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Diversity and habitat preferences of copepods in temporary tropical waters of Thailand

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Abstract

Temporary aquatic habitats are widespread in tropical regions and represent important reservoirs of freshwater biodiversity, yet their copepod fauna remains insufficiently documented. This study examines the diversity, community composition, and habitat preferences of copepods across major types of temporary aquatic habitats in Thailand, including rice fields, ponds, canals, peat swamps, and swamps. Copepods were sampled from multiple sites representing each habitat type, and community patterns were analysed in relation to habitat characteristics and environmental variables. A total of 29 calanoid, 35 cyclopoid, and 11 harpacticoid species were recorded, with species composition varying significantly among habitat types. Several species exhibited strong habitat specificity, occurring exclusively in particular habitats. Peat swamps and temporary swamps supported the highest numbers of habitat-restricted species, particularly benthic and periphytic taxa, whereas rice fields and temporary ponds were dominated by calanoid species associated with open-water conditions and recurrent disturbance. Despite these differences, overall community composition showed high similarity across environmental gradients, indicating that many species function as ecological generalists with broad environmental tolerances. These results highlight the importance of habitat heterogeneity in shaping copepod communities and underscore the need to conserve diverse temporary aquatic habitats to maintain regional copepod diversity in tropical landscapes.

Key words: Calanoida; Cyclopoid; environmental gradients; habitat heterogeneity; habitat specificity; Harpacticoida; tropical freshwater ecosystems.

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INTRODUCTION

Temporary habitats, such as ponds, rice fields, canals, and pools, are dynamic ecosystems that undergo periodic drying and refilling. These habitats play a crucial ecological role by supporting a wide range of aquatic organisms, including zooplankton, which are essential for maintaining food web stability and nutrient cycling (Céréghino *et al*., 2008). Zooplankton communities in these environments are often physiologically adapted and have developed effective and diverse mechanisms for colonization, persistence, and reproduction. The extreme environmental conditions of these habitats, including fluctuating water levels and periodic desiccation, create selective pressures that drive unique adaptations and potentially promote high levels of endemism. Therefore, in addition to supporting common species, these habitats harbor endemic and rare species (Collinson *et al*., 1995; Maiphae *et al.,* 2023).

However, despite their ecological significance, temporary habitats are often overlooked in biodiversity assessments, particularly in tropical regions where research remains limited (Freiry *et al*., 2020; Paina and Melão, 2019). Although frequently disregarded, they serve as regional biodiversity "hot spots" (Céréghino *et al*., 2008). Among the key components of zooplankton in these habitats are copepods, a diverse group of small crustaceans that function as primary consumers and predators, serve as prey for higher trophic levels, and indicators of environmental health (Dussart and Defaye, 2001). In Thailand, copepods have been extensively studied in permanent freshwater bodies (Boonmak and Sanoamuang, 2022; Boxshall and Defaye, 2008; Ding *et al*., 2024; Sanoamuang and Dabseepai, 2021), but their diversity in temporary habitats remains poorly understood (Maiphae *et al*., 2023; Saetang *et al*., 2024).

Moreover, these habitats are at risk of disappearing worldwide due to increasing human-driven pressures, such as landfilling water bodies for road construction, dredging for public park development, and climate change (Rhazi *et al*., 2012). These activities can lead to shifts in organism communities and potentially result in species loss. Despite their ecological importance and vulnerability to biodiversity decline, temporary aquatic ecosystems remain poorly studied in tropical regions. Only a few studies have focused on these habitats, leaving significant knowledge gaps. This lack of information, combined with inadequate management, contributes to their degradation and potential disappearance. Furthermore, because they are small, shallow, and temporary, they are often perceived as unproductive areas and thus receive little conservation attention.

Recent studies suggest that temporary habitats may harbor cryptic or undiscovered species, contributing to the overall biodiversity of freshwater ecosystems (Maiphae *et al*., 2023; Saetang *et al*., 2021, 2022, 2024). In Thailand, where diverse temporary water bodies are widespread, their copepod diversity remains largely undocumented. This study aims to explore the hidden diversity of copepods in temporary aquatic habitats across Thailand, providing new insights into their taxonomy, distribution, and ecological significance. By addressing these knowledge gaps, our findings aim to contribute to a better understanding of copepod biodiversity and highlight the importance of conserving temporary aquatic ecosystems.

METHODS

Sample collection and morphological identification

A total of 89 qualitative plankton samples were collected using a plankton net with a 60 µm mesh size from 52 temporary sites throughout Thailand between May 2017 and June 2019 (Figs. 1 and 2; Supplementary Tab. 1). Sampling was conducted qualitatively because the shallow nature of the habitat from 10 to more than 100 cm deep, and the high density of aquatic vegetation hindered standardized net tows. Under these conditions, the effective towing distance and filtered water volume could not be estimated accurately, precluding reliable quantitative assessments. Each sample was immediately preserved in 70% ethanol. Copepods were sorted and counted for relative abundance. Each specimen was dissected and mounted on a slide in glycerin, then sealed with nail varnish. The morphological characteristics of the specimens were examined using an Olympus CH2 compound microscope, and all copepods were identified to the species level following these keys; Sanoamuang (2002), Hołyńska *et al*. (2003), Alekseev and Sanoamuang (2006), Saetang and Maiphae (2023), Saetang *et al*. (2024). Taxa designated as "sp.", "sp.1" and "sp.2" refer to specimens that could be assigned to a genus but could not be reliably identified to the species level because diagnostic morphological characters were not fully observable in the available material. Nevertheless, these taxa were distinguishable from other identified species within the same genus. Therefore, they were retained as separate taxa and included in all subsequent statistical analyses.

Six physical parameters, namely water temperature, dissolved oxygen (DO), pH, salinity, electrical conductivity, and total dissolved solids (TDS), were measured using a YSI 30 model 30/10 FT. The habitats were classified into five types: canal, pond, peat swamp, swamp, and rice field. Sampling months were categorized into three groups based on rainfall level, namely high (July to September; rainfall more than 200 mm/month), moderate (May to June, and October; rainfall between 100 and 200 mm/month), and low (January to April, and November to December; rainfall less than 100 mm/month).

Data analysis

Species composition

Differences in species composition between habitat types and among seasons were assessed using the Bray-Curtis index of community dissimilarity (Bloom, 1981). Principal coordinates analysis (PCoA) was employed to visualize variations in the copepod community between samples, based on dissimilarity distances. This analysis was conducted using the PC-ORD program, version 7.11 (McCune and Mefford, 2016). Prior to analysis, were log-transformed to improve homogeneity of variance, and Euclidean distance was used to calculate dissimilarities among samples. Convex hull polygons were used to highlight groups of variables including habitat type, vegetation, habitat size and habitat depth. Although rainfall was recorded for each sampling site, it was not included in the statistical analyses because the sampling design was not suitable for evaluating the effects of rainfall on copepod richness and community composition. The rainfall data are provided in Supplementary Tab. 1 for reference and may be useful for future studies.

Species - environment relationship

Species distributions in relation to environmental variables were assessed using Canonical Correspondence Analysis (CCA) in PC-ORD software, version 7.11 (McCune and Mefford, 2016). Species found in fewer than 10% of the total samples were excluded from the analysis. The significance of the environmental variables was tested using a Monte Carlo test with 1,000 random permutations.

RESULTS

Diversity and distribution of copepods from temporary habitats

A total of 13,372 copepods belonging to 75 species distributed in 8 families and 25 genera were retrieved from 83 out of 89 samples collected from 48 temporary freshwater sites across Thailand (Supplementary Tab. 2), whereas no copepods were found in the remaining six samples from six sites. All species found in the present study included both pelagic and benthic species, most of which showed a wide range of habitat preferences and seasonal occurrences. Species richness varied among the five temporary habitat types. The highest number of copepod species was recorded in swamp habitats (51 species), followed by peat swamps (35 species), rice fields (32 species), ponds (30 species), and canals (26 species), respectively (Supplementary Tab. 2). Species richness across habitat types was consistently highest for Cyclopoida, followed by Calanoida, while Harpacticoida showed the lowest richness in all habitats (Fig. 3A). Swamps supported the highest overall species richness, particularly for Cyclopoida, whereas canals and rice fields exhibited comparatively lower richness. Peat swamps and ponds showed intermediate diversity, with ponds hosting relatively higher Calanoida richness than other habitats. Moreover, it was found that patterns of relative abundance differed among copepod groups and habitat types (Fig. 3B). Cyclopoid dominated most habitats, especially in ponds, swamps, and peat swamps, where they accounted for a large proportion of total abundance (63.90%). Calanoid showed moderate to high relative abundance in ponds (38.65 %) and rice fields (59.50%) and but were less dominant in swamp (27.50%) and peat swamps (21.01%). Harpacticoida contributed only a small fraction, 3.04%, of total abundance across all habitat types. Overall, the results highlight strong habitat-related patterns in copepod richness diversity and community structure in temporary aquatic habitats throughout Thailand, with Cyclopoida consistently representing the most diverse and abundant group.

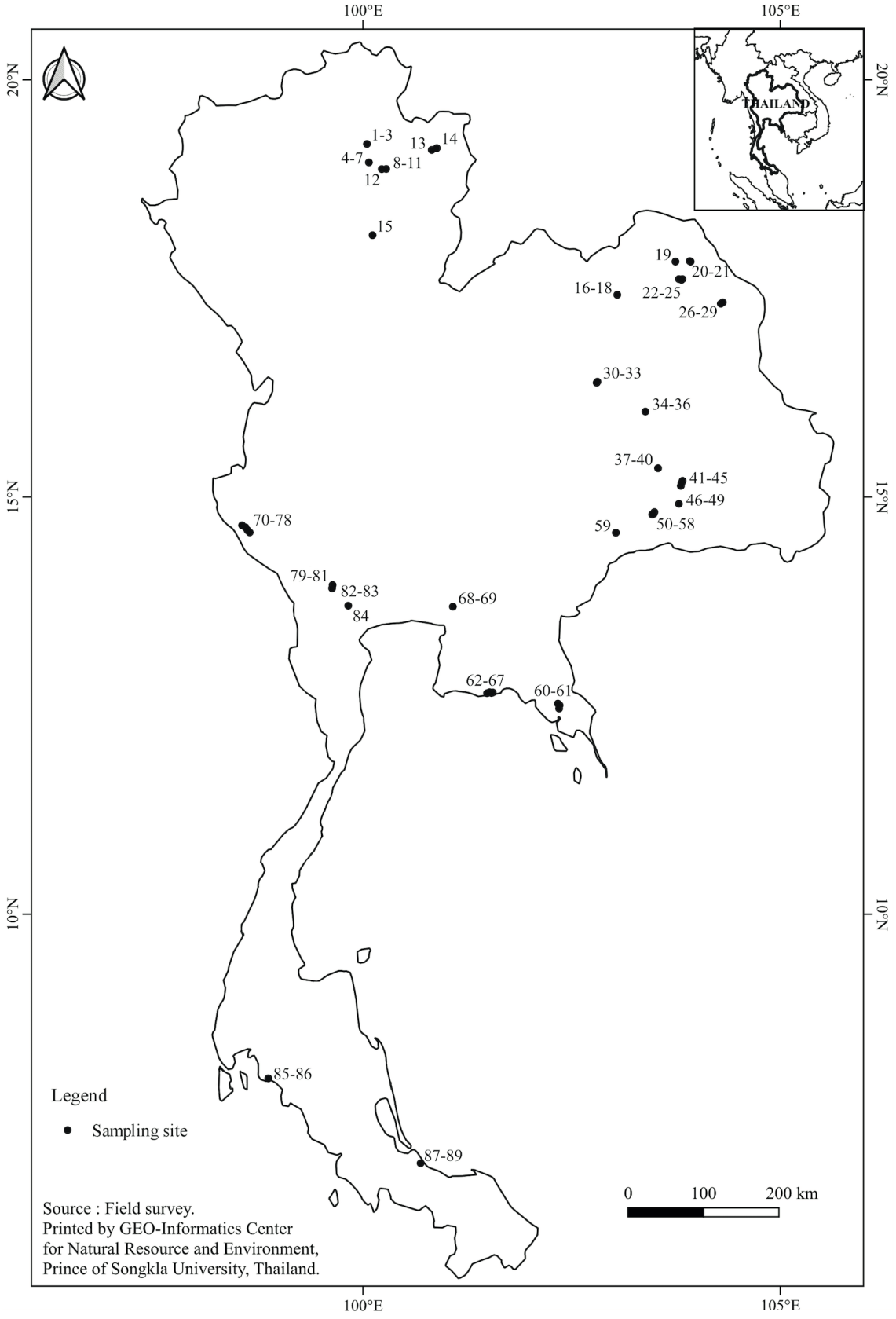

Fig. 1. Sampling sites across Thailand. Refer to Supplementary Tab. 1 for locality codes. This map was created by GEO-Informatics Research Center for Natural Resource and Environment, Prince of Songkla University and modified by authors with Adobe Illustrator CS5.

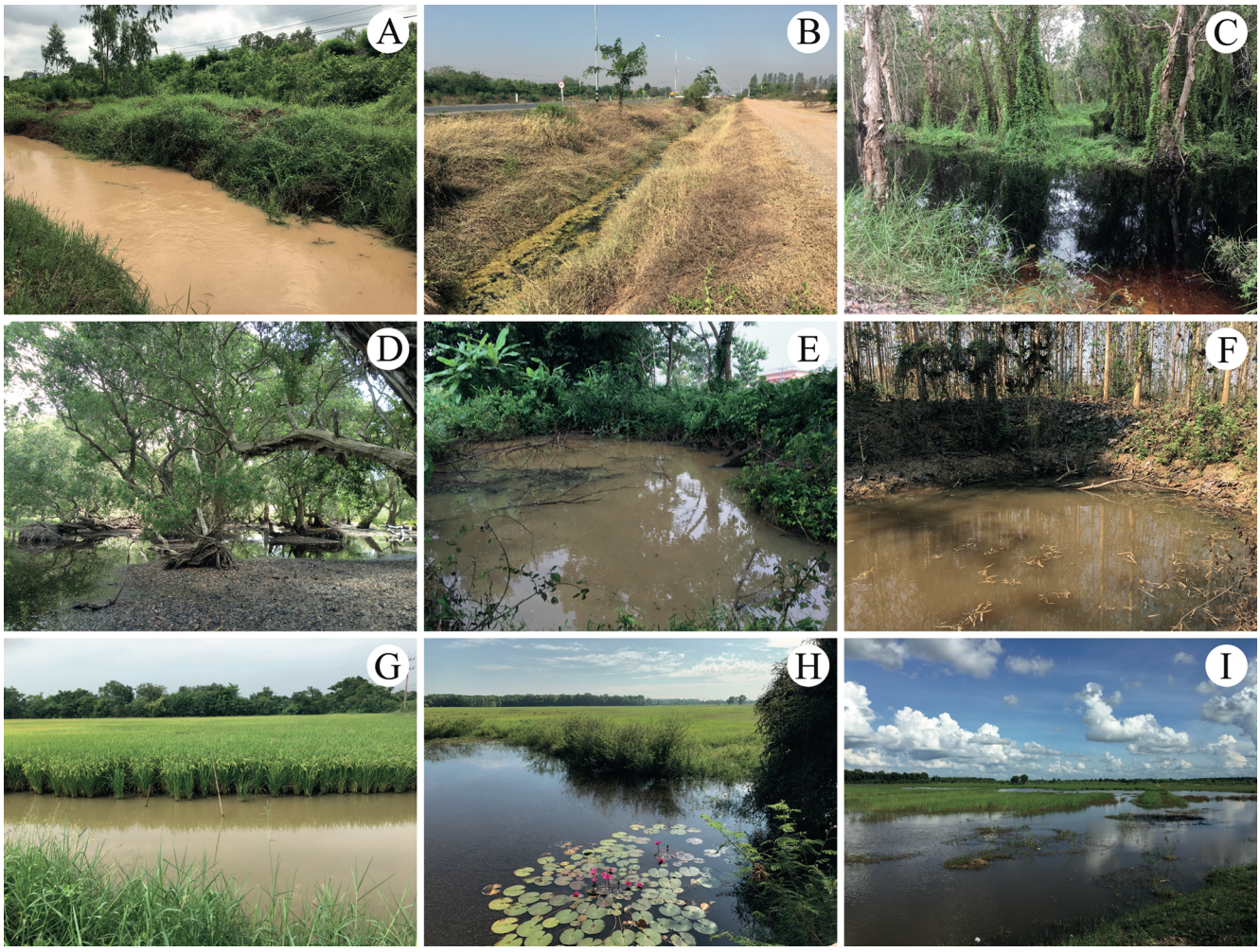

Fig. 2. Examples of sampling sites. A,B) canals; C,D) peat swamps; E,F) ponds; G) rice fields; H,I) swamps.

Most copepod species were widely distributed across all types of temporary habitats; however, several species exhibited clear habitat specificity. *Mesocyclops francisci* Holynska, 2000, *Onychocamptus mohammed* (Blanchard & Richard, 1891), *O. tratensis* Boonyanusith, Saetang, Wongkamheng & Maiphae, 2018, and *Parastenocaris* sp. occurred exclusively in peat swamps. Species restricted to rice fields included *Allodiaptomus raoi* Kiefer, 1936, *Eodiaptomus sanoamuangae* Ranga Reddy & Dumont, 1998, *Mongolodiaptomus pectinidactylus* (Shen & Tai, 1964), *Phyllodiaptomus christineae* Dumont, Ranga Reddy & Sanoamuang, 1996, *Tropodiaptomus megahyaline* Saetang, Sanoamuang & Maiphae, 2021, and *Vietodiaptomus blachei* (Brehm, 1951). In temporary ponds, only *Mongolodiaptomus calcarus* (Shen & Tai, 1965), *M. rarus* (Ranga Reddy, Sanoamuang & Dumont, 1998), *M. uenoi* (Kikuchi K., 1936), and *Tropodiaptomus* sp. were recorded. *Pseudodiaptomus dauglishi* Sewell, 1932, *Eucyclops (Denticyclops) euacanthus cognatus* Kiefer, *1929*, *Nitocra* sp., and *Elaphoidella superpedalis* Shen & Tai, 1964 were confined to temporary canals. Conversely, several species such as *Tropodiaptomus longiprocessus* Saetang & Maiphae, *2023*, *T. pedecrassum* Saetang & Maiphae, 2023, *Mesocyclops microlasius* Kiefer, 1981, *M. (Mesocyclops) pehpeiensis* Hu, 1943, *M. (Tethymesocyclops) splendidus* Lindberg, 1943, *Metacyclops* sp., *Microcyclops* sp.5, *Thermocyclops maheensis* Lindberg, 1941, *T. oryzae* Saetang, Koompoot, Watiroyram & Maiphae, 2024, *Elaphoidella bidens bidens* (Schmeil, 1893), *E. intermedia* Chappuis, 1931, *Elaphoidella* sp.2, and *Elaphoidella* sp.3 were found only in temporary swamps.

Copepod community across each variable

The PCoA results indicated a high similarity in copepod species composition across all examined environmental variables (Fig. 4). For habitat type, the first two PCoA axes accounted for a substantial proportion of the total variance (98.0%), with 52.1% explained by the first axis and 45.9% by the second axis (Fig. 4 A-D). However, the Bray-Curtis dissimilarity analysis revealed the highest dissimilarity value between rice field and swamp (24.37%), while the canal and pond showed the lowest dissimilarity value (51.03%) (Supplementary Tab. 3). Most species were distributed across all types of temporary habitats, except *Elaphoidella intermedia*, *Elaphoidella* sp.3, *Macrocyclops neuter* Kiefer, 1931,

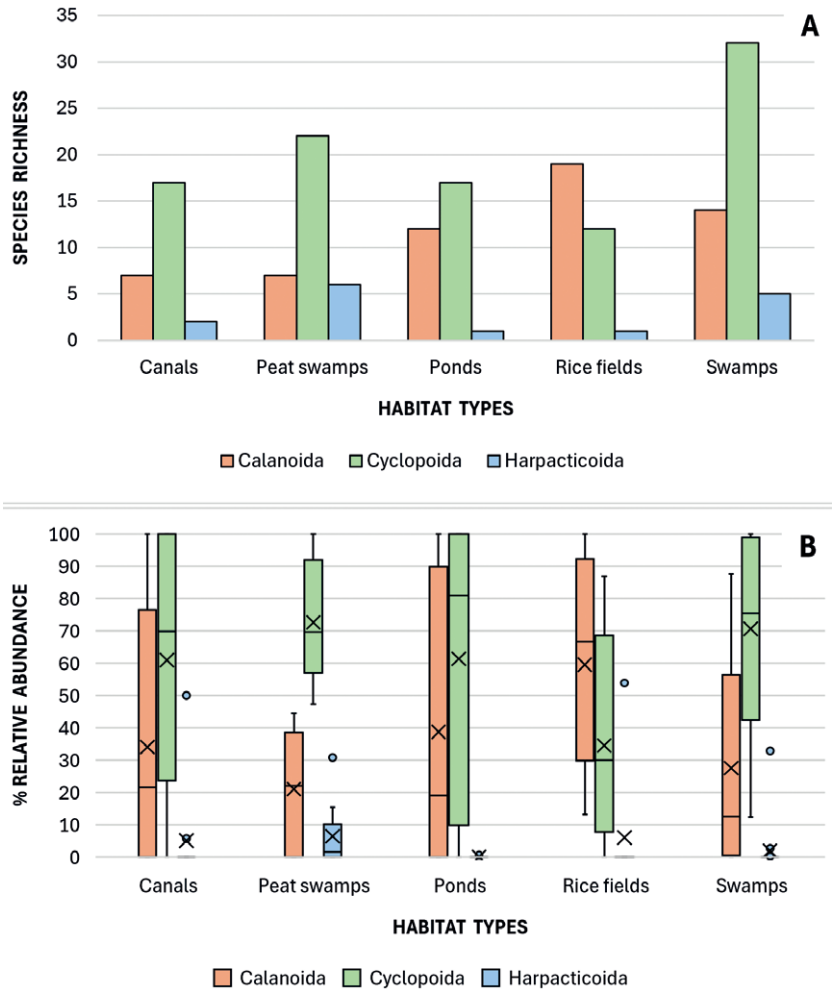

Fig. 3. A) species richness of copepods by habitat types; B) abundance of copepods by habitat types.

Mesocyclops splendidus, *Microcyclops* sp.5, and *Thermocyclops oryzae*, which were found only in temporary swamps.

When comparing habitats with and without vegetation, a similar trend was observed. The first two PCoA axes for the presence of vegetation also accounted for a substantial proportion of the total variance (98.0%), with 52.1% explained by the first axis and 45.9% by the second axis. Most species occurred in both with and without vegetation habitats. However, *Eodiaptomus sanoamuangae*, *Phyllodiaptomus surinensis* Sanoamuang & Yindee, 2001, and *P. christineae* were found only in habitats without vegetation, whereas *Elaphoidella intermedia*, *Elaphoidella* sp.3, *Macrocyclops neuter*, *Mesocyclops splendidus*, *Microcyclops* sp.5, *Onychocamptus mohammed*, *O. tratensis*, and *Thermocyclops oryzae* occurred exclusively in vegetated habitats.

Habitat size also appeared to have a limited effect on copepod community composition. The first two PCoA axes for habitat size explained a comparable proportion of the total variance (98.0%), with 52.1% attributed to the first axis and 45.9% to the second axis. Most species were present in habitats of various sizes, ranging from 0.6 to 5,700 m^2. Nevertheless, some species preferred smaller habitats, such as *Mesocyclops pehpeiensis*, *Mongolodiaptomus rarus*, *Onychocamptus mohammed*, *O. tratensis*, *Thermocyclops decipiens* (Kiefer, 1929), *Tropodiaptomus longiprocessus*, and *T. pedecrassum*, whereas others favored larger habitats, including *Elaphoidella intermedia*, *Elaphoidella* sp.3, *Macrocyclops neuter*, *Mesocyclops splendidus*, *Microcyclops* sp.5.

A similar pattern was observed with habitat depth. The first two PCoA axes for this variable accounted for a substantial proportion of the total variance (98.0%), with 52.1% explained by the first axis and 45.9% by the second axis. Most species occur across a wide range of depths, from 10 to more than 100 centimeters. However, some species were more common in shallow habitats, such as *Eodiaptomus sanoamuangae*, *Macrocyclops neuter*, *Mesocyclops splendidus*, *Microcyclops* sp.5, and *Phyllodiaptomus surinensis*, while others preferred deeper habitats, including *Elaphoidella intermedia*, *Elaphoidella* sp.3, *Thermocyclops maheensis*, and *T. oryzae*.

Influences of environmental variables on copepods

The Canonical Correspondence Analysis (CCA) revealed a significant correlation between the copepod community and environmental variables (Monte Carlo test, p=0.049) (Fig. 5). The

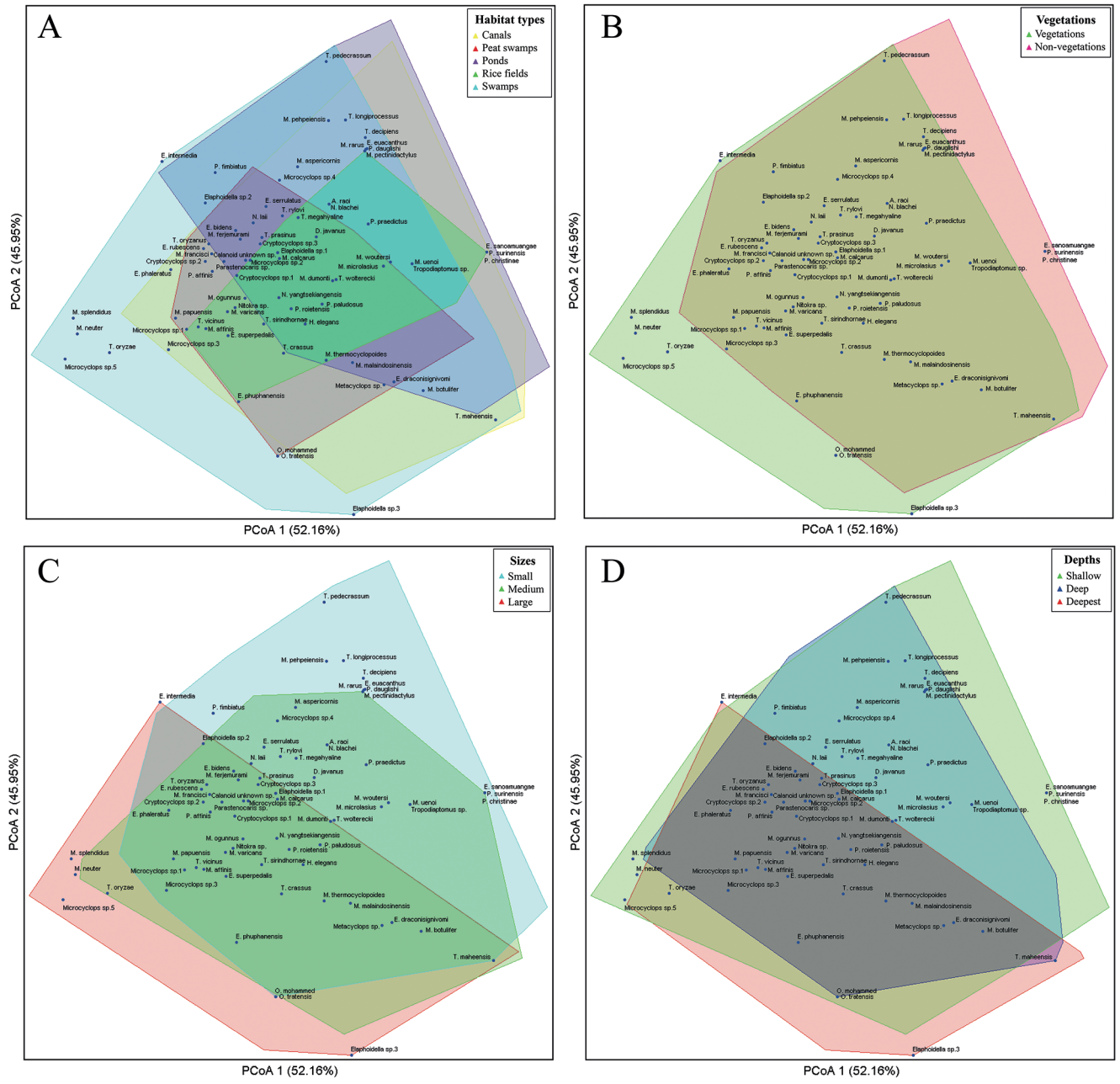

Fig. 4. Principal Coordinates Analysis (PCA) plot showing the variation in species composition among sample groups based on Euclidean distance. Each point represents a sample, and points closer together indicate higher similarity in species composition. A) habitat type; B) habitats with or without vegetation; C) size of habitat; D) depth of habitat.

eigenvalues for Axis 1 and Axis 2 were 0.270 and 0.235, respectively. Among the environmental variables, pH (Axis 1 r = 0.669, Axis 2 r = 0.227) and salinity (Axis 1 r = 0.055, Axis 2 r = 0.455) showed the strongest correlations with the copepod communities. A strong positive correlation was observed between these factors and *Ectocyclops rubescens*, *Eucyclops serrulatus* (Fischer, 1851), *Mesocyclops thermocyclopoides*, *M. woutersi*, *Thermocyclops decipiens* and *Tropocyclops prasinus*. These species were predominantly found in habitats where pH ranged from 5.43 to 8.25 and salinity varied from 0 to 1.04 PSU.

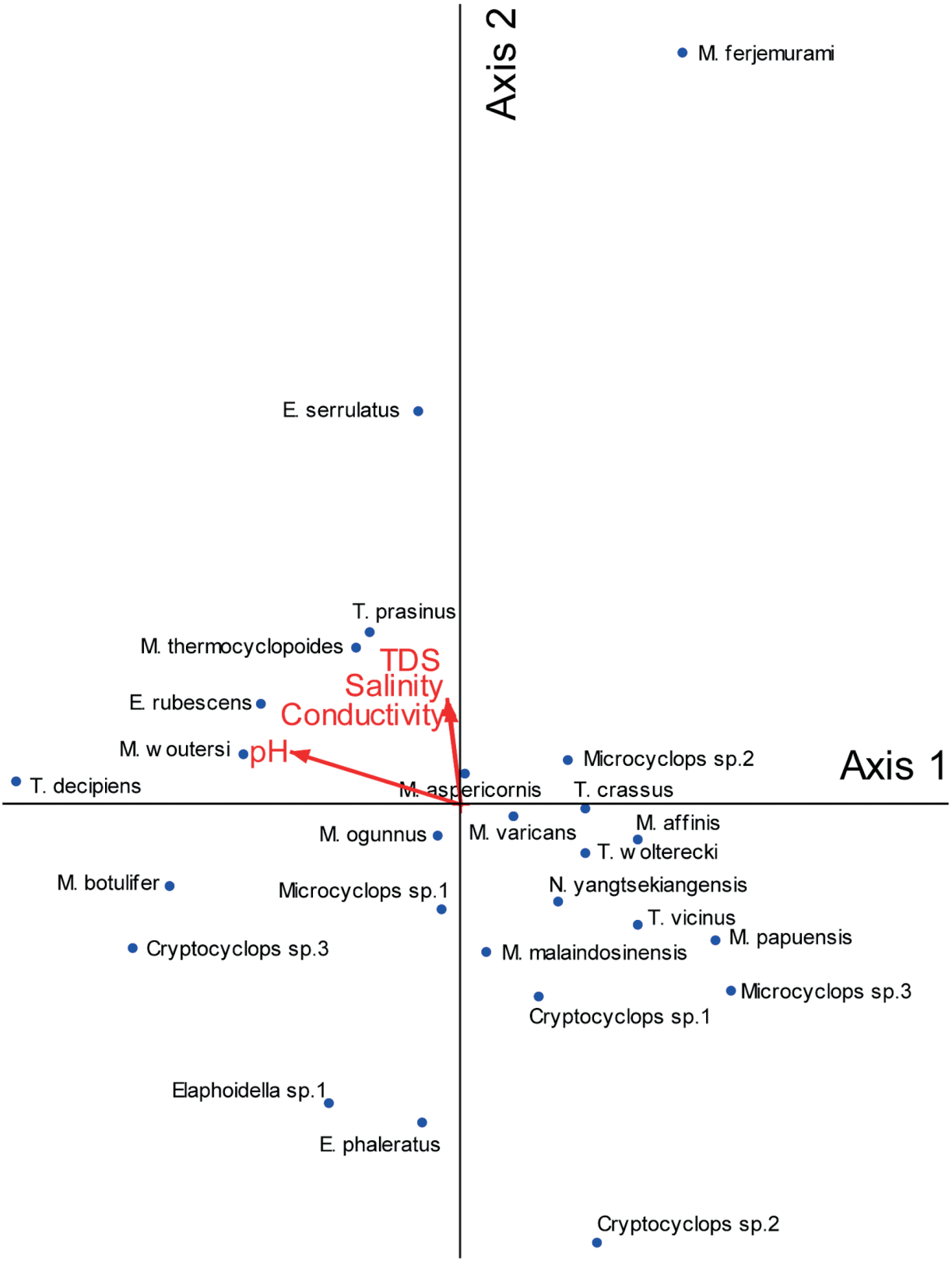

Fig. 5. Canonical Correspondence Analysis showing the correlation between copepods and environmental variables (Monte Carlo test: p=0.049; Pearson's Correlation: Axis 1 = 0.712, Axis 2 = 0.755; eigenvalue Axis 1 = 0.270, eigenvalue Axis 2 = 0.235). The blue circles represent copepod species, and the arrows represent significant environmental variables. Species and lines in the same quadrant display a positive correlation, whereas those in the opposite quadrant display a negative correlation.

DISCUSSION

Diversity and distribution of copepods from temporary habitats

The higher copepod richness observed in swamps compared with other freshwater habitats may result from their greater habitat heterogeneity and more stable hydroperiod. Swamps typically present a mosaic of microhabitats such as open water, submerged vegetation, and organic detritus, which together provide a variety of ecological niches supporting both pelagic taxa, such as calanoids, and benthic or periphytic forms, such as cyclopoids and harpacticoids (Huys and Boxshal, 1991; Maiphae *et al*., 2023; Doan *et al*., 2022; Cabral *et al*., 2020). This structural complexity increases the number of available habitats and promotes species coexistence, resulting in higher overall richness. In addition, unlike temporary rice fields or acidic peat swamps, swamp environments retain water for longer periods and exhibit relatively stable physicochemical conditions. Such environmental stability allows copepods with different life-history strategies, including those without resistant resting stages, to persist throughout the year, leading to a more diverse community (Boonmak and Sanoamuang, 2022; Caramujo and Boavida, 2010; Bruno *et al*., 2001). Therefore, the combination of high habitat complexity and a moderate, stable hydroperiod creates favorable and enduring conditions that sustain high copepod diversity in swamp habitats.

Calanoids dominate other group of copepods in rice-field because rice paddies create a temporary open-water, highly productive pelagic habitat that favours planktonic, filter-feeding, and well-dispersing taxa like calanoids (Boonmak and Sanoamuang, 2022; Maiphae *et al*., 2023). In contrast, harpacticoids are mostly benthic or meiobenthic, and cyclopoids are often epibenthic or ambush feeders, occupying habitats with substrate or vegetation (Huys and Boxshall, 1991). These ecological traits give calanoids a competitive advantage in the disturbed, shallow, and transient open-water conditions typical of flooded rice fields, where benthic microhabitats are unstable and limited (Boonmak and Sanoamuang, 2022).

The occurrence of several copepod species restricted to specific habitat types indicates pronounced habitat specificity in temporary aquatic systems. Such patterns suggest that environmental filtering influences copepod community composition across habitats with contrasting physicochemical conditions and hydroperiods (Caramujo and Boavida, 2010).

Species confined to peat swamps may be associated with distinct limnological characteristics such as high organic content and acidity, whereas those restricted to rice fields and temporary ponds likely reflect adaptations to recurrent flooding and short hydroperiods. Studies from other regions show that hydroperiod length and environmental gradients are key drivers of zooplankton diversity and species turnover in temporary wetlands (Coccia *et al*., 2024). In addition, previous studies have suggested that habitat age and historical factors can influence crustacean community composition and diversity patterns (Alfonso *et al*., 2010; Sahuquillo and Miracle, 2013). Although these factors were beyond the scope of the present study, they may represent important drivers of copepod assemblages and should be considered in future investigations.

The origin of the water body (natural *vs* artificial) may also affect copepod assemblages. Previous studies have shown that aquatic community composition and diversity can differ between natural and artificial habitats (Merrix-Jones *et al*., 2013; Naselli-Flores and Marrone, 2019). Although habitat origin was not explicitly evaluated in the present study, it may partly explain some of the variation observed among habitat types. For example, assemblages in temporary canals may be shaped by hydrological instability, favouring taxa tolerant to fluctuating water levels. In contrast, temporary swamps supported the highest number of habitat-restricted species, possibly due to greater habitat complexity and longer inundation periods that promote niche differentiation.

These habitat-specific occurrence patterns align with broader zooplankton ecology literature, which suggests that differences in hydroperiod, water stability, habitat structure, and other environmental and historical factors can shape the distribution of specialized taxa (Zokan and Drake, 2015). Together, these findings highlight the importance of conserving a variety of temporary aquatic habitats to maintain regional copepod biodiversity.

Copepod community across each variable

The copepod community composition showed a generally high degree of similarity across all examined environmental variables, indicating that most species in temporary habitats are ecological generalists capable of tolerating a broad range of habitat conditions. This finding agrees with previous reports that copepods inhabiting ephemeral or environmentally fluctuating systems often exhibit wide ecological plasticity and effective dispersal strategies, enabling them to persist across heterogeneous and unpredictable habitats (De Meester *et al*., 2002; Jocque *et al*., 2010). Such ecological flexibility is considered a key adaptive trait for colonising temporary waters, where environmental conditions can change rapidly over short time scales (Brendonck and De Meester 2003).

Among habitat types, however, subtle but distinct patterns were observed. The highest dissimilarity between rice fields and swamps likely reflects differences in hydrology, organic matter accumulation, and vegetation structure. Swamps typically provide more stable and structurally complex microhabitats that favour periphytic and benthic copepods such as *Elaphoidella* and *Onychocamptus*, genera that are frequently reported from sediments, detritus, and submerged vegetation in lentic freshwater systems (Galassi *et al*., 2012). These taxa are often associated with organic-rich substrates and macrophyte stands, where fine-scale habitat complexity offers suitable refugia and feeding surfaces (De Troch *et al*., 2006).

In contrast, rice fields experience frequent disturbance caused by fluctuating water levels and agricultural practices, which may limit the persistence of benthic and periphytic harpacticoids.

CONCLUSIONS

These findings are consistent with previous studies showing that habitat heterogeneity, vegetation complexity, and substrate stability strongly influence copepod community structure and diversity in temporary and shallow freshwater habitats (Scheffer *et al*., 2003).

The limited effect of vegetation presence, habitat size, and depth on overall community structure further supports the adaptability of many copepod species. Nonetheless, the occurrence of *Eodiaptomus sanoamuangae* and *Phyllodiaptomus surinensis* exclusively in unvegetated habitats may indicate a preference for open-water conditions typical of calanoid species, while cyclopoid and harpacticoid taxa were more common in vegetated or deeper habitats, possibly reflecting substrate dependence and refuge-seeking behaviour.

Furthermore, the limited effects of vegetation presence, habitat size, and depth on overall community composition reinforce the notion that many species in these systems are ecological generalists. Even so, some patterns were evident. The exclusive occurrence of *Eodiaptomus sanoamuangae* and *Phyllodiaptomus surinensis* in unvegetated habitats may reflect their preference for open-water conditions, a characteristic commonly reported for calanoid copepods, which are typically pelagic filter feeders adapted to the water column (Dussart and Defaye, 2001; Lampert and Sommer, 2007). In contrast, cyclopoids and harpacticoids were more frequently associated with vegetated or deeper habitats, likely reflecting their closer association with substrates and macrophytes, as well as their use of vegetation as feeding sites and refuges from predation (Williamson and Reid, 2001; Celewicz-Gołdyn and Kuczyńska-Kippen, 2017). These associations highlight the importance of microhabitat complexity in shaping the vertical and horizontal distribution of copepods within temporary aquatic environments.

Taken together, these results indicate that, although some taxa exhibited habitat-specific associations, copepod communities were not clearly separated among habitat types. This pattern may reflect the ability of many species to persist under a range of environmental conditions, resulting in substantial overlap in community composition across temporary habitats.

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Online supplementary material:

Tab. S1. Sampling sites across Thailand.
Tab. S2. List of copepod species found in temporary habitats.
Tab. S3. The Bray-Curtis Dissimilarity of habitat types.

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