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Diky Dwiyanto

IPB University

Mihwan Sataral

Universitas Tompotika Luwuk

Kurniawan P. Bandjolu

Perkumpulan Konservasi Membumi

Daisy Wowor

daisy_wowor@yahoo.com

National Research and Innovation Agency

Annawaty Annawaty

Tadulako University

Achmad Farajallah

IPB University

Dyah Perwitasari

IPB University

Thomas von Rintelen

Museum für Naturkunde

Kristina von Rintelen

Museum für Naturkunde

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Diky Dwiyanto^{a,b}, Mihwan Sataral^c, Kurniawan P. Bandjolu^{b,d}, Daisy Wowor^{e,*}, Annawaty Annawaty^{b,f}, Achmad Farajallah^g, Dyah Perwitasari^g, Thomas von Rintelen^{h,*}, Kristina von Rintelen^h

^aDiky Dwiyanto, dickydwiyanto@apps.ipb.ac.id (ORCID 0000-0002-4479-6296), Animal Bioscience Study Program, IPB University, 16680 Kampus IPB Dramaga, Bogor, West Java, Indonesia

^bMasyarakat Zoologi Wallacea (MZW), Palu, 94119 Central Sulawesi, Indonesia

^cMihwan Sataral, mihwansataral87@gmail.com (ORCID 0000-0002-0053-8375), Department of Agrotechnology, Tompotika Luwuk University, Banggai, 94711, Central Sulawesi, Indonesia

^{b,d}Kurniawan P. Bandjolu, kurniawanbandjolu@gmail.com (ORCID 0000-0002-1878-6473), Perkumpulan Konservasi Membumi, Bogor Utara, 16153 West Java, Indonesia

^eDaisy Wowor, daisy_wowor@yahoo.com (ORCID 0000-0002-4837-666X), Research Center for Biosystematics and Evolution, Research Center and Innovation Agency (BRIN), 16911 Cibinong, West Java, Indonesia

^fAnnawaty Annawaty, Annawaty09@gmail.com (ORCID 0000-0003-0112-7313), Department of Biology, Tadulako University, 94119 Kampus Bumi Tadulako Tondo, Palu, Indonesia

^gAchmad Farajallah, achamadfarajallah@gmail.com (ORCID 0000-0002-7733-6528), Dyah Perwitasari, witafar@apps.ipb.ac.id (ORCID 0000-0001-6206-1675), Department of Biology, IPB University, 16911 Kampus IPB Dramaga, Bogor, Indonesia

^hThomas von Rintelen, Thomas.Rintelen@mfn.berlin (ORCID 0000-0002-6253-3078), Kristina von Rintelen, Kristina.Rintelen@mfn.berlin (ORCID 0000-0003-4167-3570), Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, 43, D-10115 Invalidenstraße, Berlin, Germany

Corresponding authors: *daisy_wowor@yahoo.com *Thomas.Rintelen@mfn.berlin

Abstract

Ancient lakes are among the most exceptional freshwater ecosystems on Earth, characterized by long-term isolation and high levels of species endemism. Investigating how environmental filtering influences species coexistence is vital for decoding community assembly in freshwater ecosystems, including ancient lakes. Lake Poso is one of the ancient lakes in Southeast Asia that contains a species flock ($N = 11$) of the genus *Caridina*, the result of adaptive radiation. Here, we integrated occurrence and environmental data from lake-wide sampling for endemic freshwater shrimps of the genus *Caridina* across Lake Poso, Indonesia, using Hierarchical Modeling of Species Communities (HMSC) and spatial prioritization. This study aimed to (i) estimate the species relative abundance and distribution, (ii) assess how environmental filtering drives their community assembly, (iii) evaluate lineage-specific responses to these variables, and (iv) identify critical conservation areas under anthropogenic pressure. A total of 32 sites have been surveyed across the northern, western, eastern, and southern shorelines of Lake Poso. The eight lacustrine species exhibited marked variation in mean and total abundance, indicating the presence of both generalist and specialist species. Microhabitat acted as a primary abiotic filter in explaining *Caridina* spp. distribution. Notably, specific habitats strongly filtered species based on chelae morphology as a functional trait. Spatial prioritization demonstrated that areas of high habitat suitability frequently coincide with intense human disturbance. Our results highlight the critical role of microhabitat heterogeneity in maintaining the occurrence of various endemic species of the genus *Caridina*. This study establishes a predictive framework for integrating endemic communities into conservation planning for tropical ancient lakes facing accelerating anthropogenic threats.

Keywords:

Atyid shrimp, ancient lakes, community structure, conservation, environmental filtering, habitat factor

1. Introduction

Ancient lakes are geologically and biologically unique freshwater systems (Hampton et al. 2018). There are two ancient lake systems in Indonesia, i.e., Malili Lake and Lake Poso systems, that harbor rich endemic species flocks, including macroinvertebrates (von Rintelen et al. 2020). Diverse substrates and depth gradients provide heterogeneous niches that structure species communities (von Rintelen et al. 2010; Wilden et al. 2021). Understanding how microhabitats and water physiochemistry properties shape species coexistence in the littoral zone is therefore essential (Marijnissen et al. 2009). Despite of high endemism in ancient lakes, the mechanisms governing macroinvertebrate community assembly remain poorly explored (Hauffe et al. 2011). For example, previous studies on species diversity and speciation of snails and shrimps in Sulawesi's ancient lakes have proposed that species flocks arose through 'adaptive radiation' (sensu Schluter 2000) driven by habitat (substrate) specialization (von Rintelen et al. 2004; 2010). While on a global scale, stochastic processes, for example, dispersal ability, habitat fragmentation (Hernawati et al. 2020), and geological history (von Rintelen et al. 2026), played a significant role in freshwater shrimp community assembly, local species pools, such as in an isolated lake, may follow distinct assembly rules (see Keddy 1992). Determining the relative importance of deterministic processes requires evaluating both abiotic (physiochemistry and habitat) and biotic (species co-occurrence) filters (Ovaskainen et al. 2017), integrated alongside phylogenetic relationships and functional trait data (Bhaumik et al. 2025).

Macroinvertebrate communities in the littoral zone of lakes are highly dynamic due to the influence of several factors, such as temporal water fluctuations (von Rintelen et al. 2007; Špoljar et al. 2021), sedimentation (Marijnissen et al. 2009), water physiochemistry conditions (Woretaw et al. 2023), microhabitat (von Rintelen et al. 2007; 2010), including substrate (Mavromati et al. 2023), and human activities around the lakes (Hampton et al. 2018). Yet how endemic species respond to these factors in ancient lakes remains poorly explored. Lake Poso, an isolated solitary, ancient lake in Sulawesi's central highlands, harbors diverse endemic mollusks, crabs, shrimps, and fishes (von Rintelen et al. 2012; Wibowo et al. 2025). Lake Poso is unique because it has a complex geomorphology and hydrochemistry (Damanik et al. 2024). Endemic taxa depend heavily on the lake conditions, as illustrated by the absence of lacustrine shrimp species in river catchments (von Rintelen and Cai 2009).

Lake Poso is located within the area known as the 'Poso Formation', which was formerly a marine channel (see Nugraha et al. 2023) and is believed to have developed during the mid-Pliocene (~3 million years ago, Mya) to

the Pleistocene (2–1 Mya) (Hampton et al. 2018; Nugraha and Hall 2018; Nugraha et al. 2023). The total catchment area of Lake Poso is approximately 991.74 km², with a lake surface area of about 363.63 km² (Damanik et al. 2024). The lake is oligotrophic, characterised by low nutrient concentrations (von Rintelen et al. 2012; Damanik et al. 2024). A recent study reveals Lake Poso as the world's largest ferruginous lake with anoxic water (dissolved oxygen depletion) below ~90 m depth (Janssen et al. 2024). With a maximum depth of 395 m (Tournier et al. 2025) and an elevation of more than 400 m above sea level, Lake Poso is the second deepest ancient lake after Lake Matano in Southeast Asia (Vaillant et al. 2011). The western and southern shores of the lake have gentler slopes, supporting major inflowing large rivers such as the Meko and Pendolo Rivers. In contrast, the eastern side is characterised by steep slopes and is dominated by smaller streams originating from hilly terrain (Damanik et al. 2024). The substrate of Lake Poso varies across the basin in accordance with its bottom morphology, with certain areas exhibiting high-mass-transport deposits (MTDs). The shoreline is composed of coarse- and silty-sandy beaches, rocky bottoms, and bedrock ridges (Tournier et al. 2025). Lake Poso is one of the Key Biodiversity Areas (KBA) (Key Biodiversity Areas Partnership 2026) due to the uniqueness of its aquatic fauna and high levels of endemism (von Rintelen et al. 2012), including fishes, e.g., Adrianichthyidae (Miesen et al. 2015), snails, e.g., Pachychilidae and Tateidae (Haase et al. 2023), crabs, e.g., Parathelphusidae (Chia and Ng 2006), and freshwater shrimps (Atyidae) (Klotz et al. 2021).

Atyid shrimps play a crucial role in supporting aquatic ecosystems by driving nutrient cycling (as detritivores) (Crowl et al. 2001) and sustaining balanced food webs as a vital food source for other aquatic species (De Grave et al. 2015). Species flocks of shrimp genus *Caridina* represent the largest radiation of decapods in the littoral zones of Sulawesi's ancient lakes (von Rintelen et al. 2020), including Lake Poso (von Rintelen and Cai 2009; Klotz et al. 2021). Lake Poso is recognized as a hotspot for the diversity of the genus *Caridina*, with 11 species described to date (von Rintelen and Cai 2009; Klotz et al. 2021). Given that the abundance of *Caridina* species in aquatic habitats is closely linked to physiochemistry conditions (Annawaty et al. 2016) and habitat utilization (von Rintelen et al. 2010; Soomro et al. 2013), it is essential to examine the relationship between *Caridina* community structure and environmental variables, including microhabitat characteristics. In addition, it also needs to be tested whether closely related species with the same functional traits, e.g. chelipeds (see von Rintelen et al. 2010), respond similarly in habitat preferences.

Freshwater macroinvertebrates provide key evidence for conservation prioritization in lake management (Nieto et al. 2017). Conserving endemic species flocks, including freshwater shrimp, is essential to maintaining ecosystem

functioning, particularly as human disturbance intensifies. Lake Poso and other ancient lake systems in Sulawesi face severe threats (Hampton et al. 2018) from urbanization, agriculture, hydropower development (Wirachandra et al. 2024), and forest loss (Damanik et al. 2024; Sakti et al. 2026). Furthermore, the limited availability of data on species abundance raises concerns about the long-term persistence of this macroinvertebrate group, particularly under pressure from invasive species in Lake Poso (Herder et al. 2022) and habitat destruction along the lake's littoral zone. Therefore, studies that use endemic species assemblages to identify conservation priority areas around Lake Poso are crucial as science-based inputs for conservation and policy.

All *Caridina* spp. in the Lake Poso system are endemic to the lake and the surrounding area. Two species that occur only in the river within the catchment are not found in the lake proper (Klotz et al. 2021). The populations of *Caridina* spp. in Lake Poso are presumed to be declining over time due to predation by the invasive species (Herder et al. 2022). In this study, we conducted lake-wide sampling of *Caridina* spp. and converted the abundance data into a presence-absence dataset to investigate the relationship among *Caridina* community structure and environmental covariates (microhabitat and water physiochemistry) using joint species distribution modelling (JSDM) to provide evidence for conservation prioritization. Prior information on species relationships from mitochondrial DNA (cytochrome c oxidase subunit I) (von Rintelen et al. 2007; Klotz et al. 2021) was used to examine whether closely related species show similar responses to abiotic factors. In addition, we hypothesize that the shared microhabitat preferences of *Caridina* spp. in Lake Poso may influence their persistence and distribution within the lake. This phenomenon has previously been examined in the lacustrine specialists' group in the Malili Lakes system, in which each species belongs to a different 'ecogroups' according to the microhabitat and functional trait (cheliped) (von Rintelen et al. 2010). Therefore, this study were aims to: (i) estimate the relative abundance of lacustrine *Caridina* spp. and their species distribution; (ii) assess which abiotic factors (microhabitat vs water physiochemistry) are significantly acted as environmental filtering and their interspecific response; (iii) evaluate whether community responses to environmental are accommodated by functional traits; and (iv) model spatial conservation priorities (human pressure and habitat suitability) for *Caridina* spp. in Lake Poso, Sulawesi, Indonesia.

2. Material and methods

2.1 Study area and community sampling

We surveyed 32 sites distributed across the northern, western, eastern, and southern shorelines of Lake Poso (Fig. 1a; Table S1) during several fieldwork sessions, i.e., in 2022 (September), 2023 (September), 2024 (January, July, September, October, and December), and 2025 (March). Various sampling methods were employed, including SCUBA diving, snorkeling with a hand net, a tray net, and a dip net. Species abundance was assessed using Catch per Unit Effort (CPUE) over a 30-minute sampling period (Schoolmann and Arndt 2018). Sampling encompassed all known *Caridina* spp. habitat types, including submerged roots, macrophytes, leaf litter, rocks, pebbles, sand, as well as empty snail shells (von Rintelen and Cai 2009; Klotz et al. 2021) (Table S1).

2.2 Species identification and distribution

Collected specimens were placed in a large container, counted, and measured in situ for carapace length (cl) using a digital caliper (0.01 mm). Species identification was conducted based on live coloration (Fig. S2), using a pre-sorting key for living *Caridina* in Lake Poso provided by Klotz *et al.* (2021). Successfully identified individuals were subsequently released back into the lake. Specimens that could not be reliably identified in the field were preserved in 95% ethanol for future examination under a stereomicroscope. The locality of each species was recorded to build a species distribution map using QGIS version 3.36.1-Maidenhead (<https://qgis.org/>), based on a polygon lake map provided by the Geospatial Information Agency (Badan Informasi Geospasial/BIG) (available at <https://tanahair.indonesia.go.id/portal-web/>). In addition, previously surveyed locations were incorporated into the distribution map using coordinates reported in earlier studies (von Rintelen and Cai 2009; Klotz et al. 2021).

2.3 Environmental variables

Physiochemistry water parameters, including temperature (°C), pH, total dissolved solids (TDS; ppm), and conductivity (μS/cm), were measured using an AZ 86031 multi-parameter meter (Taiwan). Dissolved oxygen (DO) was measured using a DO meter (Lutron 5510, Taiwan) or a Dissolved Oxygen Tester (DO9100, China). In order to identify collinearity among variables, Spearman's rank correlation was used with Bonferroni correction in R v4.3.2 (R Core Team 2021). Eight microhabitat types for *Caridina* spp. were defined following von Rintelen and Cai (2009) and Klotz et al. (2021): submerged roots, shells of snail, sand, rocks, pebbles, macrophytes, leaf litter, and wood. The relationship between species and habitat was visualized using a chord diagram generated with the circlyze

package (Gu et al. 2014). We performed a Canonical Correspondence Analysis (CCA) to determine the influence of environmental variables on the occurrence of *Caridina* spp. using the vegan package (Oksanen et al. 2026).

2.4 Joint species distribution modelling (JSDM)

To evaluate the shrimp community response to the abiotic (physiochemistry and microhabitat) and biotic factors (residual correlation between species), we conducted an analysis for joint species distribution modeling (JSDM) using a hierarchical modeling of species communities (HMSC) approach (Ovaskainen et al. 2017), with the hmsc 3.0 package in R (Tikhonov et al. 2020). For the Y-matrix input, we converted abundance data to presence-absence (0/1, binary data) to avoid zero-inflation, as implemented in previous studies (Cranston et al. 2024; Karthick et al. 2026). The X-matrix (covariates) comprised environmental variables (water physiochemistry and microhabitat) but excluded TDS, since this variable highly correlated with conductivity ($\rho = 0.77$; $p\text{-value} < 0.001$) (Table S1; Fig. S1). Leaf litter was also excluded because it was present at only a single site. In addition, multicollinearity among environmental predictors was assessed using Variance Inflation Factors (VIF) (< 5). Prior to fitting the model, we built a C-matrix using a phylogenetic tree from eight *Caridina* species (excluding *C. lilianae*) based on partial COI gene sequences (781 bp) downloaded from GenBank (Table S2). The best substitution model was selected using jModelTest 2.1.10 (Darriba et al. 2012) based on Akaike Information Criterion (AIC). The tree was reconstructed using Maximum Likelihood (ML) with 1,000 standard bootstraps in MEGA 12 (Kumar et al. 2024). Since the selected model, TIM3 + I, was not available in MEGA, it was replaced with GTR + I, as recommended by Park and Poulin (2022). The ape package (Paradis and Schliep 2019) was used to import the NEXUS file and construct a 50% majority-rule consensus tree.

The cheliped type in lacustrine *Caridina* spp. is proposed as a functional trait by von Rintelen et al. (2010). We considered three types (generalist, specialist, and hard-substrate dweller) of traits-related habitat (T-matrix) (Gamma parameters) according to the first and second pair of cheliped, according to von Rintelen and Cai (2009) and Klotz et al. (2010). In this study, we developed only one model (the Full model) that included random (sampling site) and fixed effects (environmental variables). After fitting the model, the four independent MCMC chains were run for a total of 80,000 iterations (250,000 per chain; transient = 50,000; thin = 10; samples per chain = 20,000). Convergence was evaluated by computing the potential reduction factor for the HMSC model's beta (species response to the included variables) and omega (species-to-species associations) parameters using PSRF (Gelman and Rubin 1992). We assume MCMC convergence is adequate when the potential scale reduction factors are close to 1

(Ovaskainen et al. 2017). The area under the curve (AUC) and the Tjur R² coefficient of discrimination were used to assess the models' explanatory power. The Widely Applicable Information Criterion (WAIC) (Watanabe 2010) was used instead of Bayes Cross-Validation to compare the models, as implemented in the previous JSDMs study on freshwater mussels (da Silva et al. 2023). The heatmap of estimated parameters β , including plotTree, was constructed using plotBeta in the hmsc 3.0.13. The variance partitioning plots were generated using base R graphics.

2.5 Land use/land cover (LULC)

The analysis of land use/land cover (LULC) in the area surrounding Lake Poso was conducted using the 2024 LULC map provided by the Ministry of Environment and Forestry (<https://geoportal.menlhk.go.id/portal/>) as the primary spatial data source. Following clipping and geometric correction, land use/land cover were reclassified into seven main analytical categories: forest, shrub land, plantation, agriculture, settlement, bare land, and water, using Google Earth Engine (GEE) (Gorelick et al. 2017).

2.6 Spatial conservation prioritization

Spatial abundance datasets for *Caridina* spp. in the littoral zone of Lake Poso were mapped onto a high-resolution grid. Lake boundaries from the Geospatial Information Agency (BIG) and a 1000-m littoral zone buffer were processed using the sf (Pebesma and Bivand 2023) and terra (Hijmans et al. 2026) packages in R v4.3.2. Normalized values were aggregated into 250-m hexagonal conservation planning units using the prioritizr package (Hanson et al. 2025). Biodiversity features were weighted relative to conservation costs, defined as the level of human disturbance. According to Zhao et al. (2015), the human disturbance index applied reclassification weights ranging from weak to strong (0–3; Gu et al. 2022) across three principal categories: (a) recreational activities (value = 1; low disturbance) (Kaban et al. 2023); (b) fishing activities (value = 2; aquaculture, intensive fishing, direct shrimp harvesting) (Serdiati et al. 2020); and (c) habitat degradation (value = 3; high disturbance; pollution, land conversion, dam construction, flow alteration, invasive species, sedimentation (von Rintelen et al. 2012; Serdiati et al. 2020; Damanik et al. 2024).

Trade-off analyses between human disturbance costs (%) and *Caridina* spp representation were modeled in prioritizr (Hanson et al. 2025) with a minimum representation target of 30% per biodiversity feature. Trade-off relationships were explored using trade-off curves, and prioritization outcomes were visualized via selection frequency maps. Following non-monetary approaches to cost definition (Mantyka-Pringle et al. 2016; Rodewald et

al. 2019), candidate solutions were generated hierarchically without explicit monetary values (e.g., USD or IDR) or penalty constraints. Finally, indicator species of *Caridina* spp in Lake Poso were identified via Indicator Value (IndVal) analysis (Dufrêne and Legendre, 1997) using the labdsv package (Roberts 2019).

3. Results

3.1 Population abundance, distribution and microhabitat preferences of *Caridina* spp

We recorded a total of 1,346 individuals of lacustrine *Caridina* spp. from 32 sites in Lake Poso. During field surveys, eight of the nine known lacustrine *Caridina* spp were found (*C. caerulea*, *C. ensifera*, *C. fusca*, *C. marlenae*, *C. mayamareenae*, *C. longidigita*, *C. poso*, and *C. sarasinorum*), showing marked differences in both mean and total abundance (Fig. 1b,c). *C. ensifera* was the most abundant species (17.30 ind./CPUE) (Fig. 1d), whereas *C. poso* showed the lowest abundance (0.23 ind./CPUE) (Fig. 1b). Despite extensive sampling across several types of localities to obtain population data for all lacustrine species, *C. lilianae* was not recorded during this study. Species with high population abundance, such as *C. ensifera* and *C. longidigita*, were associated with broad microhabitat preferences (Fig. 1c,e). In contrast, rarer species with low abundance, such as *C. marlenae*, *C. mayamareenae*, and *C. poso*, were recorded in specific microhabitats (Fig. 1d). These narrowly distributed species (Fig. 2a) generally have small population sizes and occupy specific habitats (Figs. 1b-e). For instance, *C. mayamareenae*, *C. poso*, and *C. marlenae* were confined to empty snail shells, pebbles, and rocks, respectively (Fig. 1e).

Caridina spp. in Lake Poso comprise both widely distributed and narrowly distributed species (Fig. 2a). *Caridina ensifera* was the most widespread species, occurring at nearly all sampling sites (Figs. 2a,b). In addition, three other species (*C. caerulea*, *C. longidigita*, and *C. sarasinorum*) also exhibited relatively broad distributions within the lake (Figs. 2a,b). In contrast, species with restricted distributions—*C. marlenae*, *C. mayamareenae*, and *C. poso*—were recorded at only one or two sites (Fig. 2a,b). Based on species composition, the eastern shore of Lake Poso supports a higher diversity of *Caridina* spp. (eight species) than the western shore (five species) (Fig. 2).

3.2 Models evaluation, species prevalence and species richness per site

The model convergence diagnostics (PSRF) showed both β (Beta) and Ω (Omega) parameters extremely close to 1 (mean $\beta = 1.000$, $\Omega = 1.015$) (Fig. S2), and both models produced consistent results. The AUC (Full: 0.96; Environmental: 0.95) and Tjur R^2 (Full: 0.36; Environmental: 0.35) values (Table S2) demonstrated the excellent explanatory power of both the Full and Environmental models. According to the WAIC score, the Full model was

higher in predictive accuracy than the Environmental model (Table S2). Species richness per site and species prevalence were low, with the site containing only one species showing the highest frequency (Fig. S3).

3.3 Drivers of environmental factors on *Caridina* spp distributions and interspecific responses

The results of the CCA analysis showed that the species community structure was strongly influenced by microhabitat heterogeneity ($p < 0.01$) and pH gradient ($p < 0.05$), with a total explained variance of 57.4% (Fig. S4). The variance partitioning revealed 97.2% of the explained variation from fixed effects (environmental covariates) in the Full model (Fig. 3a). Among the environmental variables, microhabitat explained the most of the variation in the occurrence of *Caridina* spp. (>50%), rather than physiochemistry factors, in both the Full and the Environmental variables (Fig. 3a). The responses of *Caridina* spp. to environmental factors revealed clear interspecific variation correlated with phylogenetic relationships (Fig. 3b). The distribution of *C. longidigita* was largely explained by a significant, positive response to submerged roots (mean $\beta = 1.45$, support = 0.92). *C. caerulea* showed a significant positive response to hard substrates, wood, and rocks. Similar to its closely related species, *C. ensifera*, microhabitat (wood) was the most important variable (50%), followed by conductivity (30%) in explaining their occurrences (Figs. 3a,b). A negative response to sand but a positive response to pebbles was found in *C. sarasinorum*, with 62% occurrence, explained by microhabitat. Species with restricted distribution that are genetically close (undifferentiated clade in phylogeny comprising *C. mayamareenae*, *C. fusca*, *C. marlenae*, and *C. poso*) clearly showed a negative response with macrophytes (Fig. 3b). Among all species, a positive response to the shells of snails was found only in *C. mayamareenae* (mean $\beta = 1.66$, support = 0.90). *C. fusca* and *C. marlenae* also showed a positive response to dissolved oxygen, with proportions of 17.2% and 16.6%, respectively. Interestingly, only *C. ensifera* showed a positive association with water conductivity (Fig. 3b).

After the influence of environmental variables was removed in the Full model, the residual species correlation matrix (Ω) showed weak co-occurrence patterns (near zero), indicating that deterministic environmental filtering dominated the *Caridina* spp. community in Lake Poso (Fig. S5). The distributional variation of the species was efficiently captured by abiotic filters, leaving very little residual covariance to be explained by latent factors or micro-spatial variables (Fig. S5). In the Environmental model, only *C. mayamareenae* showed a positive correlation with *C. marlenae*, but without strong support (Fig. S5).

3.4 Trait environment relationship

The proportion of traits explained by microhabitat (0.471) was higher compared to physiochemistry variables (0.350) (Fig. 4a). Among the estimated relationships between traits and environmental responses, only the shells of snails (habitat) exhibited a strong positive association (0.90 support level) (Fig. 4b). The shell of snails was closely linked with the specialist chelae-type in *C. mayamareenae* (Table S1; Fig. 4b). This robust positive interaction showed that specific microhabitats strongly filtered species into a specialized type of chelae. No statistically supported relationships were detected for the hard-substrate or the generalist across any physiochemistry parameters (temperature, pH, DO, conductivity) or remaining microhabitat types (macrophytes, pebbles, rocks, sand, submerged roots, and wood), indicating that these abiotic factors do not strongly discriminate among the modelled functional chelae type (Fig. 4b).

3.5 Spatial Conservation Prioritization of *Caridina* spp. in Lake Poso

The prediction of species suitability for *Caridina* spp. in Lake Poso indicated that several areas with high species diversity occur within zones of elevated anthropogenic pressure (Figs. 2a, 5a,b, S6). For example, sites near Tentena town (S2, S22, and S29) supported a total of six species (*C. marlenae*, *C. sarasinorum*, *C. mayamareenae*, *C. fusca*, *C. ensifera*, and *C. longidigita*), suggesting that these areas should be prioritized for conservation (Fig. Fig. 5b, S6). However, this pattern was not consistent across all regions, as some sites were also identified as suitable habitat despite harboring only one or two species (e.g., S4 and S31) (Fig. 5b). Species indicator analysis (IndVal) identified five *Caridina* spp. (*C. fusca*, *C. sarasinorum*, *C. caerulea*, *C. longidigita*, and *C. ensifera*) as having high conservation value (above the baseline threshold; conservation weight = 1) (Fig. S7). Among these, *C. fusca* exhibited the highest value, whereas *C. ensifera*, despite being the most abundant and widespread species in Lake Poso, showed the lowest value. *Caridina poso*, *C. mayamareenae*, and *C. marlenae* exhibited weak indicator values as these species showed restricted distributions and inconsistent presence across Lake Poso.

4. Discussion

Atyid shrimps constitute a significant component of freshwater ecosystem food webs, including those in lakes (De Grave et al. 2015; von Rintelen et al. 2020). The Lake Poso system currently comprises 11 species, including nine lacustrine and two riverine taxa (Klotz et al. 2021). In the present study, we provide the first comprehensive data on the population status of eight of the nine endemic lacustrine *Caridina* spp. in Lake Poso. The population abundance of *Caridina* spp. in Lake Poso varies considerably among species, with *C. ensifera* being the

most abundant species in Lake Poso (Figs. 1b,c). Given that *C. ensifera* is a generalist species inhabiting a wide range of substrates (rock, wood, sand, and macrophytes) (von Rintelen and Cai, 2009), its capacity to exploit diverse food resources across different substrates is likely contributing to its successful adaptation within the lake. von Rintelen et al. (2010) further demonstrated that generalist species (e.g., *C. lanceolata*) tend to be widely distributed within lake systems and often occur in large population sizes.

This study provides an important baseline for estimating the population sizes of endemic species of the genus *Caridina*, whose population biology and ecology on Sulawesi remain poorly known. The lack of population data in the IUCN Red List database for all endemic species from ancient lakes limits the updating of their threatened status (De Grave et al. 2015). In addition, *Caridina* spp. can provide valuable information on ecosystem health by monitoring their population trends (Kunjulakshmi and Prakash 2025). The use of *Caridina* spp as food or for the aquarium trade led to increased overexploitation in several regions (De Grave et al. 2015). No study has yet attempted to evaluate how many shrimp species in Lake Poso have been harvested up to the present.

To our knowledge, this study is the first to apply a JSDM approach to an endemic decapod community in an ancient lake. While modeling endemic species is often hampered by rare-species data that can limit performance metrics such as AUC and Tjur's R^2 (Demir and Kalabak 2026), our focus on abiotic drivers (microhabitat vs water physiochemistry) ensures that niche and distribution estimates remain valid even with up to 50% missing data (Romera-Romera and Nieto-Lugilde 2024) or a minimum of three sites for species occurrences (Demir and Kalabak, 2026). Our study demonstrates the importance of various microhabitats to the shrimp distribution in the littoral zone of Lake Poso. Previous work that combines morphological, genetic, and ecological data has also highlighted that microhabitat specialization drives species divergence in the Malili Lake system (von Rintelen et al. 2010). Our different framework using HMSC also confirmed that the response to microhabitat is consistent with either previous studies or species-microhabitat relationships based on the chord diagram (Fig. 1e), for example, the positive association in *C. sarasinorum*, *C. caerulea*, *C. ensifera* (von Rintelen and Cai 2009), and *C. mayamareenae* (Klotz et al. 2020). In addition, the positive response of *C. longidigita* to submerged roots is supported by our study, although this species has previously been reported to be a hard-substrate dweller (von Rintelen and Cai 2009). We assume that the interspecific responses of *Caridina* spp. (phylogenetic signal = 0.53) to microhabitats follow niche conservatism after speciation, with closely related species showing similar niche responses along the phylogenetic tree (von Rintelen et al. 2010) as reported in freshwater crabs (Alves et al. 2024) and Blister beetles (Demir and

Kalabak, 2026). A higher proportion of environmental filtering than of spatial factors in explaining freshwater species distribution has also been reported in fish (Yang et al. 2026).

Our study highlights the importance of the trait (cheliped morphology) for species living in a specific habitat. The most extreme example confirmed by our study is *C. mayamareenae* (Fig. 4b), which is adapted to living in empty snail shells (Klotz et al. 2021). The species flock of *Caridina* spp. in Sulawesi's ancient lake comprises generalists and specialists, which supports the idea of phenotypic-environmental correlation or adaptive radiation (von Rintelen et al. 2010). Our study confirms the previous hypothesis that chelae morphology reflects the microhabitat use (von Rintelen et al. 2010) (Fig. 3A). The previous study showed that only five species (*C. fusca*, *C. lilianae*, *C. poso*, *C. marlenae*, and *C. mayamareenae*) (Klotz et al., 2021) could clearly be assigned to a specialist ecogroup (sensu von Rintelen et al. 2010) (Fig. 1e).

In addition to the microhabitat, water physicochemistry in tropical lakes is still a major determinant of the distribution of aquatic fauna, yet the studies evaluating the response of endemic species with physiochemistry variables remain limited. The non-significant relationship response between *Caridina* spp and water temperature in Lake Poso aligns with previous findings indicating that the genus *Caridina* exhibits broad thermal tolerance (11–30°C) (Hart 1983; Annawaty et al. 2016). Interestingly, *C. ensifera* was the only species that showed a positive effect with conductivity, which may explain its relatively wide distribution within the lake. Elevated conductivity levels may indicate increased mineral-related pollution or eutrophication due to high nitrogen and phosphorus levels (Wu et al. 2020), which could differentially affect species sensitivity in Lake Poso.

Over the past decade, extensive land conversion has occurred around Lake Poso in the northern, western, and southern parts of the lake. Despite of the increasing human activities, low nutrient levels suggest minimal immediate harm to the lake's biotic communities (Damanik et al. 2024). This is supported by our habitat suitability analysis, which identified several highly suitable sites for *Caridina* spp. in areas under elevated anthropogenic pressure. However, the direct effects of catchment deforestation on Lake Poso's substrate remain poorly documented. Deforestation-induced sedimentation is a known threat to endemic benthic fauna elsewhere, such as crabs in Lake Tanganyika (Marijnissen et al. 2009). Given the strong link between substrate and shrimp distribution in Lake Poso, sedimentation could cause localized extinctions by altering microhabitats. For example, the absence of *C. lilianae* in this survey may stem from a sedimentation-driven shift from silty to muddy sand (D. Dwiyanto pers. obs. 2025).

Our results show that conservation prioritization should rely on at least five indicator species, including *C. fusca*, *C. sarasinorum*, *C. longidigita*, *C. caerulea*, and *C. ensifera*. The northwest area (S1, 15, 23, 27) is the most suitable for *Caridina* spp, with up to four indicator species present. These species demonstrate strong ecological association, habitat specificity, and high indicator strength. Integrating conservation priority areas into land-use management and ecosystem planning is important for preserving endemic freshwater biota (Mantyka-Pringle et al. 2016). Habitat protection along the lake shore in the northwest of Lake Poso will be needed in the future, such as preventing microhabitat destruction and forest cover, promoting sustainable agricultural practices (reducing pollutant inputs and using organic fertilizer), and reducing anthropogenic activities (embankment projects, recreational and fisheries activities). We provide evidence that a particular group of macroinvertebrates should be considered, especially for their microhabitats, which are in urgent need of protection.

This study provides the first evidence on the relationship between the distribution of *Caridina* spp. and microhabitat variables in Lake Poso. Based on the JSDM analysis, our results demonstrate that interspecific community responses to abiotic factors (particularly microhabitat) are driven by phylogenetic relationships and trait utility. From an ecological perspective, these findings offer further support for the hypothesis proposed by von Rintelen et al. (2007) and Klotz et al. (2021) on adaptive radiation, suggesting that each endemic *Caridina* spp. exhibits a degree of habitat and trophic specialization in Lake Poso. Species abundance is associated with distribution range and the capacity to exploit a wide variety of microhabitats. This study also presents the first spatial conservation prioritization using endemic species of *Caridina* as model organisms. Future research should incorporate more comprehensive datasets, including temporal data (dry and wet season) and multiple taxa from Lake Poso (including fishes, crabs, and snails) to identify priority areas. Based on our results, we recommend proper management of the littoral area to maintain species occurrence and mitigate impacts from surrounding catchment, thereby maintaining the water physiochemistry properties of Lake Poso. Ultimately, preserving Lake Poso's unique ecosystem requires collaborative conservation actions among governments, researchers, NGOs and local communities for long-term monitoring, habitat protection, and threat mitigation.

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Author contributions

All authors contributed to the study conception and design. Material preparation and data collection were performed by DD, KPB, AA, DD and TvR. Data analyses were performed by DD and MS. The first draft of the manuscript was written by DD. All authors wrote and commented on subsequent versions of the manuscript. Supervision was performed by DP and AF. All authors read, critically revised and approved the final manuscript.

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Data availability statement

The data analyzed during this study are included in this article and its supplementary materials.

Declarations

Competing interests

The authors declare no competing interests

Ethical approval

All samples collected in previous study were conducted in compliance with the Ethical Guidelines according to the Directorate of Research and Innovation Licensing Governance, and Scientific Authority, Research Center and Innovation Agency, Republic of Indonesia.

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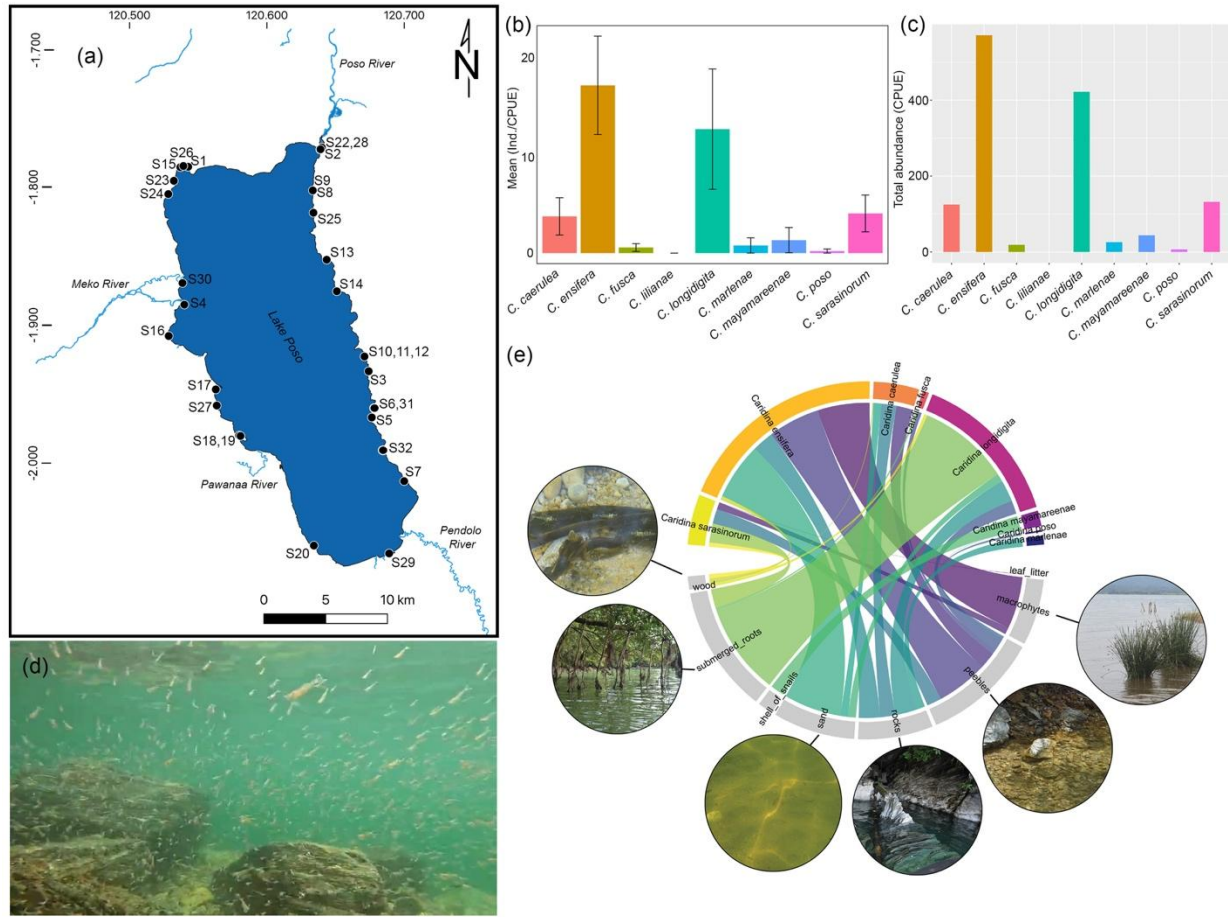


Fig. 1 (a) Study sites in Lake Poso where (b) relative abundance (mean ind./CPUE) and (c) total abundance (CPUE) data were collected. (d) Swarms of *C. ensifera*. (e) The occurrence of *Caridina* spp in habitat types shown using chord diagram. Chord thickness represents the number of individuals collected from each habitat type. The photographs show the dominant habitats

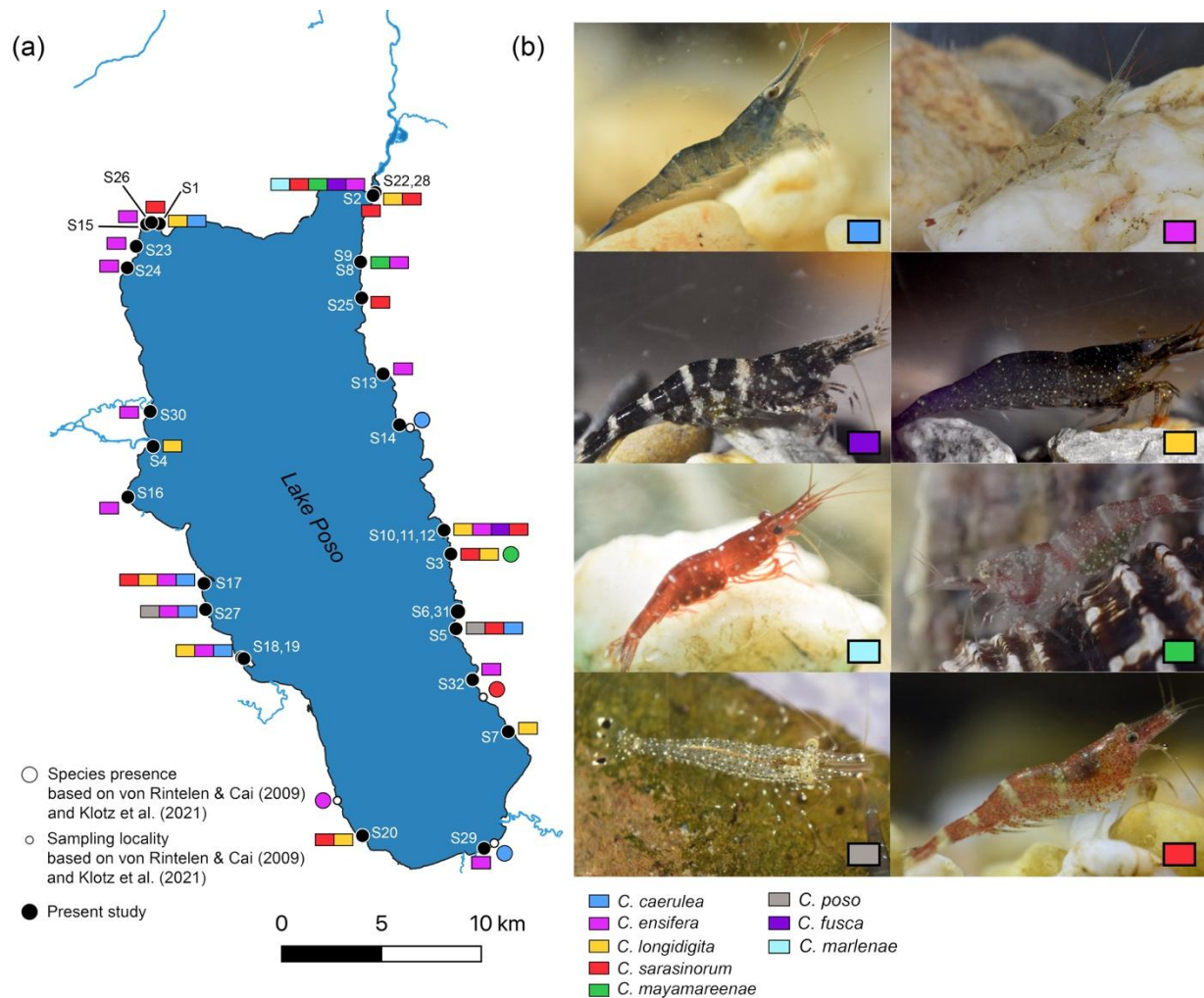


Fig. 2 (a) Distribution of *Caridina* spp. in Lake Poso. Only eight species recorded during this survey were shown. *Caridina lilianae* was not included. Black circle indicates current study and coloured circle indicates species distribution based on previous study by von Rintelen and Cai (2009) and Klotz et al. (2021). **(b)** Live coloration of *Caridina* spp. collected during this study. Photographs: Diky Dwiyanto

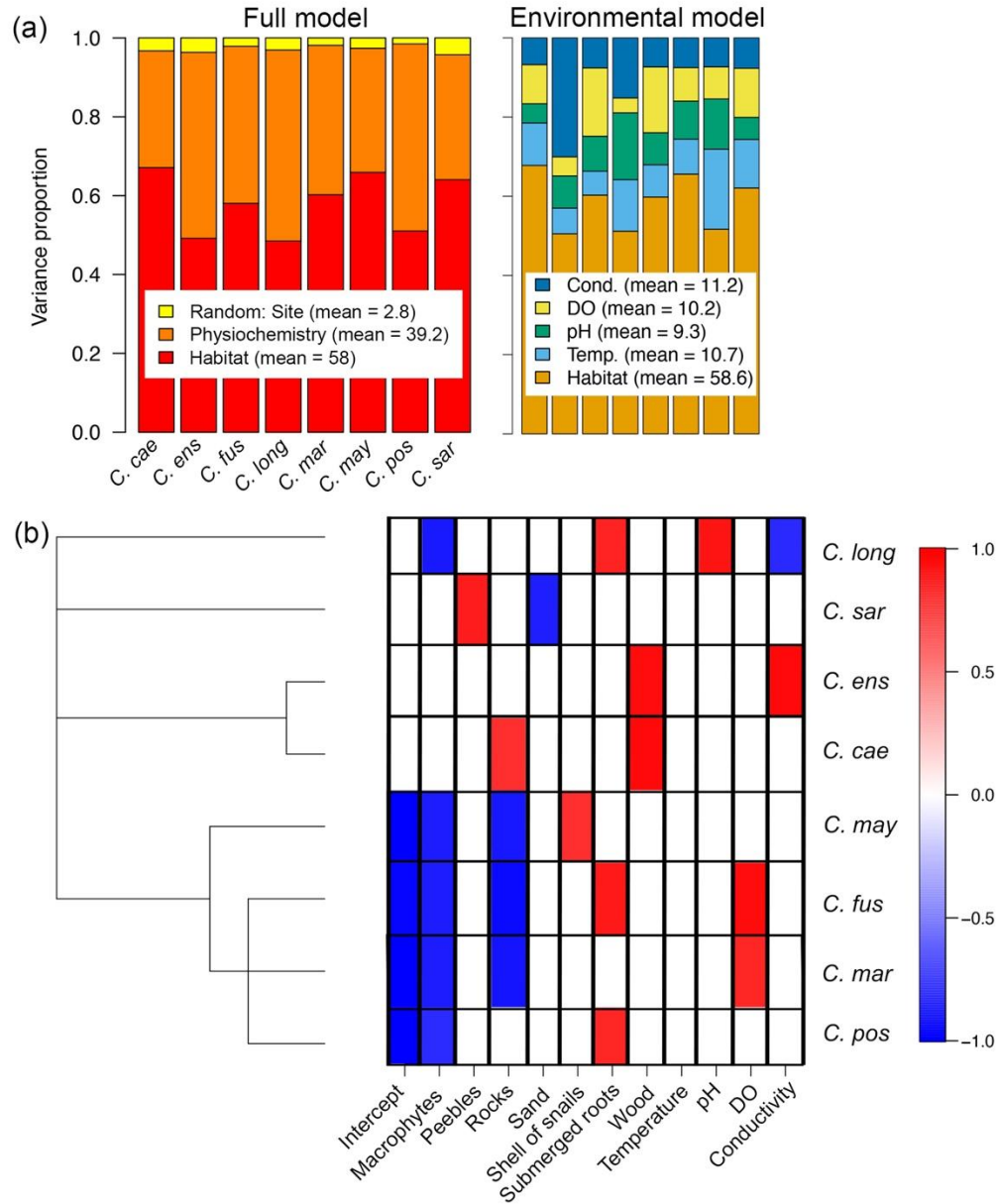


Fig. 3 The influence of environmental factors on the distribution of *Caridina* spp. in Lake Poso. **(a)** Variance partitioning of *Caridina* spp across microhabitat, water physiochemistry parameters, and random effects in full and environmental models. **(b)** Heatmap depicting species-specific responses to environmental predictors in the Joint Species Distribution Model. Red cells indicate positive associations and blue cells indicate negative associations (posterior probability ≥ 0.95); blank cells indicate non-significant relationships. Species abbreviation: *C. cae* = *C. caerulea*, *C. ens* = *C. ensifera*, *C. fus* = *C. fusca*, *C. long* = *C. longidigita*, *C. mar* = *C. marlenae*, *C. may* = *C. mayamareenae*, *C. pos* = *C. poso*, *C. sar* = *C. sarasinorum*

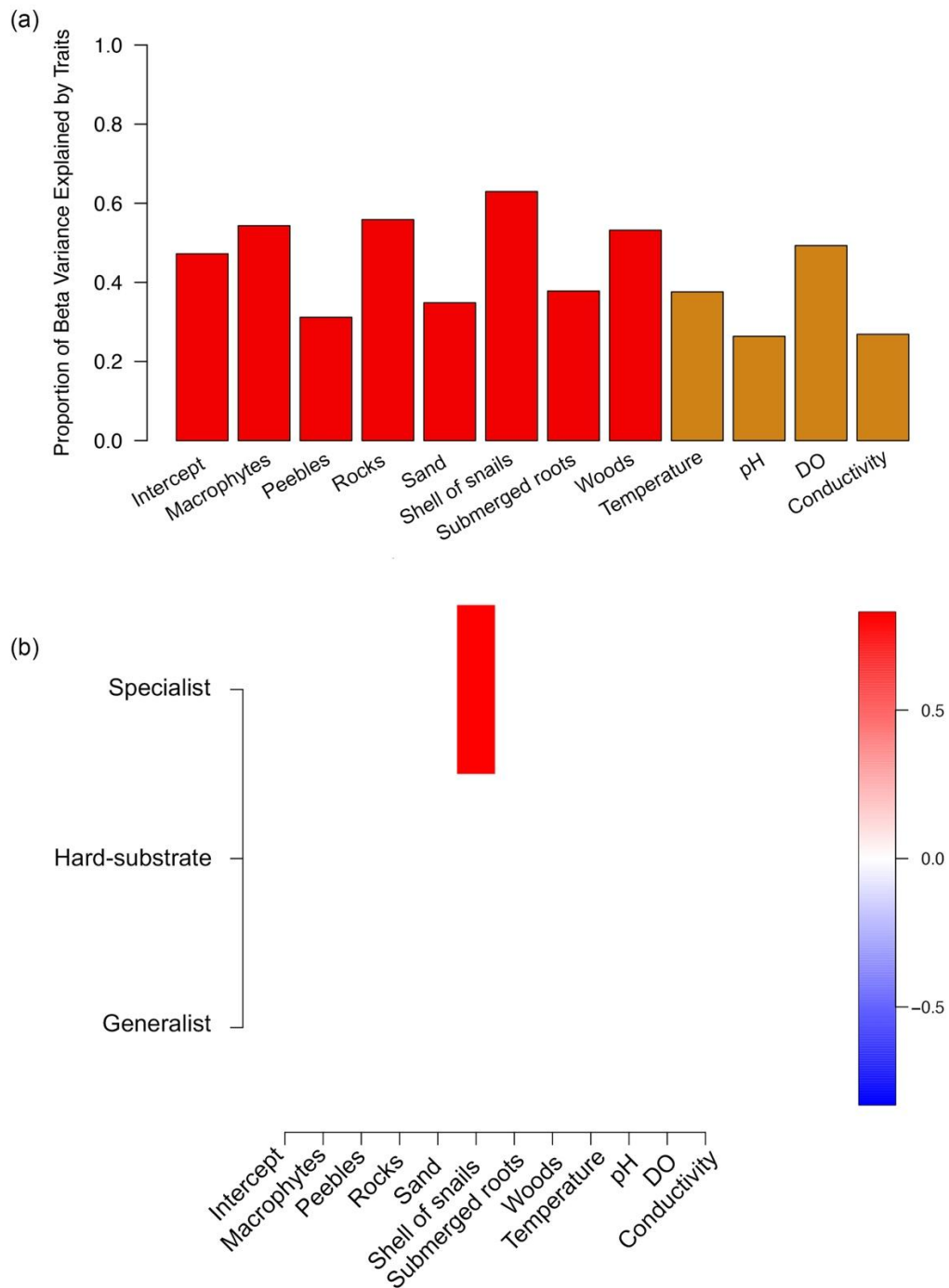


Fig. 4 The trait-environment relationships of *Caridina* spp from Lake Poso inferred from the HMSC model. **(a)** Proportion of species traits driven by environmental factors (microhabitat = red, and water physicochemistry = orange). **(b)** Positive association of *C. mayamareenae* with specialist chelae-type in shell of snails (posterior probability ≥ 0.90). Only value ≥ 0.90 was shown

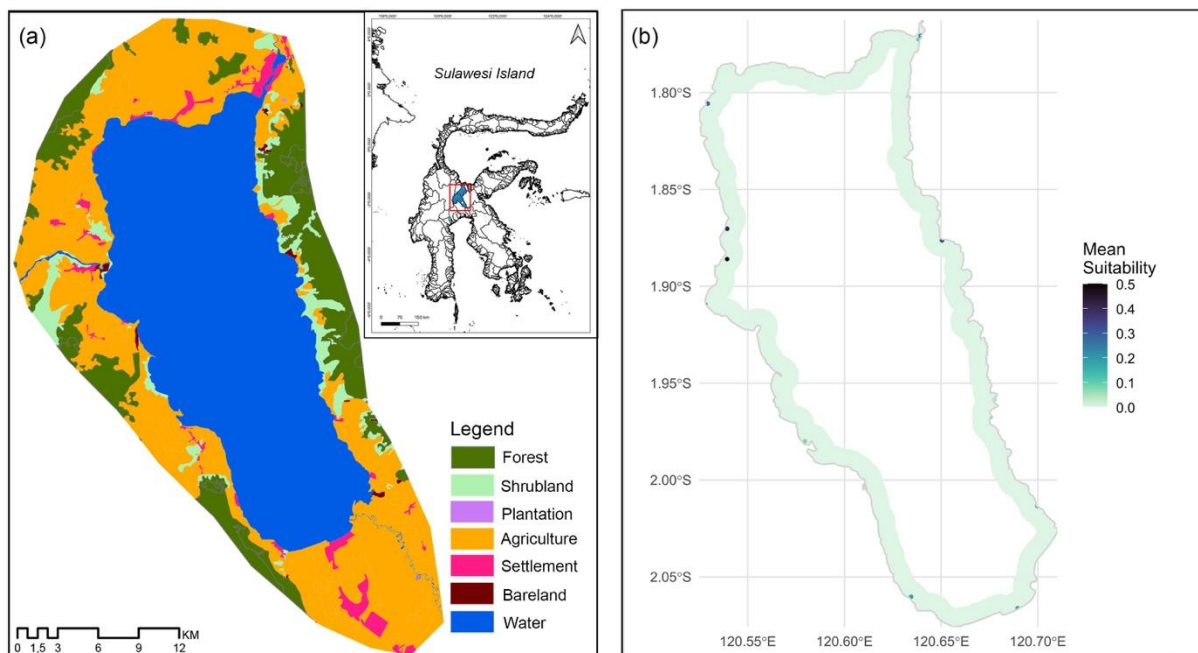


Fig. 5 (a) Land-use land cover (LULC) surrounding Lake Poso show the area with massive anthropogenic activities.

(b) Hotspot area with high species suitability for endemic *Caridina* spp. in the littoral zone of Lake Poso

Supplementary Files

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- [Supplementarymaterial.docx](#)