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REVIEW ARTICLE

Underexplored Microbiota of Testate Amoeba in Southeast Asian Ecosystems: A Systematic Review and Meta-Analysis

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ABSTRACT

Single-celled protists, such as testate amoebae, have garnered significant attention as potential bioindicators which translate into their recognition of being ecologically sensitive. They are known for their use in ecological and paleoecological studies, yet their diversity and distribution remain poorly documented in blind spot regions of the Paleotropics. This study systematically consolidates all published species records of testate amoebae, evaluates spatial research bias, and assesses regional richness from Southeast Asian countries. A comprehensive literature search was conducted across digital databases and web-based repositories. In total, there are 497 testate amoebae belonging to 70 genera, including infra-specific species from the 46 studies scoped in this review. Species richness curves revealed steep trajectories in under sampled countries, indicating untapped diversity. Despite geographical proximity, the seeming overlap of species per country was limited, pointing toward predominance of species turnover than nested clustering of richness. This disjunct pattern in species composition suggests the influence of potential ecological specialization or, perhaps, a mere result of uneven research effort in the unexplored regions. The research for testate amoebae has been in a progressive state, yet strong emphasis needs addressing species exploration in response to intensified climate change and degradation of habitats as these would mean potential biodiversity loss.

1 | Introduction

Testate amoebae are free-living shelled protists that enclose their cell in a test (Charman 2015; Delaine et al. 2017; Marcisz et al. 2020), which serves as protection against environmental changes and potential predators. Their test has a specialized, single permanent opening, the aperture or pseudotome, where the pseudopodia will emerge for movement and phagocytosis (Bogitsh et al. 2013; Kosakyan et al. 2016; Volkova and Smirnov 2016). Evolutionarily related groups of testate amoebae assemble their tests differently, resulting in a wide range of tests with various morphologies (Wilkinson and Mitchell 2010; Delaine et al. 2017). The test can be endogenous or exogenous in origin (Kuuri-Riutta et al. 2022; Silva et al. 2022). Endogenous tests (idiosomes) are secreted by the amoeba itself and can be made of proteinaceous, biosilica plates or thick organic coating. On the other hand, exogenous tests (xenosomes) are constructed using foreign particles collected from the surrounding environment, such as minerals, diatom frustules, and organic or inorganic detritus (Bobrov et al. 2004; Schwind et al. 2016; Kuuri-Riutta et al. 2022). Hence, test morphology is often used as a basis for species identification in testate amoebae (Marcisz et al. 2020; Kuuri-Riutta et al. 2022; Šímová et al. 2022). Testate amoebae, like any other Amoebozoans, exhibit a simple life cycle involving alternating stages of trophozoites and cysts. However, a key distinction that is integral to their development

is the formation of a protective test (Iudina and Sukhanova 2000; Pchelin 2010). Notably, studies have shown that species such as *Arcella* cannot undergo normal cell division in the absence of a test (Pchelin 2010; Volkova and Smirnov 2016).

Testate amoebae represent a polyphyletic group of unicellular eukaryotes, comprising unrelated taxa within the vast diversity of single-celled eukaryotes. The supergroup Amoebozoa has undergone recent taxonomic revisions, particularly in the order Arcellinida, which has been in constant restructuring of genera and families based on molecular phylogenies, uncovering significant cryptic diversity and challenging long-standing morphological classifications (Smirnov et al. 2011; Lahr et al. 2019). These taxa are grouped based on their pseudopodial morphology: Arcellinida from the clade Tubulinea (supergroup Amoebozoa) with lobose type of pseudopodia, while Euglyphida, Chlamydophryidae, and Pseudodifflugidae belong to the SAR supergroup (Stramenopiles, Alveolates, Rhizaria), exhibiting filose pseudopodia (Kosakyan et al. 2016; Delaine et al. 2017). In addition, their classification still heavily relies on traditional morphological characteristics of the test, such as its shape and material composition (Tsyganov et al. 2017). On the other hand, despite molecular advancements, it has been revealed that morphology can be misleading due to convergent evolution (González-Miguéns et al. 2021, 2022). For instance, the genus *Difflugia* was once considered monophyletic but has been shown to be non-monophyletic based on SSU rRNA gene sequences (Gomaa et al. 2012). Similarly, the genera *Hyalosphenia* and *Nebela* have been shown to be non-monophyletic (Oliverio et al. 2015). The taxonomy and phylogeny, or evolutionary relationships, of this supergroup are complex (Dumack et al. 2017; Lahr et al. 2019), but continue to be refined (Tekle et al. 2022) with ongoing debates surrounding the monophyly of major clades and the placement of testate lineages (Kosakyan et al. 2016). Although while some taxonomic value of certain morphological traits has yet to be decided (Macumber et al. 2020), recent studies incorporate integrative taxonomic approaches in combining morphological and molecular data to better resolve species delimitation (Bankov 2025).

It is well established that testate amoebae are one of the most diverse and abundant free-living protists inhabiting a wide range of aquatic and terrestrial environments. This spatial diversity makes testate amoebae important players in several ecological processes for the continued ecosystem functioning (Delaine et al. 2017; Kuuri-Riutta et al. 2022). They are key predators and among dominant microbial consumers in the microbial food web, feeding on bacteria, fungi, microalgae, other protists, and microscopic metazoans (e.g., nematodes) (Wilkinson and Mitchell 2010; Geisen et al. 2015; Marcisz et al. 2020; Kuuri-Riutta et al. 2022). As predators, they affect carbon and nutrient cycling by modifying the composition of the microbial community. Consequently, it accelerates the turnover of soil microbial biomass and soil organic matter (Wilkinson and Mitchell 2010; Jassey et al. 2015; Kuuri-Riutta et al. 2022), increasing the rate at which nitrogen and carbon are mineralized and made available for plant uptake (Schröter et al. 2003; Wilkinson 2008). Nevertheless, when prey availability declines, testate amoebae may shift from a heterotrophic to a mixotrophic mode of nutrition (Jassey et al. 2015; De Góes Cohn Freitas et al. 2022; Kuuri-Riutta et al. 2022). Under these conditions, they engage in photosynthesis by hosting endosymbiotic algae, thereby contributing to primary productivity and carbon fixation within ecosystems (Wilkinson and Mitchell 2010; Kuuri-Riutta et al. 2022), particularly in peatlands (Hamard et al. 2021). Additionally, testate amoebae are widely used bioindicators of environmental changes due to their sensitivity to various ecological conditions (De Góes Cohn Freitas et al. 2022; Kuuri-Riutta et al. 2022; Marcisz et al. 2020; Šímová et al. 2022). These organisms have been used to indicate trace element and atmospheric pollution (Fiałkiewicz-Kozieł et al. 2015; Misailidis et al. 2018), pH levels (Qin et al. 2013), and hydrological characteristics through their fluctuating abundance, distribution, and functional traits (De Góes Cohn Freitas et al. 2022; Kuuri-Riutta et al. 2022). Their potential for paleoenvironmental reconstruction has also been recognized due to their persistent test that allows tracking environmental changes over a long temporal scale (Smith and Coupe 2002; Marcisz et al. 2020; Silva et al. 2022). Such paleoecological information can be used to predict the effects of climate change and enhance our understanding of ecosystem dynamics and biodiversity shifts over time (Wingard et al. 2017).

Early discoveries of testate amoebae began in the 19th century through Joseph Leidy's description of freshwater rhizopods, including testate amoebae and their symbiosis with algae. His work was a key milestone in early taxonomic studies of testate amoebae (Leidy 1879; Wilkinson and Mitchell 2010), which led to the recognition of their ecological importance, particularly their occurrence in different terrestrial and aquatic ecosystems (Heal 1964; Beyens et al. 1990; Wilkinson and Mitchell 2010; Lansac-Tôha et al. 2014; Ju et al. 2014; Fernández et al. 2015). The importance of testate amoebae as microfossils also became apparent as their fossilized tests provided valuable insights into various geological time scales (Holocene & Pleistocene epochs, Carboniferous and Devonian periods, and Late Neoproterozoic eon), aiding in paleoclimatic and paleoecological reconstructions (Porter and Knoll 2000; Mitchell et al. 2008; Bysouth and Finkelstein 2021; Wang et al. 2023; Porfirio-Sousa et al. 2024). Moreover, the advances in the isolation and identification of testate amoebae have greatly aided researchers in studying their morphology, including test shape, size, and structure, which has led to their classification based on test characteristics (Marcisz et al. 2020; McKeown et al. 2021). Although this method is reliable and widely used, relying solely on test morphology for identification is often insufficient due to the presence of cryptic species and phenotypic plasticity (Mitchell et al. 2008; Kosakyan et al. 2016; Marcisz et al. 2020). Hence, technological advancements, such as scanning electron microscopy (SEM) and DNA sequencing, are critical for precise taxonomic work and understanding evolutionary relationships through a more detailed analysis of test morphology and genetic insights (Mitchell et al. 2008; Lahr et al. 2019; González-Miguéns et al. 2022). Evidently, these advancements in both methodology and application have expanded the field of testate amoebae from early morphological studies to their use as critical tools in paleoenvironmental reconstruction, bioindication, and ecological monitoring.

Southeast Asia (SEA) offers a unique and largely untapped avenue for such ecological applications of testate amoebae. As a known biodiversity hotspot, SEA encompasses areas, namely Indo-Burma, Sundaland, the Philippines, and Wallacea, that

host exceptional species richness and endemism across diverse ecosystems (Bellwood et al. 2012; Koh et al. 2013; Hughes 2017; Botterill-James et al. 2024). The ecological complexity within these regions is enhanced by the wide range of unique habitats it supports, including tropical rainforests, wetlands, peatlands, mangroves, and coastal zones. Unfortunately, this rich biodiversity faces severe threats from deforestation, hunting, mining, and climate change, which are rapidly degrading natural habitats (Hughes 2017; Botterill-James et al. 2024). The destruction of key ecosystems not only endangers species but also affects essential ecosystem services that are crucial for both local communities and global environmental stability (Weiskopf et al. 2020; Adla et al. 2022). Testate amoebae as bioindicators can provide essential insights into the health and functioning of these disturbed ecosystems. They reflect ecological changes linked to anthropogenic impacts through changes in their morphological traits, abundance, and diversity (Mitchell et al. 2008; Kajukało et al. 2016; De Góes Cohn Freitas et al. 2022). Thus, ecological studies on testate amoebae are integral in SEA, especially in the face of ongoing environmental pressures, as they aid in creating early warning systems for ecosystem degradation, providing crucial data for biodiversity conservation efforts and ecological management (Marcisz et al. 2020; De Góes Cohn Freitas et al. 2022).

Despite this, scientific literature documenting the presence and importance of testate amoebae in the environment is predominantly focused on temperate regions like Europe and North America, leaving tropical regions, such as SEA, severely underexplored (Wilkinson and Mitchell 2010; Kuuri-Riutta et al. 2022; De Góes Cohn Freitas et al. 2022). Moreover, there is no literature review devoted to synthesizing the available studies on testate amoebae in the SEA region. Therefore, this systematic review focused on synthesizing and evaluating the current state of research on testate amoebae in Southeast Asia, aiming to (i) consolidate existing research on testate amoebae in the SEA region, (ii) assess the geographical and temporal distribution, (iii) evaluate species richness and diversity patterns, and (iv) examine the ecological roles and research applications. The findings of this review can shed new light on research gaps in the field of testate amoebae research, thereby advancing research guidance and conservation relevance in this biodiverse region.

2 | Materials and Methods

2.1 | Literature Search Strategy

This systematic review was conducted in accordance with the guidelines established by the Preferred Reporting Items for Systematic Review and Meta-Analysis (PRISMA) Statement (Page et al. 2021). All published research studies that reported the occurrences of testate amoeba on broader ecological investigations were included across the Southeast Asian countries of Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar, Philippines, Singapore, Thailand, and Vietnam (ASEAN Secretariat). Moreover, Timor-Leste was also included in the search because of its close proximity to the ASEAN countries. The retrieval of journal articles was directed through comprehensive searches of multiple electronic databases and search engines that were recognized for extensive collections such as Google Scholar, PubMed, Web of Science, JSTOR, ScienceDirect, Wiley Online Library, Springer Link, Semantic Scholar, Taylor and Francis Online, BioONe, and WorldCatalog. The selected databases and search engines were chosen based on the commonly used by researchers within the similar research field, accessibility and familiarity, and wide-array collection of published journal articles. The method of searching followed Boolean operator combinations whereby the following keywords were applied: “Testate amoeba” AND “Brunei”; “Cambodia”; “Indonesia”; “Laos”; “Malaysia”; “Myanmar”; “Philippines”; “Singapore”; “Thailand”; “Vietnam”; and “Timor-Leste”. Independent searches were carried out for articles that had not been retrieved from the initial search as cited within journal articles (Figure 1).

2.2 | Study Selection, Extraction and Organization

The inclusion criteria for the studies or records for this study include (1a) involving first-hand observation of any testate amoebae species (1b) whether isolated morphologically or molecularly detected (2) retrieved from any environmental samples including biological samples (3) obtained and collected within the SEA countries, (4) published in peer-reviewed journals and (5) accessible through commonly used academic databases. The selected studies were restricted to publications from the 2000s forward. Upon identification of the included studies, they were designated to countries based on the origin from where the substrates were extracted. Studies that did not meet the inclusion criteria were excluded which include (a) systematic reviews and informational articles, or (b) research studies (cited or not) that were irretrievable by any means. Data extraction was conducted independently by the authors (CJMR and LLT), retrieved from November 2024 to January 2025. The identified research studies were exported to Mendeley Reference Manager (Elsevier Ltd.) for data management. The first screening was done based on the titles and abstracts of the research studies and were thoroughly reviewed against the criteria for inclusion and exclusion. After which, each article was classified “Yes” or “No” for inclusion. Consequently, the included studies that were deemed to be qualified, or in which case—uncertain or skeptical, were further evaluated. Due to the small quantity of the studies for final eligibility screening, they were subjected to full text reading.

2.3 | Data Synthesis and Analyses

The extracted research studies were subjected to analyses to determine the trend of testate amoeba research across SEA. Data information was collated from the included studies and organized in Excel Spreadsheet (Microsoft). The extracted data were gathered, including the country of origin where the samples originated, the habitat or sampling sites from where the samples were collected the objective approach on how testate amoeba were utilized, and the total species documented and recovered. The countries lacking documented studies were excluded from the figure labels to maintain relevance. The habitats were categorized into four fundamental collections, leading to particular sampling sites from which the actual samples were obtained. The objectives of the included studies were refined to the central theme of the research. Furthermore, the included studies

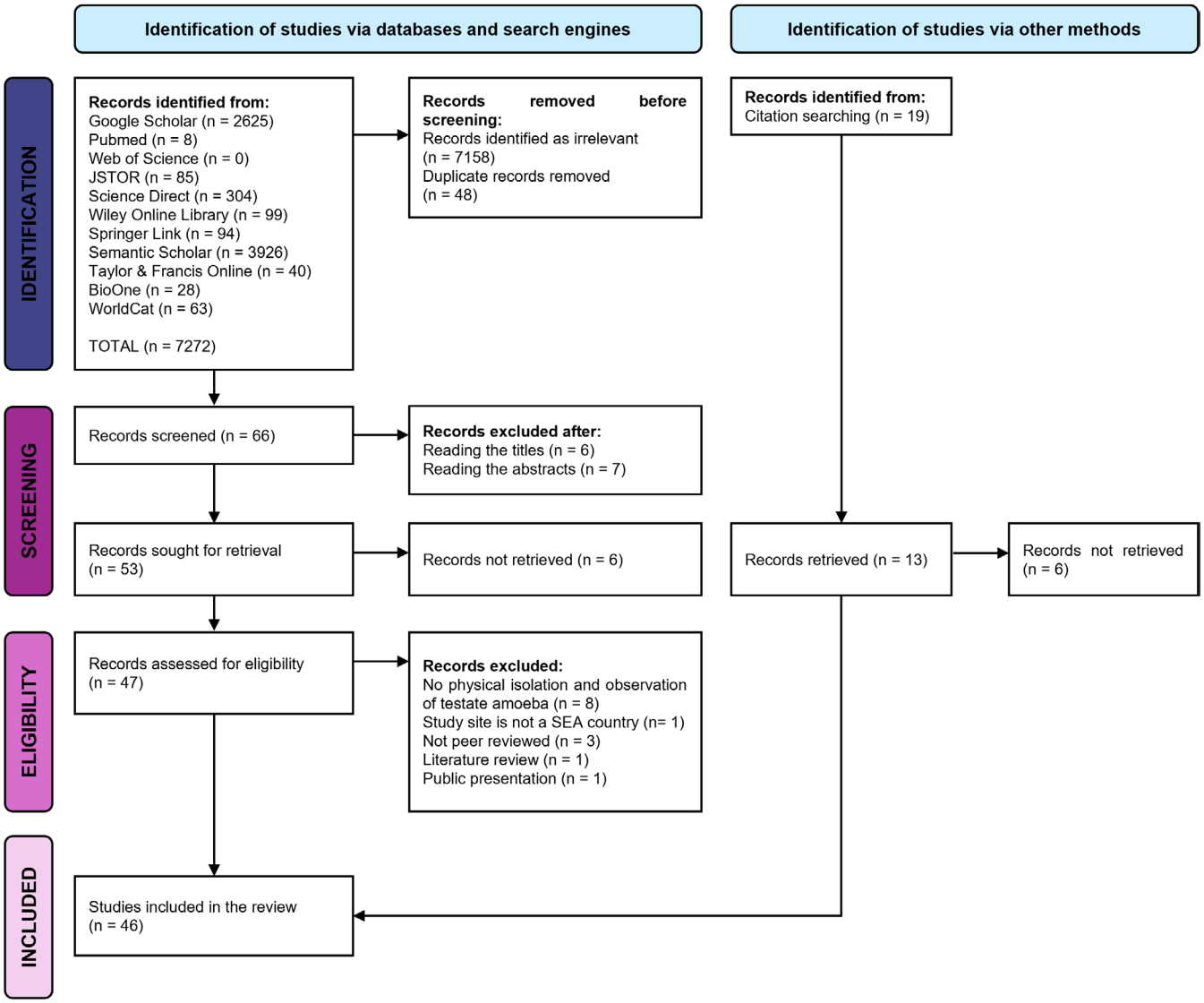

FIGURE 1 | PRISMA 2020 flowchart showing the main steps for retrieving and screening of scientific articles.

were manually examined for species count, often disregarding the declared total due to possible oversights. In this study, subspecies were treated as distinct species, whereas other studies might classify them as a single entity with the parent species. All of the recognized species with taxonomic species-level identification, including those designated with "cf." (confer) were adjoined to their nearest species-specific to maintain classification consistency. Distinct morphological variations (var.) and forms (fma.) were treated as separate species to account for potential intraspecific diversity. However, entries labeled only as "sp." without further taxonomic declaration were excluded from the final dataset to minimize ambiguity and avoid inflating species richness estimates.

The current taxonomic nomenclature of the retrieved species of testate amoebae was validated and cross-referenced based on online databases. Priority was given to "arcella.nl" (Siemensma 2025) for its amoeba-specific taxonomy, followed by "inpn.mnhn.fr"(MNHN and OFB 2025) and then "nies.go.jp" (Kuniyasu et al. 2020) if a species was not listed in the previous sources. In instances of discrepancies (e.g., synonymy and homonymy), species names were validated using the most authoritative source and verified against original literature when necessary or recorded as they appeared in the list of included studies. Although some of the studies that date back to the 1900s were successfully retrieved, a substantial portion remains inaccessible due to missing archives, language barriers, or restricted institutional access. This uneven retrieval could create a potential bias, as the available data may not fully represent the historical documentation of testate amoebae diversity in Southeast Asia.

Data analyses were performed in R version 4.3.3 (R Core Team 2013). From the comprehensive literature search, the included study counts were tallied and categorized by country and publication year. Temporal distribution was visualized using stacked bar plots with the "ggplot2" package (Wickham 2016), while spatial representation was constructed by overlaying study frequencies on a SEA map using "sf" (Pebesma 2018; Pebesma and Bivand 2023), "rnaturalearth" (Massicotte and South 2023), and "cartogram" (Jeworutzki 2016) packages to represent spatial biases in research counts. In assessing species overlap and

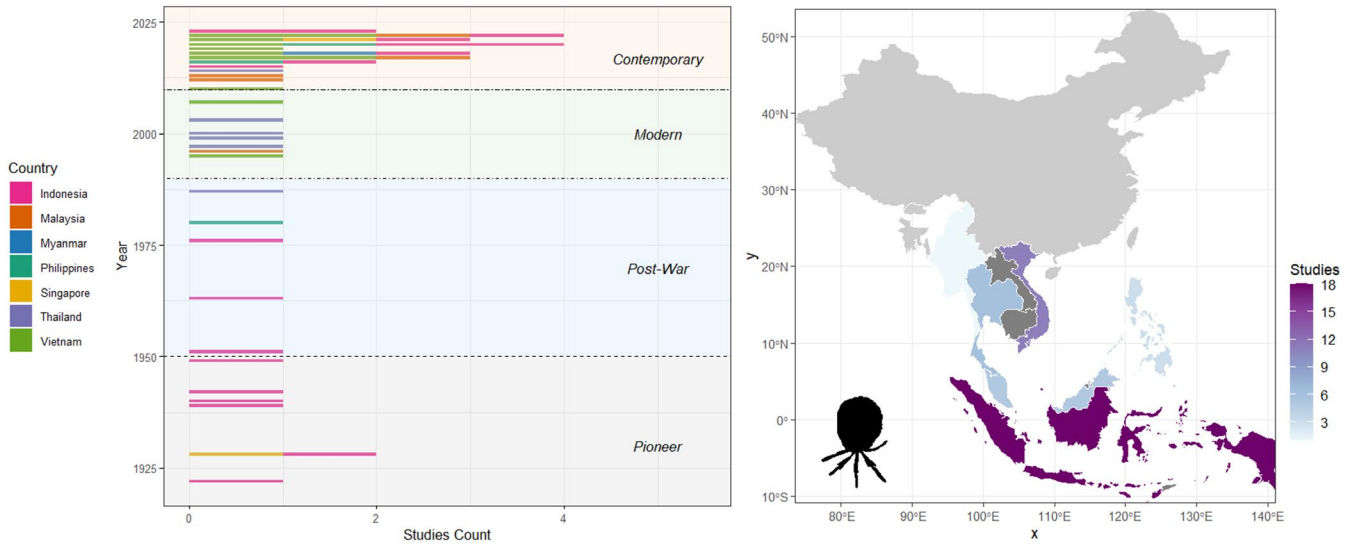

FIGURE 2 | Histogram of the research studies utilizing testate amoeba throughout the decades; Distribution map of testate amoeba research studies across SEA from the 1900s to present.

endemism, an UpSet plot was created using the "ComplexUpset" package (Lex et al. 2014), which highlights both shared and unique species across SEA countries. Species accumulation curves (Hill number, $q = 0$) were evaluated using the "iNEXT" package (Chao et al. 2014; Hsieh et al. 2016) based on incidence-frequency—where each species was counted according to the number of studies reporting its presence, not by individual abundance per study. Community composition was further analyzed using Sorensen dissimilarity utilizing the "betapart" package to evaluate multi-site beta diversity (Baselga and Orme 2012). Furthermore, a Sankey diagram was constructed utilizing the "networkD3" package (Allaire et al. 2017) to map the relationship the year of publication between the year of publication, research objectives, and sampling habitats, offering a visual trace of how study aims evolved over time and across environments. All visualizations were thematically styled using the following packages: "ggthemes" (Arnold 2021), "ggpattern" (Fc et al. 2022), "patchwork" (Pedersen 2019), "RColorBrewer" (Pedersen 2019), "viridis" (Garnier et al. 2021), and "rphylopic" (Gearty and Jones 2023).

3 | Results

3.1 | Geographical and Temporal Distribution of Research Efforts in Southeast Asia

This systematic review and meta-analysis synthesized research studies that have been conducted throughout SEA in exploring testate amoebae. A total of 46 research studies were included out of 7272 articles as submitted queries to several databases and search engines for screening and eligibility verification, including manual retrieval from in-text citations (Table S1). Research studies on testate amoeba primarily concentrated on several countries, with notable differences in terms of habitat coverage on a wide array of research objectives. The included research studies were retrieved from seven countries among the 11 countries belonging to and within the SEA, specifically: Indonesia, Malaysia, Myanmar, Philippines, Singapore, Thailand, Timor-Leste, and Vietnam. Common reasons for the rejection of the studies were exemplification of testate amoeba and/or in conjunction with studies of foraminifera, which are similar test-forming microorganisms.

It is noteworthy to mention the earlier efforts of Dammerman (1948) in Indonesia, Sudzuki (1973) and Chardez (1979) in Malaysia that have been identified through citations and initially considered for inclusion but were excluded from the final review due to the inability to access their full texts after exhaustive attempts. In addition, although the exploration of Harnisch and Thienemann (1932) was also excluded due to irretrievability, it was cited and partially summarized by Brues (1939), albeit with minor inconsistency, reporting a total of 12 testate amoeba; however, only 11 were actually listed in his account. Similarly, the same instance from Bartos (1963) cited the irretrievable study of Richters (1908), whereas only one species was accounted for since the information cannot be determined from the provided 14 species of testate rhizopods listed as found in Java, Indonesia. The included species were noted where clearly attributed, but the studies that were not retrieved were not counted in country-level study tallies. Conversely, the study of Biagioni et al. (2015) identified 78 species of testate amoebae; however, only 28 were mentioned without any supplementary data attached. Despite the advancement of technology over time, the majority of the research studies included, if not all, still remained the traditional morphological methodology for identifying testate amoeba.

The geographical distribution of testate amoeba studies was observed to be in a notably sparse pattern throughout SEA, with research efforts conducted in few countries whilst remaining infrequent or underexplored among others (Figure 2). Countries taking the lead in research efforts were from Indonesia and Vietnam, accounting for the most studies among the group with 18 and 11 research studies retrieved, respectively. The research studies were unevenly distributed across the region, with Thailand and Malaysia also contributing significant research with a fair number of six and five studies, respectively, while the

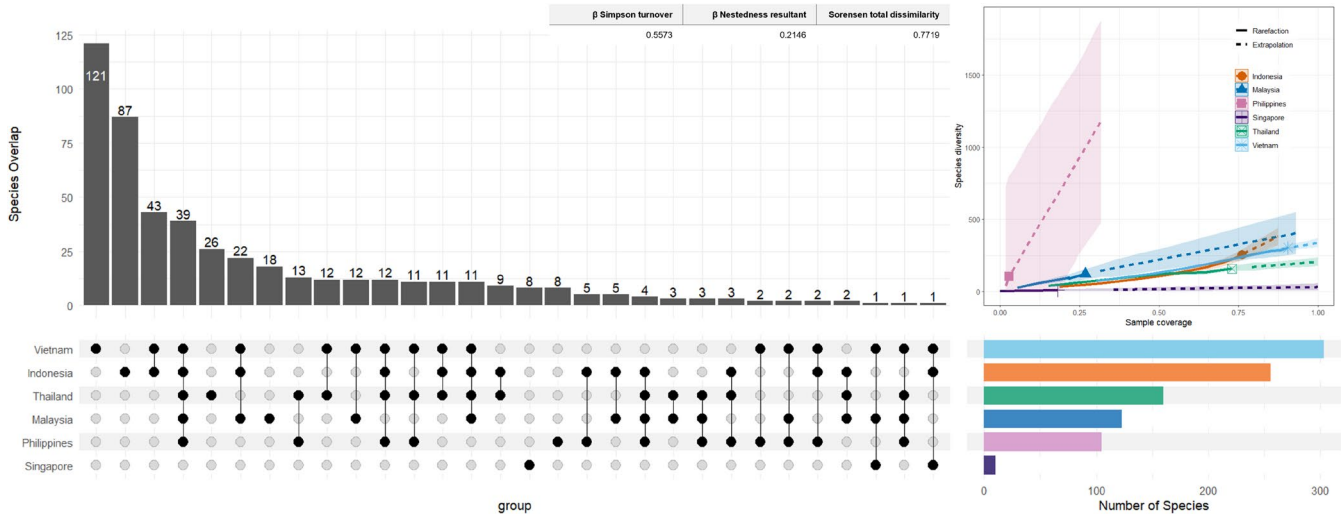

FIGURE 3 | Upset plot illustrating shared species-level diversity of testate amoebae identified across Southeast Asian countries. Each vertical bar represents the amount of a species shared, corresponding to the set of countries indicated by connected black dots; horizontal bars to the lower-right represent total species richness, respectively. Coverage-based rarefaction and extrapolation curves of testate amoebae species-level richness across Southeast Asian countries. The sample coverage represents the proportion of the total community (or species pool) that is captured by the samples. Solid lines represent interpolated richness based on observed sample sizes, while dashed lines represent extrapolated estimates. Shaded areas indicate confidence interval (0.95) based on bootstrap replicates (nboot = 999).

Philippines and Singapore had three and two studies, respectively. Subsequently, only one study was carried out in Myanmar. Despite these efforts, the distribution of testate amoeba research remains underexplored in the remaining countries of the SEA group—Brunei, Cambodia, and Laos—with no existing studies recorded to this moment.

The historical studies of testate amoebae have undergone notable shifts over time. The Pioneering Era (pre-1950) was marked by substantial foundational research, with seven studies. However, the Post-War Growth and Early Development period (1950–1989) experienced a relative decline, with only five studies, as indicated by a slowdown or stagnation in research momentum following the recovery from the world war. This was trailed by a resurgence during the Modern Consolidation period (1990–2009), where research activity increased to seven studies integrating ecological concepts and methodological improvements. The field experienced its most substantial expansion during the Contemporary Era (2010 to present), with 27 studies propelled by advancements in molecular techniques and an increasing focus on ecological and environmental applications. This temporal progression underscores a clear trend of increasing scientific interest and methodological sophistication in the study of testate amoebae over time.

3.2 | Species Discovery Dynamics and Cross-Country Biodiversity Overlaps

The studies retrieved from SEA regions have shown great richness of testate amoeba species across different habitats, making accurate identification fundamental for diversity analyses and crucial for understanding their ecological significance. The cumulative species richness of testate amoebae was recorded at an impressive total of 2132 species, taxa, morphotypes, variants, forms, and operational taxonomic units, from which 88.37% were identified to species-specific (including duplicates) resulting in a total of 497 unique species of testate amoebae, which gives a noteworthy attribution to the potential of biodiversity hotspots within the SEA regions (Table S2). However, there were evident disparities across the observed species representation among the Southeast Asian countries, reflecting differences in research intensity and habitat coverage.

Notably, Vietnam stood out as the most diverse country of testate amoebae, with the highest accumulative count of 856 species, representing nearly half of the regional total (40.15%). Furthermore, 121 of these species were unique to Vietnam, highlighting both its rich biodiversity and the emphasis on detailed species classification. Secondly, species occurrence in Indonesia, with a cumulative 751 species recorded, included 88 unique species identified exclusively within its composition. This was followed by Thailand, with 251 cumulative species records and 26 unique species. Malaysia and the Philippines exhibited comparable cumulative species counts, with 148 and 113 occurrences, respectively; whereas unique species amounted to 19 and eight, accordingly. Singapore recorded the fewest species, with 13 cumulative occurrences and eight unique species identified. The disproportion between total accumulative richness and taxonomic identification across countries reflects ongoing challenges in species identification, compounded by the morphological plasticity characteristic of testate amoebae, which continues to challenge researchers despite methodological advancements.

The coverage-based rarefaction and extrapolation curves (Figure 3) reveal striking disparities in testate amoebae diversity and sampling completeness across SEA countries. The trajectory of the curves showed that while some countries have gradual to plateauing lines, such as Vietnam and Thailand, which have relatively well-sampled communities with a high degree of completeness, others, specifically the Philippines and Malaysia, exhibited gradual to steep lines despite extremely low sampling

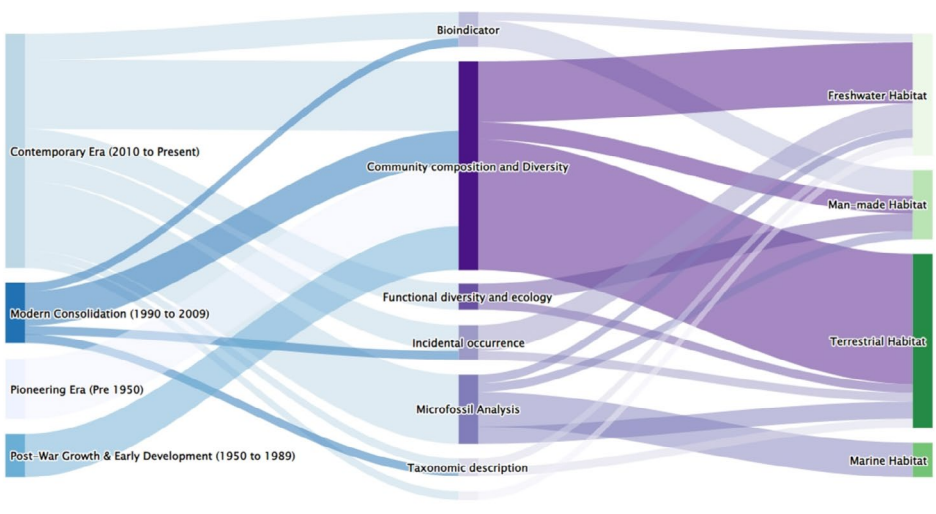

FIGURE 4 | Sankey diagram illustrating the flow of included studies from year of publication to objective or methodological approach, and subsequently to the sampling habitat from where they were conducted. The width of the links is proportional to the number of studies associated with each category.

completeness yet with high diversity estimates, reflecting both biogeographic heterogeneity and variable degrees of sampling sufficiency. Vietnam exhibited the highest observed species richness ($S = 303$) and the most robust sampling coverage, with near-exhaustive sampling estimated species richness completeness of 89.50%. Indonesia, while exhibiting a higher observed species richness ($S = 256$) than most other countries, reached only 49.17% completeness, indicating moderate under sampling, as evidenced by its estimated richness (520.65 ± 51.56). Thailand showed an observed richness of 160 species and an estimated richness of 206.69 (±13.79), resulting in 77.41% completeness, comparable in terms of species recovery efficiency to Vietnam's, though overall richness was lower. Malaysia recorded species richness of 123, yet with the estimated richness of 434.04 (±70.83), this resulted in a low sampling completeness of 28.34%, indicating a significant portion of the species remains unobserved. In contrast, sampling insufficiency was most evident in the Philippines and Singapore. The Philippines, with 105 observed species, had the most extreme incongruence, with an inflated estimate of 3710.33 (±1086.92) and only 2.83% sampling completeness, indicating severe under sampling or data heterogeneity. On the other hand, Singapore, the least species-rich, recorded only 10 observed species and an estimated 32.50 (±13.54), resulting in 30.77% sampling completeness.

Partitioning of beta diversity based on the Sørensen dissimilarity index (Figure 3) revealed pronounced compositional differentiation among SEA countries, with a total beta diversity (β.SOR) of 0.7719, indicative of a high level of compositional dissimilarity among countries. Decomposition of total beta diversity demonstrated that species turnover (β.SIM = 0.5573) overwhelmingly dominated the beta diversity pattern, accounting for over 55.70% of the observed dissimilarity rather than the nestedness-resultant component (β.SNE = 0.2146), which contributed marginally to the overall beta diversity, representing only 21.46% of compositional variation. This is consistent with the large number of unique species per country (particularly in Vietnam and Indonesia) and relatively few species shared broadly across all regions. Nevertheless, significant trends were observed such that 39 species were shared among all countries except Singapore. The remaining species were distributed across various shared geographical combinations and illustrated the complex variety of overlapping and distinct communities, which underscores the coexistence of region-specific endemism alongside broadly distributed taxa of testate amoebae. These results collectively indicate that the diversity pattern across SEA was shaped more by species turnover driven by biogeographic and environmental differentiation rather than a simple nested gradient of species loss.

3.3 | Mapping Between Sampling Sites and Objectives

The research studies conducted on testate amoebae throughout SEA established the influence of integrating diverse scientific disciplines to unravel ecological complexities, which showed clear habitat-driven patterns in study design, diversity outcomes, and analytical frameworks to the diversity and distribution of testate amoeba in SEA (Figure 4). Broadly, studies have been concentrated in four major habitat categories: terrestrial, man-made, freshwater, and marine environments. Each of the habitat types has not only shaped the geographic and methodological focus of the research but also determined the dominant ecological or taxonomic approaches applied. Terrestrial habitats have received the most comprehensive attention, particularly in countries such as Indonesia, Thailand, Vietnam, and the Philippines. These environments include a wide range of ecological settings, with most concentrations on lowland forests, then peatlands and karst wetland environments. Early exploratory studies in these environments primarily emphasized species inventories and morphological diversity, often resulting in a relatively substantial level of diversity records, particularly where methods were limited to light microscopy and descriptive checklists. However, in more recent years—particularly from peatlands in Indonesia and Vietnam—objective approaches have shifted toward functional ecology and microfossil analyses, examining how testate amoebae respond to long-term environmental changes such

as hydrological variation, fire regimes, and land-use transformation, thereby positioning these organisms as effective bioindicators in paleoecological reconstructions and ecosystem monitoring. In these contexts, the taxonomic richness and in-depth analyses have significantly increased.

On aquatic ecosystems, freshwater habitats form the second dominant research setting and exhibit the most applied objectives in the SEA region. This includes natural rivers and streams, lakes, thermal waters, ponds, estuaries, and other inland water bodies, with research predominantly focused on Vietnam, Thailand, and Malaysia. Here, testate amoebae are frequently used as bioindicators (aside from community composition and diversity) of water quality, pollution, and trophic conditions. This was also evident for incidental occurrences of testate amoebae that would likely infer and indicate the condition of the aquatic environment, even when not the primary focus of the study, emphasizing their inherent value as ecological indicators. Objective approaches in this setting were often quantitative and analytical, involving species-environment correlation analyses, multivariate ordination, and index-based water assessments. Species richness in freshwater habitats was also considerably high, although values fluctuate depending on microhabitat diversity and disturbance levels. Coastal and marine habitats, on the other hand, although significantly underrepresented, contributed to a unique perspective whereby studies from the Philippines, Indonesia, and Malaysia have investigated testate amoebae in coastal, estuarine, and inland sediments that are often in conjunction with geological or paleoenvironmental studies. The conducted investigations were usually not focused on biodiversity per se but instead leveraged testate amoebae as stratigraphic markers (palynomorphs) or proxies for paleoenvironmental reconstruction and broader tropic and ecological interpretations. In this kind of setting, species richness was typically low to almost non-existent, likely due to identifying resilient or morphologically distinct taxa that could serve as reliable indicators for layer-stratified correlation or past historical events. Exploration for testate amoebae has made its way to man-made or anthropogenically modified habitats, with most from modern-contemporary research, particularly across rural–urban landscapes, agricultural plantations, and engineered ecosystems (e.g., aerobic granular sludge systems, reconstructed wetlands and reservoirs). Despite varying sample effort and resolution, these studies share a common orientation toward taxonomic diversity, functional ecology, bioindicator, and microfossil analysis under disturbance gradients.

4 | Discussion

This synthesis and meta-analysis of conducted studies on testate amoebae in the SEA region reveals a fragmented yet informative landscape of research. There has been an increasing progression of testate amoeba research in SEA more recently, as reflected from the recognized ecological richness; however, it does not still suffice in addressing the existing knowledge gaps of underexplored diversity and unmapped distribution of these organisms within the region. Geographically, scientific efforts are heavily concentrated in a few countries such as Indonesia, Malaysia, Thailand, and Vietnam, while others—including Brunei, Myanmar, Laos, the Philippines, Singapore, and Timor-Leste—remain heavily uncharted. This spatial skew is further compounded by temporal inconsistencies, as scientific studies surge sporadically over the decades that are frequently linked to individual initiatives rather than through cohesive, long-term research agendas. Such uneven distribution not only restricts comprehensive regional assessments but also obscures and suppresses potential biogeographical trends that could emerge from more extensive spatial sampling.

It is evident that the dynamic of testate amoebae diversity in SEA is characterized by both high local endemism and modest species overlap among neighboring countries. Despite the numerous countries belonging to SEA harboring diverse ecological niches, the pooled species richness of testate amoebae documented across the region (497 species) only marginally exceeds the 416 species recorded in Chile alone (Fernández et al. 2015). Interestingly, it would not be much of a surprise if this could be seen in the case of the Philippines for its potential to harbor a comparative species, as evidenced by its steep SAC and low coverage value despite limited studies retrieved, but one would be naïve to dismiss this instance as merely a result of Bonnet (1980) precision or expertise. Speculations have already arisen within the archipelagic network of the Indo-Malay-Philippine recognized as a biodiversity hotspot, as theorized for its unsuspecting richness in species (Gaither and Rocha 2013; Hrdina and Romportl 2017), and considering its long-standing natural history of biodiversity exploration, yet still SEA would have been expected to far exceed the output for at least one single country. Although this could be associated with the difference in intensity and research effort, the comparison remains telling. The observed variation in SAC among SEA countries likely reflects not only habitat representation in the dataset but also the intensity of research input. Such countries with a predominance of freshwater and terrestrial studies, like Vietnam and Indonesia, exhibited flatter curves, consistent with higher sampling coverage and a reduced rate of new species accumulation. This is in contrast to the remaining countries, where research conducted dominantly specifically on man-made and marine habitats (compounded by limited number of studies) tended to show shallower species-specific resolution and lower coverage, resulting in SAC that rose more gradually without reaching a plateau. As aforementioned, these quite differences may be influenced by taxonomic expertise, methodological approaches, and specific aims of each study, suggesting that slope patterns are shaped by more than habitat alone.

While a few cosmopolitan species appear across national boundaries in SEA, many are reported in isolated instances, which are likely ascribed to sampling limitations or habitat specificity. Perhaps this might suggest that testate amoebae may be more geographically structured than previously assumed, which aligns with recent global debates on microbial endemism versus ubiquity. However, the reliance on morphological identification in SEA or even in other regions in particular, presents a challenge for confident species delineation, emphasizing the urgent need for molecular data integration to validate diversity and detect cryptic taxa.

The sampling habitats linking with the corresponding research objectives seem to follow a statistically evident trajectory in SEA as early investigations were predominantly conducted during

expeditions, focusing on baseline taxonomic inventories and descriptions of community structure often limited to accessible areas. Such foundational efforts laid the groundwork for more advanced research schemes—functional trait analyses, trophic interactions, and microfossil analyses using testate amoebae as bioindicators/markers. These present a clear directive for future research: to move beyond checklists and presence–absence data toward integrative studies that combine species composition, environmental parameters, and functional traits. Throughout the history of testate amoeba research in Southeast Asia is the striking trend of consistent predominance of foreign-led initiatives. From the earliest pioneering efforts—often embedded within colonial-era expeditions or externally funded biodiversity surveys—to contemporary studies, the scientific narrative of this region has largely been constructed by researchers based outside of SEA. While these contributions have been influential in building foundational knowledge, they also highlight a systemic gap: the underrepresentation of local scientists and institutions in shaping and sustaining research agendas. This external dominance not only raises important questions about long-term research sustainability, capacity building, and regional ownership of biodiversity knowledge but also the lack of locally driven programs which meant that ecological monitoring and microbial biodiversity assessments often remain episodic, fragmented, and dependent on transient foreign funding.

4.1 | Biogeographical Distribution and Regional Patterns

From a historical standpoint, the distribution of testate amoeba has been shaped continuously by present-day environmental factors which caused them to become an important indicator for ecological and biogeographical studies. Biogeographic patterns which go to be variations in species richness across space are exhibited across broad-scale diversity gradients–the latitudinal and altitudinal gradients as recognized to be the most notable geographical distribution trends in protist (Geisen et al. 2018). Although morphospecies of testate amoeba are considered generalists or cosmopolitan, some species seem to have clear geographic restrictions. For instance, the *Apodera vas*, a remarkable and flagship species, is largely confined to the Gondwanaland continents and sub-Antarctic islands, yet there is no apparent presence in the Holarctic despite suitable habitats, suggesting historical and environmental influences on distribution (Smith et al. 2008). As such, testate amoeba may seem to exhibit local endemism, whereas they may be confined to islands or specific regions, as in the case in New Zealand; however, a further molecular approach is necessary to confirm such pattern (McKeown et al. 2021). Latitudinal patterns have been reported for testate amoeba as observed in West Siberian Plain showing an interesting reversed latitudinal gradient in terms of β-diversity, with communities becoming more compositionally homogeneous toward higher latitudes, which could be explained by the influence of climate and historical constraints such as glaciation (Su et al. 2024a). Beyond latitudinal trends, altitudinal or elevational diversity gradients offer a compressed yet informative model for studying biodiversity patterns, particularly in mountainous tropical regions. This has been previously investigated with testate amoebae, revealing that species richness was highest at intermediate elevations in both tropical and temperate highlands (Krashevska et al. 2007; Tsyganov, Bobrov, et al. 2022). Nevertheless, additional research across several regional habitats is necessary to determine if this bell-shaped distribution pattern significantly influences community composition through the interplay of environmental and ecological factors. In SEA, Wanner et al. (2022) was the only one who explored the community response of testate amoeba to differing elevation yet was unable to infer a concrete relationship; however, an apparent decline was observed in the ascending elevation and further speculated on the vegetation type differences that likely inhabit per elevation. In addition, climatological variables significantly predict the diversity and community composition of testate amoeba at different rates and continental scales. These effects are often specific to microhabitats such as lawns and hollows, while hummocks show less pronounced patterns due to local stressors like low moisture and pH (Su et al. 2025). Even within seemingly uniform habitats, clearer fine-scale spatial structure is apparent in testate amoeba communities, frequently associated with microtopography and subtle environmental gradients (de Klerk et al. 2020; Mitchell et al. 2000). However, certain in-depth analyses and long-term evaluations must be conducted across different habitats, whether climatic conditions or edaphic factors could significantly impact the overall biodiversity and ecosystem dynamics. From an extensive study of Wang et al. (2020), stochastic processes (e.g., ecological drift) played a larger role than deterministic environmental factors in shaping testate amoeba community assembly over time. Yet, this has yet to be accounted for whether this holds true for testate amoebae across representative habitats, as they are considerably abundant in planktonic layers (Lansac-Tôha et al. 2014). Thus far, many regions with differing environments remain under-sampled, and future research is expected to reveal greater diversity and refine current biogeographical patterns (Smith et al. 2008; de Klerk et al. 2020; McKeown et al. 2021).

4.2 | Ecological Functions and Research Applications

Testate amoeba inhabits a range of moist environments, including peatlands, lakes, soils, mosses, and wetlands, contributing to nutrient cycling and ecosystem functioning (Mitchell et al. 2008; Koenig et al. 2015). As microbial consumers, they occupy the apex of micro-food webs by preying on bacteria, fungus, and other microscopic organisms (Zhang et al. 2020; Su et al. 2024b). It has been thought that testate amoebae participate in nutrient cycling by breaking down organic matter and recycling nutrients; albeit, the full extent of their role is still under investigation (Wilkinson and Mitchell 2010; Creevy et al. 2018). Experimental studies have begun quantifying their role in carbon and nitrogen turnover, suggesting they mediate microbial biomass dynamics and decomposition rates in soil ecosystems (Schröter et al. 2003; Jassey et al. 2015). Due to their sensitivity to environmental fluctuations, testate amoebae have demonstrated potential for ecological, environmental, and bioindicator applications across both contemporary and historical contexts. They are used in monitoring, paleoecology, and ecosystem assessment. The response of testate amoeba to dynamic variables such as moisture, pH, nutrient status, heavy metals, and organic carbon makes them effective indicators of changes in hydrology and habitat conditions (Qin et al. 2016; Beaulne et al. 2018; Carballeira and

Pontevedra-Pombal 2021; Rodas-Moran et al. 2022). The community composition of testate amoeba has demonstrated reliable indicators in peatland conservation status and hydrological changes, as reflected in diversity patterns influenced by neither natural processes nor anthropogenic disturbances (Carballeira and Pontevedra-Pombal 2021; Saldaeva et al. 2024). They have been used for assessing environmental conditions such as water quality, detecting metal and trace element pollution, and monitoring eutrophication in lakes and wetlands (Qin et al. 2011; Beaulne et al. 2018; Carballeira and Pontevedra-Pombal 2021; De Góes Cohn Freitas et al. 2022; Rodas-Moran et al. 2022).

Testate amoebae were clearly seen utilized in much more context on man-made habitats including aerobic granular sludge (Chan et al. 2021), reservoirs (Tran et al. 2021), and rural and urban areas (Nguyen-Viet et al. 2007) such that this emphasis could stem out from the well-established role as reliable indicators of ecological shifts where their assemblages respond predictably to environmental stressors as predominantly evident in human-modified landscapes, and was further employed by Tran (2019) in establishing baseline data on their diversity prior to the implementation of future major infrastructure projects such as dredging, river widening, and estate development in Coco River, Vietnam. When they leave their shells behind and are preserved in sediments, these can be utilized as natural proxies for paleoenvironmental reconstruction such as past moisture regimes, climate, sea-level changes, and ecological disturbances (Marcisz et al. 2020; Matsuoka et al. 2017; Mitchell et al. 2008; Pilarczyk et al. 2014; Šímová et al. 2022). Testate amoebae had been studied in SEA peatlands, as early as Hoogenraad and De Groot (1942) for examining diversity, and have now transitioned to complex analyses such as functional diversity ecology (Krashevska et al. 2020) and microfossil analyses, whereas they are mostly coupled with other pollen, spores, and sediments to reconstruct and reimagine past paleo-ecological, hydrological, and geochemical regimes in investigating ecosystem dynamics (Biagioni et al. 2015) and charcoal influx from fire events (Ramdzan et al. 2023). SEA being a tropical region where precipitation patterns are shaped by a complex interaction of climatic phenomena, including the El Niño-Southern Oscillation (ENSO) and monsoons (Zhou et al. 2021), which are increasingly susceptible to the effects of climate change that ultimately leads to more severe floods and droughts (Sentian et al. 2022) significantly impacting the ecology, testate amoebae may function as effective indicators of historical monsoon intensity and wetland resilience. However, the potential for tropical palaeoecological reconstruction remains largely untapped. Although there have been advances in approaches for methodology leaning toward trait-based approaches, improved statistical models, and integration with other bioindicators for more robust environmental monitoring (Gałka et al. 2017; Krashevska et al. 2016, 2020; Marcisz et al. 2020; Zhang et al. 2020; De Góes Cohn Freitas et al. 2022; Su et al. 2024a; Tsyganov, Malysheva, et al. 2022), whilst the majority of studies are empirical, focusing on community-level responses rather than individual species or functional groups (Silva et al. 2022).

Utilizing morphological and functional traits of testate amoeba is further emphasized to better understand their ecological roles and improve environmental assessments (De Góes Cohn Freitas et al. 2022). Functional traits shift in response to factors like water table depth and vegetation changes. For example, drier conditions favor smaller, heterotrophic species with specific shell adaptations (Koenig et al. 2015). A wide variety of functional traits can be exhibited by testate amoeba, including mixotrophy (combining photosynthesis and heterotrophy), biovolume, shell morphology, and aperture characteristics, which mediate their ecological functions and responses to environmental changes (Marcisz et al. 2020).

It was only in the contemporary era that this kind of research has been undertaken in SEA. Krashevska et al. (2020) showed the first species- and functional trait-based transfer functions whereby functional traits are strongly influenced by environmental variables, particularly water table depth (WTD) and pH. The sensitivity of testate amoebae, as indicators of ecosystem health and functioning affected by land-use changes (converted to plantations) significantly reduces the species richness, density, and biomass of testate amoebae, especially in the litter layer. This decline is accompanied by alterations in their functional composition, notably a decline in high trophic level species and siliceous shell-forming species (Krashevska et al. 2016). Trait-environment correlations have been progressively employed to construct functional indices that facilitate rapid evaluations of habitat integrity. These indices may function as early-warning mechanisms for wetland degradation, particularly in ecosystems such as peat domes and lowland swamps in SEA that are threatened by human settlement.

4.3 | Future Directions on Research Priorities and Conservation Relevance

Testate amoebae are important microorganisms used in ecological and paleoecological studies, but several key research gaps limit the broader application of testate amoebae, especially in tropical and understudied regions. Much of the existing knowledge is concentrated in the subtropics (North America) and temperate (Europe) (Schwind et al. 2016) and so there is a pressing need to expand ecological and biogeographical studies to better understand their global distribution, ecological roles, bioindicator potential, and methodological improvements. Aquatic ecosystems in the tropics lack baseline data on testate amoeba diversity and distribution, limiting understanding of their ecological patterns (Sigala Regalado et al. 2018; Silva et al. 2022).

Under this type of ecosystem, marine environments remain among the most underrepresented habitats in SEA, with few dedicated investigations not to mention the limited species-specific documentations, indicating that this kind of habitat is still largely underexplored in regional inventories. Since all of the studies retrieved in SEA emphasized microfossil analyses in marine settings likely stem from their application in paleoenvironmental reconstruction and biostratigraphy, where the primary objective is to infer past climatic and oceanographic conditions (Fakhruddin et al. 2021; Pilarczyk et al. 2014) and/or characterization and quantification of palynomorphs (Matsuoka et al. 2017, 2018). In these cases, rather than resolving species-level taxonomy, studies omit detailed species-specific identifications, prioritizing morphotype groupings or broader taxonomic categories that suffice for stratigraphic correlation

but underrepresent current biodiversity. This tendency to generalize taxonomic resolution extends to habitat coverage, where halotolerant species in high saline systems (e.g., mangrove and estuarine) remain poorly characterized despite their potential as indicators of coastal ecosystem resilience under sea-level rise. In SEA, this gap is reinforced by the overrepresentation of freshwater and terrestrial habitats in research, with minimal focus on brackish or transitional zones. Addressing this imbalance through targeted surveys and integrative taxonomic–ecological approaches will be essential for strengthening biodiversity baselines and anticipating climate-driven ecosystem shifts.

Expanding future efforts into these ecotones could reveal novel assemblages and refine the utility of testate amoebae as bioindicators across salinity gradients and climate-sensitive margins. Such as in the cases of the Indo-Malay-Philippine island systems, could offer more valuable opportunities to investigate various microbial biogeography concepts and hypotheses (Hrdina and Romportl 2017). Thus, a comprehensive understanding of testate amoebae and their ecological importance necessitates focused research in various prospective areas, including their roles as bioindicators in novel contexts such as pollution recovery, coastal wetlands, and sea-level rise (Mitchell et al. 2008; De Góes Cohn Freitas et al. 2022; Šímová et al. 2022). With the reliance solely on morphological characteristics, standardized and reliable methods for sampling, identification, and analysis are still evolving, with a need for improved techniques, especially for high-resolution spatial and temporal studies (Mitchell et al. 2008; de Klerk et al. 2020; Sysoev et al. 2024). Recent years have seen a trend in SEA where some studies are incorporating environmental data; yet, many still lack the necessary associations to link testate amoeba assemblages with ecological conditions (Sigala et al. 2016; Sysoev et al. 2024).

In addition, there is a shortage of in-depth knowledge about their functional traits and ecological mechanisms, especially in non-peatland habitats and across environmental gradients (Wang et al. 2020; De Góes Cohn Freitas et al. 2022; Silva et al. 2022; Šímová et al. 2022). Functional trait analyses and molecular methods are emerging but still require further development, optimization, and validation (Carballeira and Pontevedra-Pombal 2021; De Góes Cohn Freitas et al. 2022). A further expansion of testate amoebae research in covering a wider range of habitats (e.g., estuarine, lakes, saltmarshes and the like) and other underrepresented regions satisfies the understanding of their global diversity and ecological roles (Charman 2001; Smith and Coupe 2002; Mitchell et al. 2008).

This study presents a region-wide integrative synthesis of testate amoeba research across SEA, which appears to be spatially pragmatic yet temporally progressive. Despite the vast ecological heterogeneity of SEA habitats and its position within the Paleotropics, species richness remains underrepresented and unevenly distributed with disproportionate concentrations in a few countries and largely driven by foreign-led efforts. This goes to show the narrative of an overlooked microbial lineage along the most biodiverse yet underexplored tropical regions. Moreover, questions arise from the research efforts conducted in politically or logistically challenging areas within the SEA countries and raise concerns about the potential loss of undocumented species in rapidly degrading ecosystems. It calls for such action with emphasis where discovery is not only possible but overdue. Testate amoebae, just as any other protists, appear to have complex morphological plasticity, posing as one of its main challenges in studying beside difficulty in isolation. Perhaps, it cannot be overstated to say the least that there is a need to have a comprehensive literature or database (aside from those currently available databases) in describing detailed morphological characteristics, most especially regarding the occurrences of rare species. In most cases, these species are known only from the original descriptions and rudimentary sketches provided by the authors who first identified them. In any way of potential applications such as potential indicators of shifting environmental conditions and proxies for paleoclimatic reconstructions, testate amoebae transcend taxonomy, linking microbial diversity to macroscale ecological insights. Future research should broaden the ecological scope and demand more than sporadic expeditions to other underexplored habitats; and refine analytical tools by means of integrating functional and taxonomic approaches that will likely continue the documentation of new species to fully understand their significance in ecosystems.

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Data Availability Statement

The data that supports the findings of this study are available in the Supporting Information S1 of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** List of included studies of testate amoebae in Southeast Asia. **Table S2:** Listed testate amoebae species occurrences across Southeast Asian countries.