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Original Article

Community structure, spatial distribution, and species–station association of Asian horseshoe crabs from North Kalimantan, Indonesian Borneo

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Abstract: Asian horseshoe crabs are ecologically important coastal arthropods, but local community-level information from North Kalimantan, Indonesian Borneo, remains limited. This study assessed species composition, relative abundance, diversity, dominance, evenness, species-station association, occupancy, and inter-station similarity of Asian horseshoe crabs recorded from four coastal stations in North Kalimantan. A total of 205 individuals were documented through fisher-assisted bycatch records from traditional kelong trap-net fisheries and identified as *Carcinoscorpius rotundicauda*, *Tachypleus gigas*, and *T. tridentatus*. Community structure was analyzed using relative abundance, Shannon-Wiener diversity, Simpson dominance, Pielou evenness, chi-square species-station association, adjusted standardized residuals, occupancy, and Bray-Curtis similarity. *Carcinoscorpius rotundicauda* was the most abundant species, followed by *T. gigas* and *T. tridentatus*. Clear spatial differentiation was observed among stations. Bening Island was strongly dominated by *T. gigas*, whereas Karis Island and Mangkudulis Island were dominated by *C. rotundicauda*. Tanalia Island showed the most balanced community and the strongest positive association with *T. tridentatus*. Bray-Curtis similarity identified Karis Island and Mangkudulis Island as the most similar stations, while Bening Island was the most distinct. These findings provide baseline ecological information on protected horseshoe crab species in North Kalimantan and highlight the importance of habitat-based monitoring that accounts for station-specific community signatures, as well as the limitations of bycatch-derived data.

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Introduction

Horseshoe crabs are ancient marine arthropods belonging to the order Xiphosura and are recognized for their ecological, evolutionary, and conservation significance. In Asia, three extant species are important in coastal ecosystems: *Carcinoscorpius rotundicauda*, *Tachypleus gigas*, and *T. tridentatus*. These species occupy mangroves, estuaries, intertidal mudflats, sandy beaches, seagrass-associated areas, and shallow waters. Such habitats serve as movement and feeding areas, nursery grounds, shelters, and productive zones that support juvenile development and coastal food-web processes (Nagelkerken et al., 2008; Vestbo et al., 2018; Xie et al., 2019; Kwan et al., 2020, 2022; Liao et al., 2025).

Despite their ecological importance, Asian horseshoe crabs are threatened by habitat degradation, mangrove and mudflat loss, coastal reclamation, bycatch, pollution, exploitation, and coastal transformation (Liao et al., 2017; Vestbo et al., 2018; John et al., 2020; Tang et al., 2024; Liao et al., 2025). These pressures are concerning because horseshoe crabs rely on habitat mosaics during different life stages. Habitat-modifying activities can alter nursery quality, disrupt movement, and affect juvenile density and behavior (Kwan et al., 2017, 2020; Xie et al., 2019). Effective management, therefore, requires baseline data, monitoring, habitat characterization, and cross-site comparisons of population and community patterns (Wang et al., 2019; Koyama et al.,

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2020; Rozaini et al., 2023; Shih et al., 2025).

Indonesia is an important part of the regional distribution range of Asian horseshoe crabs. Studies from Indonesian coastal waters have reported the occurrence, morphometric variation, environmental associations, and genetic diversity of *C. rotundicauda* and *T. gigas* in estuarine and mangrove-associated habitats (Fauziyah et al., 2019, 2021; Sari et al., 2020; Fatimah et al., 2023; Kurniawan et al., 2024). Genetic evidence indicates high diversity and connectivity among *T. gigas* populations across Sundaland habitats, suggesting regional links through coastal and estuarine corridors (Aini et al., 2021; Fatimah et al., 2023; Kurniawan et al., 2024). Studies from Malaysia, Brunei Bay, and the Sunda Shelf show that horseshoe crab populations are shaped by mangrove connectivity, estuarine structure, salinity gradients, substrate conditions, and regional biogeographic history (Fairuz-Fozi et al., 2021; Rozaini et al., 2023; Tang et al., 2024; Liao et al., 2025).

North Kalimantan, located in Indonesian Borneo, contains coastal islands, estuarine waters, mangrove systems, intertidal flats, and muddy-to-sandy-muddy substrates that may support Asian horseshoe crab communities. However, local community-level information from this region remains limited. Nearby Borneo records, including Pulau Bedukang in Brunei Bay, show that mangrove-mudflat nursery habitats can support co-occurring horseshoe crab populations and provide baseline data for conservation planning (Rozaini et al., 2023). Data from North Kalimantan are needed to complement Indonesian and Borneo records and clarify whether local stations differ in species composition, dominance, and similarity.

Several research gaps remain unresolved. First, community-level data on Asian horseshoe crabs from North Kalimantan are scarce. Second, many Indonesian studies have focused on occurrence records, morphology, morphometrics, environmental conditions, or genetic diversity, whereas fewer studies have quantified station-level community structure using abundance, diversity, dominance, evenness, occupancy, and similarity metrics. Third, species–station association has rarely been used to identify over- or under-representation of species at coastal locations. Fourth, abundance-based inter-station similarity remains underused, although it can reveal whether stations share comparable community structure or differ in dominance patterns (Beck et al., 2013; Legendre and Cáceres, 2013; Wang et al., 2019; Rozaini et al., 2023; Liao et al., 2025).

To address these gaps, this study documents the community structure and spatial distribution of three Asian horseshoe crab species from coastal stations in North Kalimantan. The novelty lies in its integrated station-level community approach. To the best of our knowledge, this is one of the first assessments from North Kalimantan to combine species composition, relative abundance, Shannon diversity, Simpson dominance, Pielou evenness, chi-square species–station association, adjusted standardized residuals, occupancy, Bray–Curtis similarity, and clustering within a single analytical framework. This approach moves beyond species occurrence records by identifying species–station signatures and abundance-based community differentiation. The objectives of this study were to: (1) analyze species composition and relative abundance; (2) evaluate diversity, dominance, and evenness across stations; (3) test species–station association; (4) assess occupancy and inter-station similarity; and (5) provide baseline ecological information to support monitoring and conservation of Asian horseshoe crabs in North Kalimantan, Indonesian Borneo.

Materials and Methods

Study area and sample collection: This study was conducted in the coastal waters of North Kalimantan, Indonesian Borneo, from January to April 2025. Sampling was carried out at four stations representing shallow coastal, estuarine, intertidal, and mangrove-associated habitats: ST1PB/Bening Island, ST2PK/Karis Island, ST3PM/Mangkudulis Island, and ST4PT/Tanalia Island. The stations were generally characterized by shallow waters, tidal influence, mangrove-associated shorelines, and muddy-to-sandy-muddy substrates. These habitat descriptions were used to contextualize station-level

Figure 1. Map of horseshoe crab sampling sites in the waters of North Kalimantan, Indonesia.

community patterns, but they were not included as inferential environmental predictors in the present analysis (Fig. 1).

A total of 205 horseshoe crab individuals were recorded during the study using a fisher-assisted opportunistic bycatch sampling approach. Field observations were conducted by following local fishers operating traditional stationary trap nets locally known as kelong. These passive gears are commonly installed in shallow mangrove-associated waters and use tidal currents to guide fish, shrimp, and mangrove crabs into the trap chamber. Horseshoe crabs were not target organisms in this fishery and were recorded only when they occurred as incidental bycatch. The field sampling context is illustrated in Figure 2, showing (Fig. 2A) the traditional stationary trap net locally known as kelong installed in shallow mangrove-associated waters and (Fig. 2B) horseshoe crabs recorded as incidental bycatch during fisher-assisted sampling at Tanalia Island on 24 January 2025.

Species identification and morphometric measurement: Each individual was identified to species level based on external morphological characters. The species analyzed in this study were *C. rotundicauda*, *T. gigas*, and *T. tridentatus*. Species codes used in the analysis were CR for *C. rotundicauda*, TG for *T. gigas*, and TT for *T. tridentatus*. Morphometric measurements were recorded to the nearest 1 cm. The measured parameters included total length (TL), telson length (TEL), prosoma width (PW), and carapace length (CL). Total length was measured from the most anterior part of the carapace to the distal end of the telson. Telson length was measured from the telson base to the distal tip. Prosoma width was measured

Figure 2. Fisher-assisted bycatch sampling using traditional kelong trap nets. (A) Traditional kelong trap net in shallow mangrove-associated waters. (B) Horseshoe crabs were recorded as incidental bycatch at Tanalia Island on 24 January 2025.

horizontally across the widest part of the prosoma, whereas carapace length was measured vertically from the anterior margin to the posterior margin of the carapace (Fig. 3).

Data analysis: Analyses were performed in R 4.3.0 using dplyr for data handling, ggplot2 for visualization, and vegan for diversity and community similarity analyses, while selected statistics were also verified by manual calculation. The analytical focus was community structure, spatial distribution, species–station association, naive station occupancy, and inter-station similarity. Because the study was based on four stations, three species, and opportunistic bycatch records, the results were interpreted primarily as descriptive community ecology supported by categorical association and similarity analyses. Environmental variables were not tested inferentially; therefore, habitat-related explanations were treated as ecological interpretations rather than causal conclusions. All community indices and similarity measures were calculated from raw abundance counts obtained from fisher-assisted bycatch records, rather than from standardized catch-per-unit-effort data. Therefore, the resulting values should be interpreted as patterns of relative community composition among stations, not as standardized estimates of population density or fishing-corrected abundance.

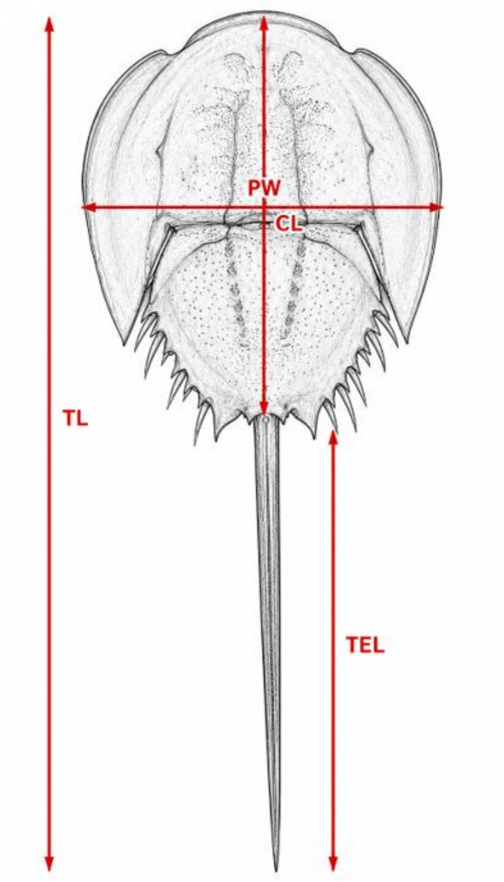

Figure 3. Sketch of morphometric measurements of horseshoe crabs.

Species composition and relative abundance: Species composition was calculated as the number of individuals of each species, expressed as a percentage of the total. Relative abundance was calculated for the overall dataset and within each station using the formula: $RA_i = (n_i / N) \times 100\%$, where RA_i is the relative abundance of species i, n_i is the number of individuals of species i, and N is the total number of individuals observed. Station-level relative abundance was used to identify the dominant species at each sampling station.

Diversity, dominance, and evenness indices: Community diversity and dominance were calculated for each station using species richness, total abundance, the Shannon–Wiener diversity index, the Simpson dominance index, the Simpson diversity index, and the Pielou evenness index. Species richness (S) was defined as the number of species recorded at each station, whereas total abundance (N) was the total number of individuals recorded at each station. The Shannon–Wiener diversity index was calculated as: $H' = - \Sigma_{i=1}^{s} (p_i \ln p_i)$, where p_i is the proportional abundance of species i in a station. Simpson dominance was calculated using the formula $D = \Sigma_{i=1}^{s} p_i^2$, and Simpson diversity was expressed as $1 - D$. Pielou evenness was calculated as $J = H' / \ln(S)$, where J describes how evenly individuals are distributed among the species present in each station. These indices were used to compare the balance of community structure among stations.

Species–station association: Species-station association was evaluated using a chi-square test of independence based on a contingency table of species abundance by station. The chi-square statistic was calculated as: $\chi^2 = \Sigma_i \Sigma_j [(O_{ij} - E_{ij})^2 / E_{ij}]$, where O_{ij} is the observed count of species i at station j, and E_{ij} is the expected count under the null hypothesis that species distribution is independent of station identity. Expected counts were calculated as: $E_{ij} = (R_i \times C_j) / N$, where R_i is the row total for species i, C_j is the column total for station j, and N is the grand total. The degrees of freedom were calculated as: $df = (r - 1)(c - 1)$, where r is the number of species categories, and c is the number of station categories. Because some expected cell counts were below five, a Monte Carlo p-value was used to support the interpretation of the chi-square test.

The strength of species–station association was quantified using Cramer's V: $V = \sqrt{[\chi^2 / \{N \times \min(r - 1, c - 1)\}]}$, where $\min(r - 1, c - 1)$ is the smaller dimension of the contingency table. Cramer's V ranges from 0 to 1, with higher values indicating a stronger association between species and stations. Adjusted standardized residuals were used to identify the species–station combinations contributing most strongly to the association pattern. Adjusted residuals were calculated as: $AR_{ij} = (O_{ij} - E_{ij}) / \sqrt{[E_{ij}(1 - R_i/N)(1 - C_j/N)]}$, where AR_{ij} is the adjusted residual for species i at station j. Positive residuals indicate that a species was observed more frequently than expected at a station, whereas negative residuals indicate under-representation. Residuals with large absolute values were interpreted as the main contributors to species–station differentiation.

Presence–absence, occupancy, and similarity among stations: A presence-absence matrix was constructed by assigning a value of 1 when a species was present at a station and 0 when absent. Species occupancy was calculated as: $\text{Occupancy}_i = (S_i / S_t) \times 100\%$, where S_i is the number of stations where species i was recorded, and S_t is the total number of sampling stations. Inter-station similarity based on presence–absence data was evaluated using Jaccard and Sørensen similarity indices. Jaccard similarity was calculated as: Jaccard similarity = a / (a + b + c), where a is the number of species shared by two stations, b is the number of species present only in the first station, and c is the number of species present only in the second station. Sørensen similarity was calculated as: Sørensen similarity = 2a / (2a + b + c).

Abundance-based similarity among stations was calculated using Bray-Curtis similarity: $\text{BC similarity}_{jk} = 1 - [\Sigma_i |x_{ij} - x_{ik}| / \Sigma_i (x_{ij} + x_{ik})]$, where x_{ij} and x_{ik} are the abundances of species i at stations j and k, respectively. Bray–Curtis similarity values range from 0 to 1, where values closer to 1 indicate a more similar abundance structure between stations. A UPGMA clustering approach was used to visualize station grouping based on Bray-Curtis dissimilarity.

Results

Species composition and relative abundance: A total of 205 horseshoe crab individuals were recorded from four coastal stations in North Kalimantan, Indonesian Borneo. Three Asian horseshoe crab species were identified: *C. rotundicauda*, *T. gigas*, and

Table 1. Species composition of horseshoe crabs in North Kalimantan.

Species	Species code	Number of individuals (n)	Composition (%)
Carcinoscorpius rotundicauda	CR	109	53.17
Tachypleus gigas	TG	75	36.59
Tachypleus tridentatus	TT	21	10.24
Total	-	205	100.00

Table 2. Species abundance and relative abundance of horseshoe crabs by station.

Station	Location	CR n (%)	TG n (%)	TT n (%)	Total N	Dominant species
ST1PB	Bening Island	1 (1.92)	49 (94.23)	2 (3.85)	52	TG
ST2PK	Karis Island	32 (76.19)	6 (14.29)	4 (9.52)	42	CR
ST3PM	Mangkudulis Island	62 (82.67)	13 (17.33)	0 (0.00)	75	CR
ST4PT	Tanalia Island	14 (38.89)	7 (19.44)	15 (41.67)	36	TT

Note: CR = *Carcinoscorpius rotundicauda*; TG = *Tachypleus gigas*; TT = *Tachypleus tridentatus*. Values in parentheses indicate relative abundance within each station (%).

Table 3. Diversity and dominance indices of horseshoe crab communities by station.

Station	Location	N	S	Shannon H′	Pielou J	Simpson D
ST1PB	Bening Island	52	3	0.2573	0.2342	0.8898
ST2PK	Karis Island	42	3	0.7091	0.6455	0.6100
ST3PM	Mangkudulis Island	75	2	0.4611	0.6653	0.7134
ST4PT	Tanalia Island	36	3	1.0505	0.9562	0.3627

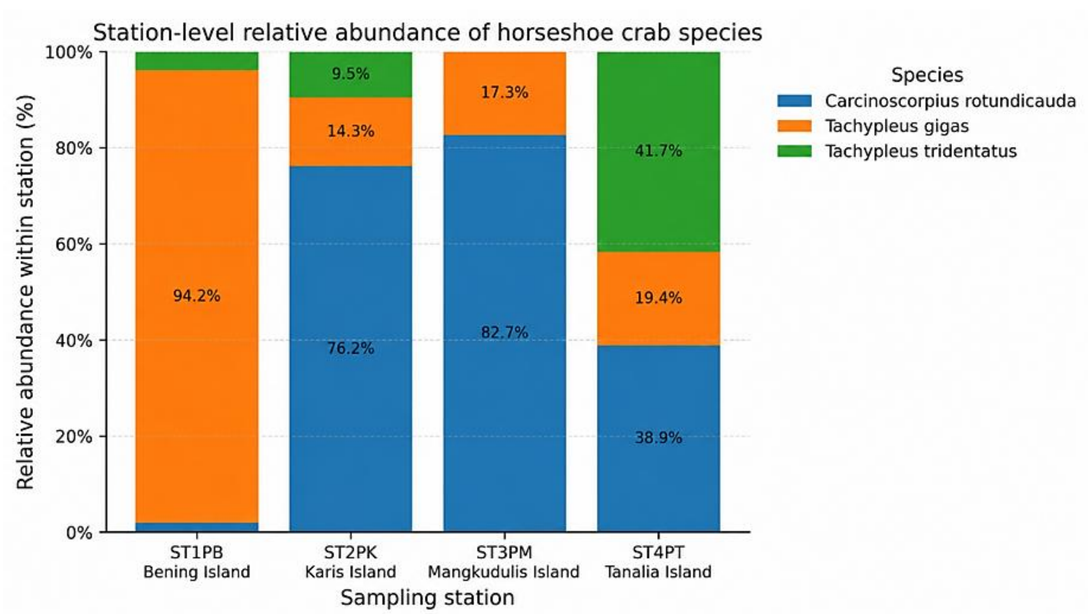

Figure 4. Relative abundance of horseshoe crab species across sampling stations.

T. tridentatus. Overall, *C. rotundicauda* was the dominant species, with 109 individuals (53.17%), followed by *T. gigas* with 75 individuals (36.59%) and *T. tridentatus* with 21 individuals (10.24%) (Table 1).

Species composition differed markedly among stations (Table 2; Fig. 4). Bening Island was strongly dominated by *T. gigas*, which represented 49 of 52 individuals (94.23%). In contrast, Karis Island and Mangkudulis Island were dominated by *C. rotundicauda*, contributing 76.19% and 82.67% of individuals, respectively. Tanalia Island showed the most balanced species composition, with *T. tridentatus* contributing the highest proportion (41.67%), followed by *C. rotundicauda* (38.89%) and *T. gigas* (19.44%).

Community diversity, dominance, and evenness: Community indices confirmed that the four stations differed not only in abundance but also in the balance

Table 4. Results of species-station association analysis.

Statistic / result	Value / interpretation
Chi-square	151.4341
Degrees of freedom	6
p-value	< 0.001
Monte Carlo p-value	0.00001
Cramer's V	0.6077; strong species–station association
Expected cells < 5	2 of 12 cells
Main over-represented associations	ST1PB × *Tachypleus gigas*; ST2PK × *Carcinoscorpius rotundicauda*; ST3PM × *Carcinoscorpius rotundicauda*; ST4PT × *Tachypleus tridentatus*

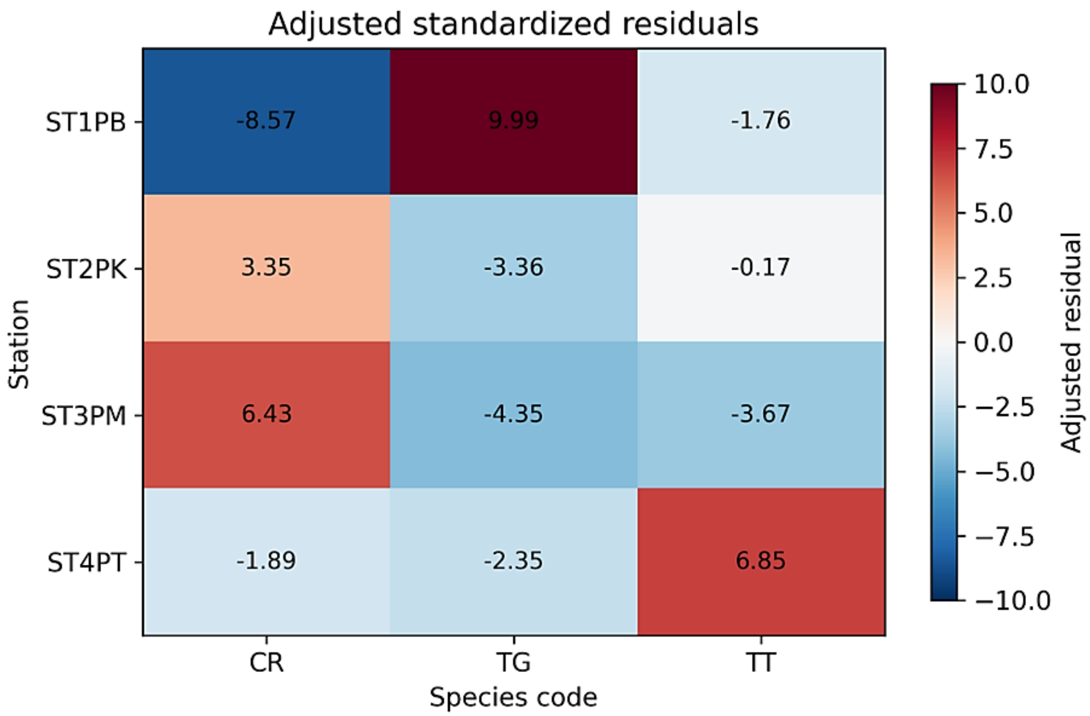

Figure 5. Heatmap of adjusted standardized residuals for species-station associations.

of species within their communities (Table 3). Tanalia Island had the highest Shannon diversity, highest Pielou evenness, and lowest Simpson dominance, indicating the most even community structure. By contrast, Bening Island had the lowest Shannon diversity, lowest evenness, and highest dominance, reflecting the overwhelming dominance of *T. gigas*. Karis Island and Mangkudulis Island showed intermediate values but remained dominated by *C. rotundicauda*.

Species-station association: The chi-square test showed that species distribution differed significantly among stations, and Monte Carlo support confirmed the observed pattern of association. Cramer's V indicated a strong association between species identity and station (Table 4). Adjusted standardized residuals identified the main species-station combinations driving this pattern (Fig. 5). Bening Island was strongly associated with *T. gigas*, Karis Island and Mangkudulis Island were associated with *C. rotundicauda*, and Tanalia Island was associated with *T. tridentatus*.

Occupancy and community similarity among stations: Presence-absence analysis showed that *C. rotundicauda* and *T. gigas* occurred at all four stations, resulting in full station occupancy, whereas *T. tridentatus* occurred at three stations. Bray-Curtis similarity provided an abundance-based representation of community resemblance (Fig. 6). Karis Island and Mangkudulis Island were the most similar pair of stations, mainly because both were dominated by *C. rotundicauda*. Bening Island showed

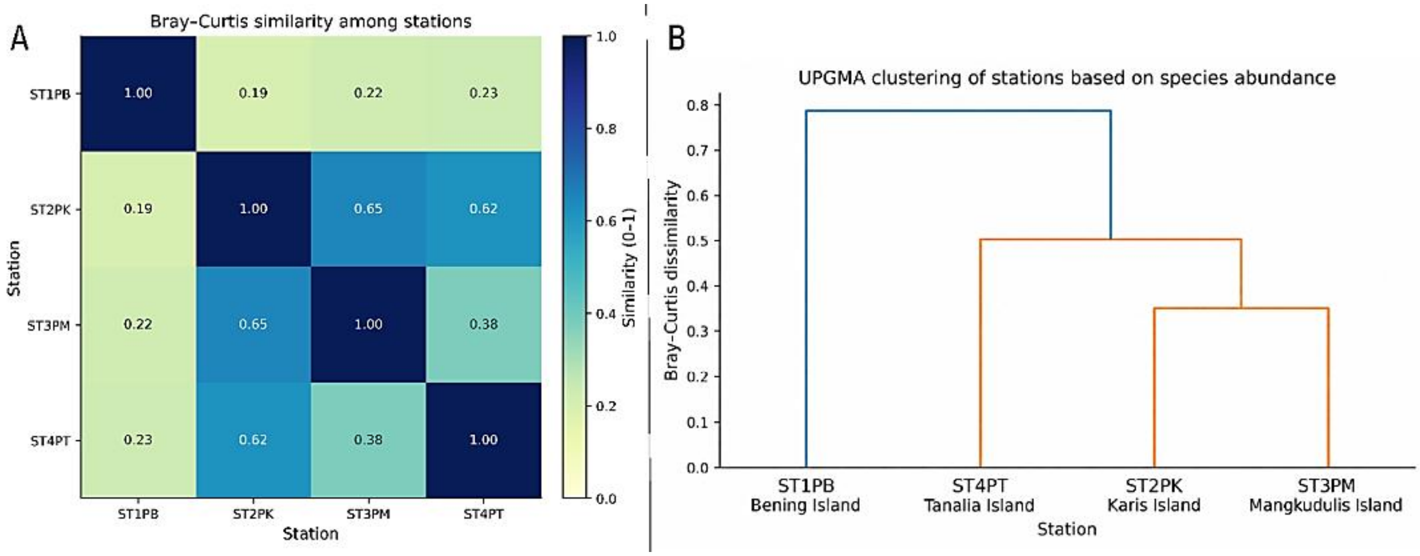

Figure 6. Bray-Curtis similarity heatmap and station clustering based on species abundance.

low similarity to all other stations, reflecting its strong dominance by *T. gigas*. The clustering pattern grouped Karis Island and Mangkudulis Island most closely, followed by Tanalia Island, while Bening Island remained the most distinct station.

Discussions

The occurrence of all three Asian horseshoe crab species in the same coastal region indicates that North Kalimantan supports a habitat mosaic suitable for multiple xiphosuran taxa. This finding is consistent with previous reports that Asian horseshoe crabs occupy estuaries, mangrove-associated mudflats, sandy-muddy intertidal zones, shallow bays, and coastal waters across Southeast Asia (Vestbo et al., 2018; Fauziyah et al., 2019; Xie et al., 2019; Rozaini et al., 2023). The dominance of *C. rotundicauda* suggests that several sampling sites may provide conditions commonly associated with mangrove estuaries and muddy substrates, whereas the substantial contribution of *T. gigas* reflects the availability of more open coastal or sandy-muddy habitats. However, because the present study did not directly model environmental variables, these habitat interpretations should be treated as ecological inferences rather than causal explanations.

The station-level differences indicate that the horseshoe crab community in North Kalimantan is spatially heterogeneous rather than regionally uniform. Similar spatial structuring has been reported in other Asian horseshoe crab habitats, where species occurrence and juvenile density are influenced by estuarine gradients, substrate type, tidal exposure, vegetation, and proximity to nursery grounds (Xie et al., 2019; Kwan et al., 2020; Rozaini et al., 2023; Liao et al., 2025). Therefore, the strong dominance of different species at different North Kalimantan stations likely reflects local habitat filtering, species-specific habitat use, and the spatial arrangement of mangrove-estuarine and open coastal environments.

The contrast between total abundance and diversity is ecologically important. Mangkudulis Island had the highest number of individuals but only two species, whereas Tanalia Island had fewer individuals but a more even distribution among all three species. Thus, total catch alone would not adequately describe community condition. Diversity, dominance, and evenness indices are useful because they capture different dimensions of community structure, including proportional contribution, degree of dominance, and balance among co-occurring species. The species-station association provides a clearer ecological interpretation than abundance summaries alone, as it shows where each species was over- or under-represented relative to the expected distribution. In practical terms, each station had a distinct community signature: Bening Island was characterized by *T. gigas* dominance, Karis Island and

Mangkudulis Island by *C. rotundicauda* dominance, and Tanalia Island by a comparatively high contribution of *T. tridentatus*.

Stations with similar species lists may still differ substantially in community structure if dominance patterns differ. Abundance-based similarity can help identify groups of stations that may require different monitoring or management attention. In this study, Karis Island and Mangkudulis Island may represent a *C. rotundicauda*-dominated community type, Bening Island a *T. gigas*-dominated type, and Tanalia Island a more balanced assemblage with a relatively high proportion of *T. tridentatus*.

Overall, the results show that North Kalimantan supports all three Asian horseshoe crab species but that their local community structures are strongly differentiated among stations. This finding strengthens the role of Indonesian Borneo as part of a broader Southeast Asian and Sundaland conservation landscape for Asian horseshoe crabs, where connectivity, genetic diversity, nursery habitat availability, and habitat degradation are important conservation concerns (Aini et al., 2021; Fairuz-Fozi et al., 2021; Fatimah et al., 2023; Kurniawan et al., 2024; Liao et al., 2025). The conservation value of this study lies primarily in its local baseline contribution. North Kalimantan remains poorly represented in horseshoe crab ecological literature, yet the present data show clear evidence of species co-occurrence, station-level dominance, and abundance-based differentiation. These findings can support future monitoring by identifying stations that may function as priority sites for different species. Bening Island may be important for tracking *T. gigas*, Karis Island and Mangkudulis Island for *C. rotundicauda*, and Tanalia Island for multispecies coexistence and *T. tridentatus* occurrence.

At the same time, several limitations must be recognized. First, the data were obtained through fisher-assisted opportunistic bycatch records from traditional kelong trap nets. Capture probability may have been influenced by trap placement, fishing effort, tidal conditions, season, gear selectivity, and fisher activity. Therefore, the abundance values reported here should be interpreted as relative abundance in bycatch records, not as standardized estimates of population density. Second, environmental variables such as salinity, substrate composition, water depth, mangrove cover, distance to estuary, and anthropogenic pressure were not analyzed inferentially. As a result, the study can identify spatial community patterns but cannot test the environmental mechanisms responsible for those patterns. Despite these limitations, bycatch-based information remains valuable when interpreted carefully. In coastal regions where systematic monitoring remains limited, fisher-assisted records can reveal the presence of protected and conservation-relevant species, provide preliminary spatial information, and guide the design of more standardized surveys.

Conclusion

This study recorded three Asian horseshoe crab species in the coastal waters of North Kalimantan, Indonesian Borneo, namely *C. rotundicauda*, *T. gigas*, and *T. tridentatus*. Overall, *C. rotundicauda* was the most abundant species, but community dominance varied clearly among sampling stations. Bening Island was characterized by the dominance of *T. gigas*; Karis Island and Mangkudulis Island by *C. rotundicauda*; and Tanalia Island by a more balanced community structure, with the highest contribution from *T. tridentatus*. The diversity, association, and similarity analyses confirmed that horseshoe crab communities in North Kalimantan were spatially differentiated. Tanalia Island showed the highest diversity and evenness, whereas Bening Island had the strongest dominance pattern. The significant species–station association and high Cramer's V value indicated that species composition was strongly related to station identity. This pattern was further supported by Bray–Curtis similarity and UPGMA clustering, which identified Karis Island and Mangkudulis Island as the most similar stations and Bening Island as the most distinct. These findings provide baseline ecological information for Asian horseshoe crabs in North Kalimantan and emphasize the importance of habitat-specific conservation and monitoring.

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Ethical and conservation considerations: Horseshoe crabs recorded in this study were incidental bycatch from traditional kelong or stationary trap-net fisheries, not target catch. Based on field observations and information from local fishers, they were considered unwanted catch because they had no direct market value, could damage kelong nets, and were protected wildlife in Indonesia. Live individuals were identified, measured, when possible, recorded by station and date, and released back into their habitat after handling. This procedure was applied to minimize harm and ensure that the study generated baseline ecological information without encouraging the retention or use of protected horseshoe crabs. To support the protected-species statement, the manuscript should cite the relevant Indonesian legal source, such as the Ministry of Environment and Forestry Regulation No. P.20/MENLHK/SETJEN /KUM.1/6/2018 concerning protected plant and animal species.

Sampling limitation and interpretation of bycatch records: The fisher-assisted opportunistic bycatch approach provided access to horseshoe crab records from local fishing grounds, but it also introduced important methodological limitations. Capture probability may have been affected by trap placement, fishing effort, tidal conditions, season, gear selectivity, and fisher activity. Therefore, the abundance data should be interpreted as station-level relative abundance and community composition within bycatch records, rather than as standardized estimates of population density. This limitation is important when comparing stations because differences in observed abundance may reflect both ecological variation and sampling-related effects.

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