the dwindling availability of refuges that provide habitat and protection, rather than processes involved in species interactions.

Interestingly, ungulate space use was positively correlated with the space use of both medium and small carnivorans. The cause of this relationship is unclear, but might be influenced by the need for smaller areas to survive or the greater ability to adapt to anthropized environments (Crooks 2002; Barbosa Júnior et al. 2022). However, it seems hard to explain such results without considering the inevitable influence that rapid biodiversity collapse has in producing nonequilibrium patterns of species richness in remnant habitats where broad ranges of mammal biodiversity have not yet been eliminated and which provide remnant patches of suitable remaining habitats.

Site importance ranking

Unlike previous studies pursuing similar goals, our data analysis directly reports space use rates for the species that have actually been recorded in each area, rather than relying on spatial statistical models to extrapolate observations. Nonetheless, the ranking of sites emerging from our analysis has some congruence with the patterns of species richness modelled by other authors (Catullo et al. 2008; Chiaverini et al. 2022; Hughes 2017b; Macdonald et al. 2020). Most importantly, the peninsular region of Thailand, which was also identified by Catullo et al. (2008), Hughes (2017b) and Macdonald et al. (2020) as highly suitable for species richness, emerged from our analysis as one of the most important sites across the guilds we assessed. Additionally, our analyses accord with the findings of Catullo et al. (2008) Chiaverini et al. (2022), Hughes (2017b) and Macdonald et al. (2020) in identifying Cambodia West, Sumatra South, and Sumatra North as priority areas for biodiversity. The fact that distinct methods identified these areas as substantially important highlights the significance of these areas for conservation.

However, there are also discrepancies between our results and those of previous studies. Nepal North was ranked as one of the most important sites in our analysis, which accords with Gil-Sánchez and Sánchez-Cerdá (2023) who concluded that it is one of the last areas of intact communities of megaherbivores and top predators. In contrast, Macdonald et al. (2020) had predicted very low species richness for this area and high species richness in Singapore, whereas our results usually identify Singapore as one of the lowest richnesses for all species groups across all studied sites. Finally, the Kalimantan region in Borneo was predicted by Chiaverini et al. (2022) to have low species richness, but in our work the Kalimantan sites were ranked as important for some species groups. These contrasting results demonstrate the value in estimating the site importance for species richness using different measures and methods, allowing the integration of distinct species abundance and richness measures.

Conclusions

Given the limited resources available for conservation and the rapidly diminishing areas of natural lands remaining, identifying critical areas for biodiversity conservation has become extremely important (McIntosh et al. 2017; Wilson et al. 2007). Our results highlight the differences in species occurrence patterns and the need to account for different mammalian guilds when prioritizing conservation areas. This also emphasizes the need for cautious consideration when establishing umbrella species (Branton & Richardson 2011) for the protection of certain areas, particularly in regions experiencing environmental disequilibrium on species trophic guilds. We identified Thailand Northwest, Thailand Central, and Thailand South/Malaysia North as areas that represent some of the most important strongholds for biodiversity conservation in Southern Asia and should be given precedence in conservation efforts to ensure their sustained biodiversity value and enhanced dispersal linkages among them. Although we did not survey the central part of Peninsular Malaysia, this area likely also is an important stronghold for biodiversity conservation, because it is well protected and has maintained its biodiversity of large carnivorans and other species over the long-term (Rostro-García et al. 2016; Clements et al. 2021). However, the unexpected correlations between species groups suggest a major disequilibrium among species trophic guilds, indicating that biodiversity collapse caused by high levels of poaching and habitat loss is superseding species interactions, forcing species to coexist in the short-term within small and dwindling suitable areas that are still available. Further research at a continental level that asses the impacts of anthropogenic factors on different species groups is necessary to develop a deeper understanding of their effects for biodiversity conservation in the region. Although we highlight the need of protecting different areas for the conservation of distinct species groups, we acknowledge the importance of taking into consideration the impact and/or importance that these areas have on local people's livelihood. In undeveloped countries, forest products often represent an important monetary source for local families and, sometimes, even governments (Abukari et al. 2020; Chowdhury et al. 2022). Therefore, when determining conservation measures, one must consider the implications this may hold for local communities and which approach can be taken to allow both biodiversity and local people to live together in a sustainable way.

Finally, our analysis is limited by our sampling areas and there are notable geographic gaps between them. Thus, future research should focus on these areas to evaluate the current conservation state of distinct mammalian guilds in these areas. Still, it is important to highlight that the camera trap dataset used in this work was collected spanning more than a decade. Considering the high rates of habitat loss and poaching in the region, the species composition in many study sites might have drastically changed during those years. We know, for example, that such rapid change has been documented in the Laotian and Cambodian sites. These sites had one of the highest space use values for large carnivorans (Fig. 2, Supporting Information, Table S6). However, both tigers and leopards have recently become functionally extinct in these countries and other carnivoran and ungulate species are declining rapidly within the best protected areas of those countries (Rasphone et al. 2019, 2021; Rostro-García et al. 2023). Therefore, the high ranking of the areas now stands as a tragic memorial to a splendour that has been lost during the course of our research, and is a sinister warning signal for biodiversity conservation elsewhere in Southern Asia as a whole. This further emphasizes the rapid biodiversity collapse and nonequilibrium pattern of remnant biodiversity in Southern Asia.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-024-02902-0.

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Author contributions Conceptualization: CCS, SAC and DWM; Field work: JK, AJH, EA, AR, AF, BPY, CKWT, GB, IAH, ML, OEC, PC, PS, PPK, SC; Formal analysis and investigation: CCS, ZK, SAC; Writing—original draft preparation: CCS, ZK, SAC, DWM; Funding acquisition: DWM; Supervision: DWM and SAC. All authors read and approved the final manuscript.

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Data availability The data generated during and/or analysed during the current study is partially available at: Mendes et al. (2024) CamTrapAsia: A dataset of tropical forest vertebrate communities from 239 camera trapping studies. Ecology, p. e4299. The complete data can be available from the corresponding author on reasonable request. The script used to perform the analysis is available on Figshare repository at: https://doi.org/10.6084/m9.figshare.25995973

Declarations

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