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Human and apex predators shape lower trophic levels through top-down control

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ABSTRACT

Apex predators are thought to regulate ecosystems through top-down control, but the extent of their impact often varies, potentially due to differences in their abundance and other aspects of the ecosystem, including human disturbances. Here, we analyzed three years of data collected from 114 camera traps placed in Htamanthi Wildlife Sanctuary, northwestern Myanmar. Using multigroup piecewise structural equation modeling, we explored associations among multiple trophic levels, including humans, apex predators, mesopredators, prey species and vegetation across varying apex predator biomass levels within similar environments. We found that variation in apex predator biomass significantly influences trophic associations, especially concerning top-down control exerted by humans and apex predators. Human disturbances had a regulatory role on apex predators and large prey populations and alter their behavior. Apex predators both suppressed and facilitated prey populations, underscoring the crucial role of sustaining apex predator populations in ecosystems. Furthermore, our study highlights positive associations between mesopredators and prey species, demonstrating their coexistence within the ecosystem. Bottom-up effects from vegetation were weaker than top-down processes. Nevertheless, the observed positive link between vegetation and small prey suggests that this bottom-up component also plays an important role in the trophic network. Our study highlights the complex associations between different trophic levels and underscores the importance of considering multiple species for effective conservation and ecosystem stability.

1. Introduction

Understanding the structure and functioning of trophic networks is a fundamental goal in ecology (Polis and Strong, 1996; Ripple et al., 2016; Tossens et al., 2024). When discussing trophic networks, two diametrically different but complementary processes that are often discussed: top-down process, where top consumers or predators shape lower trophic levels, and bottom-up process, where primary producers and associated consumers regulate the energy transfer among above trophic levels (Estes et al., 2011; Paine, 1980; Terborgh, 2015). For top-down control, apex predators play a crucial role largely due to their ability to trigger top-down trophic cascades (Suraci et al., 2016; Zhang et al., 2018). Without apex predators, mesopredator and herbivore abundance are supposed to increase in abundance, which can impact small mammal populations (mesopredator release hypothesis, see, e.g., Hoeks et al., 2020; Takimoto and Nishijima, 2022; Soule et al., 1988). It has also been suggested that this increase in herbivores may reduce vegetation biomass (green world hypothesis, see, e.g., Atkins et al., 2019; Wilkinson

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and Sherratt, 2016; Hairston et al., 1960). However, a significant knowledge gap remains in understanding how these general ideas about the effects of reduction or extirpation of apex predators play out in real ecosystems, particularly regarding possible trophic cascades and ecosystem stability.

When analyzing trophic networks, intraguild predation (predation and competition among apex or mesopredators) introduces an additional layer of complexity. Intraguild predation mainly occurs when the landscape contains more than one predator occupying a similar ecological niche (Heithaus, 2001). In such a case, subordinate predators try to minimize their co-occurrence pattern with predators (Carter et al., 2012; Lima and Dill, 1990) and adapt their behavior, such as increasing vigilance and adapting foraging strategies (Wikenros et al., 2014; Wooster et al., 2022). For example, not only medium to small felid species such as the Asian golden cat (*Catopuma temminckii*), marbled cat (*Pardofelis marmorata*) and leopard cat (*Prionailurus bengalensis*), but also other mesopredators such as red fox (*Vulpes vulpes*), Asian badger (*Meles leucurus*), masked palm civet (*Paguma larvata*), yellow throated marten (*Martes flavigula*), are avoiding the top predators such as tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) by adapting their spatiotemporal activity pattern (Allen et al., 2020; Bitetti et al., 2010; Vernes et al., 2022; Zhao et al., 2020).

Human impacts, including poaching, recreation activities, and habitat modification pose a further complication to understanding trophic networks. These impacts can cause lethal and non-lethal effects on apex predators (Lennox et al., 2022; Ordiz et al., 2021). Apex predators need large home ranges to fullfill their food requirements due to their larger body size, low population densities, and low reproduction rates (Estes et al., 2011; Ripple et al., 2014, 2017). Darimont et al. (2015) found that human's exploitation rate of large carnivores exceeds that of herbivores by 3.7 times, indicating a significant influence on carnivore populations and suggesting humans may be regarded as "super predators". On the other hand, some studies indicated that humans exert not only a top-down trophic cascade by suppressing lower trophic levels but also bottom-up effects through the modification of the landscape (Dorresteijn et al., 2015; Muhly et al., 2013; She et al., 2023; Sun et al., 2021). For example, human activities change the vegetation structure through agricultural practices such as fertilization, grazing and forage biomass, strengthening the bottom-up forces in the ecosystems (Foley et al., 2005; Muhly et al., 2013; Zhang and Huang, 2019). However, the top-down process resulting from human impacts on different apex predators, and their associations with mesopredators, prey, and vegetation, are complex and not yet fully understood.

Among apex predators, the tiger is one of the world's most iconic species. As the largest living cat species, it has been recognized as Asia's largest apex predator, attributed to its remarkable morphological and physiological characteristics (Joshi et al., 2016; Louys, 2014). They predate mainly on larger prey and mesopredators to fulfil their high metabolic requirements. Intact contiguous landscapes are essential for their long-term survival (Ripple et al., 2014). However, human disturbances such as hunting, illegal wildlife trade, habitat fragmentation, agricultural expansion, and human encroachment threaten their populations (Gray et al., 2023; Joshi et al., 2016; Sarkar et al., 2021; Thinley et al., 2018). According to the International Union for Conservation of Nature (IUCN), the global wild tiger population has dramatically declined from 100,000 to 3500 individuals from the early 1900s to 2014, especially in Southeast Asia. Their current distribution range has diminished to <6 % of their historical range during the last century (Gray et al., 2023; IUCN, 2022). Subsequently, numerous ecological interactions changed, triggering trophic downgrading due to imbalances in the predator-prey system (Estes et al., 2011; Ritchie and Johnson, 2009; Rodríguez-Lozano et al., 2015).

An ideal location for studying the effects of apex predators on ecosystems is the Htamanthi Wildlife Sanctuary (HWS) in northwestern Myanmar, recognized as one of the global tiger conservation landscapes. This sanctuary provides essential habitat for numerous endangered, rare and endemic species. As part of a global tiger conservation landscapes, HWS plays a crucial role in conserving of apex predators and their prey populations. Unfortunately, humans' encroachment with unlawful activities: poaching, gold mining, and logging, occurs throughout the sanctuary (Bhagwat et al., 2017; Grffi et al., 2020; Naing et al., 2019a), resulting in significant impacts on mammal populations. Therefore, this area offers a unique opportunity to examine trophic associations involving apex predators and their interplay with human disturbances.

In this study, we examined the impact of trophic associations across different trophic levels, including humans, apex predators, medium predators, small predators, large to medium prey, semi-arboreal prey, small prey, and vegetation, within two areas differing in apex predator biomass. The primary objective of this study is to understand how humans as super predators and apex predators, influence trophic associations, as well as to understand the consequences of reduced apex predators from the community. In accordance with this objective, we developed eight different hypotheses (Fig. S1, Table 1) to investigate the complex associations among various trophic levels within both top-down and bottom-up trophic networks of tropical Southeast Asian forest ecosystems.

2. Materials and methods

2.1. Study area

Our study area is the Htamanthi Wildlife Sanctuary (HWS) (25° 21′ 50" N, 95° 33′ 36″ E), covering an area of 2151 km^2, in northwestern Myanmar. It is situated in the transition zone between the eastern Himalaya, Indo-Burma, and the mountains of Southwest China (Fig. 1). Established in 1974, the sanctuary was declared an ASEAN heritage park in 2019. The HWS acts as a reservoir for seven endangered cat species (i.e., tiger, leopard, clouded leopard (*Neofelis nebulosa*), Asian golden cat, marbled cat, jungle cat (*Felis chaus*) and leopard cat) together with many other rare and threatened species (i.e., dhole, sun bear (*Helarctos malayanus*), Asian black bear (*Ursus thibetanus*), etc.) (Thu et al., 2024). The elevation ranges from 141 to 618 m, and the vegetation in this region comprises semi-evergreen forest, swamp forest, and upper-mixed deciduous forest (Kyaw et al., 2021; Latt and Park, 2022). The total annual precipitation in this region is around 2695 mm and mean annual minimum and maximum temperatures are around 20 °C and 30.1 °C (Fig. 1). For effective management, the sanctuary is divided into four distinct zones: Nam Yan Yin, Nam Pa Gon, Nam E Zu, and Nam Phi Lin, based on the involvement of patrol rangers and the placement of guard posts.

2.2. Camera trap survey

We deployed 142 camera traps, with 59 placed in Nam Pa Gon and 83 in Nam E Zu, over various periods between May 2019 and May 2021 (Table S1). Due to malfunctions and losses, data from only 114 of the 142 camera traps could be used, 50 from Nam Pa Gon and 64 from Nam E Zu (Table S1). Each camera trap was configured to capture three consecutive pictures with five-second intervals between every detection. The camera traps were positioned approximately 500 m apart from each other and mounted at a height of 0.5–1 m above the ground. No bait was used, and the traps were distributed throughout the forest without predetermined selection of specific features, to cover diverse habitats and topographic features while minimizing selection bias in site placement. Each camera trap location was recorded using handheld GPS (Garmin 62 S), and the dataset was compiled using Microsoft Excel.

2.3. Data analysis

In this study, we utilized multiple species to understand the impact of humans and apex predators in areas with varying apex predator biomass. Before starting the analysis, we determined independent events

Table 1
Proposed trophic pathways based on our predictions in higher and lower apex predator biomass area in Htamanthi Wildlife Sanctuary, northwestern Myanmar.

	Trophic levels*	Higher apex predator biomass area (HAB)	Lower apex predator biomass area (LAB)
H1	Humans to Predators Humans to Prey	➢ Human disturbances will suppress (negative association) not only apex predators, but also lower trophic levels, including mesopredators, and prey species, in both HAB and LAB (Darimont et al., 2015).	
H2	APred to MPred APred to SPred	➢ According to mesopredators release theory (Soule et al., 1988), apex predators would suppress (negative association) both medium and small predators due to higher apex predator biomass in HAB.	➢ Medium and small predator population will increase (positive association) due to lower apex predator biomass in LAB (Soule et al., 1988).
H3	APred to LPrey APred to SAprey	➢ In HAB, apex predators will suppress (negative association) prey species due to increased predation pressure and competition for resources (Ripple et al., 2014).	➢ In LAB, populations of prey will increase (positive association) due to reduced predation pressure (Ripple et al., 2014).
H4	MPred to SPred	➢ Coexistence among medium and small predators is expected due to top-down regulation by apex predators, which reduce competitive exclusion among mesopredators according to coexistence theory (positive association) (Schoener, 1974).	➢ Higher competition among medium and small predators is expected due to mesopredator release resulting from reduced predation pressure by apex predators (negative association) (Prugh et al., 2009).
H5	MPred to LPrey MPred to SAprey SPred to LPrey SPred to SAprey	➢ Medium and small predators are expected to coexist (positive association) with large and semi-arboreal prey in both regions due to different body size and feeding habit (Cohen et al., 1993).	
H6	MPred to SPrey SPred to SPrey	➢ In HAB, small prey populations will increase (positive association) as a result of potential mesopredator suppression by apex predators (Gordon et al., 2015).	➢ In LAB, small prey populations will decrease (negative association) as a result of potential mesopredator released by apex predators (Gordon et al., 2015).
H7	LPrey to SAprey SAprey to SPrey	➢ We predicted that large prey will exhibit positive associations with semi-arboreal prey. Additionally, semi-arboreal prey will also coexist (positive association) with small prey due to their distinct feeding habits and behaviors (Heymann and Hsia, 2015; ter Schure et al., 2020).	
H8	EVI and Forest canopy height	➢ We proposed that both vegetation-related variables would transfer the energy (positive association) to upper trophic levels, whether predator biomass is higher or lower (Cano-Martínez et al., 2024; Villamuelas et al., 2016).	

* APred = Apex predators, MPred = Medium predators, SPred = Small predators, LPrey = Large prey, SAprey = Semi-arboreal prey, SPrey = Small prey.

using 30-min intervals, following the methodology established by O'Brien et al. (2003). As a proxy for human disturbances, we used all human activities that was detected in camera traps, including hunters (i.e., people with guns or crossbow), pedestrians, cattle presence and collection of non-wood forest products. We then ran a negative binomial generalized additive model via tensor spline that accounted for spatial autocorrelation on these observations, using distance to settlements, distance to road, and distance to water courses (since the local population mainly uses waterways for transportation) as predictor variables. We then incorporated the predictions of this model as proxy for human disturbance in our final multigroup piecewiseSEM model.

We included two vegetation-related variables for the bottom-up approach: the Enhanced Vegetation Index (EVI) and forest canopy height data. To obtain EVI data, we accessed the MOD13Q1 product (LP DAAC - MOD13Q1 (usgs.gov)) and extracted 16-day composite EVI measurements at a spatial resolution of 250 m for the period from January 1, 2019, to December 31, 2019. Subsequently, we calculated the mean EVI values across all camera trap locations. For forest canopy height, we downloaded data from the 2019 Global Forest Canopy Height dataset (~30 m resolution) available at (Global Forest Canopy Height, 2019 | GLAD - umd.edu). We then applied a circular buffer with a radius of 250 m around each camera trap to extract the average forest canopy height for each camera trap location. To establish our study objectives, we performed two primary steps: comparing biomass and analyzing causal pathways to show species associations.

2.3.1. Biomass comparison

We analyzed data from 27 mammalian species with a minimum of 10 recorded events to explore trophic associations between predators and prey species, considering human disturbances. We grouped these species into six groups based on their body size and functional roles: apex predators (i.e., tiger, leopard, clouded leopard, Asiatic black bear, Malayan sun bear and dhole), medium predators (i.e., large Indian civet, hog badger and Asian golden cat), small predators (i.e., yellow throated marten, common palm civet, leopard cat, marbled cat and crab eating mongoose), large to medium prey (hereafter large prey) (i.e., gaur, sambar, Chinese serow, wild boar and northern red muntjac), semi-arboreal prey (i.e., shortridge's langur, stump-tailed macaque, rhesus macaque and northern pig tailed macaque), and small prey (i.e., Malayan porcupine, Asiatic brush tailed porcupine, squirrels and rat), utilizing the functional database provided by the PanTHERIA (Jones et al., 2009) (Table 2). We excluded Asian elephants as prey in our study because tiger usually avoid adult elephant and only target young and weak individuals (Pakpien et al., 2017; Seidensticker and McDougal, 1993). Consequently, we computed the biomass for each group by using the relative abundance index (RAI) alongside adult species body mass data sourced from the PanTHERIA database. The RAI was calculated by using the number of independent events divided by the camera trapping days multiplied by 100 (O'Brien et al., 2003). This value represents an index of relative abundance, not a percentage, with the multiplication by 100 serving as a scaling factor making the index easier interpretable. Following this, we multiplied each species' RAI value by its corresponding adult species body mass to determine the biomass of each species and then aggregated species-level biomass by group (She et al., 2023).

Finally, we compared the biomass within the six groups across the two areas - Nam Pa Gon and Nam E Zu - using the Mann-Whitney *U* test (for example, apex predators in Nam Pa Gon vs. apex predators in Nam E Zu). Based on the biomass comparison results, we proposed two different areas as higher apex predator biomass area (hereafter HAB) and lower apex predators' biomass area (hereafter LAB) and developed eight different hypotheses, focusing on top-down and bottom-up pathways to achieve our study objective (Table 1, Fig. S1). The camera traps from these two areas are <20 km apart and share nearly identical environmental conditions, including vegetation, topography, and climate. Therefore, we assumed that these similarities make the regions suitable for a comparative analysis of the impact of varying apex predator biomass on the trophic association of the ecosystem. To further investigate variation in detection rate (i.e., number of independent detections per effective camera-days) between regions (i.e., HAB vs LAB) and seasons (i.e., dry: October to March, and wet: April to September) for each species group across regions, we used the Mann-Whitney *U* test to compare the mean detection rate.

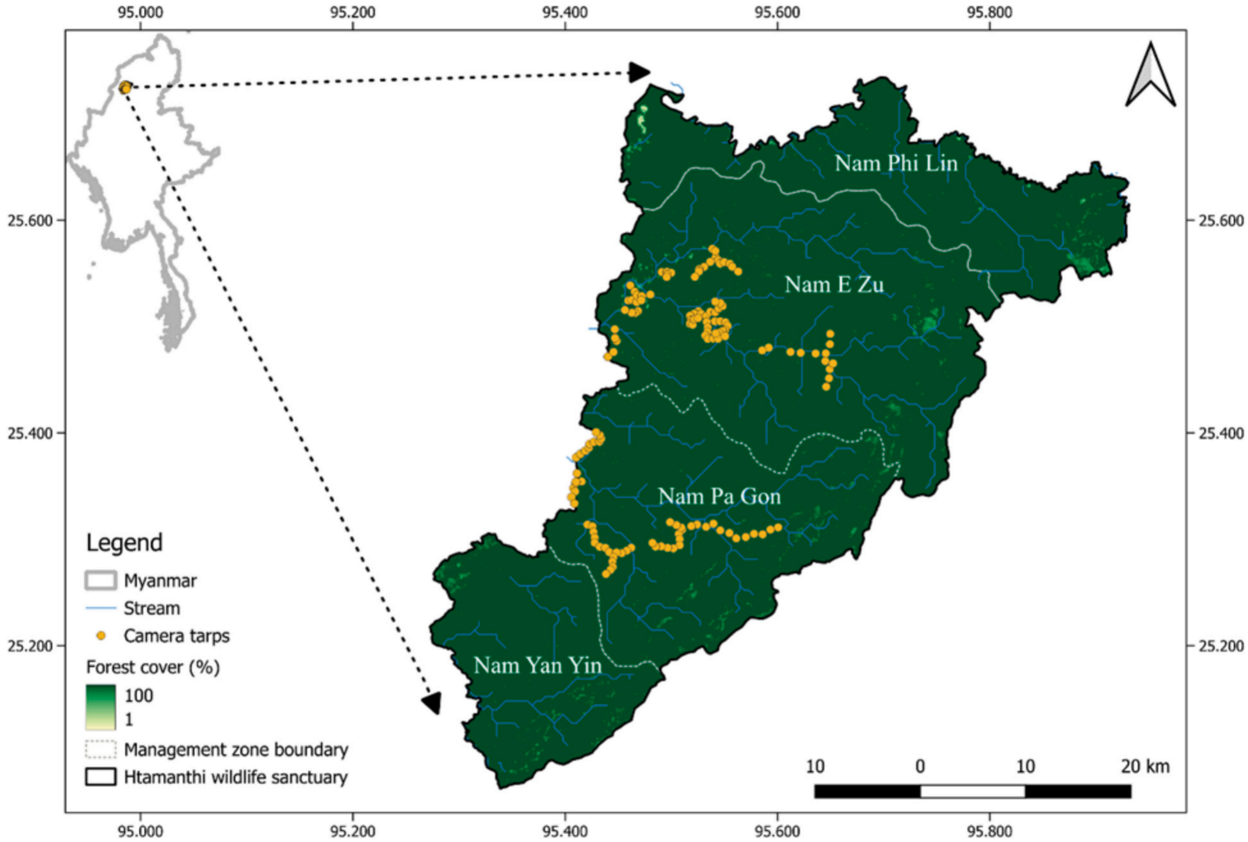

Fig. 1. Study area map showing the location of camera traps in Htamanthi Wildlife Sanctuary, northwestern Myanmar.

Table 2
List of mammal species together with their independent events (> 10), body weight, average biomass (kg) per camera trap station, diet and proposed group in the Htamanthi wildlife sanctuary.

No	Common name	Scientific name	Independent events	Body weight (kg)	Average biomass kg/station	Diet*	Group**
1	Tiger	*Panthera tigris*	207	161.9	101.47	C	APred
2	Asian black bear	*Ursus thibetanus*	19	99.71	4.06	O	APred
3	Sun bear	*Helarctos malayanus*	216	57.08	23.45	O	APred
4	Leopard	*Panthera pardus*	84	52.39	9.79	C	APred
5	Dhole	*Cuon alpinus*	88	15.8	2.53	C	APred
6	Clouded leopard	*Neofelis nebulosa*	207	14.95	6.43	C	APred
7	Large Indian civet	*Viverra zibetha*	504	9.15	9.22	C	MPred
8	Hog badger	*Arctonyx collaris*	222	8.17	4.03	C	MPred
9	Asian golden cat	*Catopuma temminckii*	173	7.73	2.42	C	MPred
10	Common palm civet	*Paradoxurus hermaphroditus*	561	3.2	3.01	C	SPred
11	Marbled cat	*Pardofelis marmorata*	82	2.83	0.43	C	SPred
12	Leopard cat	*Prionailurus bengalensis*	287	2.78	1.38	C	SPred
13	Yellow throated marten	*Martes flavigula*	82	2.51	0.43	C	SPred
14	Crab eating mongoose	*Herpestes urva*	55	2.38	0.23	C	SPred
15	Gaur	*Bos gaurus*	486	800.14	861.95	H	LPrey
16	Sambar	*Rusa unicolor*	238	177.52	76.52	H	LPrey
17	Chinese serow	*Capricornis sumatraensis*	13	110.94	1.86	H	LPrey
18	Wild boar	*Sus scrofa*	2540	84.47	443.46	O	LPrey
19	Northern red muntjac	*Muntiacus vaginalis*	5071	17.61	199.39	H	LPrey
20	Shortridge's langur	*Trachypithecus shortridgei*	24	11	0.44	H	SAprey
21	Stump tailed macaque	*Macaca arctoides*	276	9.36	5.7	H	SAprey
22	Northern pig tailed macaque	*Macaca leonina*	49	9.1	0.69	H	SAprey
23	Rhesus macaque	*Macaca mulatta*	16	6.46	0.22	H	SAprey
24	Malayan porcupine	*Hystrix brachyura*	799	8	13.55	H	SPrey
25	Asiatic brush tailed porcupine	*Atherurus macrourus*	1851	2	7.68	H	SPrey
26	Squirrel		212	0.8	0.61	O	SPrey
27	Rat		52	0.5	0.09	O	SPrey

[*] C = Carnivore, H = Herbivore, O = Omnivore.

[**] APred = Apex predator, MPred = Medium predator, SPred = Small predator, LPrey = Large prey, SAprey = Semi-arboreal prey, SPrey = Small prey.

2.3.2. *Trophic associations*

To explore the associations between the species at different tropic levels, and how those change between the regions (HAB and LAB), we fitted a piecewise structural equation model based on the eight previously identified putative causal pathways (Table 1, Fig. S1) by using series of regression models. We also checked the residual spatial autocorrelations for linear models using DHARMa package in R (Hartig and Lohse, 2022). If residual spatial autocorrelation was detected, we used a generalized least square (gls) model with exponential spatial correlation structure by using corExp argument in the gls function, and checked the successful removel of the residual autocorrelation using spline correlograms implemented in the 'ncf' R package. Finally, we fitted the final piecewise structural equation model (piecewiseSEM) with the "psem" function in R and used the multigroup function to understand the path coefficients different between HAB and LAB (Lefcheck, 2016). The multigroup approach evaluates how the model interacts with the grouping variables (i.e., HAB and LAB). If the interaction is significant, the path coefficients differ between groups; if not, they follow the global dataset (Lefcheck, 2016). The model goodness of fit was evaluated using Shipley's d-sep test (Fisher's C statistics) where $p > 0.05$ indicated a good fit by confirming conditional independence among unconnected variables (Shipley, 2009). The model was then revised by adding significant paths ($p < 0.05$) and re-evaluating fit until an optimal structure was achieved.

3. Results

We recorded 16, 263 independent events from 47,021 trapping days. We detected 36 mammal species (i.e., 31 terrestrial mammals including squirrel and rat species, 5 semi-arboreal species), one reptile (i.e., common water monitor lizard), plus birds (Table 2). According to the biomass comparison, HAB (i.e., Nam Pa Gon) showed significantly higher apex predators' biomass ($W = 2362$, $p < 0.001$) than LAB (i.e., Nam Ei Zu) and other species groups such as small predators ($W = 2013.5$, $p < 0.05$) and small prey biomass ($W = 2041$, $p < 0.05$) were also higher in HAB (Fig. 2). On the other hand, LAB supported higher semi-arboreal prey biomass ($W = 816$, $p < 0.001$) and large prey tended to be higher in LAB, though this difference was only marginally significant ($W = 1270$, $p = 0.059$) (Fig. 2). Our results showed no significant differences in detection rates between regions (i.e., HAB vs LAB) ($W = 1416.5$, $p > 0.05$) and seasons, except for the large prey between the dry and wet seasons ($W = 2316.5$, $p < 0.001$) in the LAB (Fig. S2).

3.1. *Trophic association among high and low apex predator biomass region*

Our initial multigroup piecewiseSEM model excluded the direct path from large prey to small prey, but Shipley's d-sep test (Fisher's $C = 18.329$, $df = 4$, $p = 0.001$, $AIC = 110.329$) indicated this path was significant. To improve fit, we incorporated this path in our final model and our final result demonstrated a good fit (Fisher's $C = 4.561$, $df = 2$,

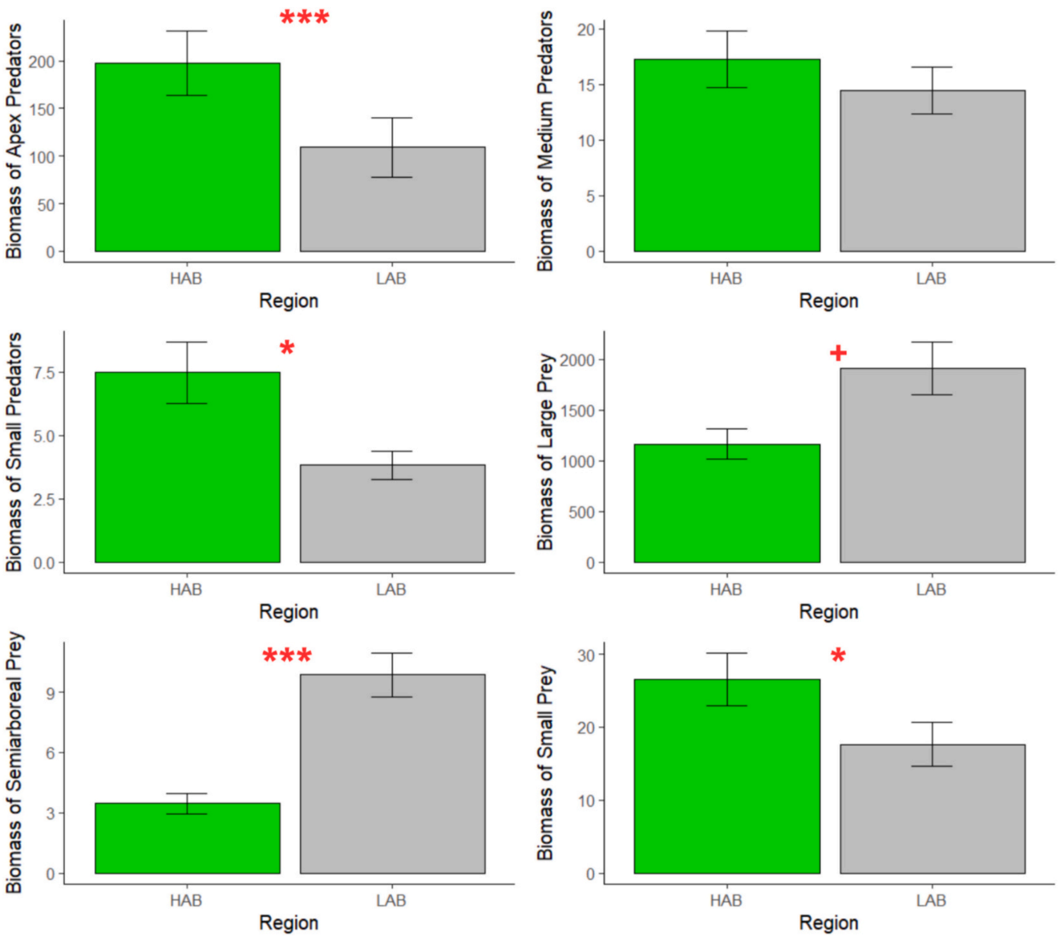

Fig. 2. Relative species community biomass comparison in two different areas: higher apex predator biomass area (HAB, green color), and lower apex predator biomass area (LAB, grey color) of Htamanthi Wildlife Sanctuary. Relative species community biomass was calculated by multiplying the relative abundance index by the respective adult species body mass. Error bars represent the mean ± standard error. Statistical significance was determined using the Mann-Whitney U test. (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, $^{+}$ $P < 0.1$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

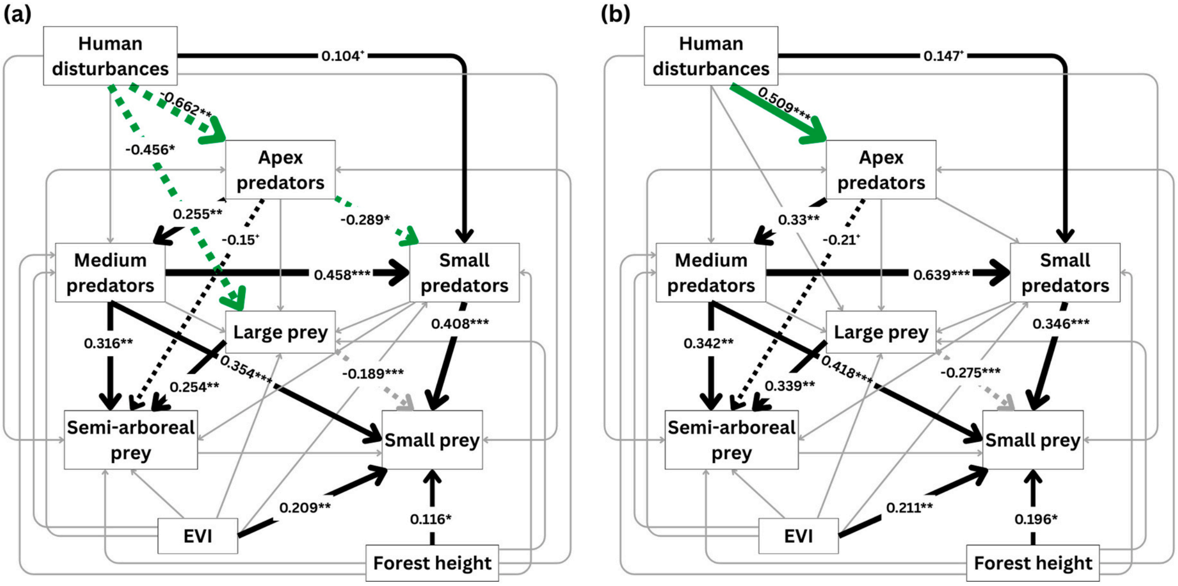

Fig. 3. The multigroup piecewise structural equation model of trophic association in Htamanthi wildlife sanctuary (Fisher's C = 4.561, df = 2, p = 0.102, AIC = 98.561). The green lines highlighted the causal paths with significant differences between the two regions: (a) higher apex predator biomass area (HAB) and (b) lower apex predator biomass area (LAB) respectively. If there is a significant causal path globally, but no significant association between groups (i.e., HAB and LAB), the lines are highlighted in black. The solid and dotted lines represent the positive and negative association among response and predictor variables and significant levels are denoted by asterisks (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, + $P < 0.1$). The strength of standardized coefficients is represented by varying line widths. Non-significant paths are shown in grey, and the grey dotted line indicates a path added based on the results of the goodness-of-fit test in the piecewiseSEM analysis. The full model output is provided in Tables S2 and S3. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

$p = 0.102$, AIC = 98.561) (Fig. 3a, b, Table S2, S3). The results revealed that the two locations HAB and LAB (presumably differing mainly in their apex predator biomass) showed significant differences in certain pathways.

Specifically, human disturbances were significantly negatively associated with apex predators in HAB, whereas in LAB, this association shifted to positive (Fig. 3a, b, human ➔ apex predators) (H1). Additionally, we found significant negative association between human disturbances and large prey in HAB, but their association was not significant in LAB (H1). Interestingly, human disturbances showed significant positive association with small predators in both regions (H1) (Fig. 3a, b, human ➔ small predators). Conversely, human exhibited a negative indirect effect on medium predators through apex predators (−0.168, human ➔ apex predators * apex predators ➔ medium predators), as well as on semi-arboreal prey mediated by large prey (−0.116, human ➔ large prey * large prey ➔ semi-arboreal prey) in HAB.

As hypothesis (H2), we found a significant negative association between apex predators and small predators in HAB. Surprisingly, there was a positive association between apex predators and medium predators in HAB, contrary to expectations (H2). In LAB, as predicted, a significant positive association between apex predators and medium predators was observed (H2) (Fig. 3b, apex predators ➔ medium predators). Hypothesis 3 was generally not supported, except for a significant negative association between apex predators and semi-arboreal prey in both regions (Fig. 3a, b, apex predators ➔ semi-arboreal prey) and apex predators exerted negative indirect effect on small prey via small predators (−0.118, apex predators ➔ small predators * small predators ➔ small prey) in HAB. Although we expected a positive association between medium and small predators in HAB and a negative association in LAB (H4), we found a consistent positive association between these predators in both regions (Fig. 3a, b, medium predators ➔ small predators). There were no significant associations between small predators with large and semi-arboreal prey in both regions, but a positive association between medium predators and semi-arboreal prey in both regions, supported hypothesis 5 (Fig. 3a, b, medium predators ➔ semi-arboreal prey).

Despite expecting variation in the association between mesopredators and small prey between HAB and LAB in hypothesis 6, our results showed a consistently significant positive association in both regions (Fig. 3a, b, mesopredators ➔ small prey). Additionally, hypothesis 7 was partially supported, found positive association between large prey and semi-arboreal prey in both regions, but no significant associations between semi-arboreal prey and small prey (Fig. 3a, b, large prey ➔ semi-arboreal prey). However, vegetation-related variables, EVI and forest canopy height, consistently showed a positive association with small prey (Fig. 3, EVI and forest height ➔ small prey) in both regions, as hypothesis 8. There were no significant associations between vegetation-related variables and other species groups (H8).

4. Discussion

Our study explored the complex trophic associations involving humans, predators, prey, and vegetation-related variables across regions with varying apex predator levels in Myanmar. The biomass in our study does not reflect total biomass, as individuals may be captured multiple times. Multiple captures are interpreted as higher site usage and greater ecological impact. Therefore, the calculated biomass serves as a relative measure of species presence and ecosystem impact (Grella et al., 2024: Gebert et al., 2019). We found that apex predator biomass significantly influences trophic associations, particularly through top-down control by both humans and apex predators. Human disturbances, especially in HAB, strongly suppressed apex predators and large prey, affecting both populations and behaviors. Apex predators exhibited both suppressive and facilitative effects on lower trophic levels, though their regulatory capacity weakened under human pressure. Additionally, positive associations within lower trophic levels were consistent across HAB and LAB. Lastly, the top-down effects of apex predators and humans predominance over the bottom-up effects of vegetation.

4.1. Trophic associations

4.1.1. Human impact on lower trophic levels (H1)

We hypothesized that human disturbances would be negatively associated with lower trophic levels in both regions (H1). However, our finding showed that in HAB, human disturbances were negatively associated with apex predators, while in LAB the association was positive (Fig. 3a, human ➔ apex predators). Moreover, apex predators serve as mediators for the negative association between human and medium predators. This suggested that apex predators are more likely to encounter humans when their biomass is higher and the potential role of humans as super predators controlling apex predators, with far-reaching ecological consequences that cannot be overlooked in trophic associations (Darimont et al., 2015; Dorresteijn et al., 2015).

The significant positive association observed between human disturbances and apex predators in LAB may be linked to the fine scale behavior of these predators (Fig. 3b, human ➔ apex predators). Kyaw et al. (2021) noted that many felid species in HWS use old logging roads to facilitate movement, expanding their range and accessing resources by adjusting their spatiotemporal activities to minimize human contact and reduce the risk of human-caused mortality (Oriol-Cotterill et al., 2015; Smith et al., 2024). For instance, tigers have been found to coexist with humans on a fine spatial scale by adapting their temporal behavior to avoid disturbances (Carter et al., 2012; Li et al., 2019). The positive association in LAB could be attributed to this movement pattern. Also, Cremonesi et al. (2021) found that some apex predators in HWS, such as the Malayan sun bear and clouded leopard, exhibited medium to low activity overlap with humans, respectively. Therefore, we suspected that human disturbances in LAB influence species behavior (i.e., anthropogenic behaviorally mediated trophic effect) rather than population density (i.e., anthropogenic density mediated trophic effect) (Kuijper et al., 2016).

We also anticipated a negative association between human disturbances and small predators in both regions. However, our study revealed a consistent positive association in both HAB and LAB (Fig. 3a, b, human ➔ small predators). One plausible explanation for this pattern is the dietary and foraging flexibility observed in certain small predators, such as martens, civets, and mongooses, which thrive in disturbed environments due to their broad diets and ability to exploit human-generated food waste and crops (Hasan and Csanyi, 2023). Moreover, species like leopard cats, exhibited high tolerance to human-impacted landscapes (Srivathsa et al., 2015; Wearn et al., 2013; Rajaratnam et al., 2007), further supporting the positive association between small predators and human disturbances observed in our study. Another factor potentially contributing to this positive association is the behavioral response of small predators to human disturbances. We suspected that these small predators perceive human disturbances as a protective shield against apex predators, strategically using it to reduce their risk of predation, especially in HAB, where apex predators suppressed their populations.

Human disturbances had a significant negative association with large prey in HAB, as expected (H1) (Fig. 3a, human ➔ large prey), which in turn mediated the negative effect of human disturbances on semi-arboreal prey, since humans often hunt these species. This suggested that human disturbances have potentially replaced apex predators in exerting top-down control on prey populations (Suraci et al., 2019). She et al. (2023) observed a similar pattern, suggesting that human impacts on prey are driven more by avoidance of predation risk than by direct killing, as hunting has been banned in their study area for decades. However, in our study area, despite the sanctuary being legally protected, human disturbances such as illegal hunting, non-wood forest product harvesting, gold mining, and illegal timber harvesting could affect both prey species not only through fear but also through direct killing (Naing et al., 2019a; Rabinowitz et al., 1995).

4.1.2. Top-down control by apex predators (H2,H3)

We initially hypothesized that apex predators would suppress lower trophic levels in HAB and that prey release would occur in LAB (H2, H3). However, the association of apex predators with medium predators and large prey in HAB contradicted this expectation. Surprisingly, we found a positive association between apex predators and medium predators, but there was no association with large prey in HAB. We suspect this unexpected association may stem from interspecific competition among apex predators, which can weaken their regulatory role and reduce predation pressure on medium predators and large prey in HAB. For example, Naing et al. (2019b) reported a leopard preying on a sun bear cub, illustrating such associations, including resource competition and intraguild predation, can disrupt typical top-down control. Secondly, it may be that human disturbances hinder apex predators from reaching their carrying capacity, thereby compromising their ability to control lower trophic levels through top-down predation dynamics effectively.

Regarding the large prey, the higher prey species richness in our survey region could be an additional factor explaining the unexpected no significant association between apex predators and large prey in our study (Fig. 3a, b, apex predators ➔ large prey, H3). In prey-rich environments, apex predators exert less pressure on individual prey species due to their broader dietary range. Ferretti et al. (2020) found that apex predators diversify their diet, switching between available prey types, which diminishes significant suppression of any single prey population. Apart from these findings, we observed the expected negative association between apex predators and small predators in HAB (Fig. 3a, apex predators ➔ small predators, H2). This supports the mesopredator release hypothesis, indicating that apex predators can still regulate small predators, even under human disturbance. This negative association may cause smaller predators to adjust their behaviors, such as changing foraging locations or times, to avoid apex predators. These adaptations are crucial for survival in landscapes where apex predators still exert influence.

Moreover, we found that apex predators exhibited a significant negative association with semi-arboreal prey in both regions, indicating that these semi-arboreal prey are sensitive to apex predators (Fig. 3a, b, apex predators ➔ semi-arboreal prey, H3). This suppression could be due to the dietary habits of certain apex predators, such as clouded leopards and leopards, which are known to have a broad diet that includes arboreal primates among other prey species (Brodie and Giordano, 2013; Shwe et al., 2023; Karanth and Sunquist, 1995; Steinmetz et al., 2013). Their adept climbing abilities and hunting strategies allow them to effectively access and prey upon semi-arboreal species that utilize ground and tree habitats. Moreover, apex predators exhibited a negative indirect association with small prey in HAB, mediated by small predators. Overall, apex predators possess dual roles in ecosystems, exhibiting suppressive and facilitative effects on lower trophic levels (Prugh and Sivy, 2020).

4.1.3. Lower trophic levels associations (H4, H5, H6, H7)

The consistent positive association between medium and smaller predators in both regions (Fig. 3a, b, medium predators ➔ small predators, H4) could results from temporal and spatial segregation among mesopredators. Kyaw et al. (2021) observed that small predators, such as marbled cats, minimize spatial and temporal overlap with Asian golden cats, and leopard cats partially avoid them in timing in HWS. This avoidance likely reduces competition among mesopredators, resulting in a positive association between medium and small predators. Another explanation is the trophic generalist nature of mesopredators, which allows them to consume a wide range of food sources based on availability (Nakashima et al., 2010). This dietary flexibility reduces direct competition through niche differentiation, facilitating coexistence within ecological communities (Chutipong et al., 2017).

The positive association between medium predators and semi-arboreal prey in both HAB and LAB (Fig. 3a, b, medium predators ➔ semi-arboreal prey, H5) is likely due to semi-arboreal prey, like primates, living in social groups that offer protection and employ diverse foraging strategies. Their broad diet and ability to exploit arboreal and terrestrial resources minimize direct competition with medium predators (Sengupta and Radhakrishna, 2016; Zhang et al., 2023; Estrada et al., 1978). Moreover, although we anticipated that small prey would be released in HAB and suppressed in LAB (Gordon et al., 2015), small prey populations thrived in both regions due to the presence of mesopredators (Fig. 3a, b, mesopredators ➔ small prey, H6). The unexpected pattern of small prey released in LAB could be attributed to two primary reasons. First, increased food resources, such as seeds and fruits, are associated with bottom-up variables like EVI and forest canopy height, enhancing the availability of food for small mammals, supporting their population growth despite predation. Second, the high reproductive rates of small mammals enable rapid population recovery, allowing their numbers to rebound quickly even in the face of predation pressure.

We found a positive association between semi-arboreal prey and large prey in both HAB and LAB, as expected (Fig. 3a, b, large prey ➔ semi-arboreal prey, H7). Semi-arboreal prey and ungulates often benefit from each other presence while sharing the same habitat, occupying different ecological niches, primates on trees and ungulates on the ground, to reduce direct competition for resources. They typically consume different parts of plants or different plant species, such as fruits and leaves versus grasses and shrubs (ter Schure et al., 2020). Moreover, primates play a crucial role in seed dispersal by eating fruits and spreading seeds through their faeces. This provides ungulates by ensuring a continuous food supply from new plant growth. Additionally, both groups benefit from mutual vigilance, with primates in trees spotting predators from afar and alerting ungulates (Heymann and Hsia, 2015).

4.1.4. Potential bottom up effects (H8)

The observed significant positive association between forest canopy height, EVI, and small prey populations in both regions can be attributed to several ecological factors (Fig. 3a, b, forest height and EVI ➔ small prey, H8). Healthier vegetation, indicated by higher EVI values, generally provides more food resources and shelter for smaller animals, leading to increased population densities. Taller forests offer greater structural complexity, creating a variety of niches and providing protection from mesopredators (Jacob, 2008). This habitat complexity is crucial for small prey species as it enhances their chances of survival and reproductive success. Additionally, dense vegetation offers numerous hiding places and escape routes, reducing the vulnerability of small prey to predators and allowing their populations to grow.

Our study found that the absence of significant direct associations between vegetation and both apex predators and large prey (Fig. 3a, b, forest height and EVI ➔ apex predators, large prey, H8). Apex predators do not directly depend on vegetation characteristics due to their broad dietary preferences and diverse hunting strategies. Their presence and behavior are influenced by prey availability, habitat suitability, and competition dynamics rather than solely by vegetation structure (Kuijper et al., 2016; Colman et al., 2015). Additionally, apex predators exhibit high behavioral flexibility, enabling them to adapt to various environmental conditions and utilize diverse habitats, making their distribution less reliant on specific vegetation features than smaller predators. Similarly, the absence of significant associations between vegetation and large prey could be due to the stable, year-round primary productivity driven by relatively constant temperature, precipitation and consequently productivity in tropical region. The stable primary productivity results in more balanced and less variable trophic associations, making bottom-up effects less pronounced compared to regions with low productivity (Cano-Martínez et al., 2024; Stoessel et al., 2018; Terborgh, 2015).

4.2. Study limitations and future directions

This study utilized camera trap data to infer mammal trophic associations; however, this approach may provide less detailed information compared to direct methods such as scat analysis or stable isotope analysis (Meyer et al., 2020; Reum et al., 2020). We acknowledge that imperfect detection may have influenced our results, particularly due to factors such as camera position, deployment period and the varying detectability of species (e.g., ground-dwelling vs arboreal species). Unfortunately, we could not account for this in our model, as our focus was on community-level patterns. Future studies should address this limitation by incorporating methods that account for imperfect detection. Our research defined human activities in the camera traps as indicators of human disturbances, but recent studies by Nickel et al. (2020) showed that different anthropogenic disturbances (i.e., human presence and human footprint) can have diverse impacts on mammal communities.

Also, we grouped multiple species based on their functional roles within trophic groups instead of solely focusing on individual species to align with our objective. While this approach may result in a loss of species-level information, further studies focusing on the species level are essential for a comprehensive understanding of predator-prey association at different trophic levels. Moreover, incorporating bottom-up factors related to primary productivity is crucial, as they support upper trophic levels by providing essential resources. Due to a lack of data accessibility in our study area, we relied on EVI and forest canopy height data as proxies for primary productivity, which may not sufficiently capture ecosystem productivity. Additional research should incorporate more comprehensive variables to facilitate a deeper understanding and precise representation of ecosystem dynamics and productivity.

4.3. Conclusion

We studied trophic cascades in tropical Southeast Asia forest, exploring the impacts of human disturbances and apex predators across different levels of apex predator biomass and involving multiple species. Our study supported Darimont et al.'s (2015) assumption of human as 'super predator' and they can reduce the regulatory role of apex predators. We found apex predators exert both suppression and facilitation on lower trophic levels, whereas their regulatory role was relatively weak, even in HAB. This may aligned with Kyaw et al. (2021), who suggested that apex predators in HWS face pressure from human disturbances, impacting their ability to regulate lower trophic levels. Therefore, our result highlighted that prioritizing protecting and restoring apex predator populations alone is insufficient to maintain ecosystem balance; it is also necessary to reduce human pressures.

We found predominant positive associations among lower trophic levels, which can facilitate mutualistic associations and adaptive behaviors, reduce direct competition among species, and promote coexistence (Schoener, 1974). These facilitative associations suggested that biodiversity conservation should prioritize preserving entire species assemblages rather than focusing solely on charismatic species. Although our study highlighted that bottom-up processes from vegetation, given that it is a rough approximation, are weaker than top down processes from humans and apex predators, we recommend considering both processes as influential factors in trophic associations. Vegetation variables linked to bottom-up process, such as key food sources for small prey, are vital for seed dispersal, forest regeneration, and overall ecosystem resilience. Maintaining keystone plant resources is crucial for supporting prey populations and promoting forest recovery. Unfortunately, tropical Southeast Asian forests face significant anthropogenic pressures, disrupting both trophic mechanisms by altering habitats, reducing forest productivity, and changing vegetation composition. While not immediately evident, these changes can have profound ecological implications over time, affecting entire trophic associations and necessitating conservation efforts to mitigate disturbances and safeguard long-term ecosystem health and stability.

To enhance conservation effectiveness, apex predator conservation should extend beyond designated protected areas by establishing habitat corridors. For example, the Yaybawmee Corridor, spanning 3213 km^2 of unprotected forest north of Htamanthi, could link Htamanthi to the Hukaung Valley Wildlife Sanctuary, as recommended by Naing et al. (2019a). Law enforcement efforts should also be aligned with customary practices and supported by public awareness initiatives to ensure effective conservation. However, challenges such as inadequate infrastructure, a limited number of skilled professionals, and political instability hinder successful management. To address these obstacles, local communities need to take an active role in conservation through community-based efforts (Lwin et al., 2023). This approach will strengthen local stewardship and resilience, even amid political challenges. By integrating biodiversity conservation with indigenous rights, this inclusive strategy can promote sustainable environmental protection while respecting the needs and knowledge of local communities.

Overall, we tested eight different hypotheses with multiple causal paths to understand the trophic associations among multiple species, incorporating human disturbances and vegetation into the networks. The associations between multiple species proved to be more complex than we initially expected, and our results did not fully align with all of our initial predictions. Nonetheless, our systematic modeling and analytical approach significantly enhances understanding of these complex trophic associations, primarily through examining the interplay among human disturbances, apex predators, and multiple prey communities in tropical forest ecosystems.

CRediT authorship contribution statement

Ye Htet Lwin: Writing – original draft, Formal analysis, Writing – review & editing, Methodology, Conceptualization, Visualization, Data curation. **Rui-Chang Quan:** Funding acquisition, Supervision, Writing – review & editing, Conceptualization. **Florian Hartig:** Formal analysis, Supervision, Writing – review & editing. **Hjalmar S. Kühl:** Conceptualization, Supervision, Writing – review & editing. **Marco Heurich:** Writing – review & editing, Conceptualization, Funding acquisition, Supervision.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111352.

Data availability

Due to the sensitive location of threatened species, the data are not publicly available but can be requested from the corresponding author.

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