Diversity and habitat preferences of bdelloid rotifers in mosses and liverworts from beach forests along sand dunes in Thailand

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Microscopic animals are often thought to be widely distributed due to their small size and specific capabilities. However, evidence shows that bdelloid rotifers in bryophytes exhibit habitat specialization, with species composition varying by microhabitat. This suggests that their distribution is influenced by complex ecological processes, warranting further research, especially at the microscale. Therefore, we aimed to test whether species richness and composition of bdelloid rotifers differ across bryophyte species, forms, characteristics, and seasons to understand their distribution and habitat preferences in limnoterrestrial environments. Rotifers were identified and counted from bryophyte samples collected in April (low rainfalls), August (moderate rainfalls), and December 2022 (high rainfalls) at Bang Berd Beach Forest, Chumphon Province, Thailand. The results revealed high bdelloid diversity, with 22 species identified, 14 of which are new records for Thailand, raising the known number to 30. Species richness did not vary significantly across bryophyte variables or seasons, and there was no strong habitat preference between bdelloid rotifers and bryophytes, except for a few species. However, species composition showed high variation across bryophyte variables, confirming the limitation of their distribution.These findings indicate that this highly variable bdelloid rotifer community is surprising for several reasons. First, it suggests that bdelloid rotifers are not as vagile as previously thought. Second, it implies some local adaptation or competitive interactions between species that generate local and unique communities.

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Abstract

Microscopic animals are often thought to be widely distributed due to their small size and specific capabilities. However, evidence shows that bdelloid rotifers in bryophytes exhibit habitat specialization, with species composition varying by microhabitat. This suggests that their distribution is influenced by complex ecological processes, warranting further research, especially at the microscale. Therefore, we ~~aimed to test~~ whether species richness and composition of bdelloid rotifers differ across bryophyte species, forms, characteristics, and seasons to understand their distribution and habitat preferences in limnoterrestrial environments. Rotifers were identified and counted from bryophyte samples collected in April (low rainfall~~s~~), August (moderate rainfall~~s~~), and December 2022 (high rainfall~~s~~) at Bang Berd Beach Forest, Chumphon Province, Thailand. The results revealed high bdelloid diversity, with 22 species identified, 14 of which are new records for Thailand, raising the known number to 30. Species richness did not vary ~~significantly~~ across bryophyte variables or seasons, and there was no strong habitat preference between bdelloid rotifers and bryophytes, except for a few species. However, species composition ~~showed high variation~~ across bryophyte variables, confirming the limitation of their distribution.These findings indicate that this highly variable bdelloid rotifer community is surprising for several reasons. First, it suggests that bdelloid rotifers are not as vagile as previously thought. Second, it implies some local adaptation or competitive interactions between species that generate local and unique communities.

Introduction

The distributions and abundances of microscopic organisms (< 1 mm) may not follow the patterns typically attributed to larger organisms (Fontaneto et al., 2008; Segers & De Smet, 2008; Kaya & Erdoğan, 2015; Zawierucha et al., 2023). It has been hypothesized that microscopic organisms tend to be more widely distributed because they are small enough to be passively dispersed by wind over long distances, a concept known as the ‘everything is everywhere’ or ubiquity hypothesis (Finlay, 2002; Fenchel & Finlay, 2004; Fontaneto & Hortal, 2013). Additionally, certain microscopic organisms, such as rotifers, possess efficient resting stages that allow them to endure prolonged periods of dormancy, and their asexual and parthenogenetic reproduction enables them to rapidly colonize suitable habitats (Fontaneto, 2019). This suggests that they can be considered cosmopolitan (Fontaneto, 2011). Furthermore, Fontaneto, Westberg, and Hortal (2011) confirmed that microscopic organisms, such as bdelloid rotifers, have a lower degree of habitat specialization than larger organisms. However, this occurs within a complex scenario of ecological processes; therefore, more research is needed to explain the effects on species composition, especially at the microscale.

The distribution of microinvertebrates, such as tardigrades (Nelson & Adkins, 2001; Ramsay et al., 2021) and bdelloid rotifers (Kaya, De Smet & Fontaneto, 2010; Dražina et al., 2013; Kaya & Erdoğan, 2015), in bryophytes has been extensively studied. Bryophytes have ecological associations with microorganisms, including protozoans and rotifers, as well as other invertebrates, plants, and fungi (Gerson, 1982). They provide food, shelter, and nesting material

for small animals and invertebrates, indirectly serving as a matrix for various interactions among all these organisms (Bahuguna et al., 2013). Several studies have illustrated significantly enhanced invertebrate densities in bryophytes compared to unstable gravels (Suren, 1991; Suren, 1993). Furthermore, it has been reported that the species richness and composition of bdelloid rotifers living in bryophytes differ significantly among microhabitats, providing evidence of habitat specialization (Kaya & Erdoğan, 2015; Heatwole & Miller, 2019). In contrast, no relationships have been found between bdelloids and moss species (Burger, 1948; Kaya, De Smet & Fontaneto, 2010). Therefore, it appears that the species composition inhabiting bryophytes may change over time, or certain species may coexist in specific patterns.

Bdelloid rotifers are microscopic organisms capable of reproducing without fertilization and resisting dry and frozen conditions, which allows them to disperse across a variety of terrestrial and aquatic habitats (Fontaneto, Melone & Ricci, 2003; Ricci & Caprioli, 2005; Fontaneto & Ricci, 2006; Wilson, 2011; Debortoli, Laender & Doninck, 2018). Currently, approximately 460 species of bdelloid rotifers have been reported worldwide (Segers, 2007). In recent decades, bdelloid diversity in terrestrial environments has been extensively studied across various regions, including Central and Eastern Europe (Donner, 1965; Koste, 1975, 1978a, 1978b; Schmid-Araya, 1995), Turkey (Kaya, 2013), Korea (Song & Kim, 2000; Song & Min, 2015; Song & Lee, 2017), China (Zeng et al., 2020; Wang et al., 2023), the Arctic (Svalbard) (Kaya et al., 2010), and Antarctica (Velasco-Castrillón et al., 2014; Iakovenko et al., 2015). These studies have contributed to extensive species lists, resulting in numerous species being recorded (Fontaneto et al., 2007; Zeng et al., 2020).

In Thailand, studies on bdelloid rotifers have predominantly focused on freshwater habitats, with 16 species reported (Sa-Ardrit, Pholpunthin & Segers, 2013; Maiphae, 2017; Jaturapruek et al., 2018, 2021). While their niche preferences and distribution patterns in freshwater environments have been explored (Jaturapruek et al., 2021), there remains limited knowledge about their distribution in limnoterrestrial habitats. This study was the first to investigate the habitat preferences of bdelloid rotifers in tropical terrestrial environments, where water availability may influence dispersal and distribution patterns, potentially differing from those in drier or colder regions. The Bang Burd Forest, the largest beach forest on sand dunes in Thailand, is a unique ecosystem characterized by a diverse plant community, including climbers and trees adapted to sandy soils, intense sunlight, high winds, dryness, and constant seawater spray (Inuthai, 2007). This forest is significant not only for its distinct environmental conditions but also for the rich biodiversity it supports. Previous research has documented a high diversity of bryophytes—specifically, 16 species of mosses and liverworts (Inuthai, 2007)—indicating a variety of microhabitats that could be crucial for supporting invertebrate communities (Budke et al., 2018). As a result, this study aims to examine the distribution patterns of bdelloid rotifers in relation to bryophyte species and their characteristics. By understanding these relationships, we hope to gain insights into the habitat preferences of bdelloid rotifers in this distinctive ecosystem.

Materials & Methods

Sampling site

Bang Berd Beach Forest in Chumphon Province, Thailand, is located near the coast (10.987531700278218, 99.49570988282339) with an elevation ranging from 6 to 54 meters above sea level. This forest is characterized by sand dunes and scattered patches of plants. The surrounding area is dry and sunny, while the interior is more humid. The plant community includes shrubs, trees, and climbers, which provide habitats for bryophytes (Fig. 1).

Sample collection, species identification and count

A total of 173 bryophyte samples were collected in April 2022 (low rainfalls), August 2022 (moderate rainfalls) and December 2022 (high rainfalls), and the average rainfalls of each periods based on data during 2019-2021 were 6.96, 15.04 and 21.64 mm, respectively (Hydro-Informatics Institute (Public Organization), 2021). (Approved by the Institutional Animal Care and Use Committee, Kasetsart University, approval no. ACKU66-SCI-018). All samples were stored in zip-lock plastic bags for bdelloid studies and bryophyte identification. There are 11 species of mosses and 31 species of liverworts which were classified into groups (mosses, liverworts), life forms (cushion, turf, mat) (Inuthai, 2007; Suwanmala & Chantanaorrapint, 2016), and morphological characteristics. The morphological characteristics of mosses and liverworts were classified by the complexity of their structure that may be linked to the ability to harbor water, which is an environment for rotifers. Mosses are classified into two characters including leaves curl when dry and leaves do not curl when dry (in this context, ‘leaves’ refers to a leave-like structure or phyllids) and liverworts are classified into two characters including large lobules (a ratio of lobules is about half or more than half of lobe length) and small lobules (a ratio of lobules is less than half of lobe length) (Table 1, Figs. 2-3). Samples containing mixed bryophyte species (Table S1) and those where bdelloid rotifers were not found were excluded from the analysis. Therefore a total of 52 samples were used for data analysis. In the laboratory, samples were prepared for identification using a modified method from Peters et al. (1993). A 3x3 cm^2 of each sample was soaked in mineral water for 24 hours, then shaken thoroughly before collecting the water samples for bdelloid rotifer identification and counting.Bdelloid rotifers in each water sample were sorted using a stereomicroscope (Olympus SZ51). The morphological characteristics of each specimen were examined live with a light microscope (Olympus CH2). All taxonomic characters were photographed and recorded on video. Identifications were based on morphological characteristics, following Donner (1965) and Ricci & Melone (2000).

Data analysis

Species diversity

Shannon diversity and species evenness index was used to compare species diversity of bdelloid rotifers among bryophyte species, among seasons (low, moderate and high rainfalls), among bryophyte forms (cushion, turf, mat) and among bryophyte characters (mosses: leaves curl when

dry and leaves do not curl when dry; liverworts: large lobules and small lobules). These analyses used the Microsoft Excel program (Microsoft 365).

Species composition and habitat preferences

Differences in species composition were assessed using a Jaccard similarity index (Wolda, 1981). To visualize the relationship between species composition and bryophyte species, between species composition and bryophyte forms and between species composition and season, Principal Components Analysis (PCA) was performed using PC-ORD program version 7.11 (McCune & Mefford, 2016). Before performing the analyses, species composition was transformed to normalize the data using log transformation and relativization. PCA was conducted using a correlation cross-products matrix, and scores for species were calculated through weighted averaging. Convex hull polygons were used to highlight groups of variables including bryophyte group, bryophyte species, bryophyte form, bryophyte characters and season. The habitat preference of each species was calculated following the equation of Dufrêne & Legendre (1997). According to the results, three groups of preference degree were classified: high ($\geq$ 50%), moderate (30-49%) and low ($<$ 30%).

Results

Species diversity

A total of 22 bdelloid species were identified (Tables 2-4), 14 of which are newly recorded in Thailand. In addition, five bdelloid species, including *Adineta vaga*, *Adineta* sp. 2, *Habrotrocha* cf. *brocklehursti*, *Macrotrachela* cf. *plicata*, and *Philodina rugosa*, were found exclusively in samples of mixed bryophyte species (Table 4), making it difficult to determine the exact bryophyte species they inhabited. In each example, a range of 1 to 7 bdelloid species was identified, which corresponds to the number of species observed in other variables, including the bryophyte group, form, morphological characteristics, and across different seasons. Moreover, only two species, *Macrotrachela multispinosa* and *Rotaria sordida*, were distributed in more than 50% of the 83 samples, accounting for 51.81% and 53.01%, respectively. They were followed by *Habrotrocha angusticollis* (25.30%) and *Habrotrocha bidens* (19.28%), which were relatively widespread. In contrast, most other species were found in only 1 to 8 samples (Fig. 4).

The species richness of bdelloid rotifers across different bryophyte species ranged from 1 to 8 and did not differ significantly (ANOVA, p = 0.43). *Lejeunea adpressa* and *Schiffneriolejeunea tumida* var. *haskarliana* contained the most diverse bdelloid rotifer species (8 species), followed by *Cololejeunea planissima* and *Microlejeunea punctiformis* (7 species), although the diversity index of *Lejeunea adpressa* was highest, followed by *Cololejeunea planissima* (Table 5). In addition, the bdelloid rotifer species richness found in liverworts (14 species) was higher than in mosses (10 species), which is in agreement with the trend in the diversity index, although these differences were not significantly (t-test, p = 0.11) (Table 6). Moreover, the highest species richness was observed in bryophytes with a mat life form, which supported 14 species, followed

by turf with 8 species and cushion with 3 species, although the differences were not statistically significant (t-test, $p = 0.46$). This finding largely aligns with the trends observed in the diversity index, with the exception of the cushion life form, which exhibited the highest evenness value. Additionally, large-lobule liverworts displayed the highest richness, also at 14 species; however, this was not significantly different from the richness found in small-lobule species, which had 8 species (t-test, $p = 0.91$). Similarly, mosses with leaves that curl when dry supported 9 species, which did not differ significantly from the species richness of mosses whose leaves do not curl when dry, which had 5 species (t-test, $p = 0.27$). Notably, the highest diversity index was recorded for large-lobule bryophytes (1.93), followed by small-lobule bryophytes (1.68) (Table 6). Furthermore, species richness among the three periods exhibited significant differences (ANOVA, $p = 0.05$). The low rainfalls period had the highest species richness and diversity index, with 14 species and a diversity index of 1.85. This was followed by the high rainfalls period with 9 species and a diversity index of 1.67, and the moderate rainfalls period with 8 species and a diversity index of 1.52 (Table 6).

Notes on taxonomy of some unidentified bdelloid rotifers

Of the 22 recorded taxa, 6 species remain unidentified: *Adineta* sp.1, *Adineta* sp.2, *Habrotrocha* sp., *Macrotrachela* sp., *Didymodactylos* sp., and *Pleuretra* sp. (Figs. 5A–N) due to insufficiently detailed characteristics. Additionally, some of these species exhibit characters that do not align with other members of their genera.

Adineta sp.1 is notably small, measuring approximately 74.04 μm (Fig. 5A), while *Adineta* sp.2 is larger, measuring 176.92–197.12 μm (Fig. 5B), although it is still smaller than *A. vaga* (200–700 μm, according to Donner, 1965). *Adineta* sp.2 has an oval head that is wider than its trunk, but the rake apparatus is not clearly visible (Fig. 5C), and its foot is relatively short. These distinctive characteristics suggest that both *Adineta* sp.1 and *Adineta* sp.2 differ significantly from *A. vaga.* Additionally, the morphology of *Didymodactylos* sp. differs from the only known species in the genus, *Didymodactylos carnosus* (Fig. 5D–F), notably lacking the bulbous base on the spurs characteristic of *D. carnosus* (Fig. 5E). *Habrotrocha* sp. has a shuttle-shaped body, with a neck nearly half the body length (Fig. 5G). Small pellets inside the stomach are visible. The spurs are short with 3 toes (Fig. 5H), and the trophi are relatively large with 3/4 teeth. In *Macrotrachela* sp., it is unclear whether the body is fully extended, as the first segment of the trunk is swollen (Fig. 5I). The spurs are short with 3 toes (Fig. 5J), and the trophi are small, with 2/2 teeth. *Pleuretra* sp. exhibits distinct morphological differences from known species and is considered a putative new species. It has a short head and neck, with a stiff, sculptured trunk covered in broad, blunt spines (Fig. 5K). The first trunk segment shows triangular processes in dorsal view (Fig. 5L). The foot and spurs are short, with four toes (Figs. 5M–N), and the trophi are small and symmetrical, with 3/3 teeth.

Bdelloid rotifer community in bryophytes

The PCA results indicate a correlation between the species composition of bdelloid rotifers and bryophytes, life forms, and seasons. The first two PCA axes explained 15.43% and 11.37% of the total variation, respectively. Notably, the similarity among most bdelloid rotifer groups, life forms, characteristics, and seasons was less than 60%. The bdelloid rotifer species associated with mosses and liverworts exhibited a 41% similarity, with the majority found in liverworts and only a few species distributed across both mosses and liverworts. In total, eight bdelloid rotifer species were specifically associated with bryophytes, either mosses or liverworts. Five of these species were exclusive to liverworts, including *Adineta* cf. *glauca*, *Didymodactylos* sp., *H. gracilis*, *Macrotrachela papillosa*, and *Scepanotrocha simplex*. The remaining three species were found only in mosses: *Adineta* sp.1, *Habrotrocha* sp., and *Macrotrachela* sp. (Fig. 6, Table S2). At the species level, bryophytes exhibited similarities ranging from 0% to 67%, with bdelloid rotifers distributed among various bryophyte species, categorized into four distinct groups. Notably, one species of moss (*Frullania ericoides*) and one species of liverwort (*Taxithelium instratum*) were found to host the same bdelloid rotifer species (Fig. 7, Table S3). Furthermore, species composition among life forms showed the lowest similarity, with the cushion form being the most dissimilar from the others, exhibiting only 10% similarity with the turf form and 21% similarity with the mat form. The life forms can be divided into two groups: mat and turf. Most species are distributed among the mat life forms, while cushion life forms do not show a clear grouping (Fig. 8, Table S4). Moreover, the similarity in species composition based on the characteristics of mosses was only 40%. Most bdelloid rotifers are distributed in leaves that curl when dry, with some species exhibiting both types of character distributions. The first two axes of the PCA explained 20.82% and 17.55% of the variability, respectively (Fig. 9, Table S5). In contrast, the similarity in species composition for the characteristics of liverworts was 57%. Most bdelloid rotifer species are found only in large lobules or in both small and large lobules. Six species—*Adineta* cf. *glauca*, *Didymodactylos* sp., *Habrotrocha* cf. *alacris*, *H. gracilis*, *Macrotrachela papillosa*, and *Philodina verrucosa*—were found exclusively in the large lobules, whereas other bdelloid rotifers were distributed in both small and large lobules. The first two axes of the PCA explained 24.01% and 13.93% of the variability, respectively (Fig. 10, Table S5).

In addition, bdelloid rotifer species exhibit seasonal similarities ranging from 44% to 55%, which can be grouped into three seasons, with most species occurring during periods of low rainfalls. The first two PCA axes in these relationships explained 15.43% and 11.37% of the total variation, respectively. Specifically, *Adineta* cf. *glauca*, *Adineta* sp. 1, *Habrotrocha* cf. *alacris*, *H. flaviformis*, *H. gracilis*, and *Philodina verrucosa* were found exclusively during low rainfall, while *Macrotrachela* sp. was observed only in moderate rainfalls. Didymodactylos sp. and Habrotrocha sp. were identified only during high rainfalls. Other bdelloid rotifers were distributed across both low and moderate rainfalls or were found in all seasons (Fig. 11, Table S6).

Ind indices and Habitat preference degree

All bdelloid rotifer species exhibited indicator values for bryophyte groups (mosses and liverworts) of less than 30%, indicating that these species are generally low indicators of mosses and liverworts. Although most bdelloid rotifers showed non-specific habitat preferences for bryophyte species, *Scepanotrocha simplex* and *Habrotrocha* cf. *alacris* displayed strong habitat preferences (IndVal ≥ 50%) for the liverwort species Cheilolejeunea ceylanica and *Schiffneriolejeunea tumida* var. *haskarliana*, respectively (Table 7).

Discussion

Species diversity

The surprising species richness and distribution patterns of rotifers support the suggestion that different processes determine how they are dispersed. A total of 22 taxa were found in the present study, accounting for about 4% of bdelloid species worldwide (Seger, 2007; Jersabek & Leitner, 2024). Moreover, 14 new records have increased the number of bdelloid rotifers in Thailand from 16 to 30 species (Sa-Ardrit, Pholpunthin & Segers, 2013; Maiphae, 2017; Jaturapruek et al., 2018; Jaturapruek et al., 2021). Therefore, the present study confirms the rich diversity of bdelloid rotifers in terrestrial habitats.

These results reveal that *Habrotrocha flaviformis*, *Philodina verrucosa*, and *Scepanotrocha simplex*, which were recorded for the first time in the Oriental region, have a broader distribution range than other species. Moreover, most species found in this study were reported for the first time in liverworts, except for *Habrotrocha angusticollis* and *Macrotrachela multispinosa* (Donner, 1965). *Macrotrachela multispinosa* and *Rotaria sordida*, found in every region except Antarctica (Segers, 2007), were the most numerous and frequently encountered in the present bryophyte samples. In particular, *R. sordida* has been recognized as a successful anhydrobiotic species (Eyres et al., 2015), suggesting it is an effective disperser that may have colonized this area before spreading more widely. However, the degree of tolerance to environmental variables of each species also contributes to the explanation of its distribution and abundance (Ricci, 1998).

The results showed that more bdelloid species inhabit liverworts than mosses, possibly because liverworts offer a more suitable habitat for bdelloid rotifers. Liverworts often have a thinner and more delicate structure compared to mosses, which can provide more intricate and varied microhabitats for bdelloids. The surface of liverworts may possess specialized structures, such as underleaves, imbricate leaves, or lobules, that offer hiding places or protection for small organisms (Inuthai, 2007; Kraichak, 2012). There have been reports of high numbers of bdelloid rotifer species inhabiting lobules, whether the lobule was characterized as a sac (Puterbaugh, Skinner & Miller, 2004) or not (Glime, 2017a). *Microlejeunea punctiformis*, which has large lobules and small leaves but a higher number of leaves than other species, was found to maintain a high number of bdelloid rotifer species. Therefore, these characteristics might increase microhabitat diversity or complexity. However, *Lejeunea adpressa*, characterized by its small lobules and simple lobule shape, also supports a high number of bdelloid rotifer species. This

suggests that other factors, such as phytochemicals, may play a significant role in determining habitat suitability (Puterbaugh, Skinner & Miller, 2004; Xie & Lou, 2009).
Additionally, while the complexity of the bryophyte is an important factor, moisture content likely contributes to the greater richness and abundance of individuals observed (Hirschfelder et al., 1993). Unfortunately, moisture content was not measured in the present study, making it a crucial consideration for future research. Furthermore, liverworts were frequently found in areas protected by trees, which helped slow water loss, whereas mosses were found in more open areas, increasing the risk of desiccation. Moreover, most liverworts found in the present study grew in a mat life form, which retains moisture well (Proctor, 1990). This moisture retention is crucial for many invertebrates that require high humidity levels to survive, especially in dry environments (Schwarz et al., 1993; Ricci & Fontaneto, 2009; Velasco-Castrillón et al., 2014; Devetter et al., 2017). Additionally, it has been reported that liverworts tend to decompose more readily than mosses, releasing nutrients into the environment at a faster rate (Lang et al., 2009). This decomposition process supports a diverse community of microorganisms and detritivores, which in turn attract various invertebrates that feed on them or utilize them as a resource. Some invertebrates directly consume liverwort tissues or use them as a substrate for feeding and reproduction (Haines & Renwick, 2009). Liverworts may offer a richer source of food or organic matter compared to mosses in certain ecosystems. Further study on the effect of food availability in liverworts and mosses on bdelloid rotifers and other invertebrates is needed.
However, surprisingly, in periods with moderate and high rainfalls, which are characterized by high humidity, fewer species were found. One possible explanation is that during the dry season, the availability of water and suitable habitats may be limited. Under these conditions, bryophytes can serve as refuges for bdelloid rotifers, offering protection from desiccation and potentially reducing competition with other organisms. Additionally, the reduced water volume and simpler community structure in bryophyte-associated microhabitats during the dry season may lower predation and parasite pressure on bdelloid rotifers, allowing for higher species diversity to be sustained (Wilson, 2011; Wilson & Sherman, 2013). Moreover, the observed patterns in low-rainfalls tropical regions may be similar to those found in other environments (Fontaneto, Iakovenko & De Smet, 2015). However, this hypothesis should be further tested in tropical ecosystems. Another possible reason is that bdelloid rotifers have unique adaptations, such as desiccation tolerance and dormancy strategies, that allow them to survive the harsh environmental conditions characteristic of the dry season (Caprioli & Ricci, 2001; Hespeels et al., 2023). For example, *Habrotrocha gracilis*, found during the low rainy season, can secrete mucus to cover its body or combine with detritus to form a nest (Donner, 1965; Song & Kim, 2000). This trait, commonly found in this genus, may help *Habrotrocha gracilis* survive in harsh environments (Kutikova, 2003). Additionally, *Philodina verrucosa* has a thick and rough integument (Donner, 1965), a feature often seen in species that live in dry environments (Kutikova, 2003). These adaptations enable rotifers to persist within bryophytes despite fluctuating moisture levels and other environmental stressors, thereby contributing to sustained species diversity. In addition, the seasonal dynamics of bryophyte-associated habitats, influenced

by moisture availability and temperature fluctuations, may create temporal niches that favour different stages of bdelloid rotifers (Ricci, Pagani & Bolzern, 1989). Consequently, this temporal variation can enhance species diversity by supporting a succession of bdelloid rotifer species adapted to varying ecological conditions throughout the dry season.

Habitat preference

The similarities in species composition among bryophyte groups, life forms, and bryophyte characteristics are low. These results confirm the narrow distribution of bdelloid rotifers in this limnoterrestrial habitat, which may be due to several factors, including habitat characteristics and the species' capacities for surviving desiccation, achieving long-term colonization, and being dispersed by wind and raindrops (Burger, 1948; Örstan, 1998; Fontaneto et al., 2007; Bielańska-Grajner, Mieczan & Cieplok, 2017). Bryophytes provide a moist environment, which is crucial for bdelloid rotifers and other microorganisms, as they rely on water films to move and feed (Hingley, 1993). Moreover, the dense structure of bryophytes offers protection against environmental stressors such as UV radiation and desiccation, while bdelloid rotifers contribute to nutrient cycling within the bryophyte ecosystem by feeding on detritus, bacteria, and other microorganisms (Glime, 2017b). In the present study, the cushion form of bryophytes showed the lowest similarity in species composition with other forms. This may be because the cushion form has a more complex structure that supports different species compared to the more uniform structures of mats and turfs. Additionally, cushions may maintain more varied moisture levels, microclimates, and food resources, attracting specialized species and leading to distinct bdelloid communities. In this study, only *Macrotrachela pinnigera* and *Pleuretra* sp. were highly abundant in the cushion form. It has been reported that both species can disperse well in moss. Therefore, the cushion form, which is most likely to have high internal moisture, may be a suitable habitat for the growth of these two species (Donner, 1965; Ricci & Melone, 2000; Glime, 2017c). Additionally, we detected the genus *Adineta* only in the low rainy season, though with low abundance. This common genus, which is highly desiccation-tolerant (Örstan, 1995; Ricci, 1998; Hespeels et al., 2020), may prefer to avoid competition and predation in the high rainy season and disperse more in the low rainy season (Ricci & Melone, 2000; Ricci & Covino, 2005). Our results showed no specificity between bdelloid rotifer species and bryophytes, except for *Scepanotrocha simplex* and *Habrotrocha* cf. *alacris*, which were found only in liverworts (i.e., *Cheilolejeunea ceylanica* and *Schiffneriolejeunea tumida* var. *haskarliana*, respectively). However, neither species has previously been reported in liverworts. *S. simplex* has been observed in soil and leaf litter (De Koning, 1947; Donner, 1965), and *Habrotrocha* cf. *alacris* has been documented in mosses (Milne, 1916; Donner, 1965). Nevertheless, due to the low abundance observed in both species, it cannot be concluded that they are specific to these two species of liverworts unless further studies are conducted. Therefore, to better understand the impact of these factors on the species composition of bdelloid rotifers, more research is needed.

Conclusions

~~The distribution pattern of small animals on a micro scale remains a subject of debate.~~ The results of the present study on bdelloid rotifers in bryophytes confirm their limited distribution across different microhabitats and seasons. Regardless of lobule size, bryophytes with mat life forms, particularly liverworts, were the primary habitat for most bdelloid rotifers found. In contrast, mosses exhibited high species diversity only in those with leaves that curl when dry. Additionally, bdelloid species diversity was higher during periods of low rainfalls, likely due to their desiccation tolerance. Bdelloid rotifers showed low similarity in species composition across different bryophyte species, forms, and characteristics, generally exhibiting no specific relationship with bryophyte species, with a few exceptions. Therefore, further studies are needed to fully evaluate their potential as ecological indicators. While more research is required, the current findings suggest a possible relationship between bdelloid rotifer species and bryophyte characteristics.

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Table 1(on next page)

Bryophyte species that were used for data analysis

Bryophyte species	Groups	Seasons	Life forms	Characters
Acrolejeunea recurvata Gradst.	liverwort	low rainfalls	mat	large lobule
Cheilolejeunea ceylanica (Gottsche) R.M.Schust. & Kachroo	liverwort	low rainfalls	mat	large lobule
Cheilolejeunea cf. *intertexa*	liverwort	low rainfalls	mat	large lobule
Cololejeunea planissima (Mitt.) Abeyw.	liverwort	low, moderate, high rainfalls	mat	large lobule
Frullania ericoides (Nees) Mont.	liverwort	moderate rainfalls	mat	large lobule
Lejeunea adpressa Nees	liverwort	low, moderate, high rainfalls	mat	small lobule
Lejeunea cocoes Mitt.	liverwort	high rainfalls	mat	small lobule
Microlejeunea punctiformis (Taylor) Steph.	liverwort	low, moderate, high rainfalls	mat	large lobule
Schiffneriolejeunea cumingiana (Mont.) Gradst.	liverwort	low rainfalls	mat	small lobule
Schiffneriolejeunea tumida var. *haskarliana* (Gottsche) Gradst. & Terken	liverwort	low, high rainfalls	mat	large lobule
Brachymenium sp.	moss	moderate rainfalls	cushion	leaves curl when dry
Calymperes erosum Müll. Hal.	moss	moderate, high rainfalls	turf	leaves curl when dry
Calymperes tenerum Müll. Hal.	moss	low, moderate rainfalls	turf	leaves curl when dry
Octoblepharum benitotanii Salazar Allen & Chantanaorr.	moss	moderate, high rainfalls	turf	leaves do not curl when dry
Octoblepharum poscii Magill & B. H. Allen	moss	moderate rainfalls	turf	leaves do not curl when dry
Taxithelium instratum (Brid.) Broth.	moss	moderate, high rainfalls	mat	leaves do not curl when dry

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Table 2(on next page)

Bdelloid rotifer species found in the present study and their distribution in mosses.* = new records in Thailand

Bdelloid rotifer species	Mosses					
	***Brachymenium* sp.**	***Calymperes erosum***	***Calymperes tenerum***	***Octoblepharum benitotanii***	***Octoblepharum poscii***	***Taxithelium instratum***
Adineta sp.1			+			
Habrotrocha angusticollis (Murray, 1905)		+		+		+
**H. bidens* (Gosse, 1851)		+	+	+		
Habrotrocha sp.		+				
**Macrotrachela multispinosa* Thompson, 1892		+	+	+	+	+
M. pinnigera (Murray, 1908)	+					
Macrotrachela sp.				+		
**P. verrucosa* Song & Lee, 2020			+			
Pleuretra sp.	+					
**Rotaria sordida* (Western, 1893)	+		+		+	+

Table 3(on next page)

Bdelloid rotifer species found in the present study and their distribution in liverworts.* = new records in Thailand

Bdelloid rotifer species	Liverworts									
	Cheilolejeunea ceylanica	***Acrolejeunea recurvata***	***Cheilolejeunea* cf. *intertexa***	***Cololejeunea planissima***	***Frullania ericoides***	***Lejeunea adpressa***	***Lejeunea cocoes***	***Microlejeunea punctiformis***	***Schiffneriolejeunea cumingiana***	***Schiffneriolejeunea tumida var. haskarliana***
**Adineta* cf. *glauca* Murray, 1911			+							
Didymodactylos sp.								+		
Habrotrocha angusticollis (Murray, 1905)				+	+	+		+		+
**H.* cf. *alacris* Milne, 1916										+
**H. bidens* (Gosse, 1851)			+	+		+		+		+
**H. flaviformis* De Koning, 1947				+		+				+
**H. gracilis* Montet, 1915	+		+							
**Macrotrachela multispinosa* Thompson, 1892	+			+	+	+	+	+		+
**M. papillosa* Thompson, 1892	+			+				+		+
M. pinnigera (Murray, 1908)		+				+				
**P. verrucosa* Song & Lee, 2020										+
Pleuretra sp.				+		+	+			
**Rotaria sordida*	+	+	+	+	+	+	+	+	+	

(Western, 1893)				
**Scepanotrocha simplex* De Koning, 1947	+	+	+	+

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Table 4(on next page)

Bdelloid rotifer species found in the present study and their distribution in mixed bryophyte species samples.* = new records in Thailand

Bdelloid rotifer species
**A. vaga* (Davis, 1873)
Adineta sp.2
Habrotrocha angusticollis (Murray, 1905)
**H. bidens* (Gosse, 1851)
**H.* cf. *brocklehursti* Murray, 1911
**H. flaviformis* De Koning, 1947
**Macrotrachela multispinosa* Thompson, 1892
**M. papillosa* Thompson, 1892
M. pinnigera (Murray, 1908)
**M.* cf. *plicata* (Bryce, 1892)
**Philodina rugosa* Bryce, 1903
**P. verrucosa* Song & Lee, 2020
Pleuretra sp.
**Rotaria sordida* (Western, 1893)

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Table 5(on next page)

Shannon Diversity of bdelloid rotifer species that are found in each bryophyte species. Bold number indicated the highest value.

Bryophyte species	Species richness	Shannon Diversity Index	Evenness
Acrolejeunea recurvata	2	0.33	0.47
Brachymenium sp.	3	1.03	0.94
Calymperes erosum	4	0.87	0.63
C. tenerum	5	1.00	0.62
Cheilolejeunea ceylanica	5	1.49	0.93
C. cf. *intertexa*	4	1.21	0.87
Cololejeunea planissima	7	1.58	0.81
Frullania ericoides	3	0.85	0.77
Lejeunea adpressa	**8**	**1.73**	0.83
L. cocoes	3	1.04	**0.95**
Microlejeunea punctiformis	7	1.40	0.72
Octoblepharum benitotanii	4	0.95	0.69
O. poscii	2	0.45	0.65
Schiffneriolejeunea cumingiana	1	0	0
S. tumida var. *haskarliana*	**8**	1.54	0.74
Taxithelium instratum	3	0.72	0.66

Table 6(on next page)

Diversity Index of bdelloid rotifer species in each group, life forms, characters and seasons. Bold number indicated the highest value.

Bryophytes	Species richness	Shannon Diversity Index	Evenness
Groups			
mosses	10	1.61	0.70
liverworts	**14**	**1.97**	**0.75**
Life forms			
cushion	3	1.03	**0.94**
mat	**14**	**1.87**	0.71
turf	8	1.54	0.74
Characters			
leaves curl when dry	9	1.67	0.76
leaves do not curl when dry	5	1.22	0.76
large lobule	**14**	**1.93**	0.73
small lobule	8	1.68	**0.81**
Seasons			
low rainfalls	**14**	**1.85**	0.70
moderate rainfalls	8	1.52	0.73
high rainfalls	9	1.67	**0.76**

Table 7 (on next page)

IndVal value and habitat preferences of species found in bryophyte species.

Bdelloid rotifer species	Relative abundance		IndVal (%) in bryophyte group	IndVal (%) in bryophyte species	Bryophyte species preference	Preference degree in bryophyte species
	mosses	liverworts				
A. cf. *glauca*	0	0.35	3.33	33.33	without preference	**moderate**
Adineta sp.	0.79	0	4.55	14.29	without preference	**low**
Didymodactylos sp.	0	0.35	3.33	14.29	without preference	**low**
H. angusticollis	26.19	4.55	22.90	38.41	without preference	**moderate**
H. cf. *alacris*	0	0.35	3.33	50.00	*S. tumida* var. *haskarliana*	**high**
H. bidens	4.76	9.09	16.24	11.30	without preference	**low**
H. flaviformis	0	1.40	10.00	27.70	without preference	**low**
H. gracilis	0	3.5	6.67	29.41	without preference	**low**
Habrotrocha sp.	1.59	0	4.55	33.33	without preference	**moderate**
M. multispinosa	33.33	11.19	29.56	24.06	without preference	**low**
M. papillosa	0	2.45	16.67	35.61	without preference	**moderate**
M. pinnigera	2.38	19.58	2.95	32.74	without preference	**moderate**
Macrotrachela sp.	1.59	0	4.55	33.33	without preference	**moderate**
P. verrucosa	0.79	0.35	4.08	17.51	without preference	**low**
Pleuretra sp.	1.59	8.04	10.57	27.65	without preference	**low**
R. sordida	26.98	23.78	26.33	17.64	without preference	**low**
S. simplex	0	15.03	16.67	55.17	*C. ceylanica*	**high**

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Figure 1

Sampling site

(A) Sampling site at Bang Berd Beach Forest, Chumphon Province, Thailand and (B-C) Bang Berd Beach Forest environment area.

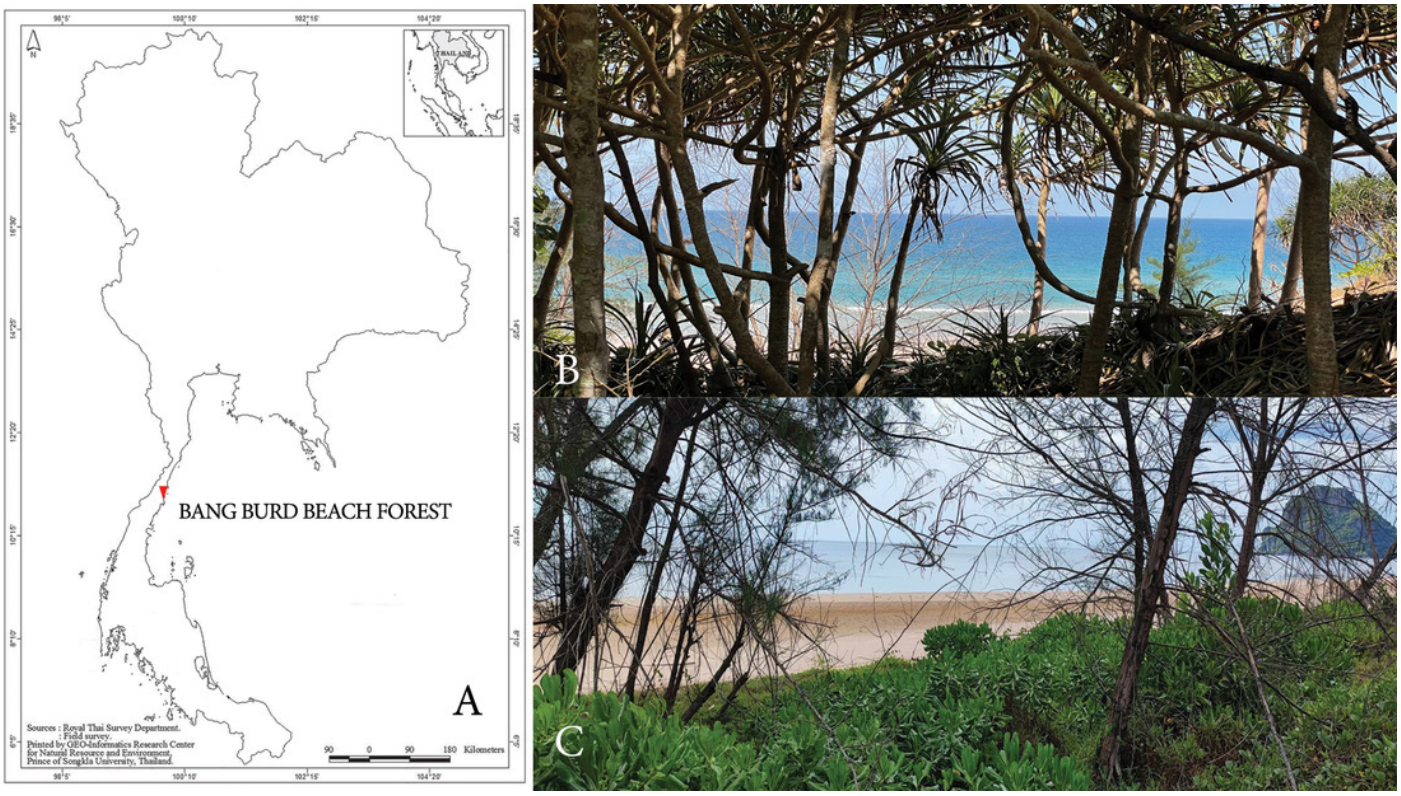

Figure 2

Bryophyte life forms.

(A) cushion (*Brachymenium* sp.). (B) turf (*Calymperes erosum*). (C) mat (*Frullania ericoides*).

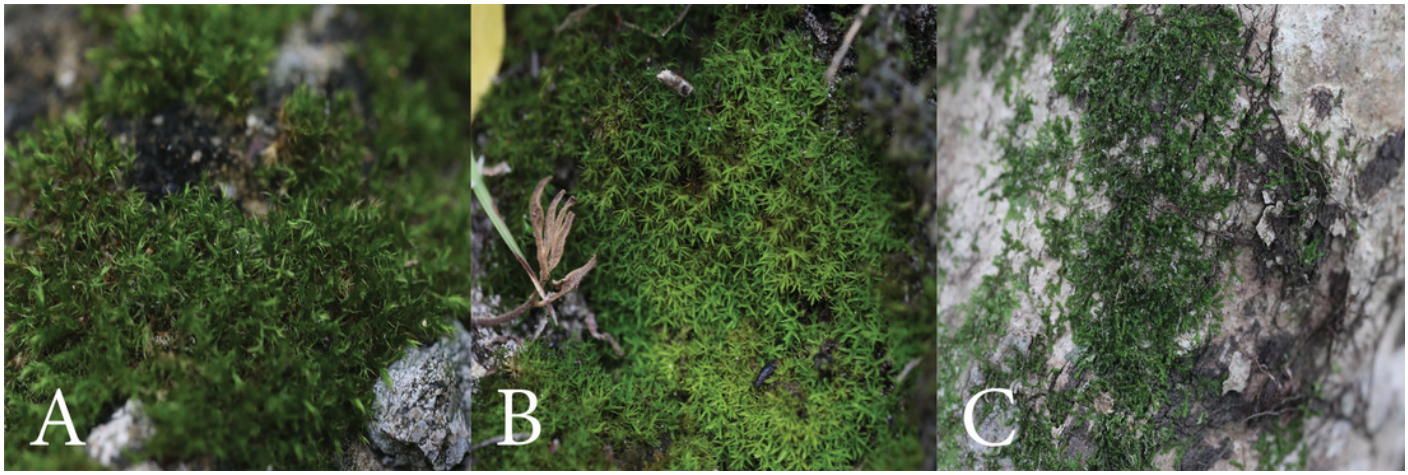

Figure 3

Bryophyte characters

(A) leaves curl when dry (*Taxithelium instratum*). (B) leaves do not curl when dry (*Octoblepharum benitotanii*). (C) large lobule (*Schiffneriolejeunea tumida* var. *haskarliana*). (D) small lobule (*Lejeunea adpressa*). Red circles indicate lobules.

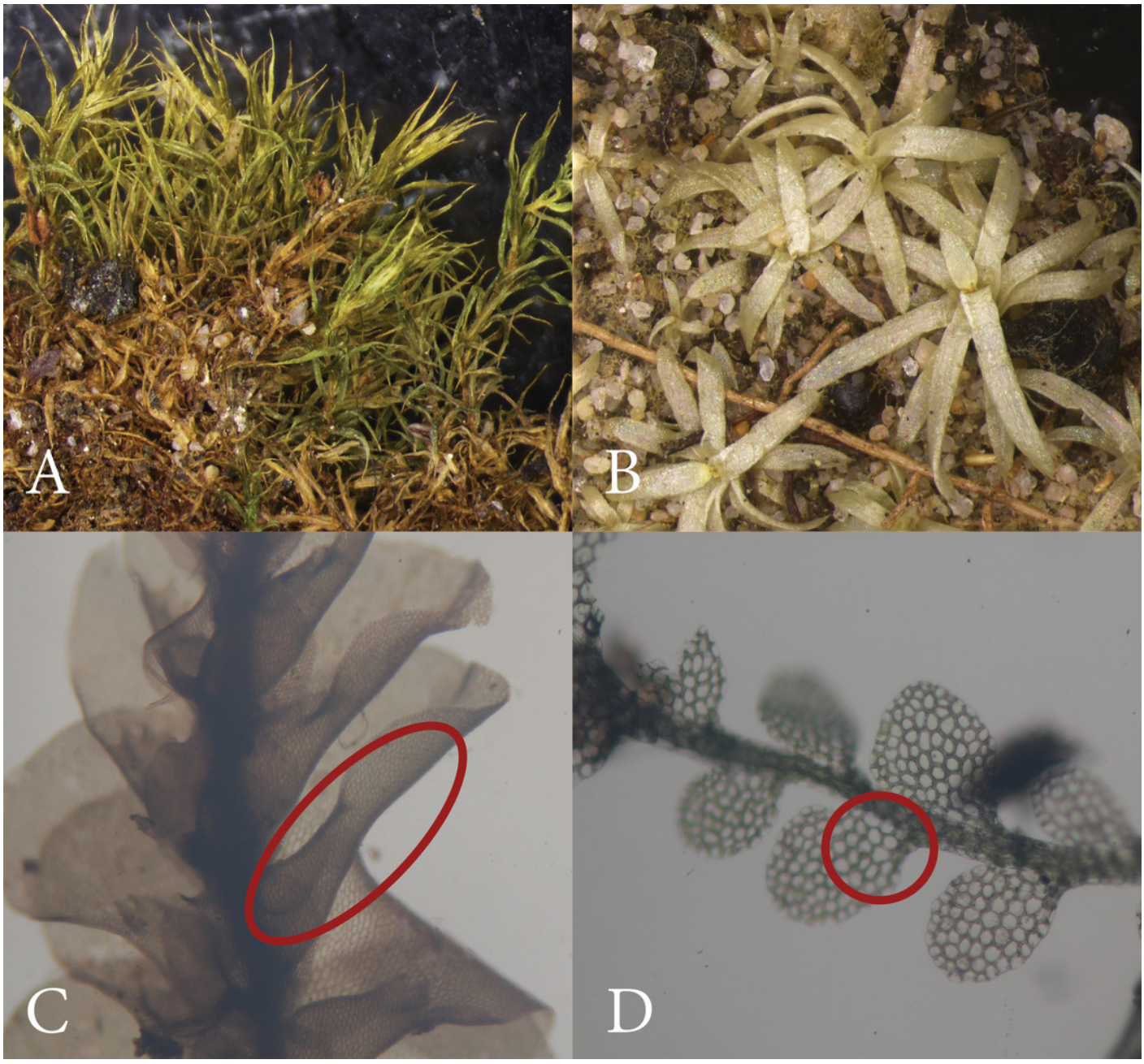

Figure 4

The number of bryophyte samples found for each bdelloid rotifer taxon

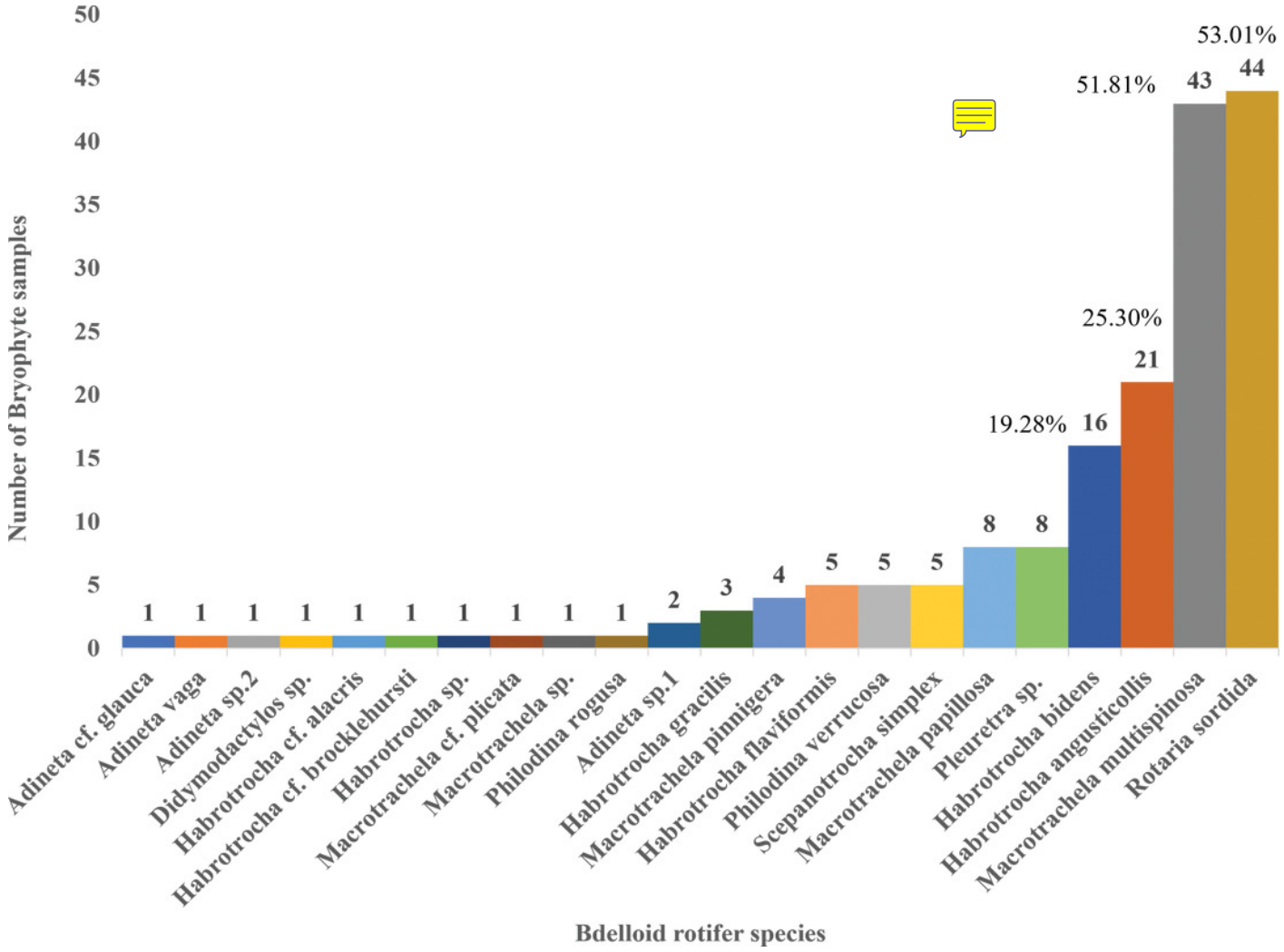

Figure 5

Photo of some bdelloid species

Adineta sp.1 (A) feeding, dorsal view. *Adineta* sp.2 (B) creeping, dorsal view; (C) creeping head, dorsal view. *Didymodactylos* sp. (D) creeping, dorsal view; (E) foot and spurs, lateral view; (F) toes, ventral view. *Habrotrocha* sp. (G) creeping, dorsal view; (H) foot and spurs, dorsal view. *Macrotrachela* sp. (I) creeping, dorsal view; (J) foot and spurs, dorsal view. *Pleuretra* sp. (K) trunk, lateral view; (L) trunk, dorsal view; (M) foot and spurs, dorsal view; (N) toes, ventral view (scale bars: B, E-F, H-I, M-N = 10 µm; A, C, D, G, J, K-L = 50 µm). The explanation of the arrows is given in the text.

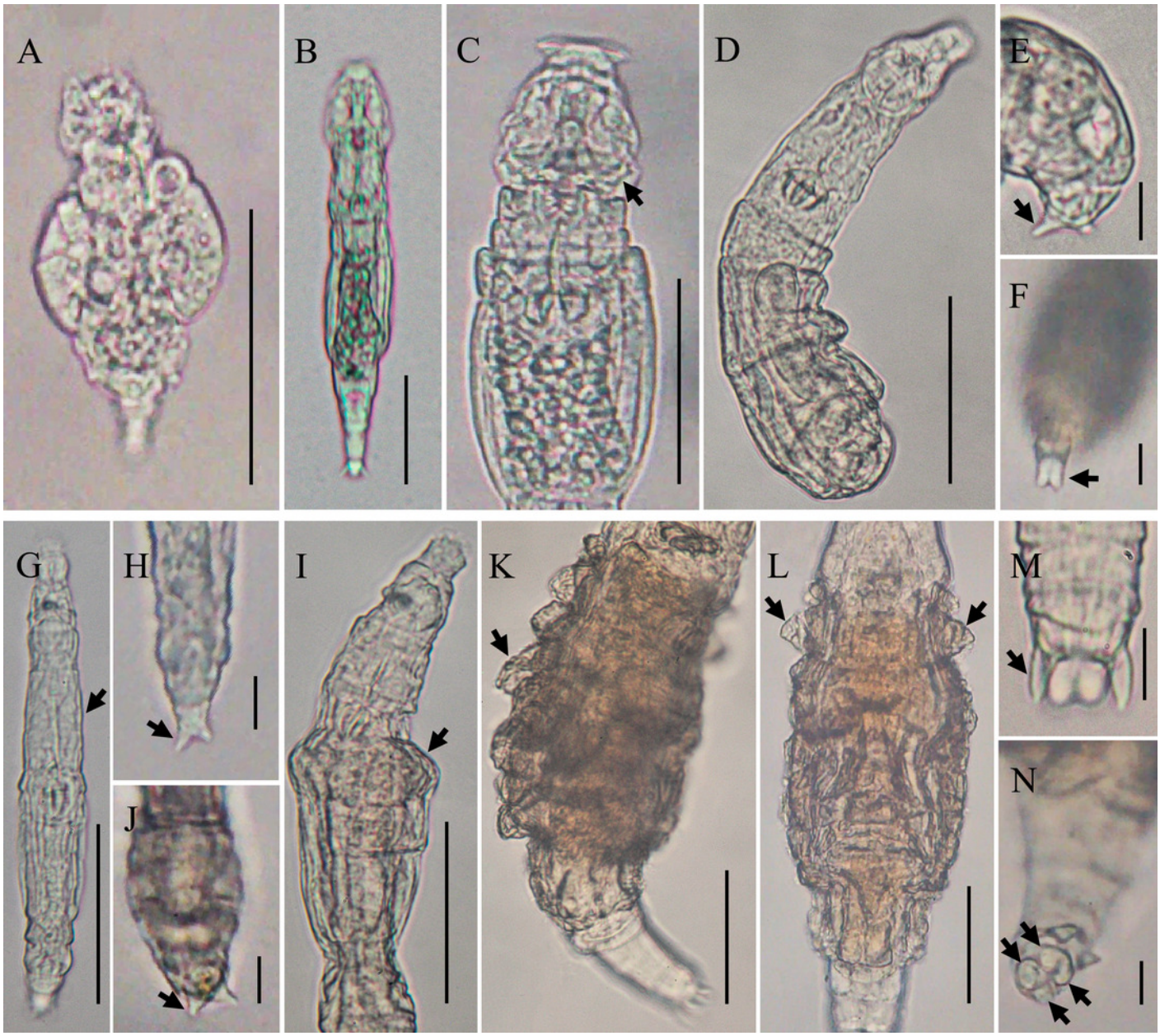
A
B
C
D
E
F
G
H
I
K
L
M
N
J

Figure 6

Principal Components Analysis (PCA) illustrates the distribution of bdelloid rotifers among bryophyte groups. The first two PCA axes explain 15.43% and 11.37% of the total variation, respectively. The polygons represent groups of bryophytes, differentiate

The first two PCA axes explain 15.43% and 11.37% of the total variation, respectively. The polygons represent groups of bryophytes, differentiated by color. Blue circles indicate bdelloid rotifer species.

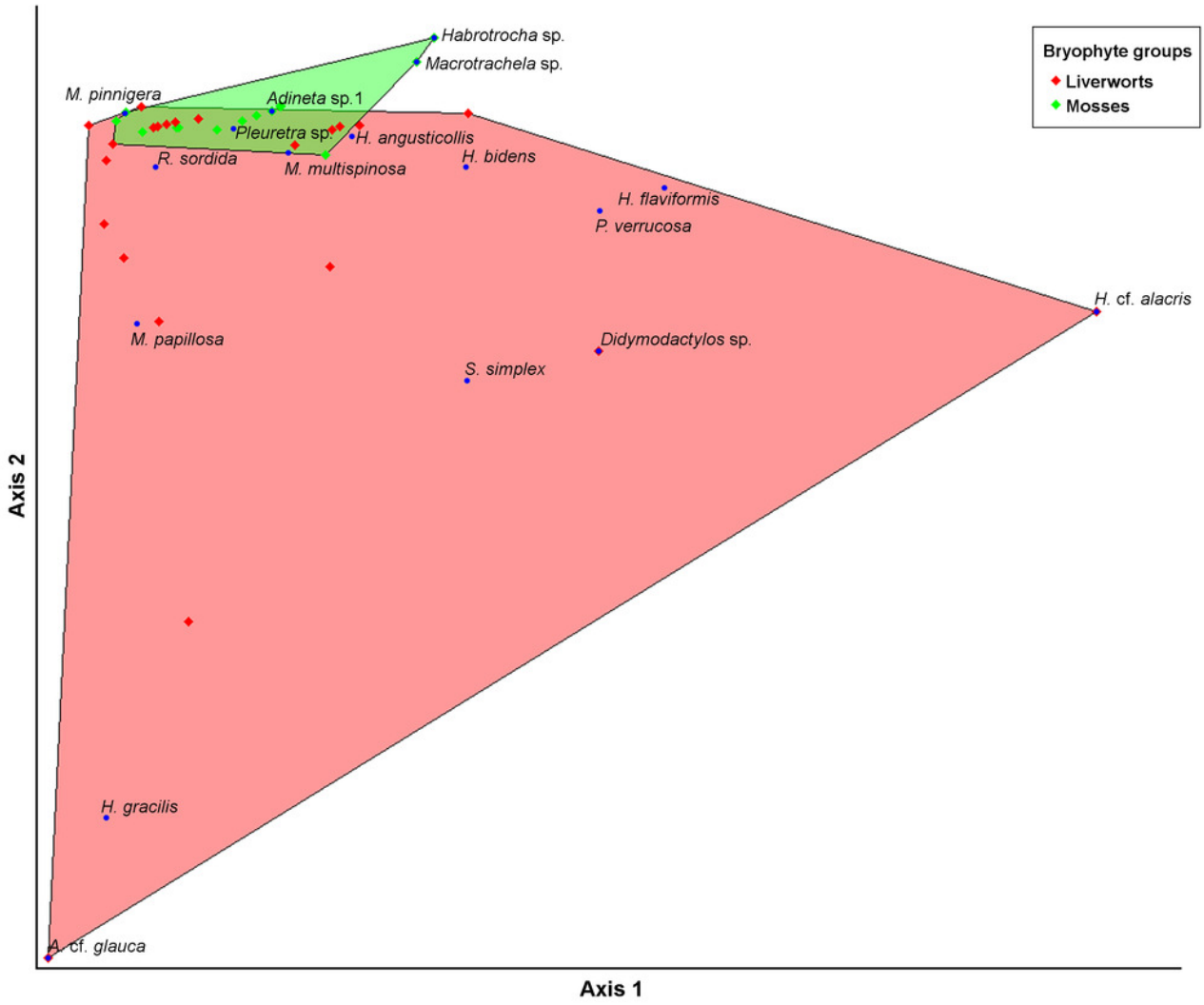

Figure 7

Principal Components Analysis (PCA) illustrates the relationship between bdelloid rotifers and bryophyte species. The first two PCA axes explain 15.43% and 11.37% of the total variation, respectively. The polygons represent groups of bryophyte species, di

The first two PCA axes explain 15.43% and 11.37% of the total variation, respectively. The polygons represent groups of bryophyte species, differentiated by color. Blue circles indicate bdelloid rotifer species.

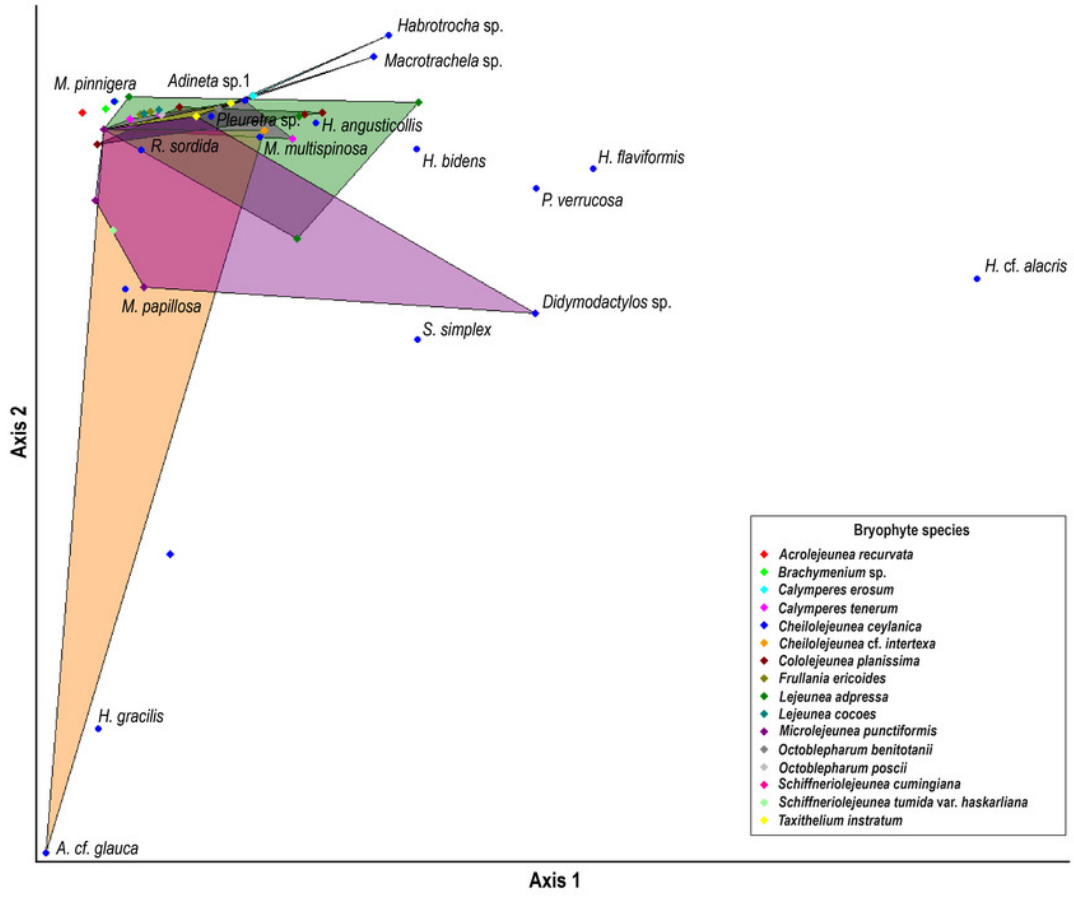

Figure 8

Principal Components Analysis (PCA) illustrates the distribution of bdelloid rotifers among various life forms. The first two PCA axes explain 15.43% and 11.37% of the total variation, respectively. The polygons represent groups of life forms, differentia

The first two PCA axes explain 15.43% and 11.37% of the total variation, respectively. The polygons represent groups of life forms, differentiated by color. Blue circles indicate bdelloid rotifer species.

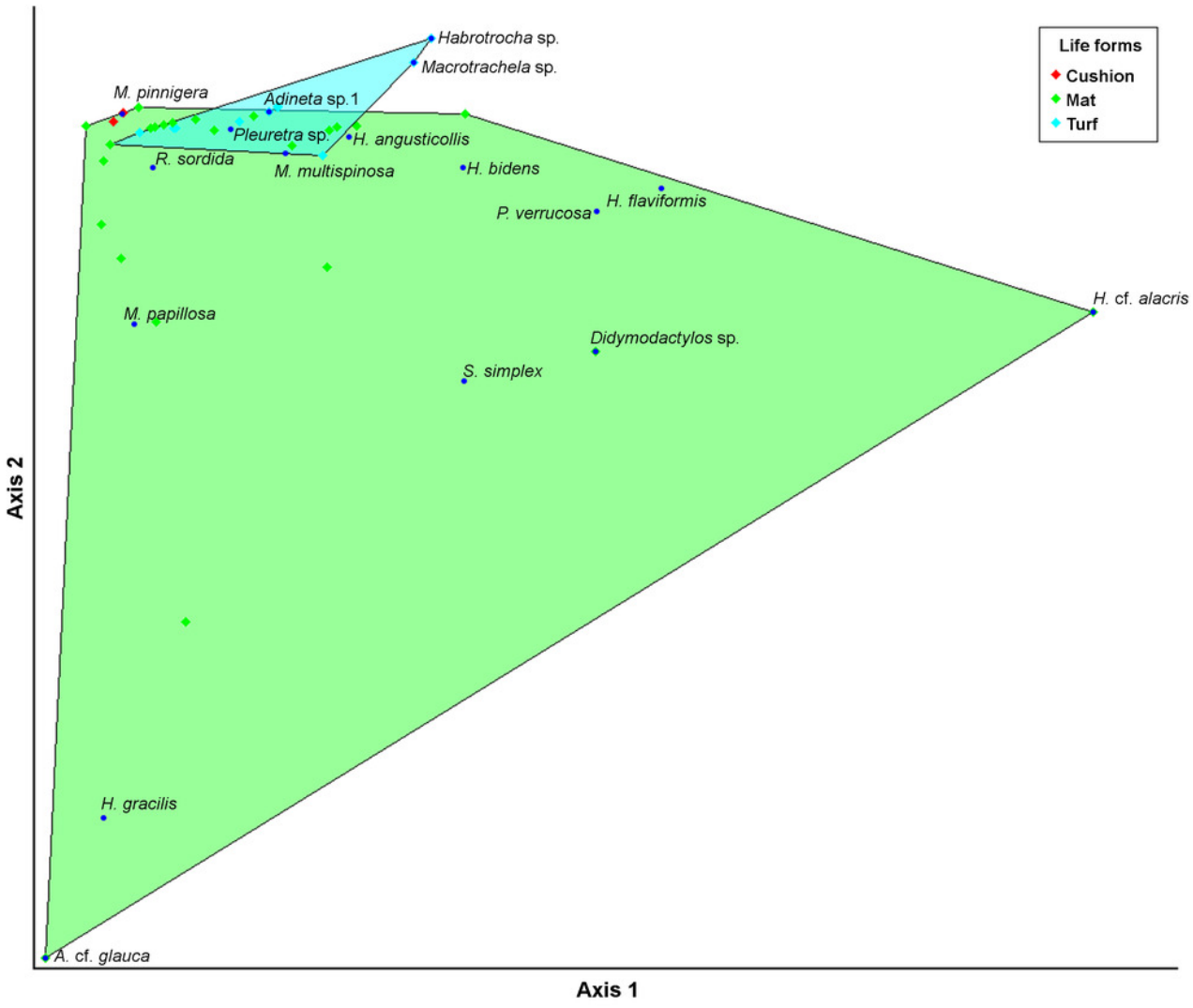

Figure 9

Principal Components Analysis (PCA) illustrates the distribution of bdelloid rotifers among moss characters.

The first two axes of the PCA explained 20.82% and 17.55% of the variability, respectively. The polygons represent groups of moss characters, differentiated by color. Blue circles indicate bdelloid rotifer species.

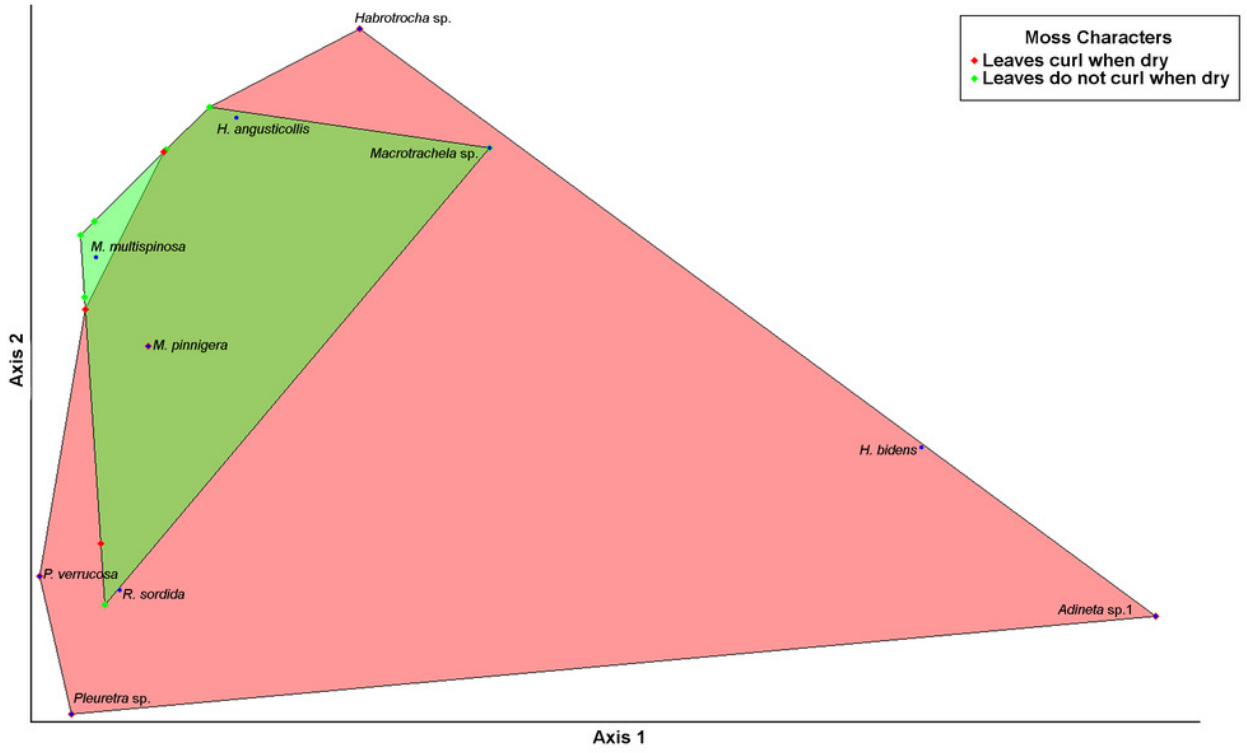

Figure 10

Principal Components Analysis (PCA) illustrates the distribution of bdelloid rotifers among liverwort characters. The first two axes of the PCA explained 24.01% and 13.93% of the variability, respectively. The polygons represent groups of liverwort charac

The first two axes of the PCA explained 24.01% and 13.93% of the variability, respectively. The polygons represent groups of liverwort characters, differentiated by color. Blue circles indicate bdelloid rotifer species.

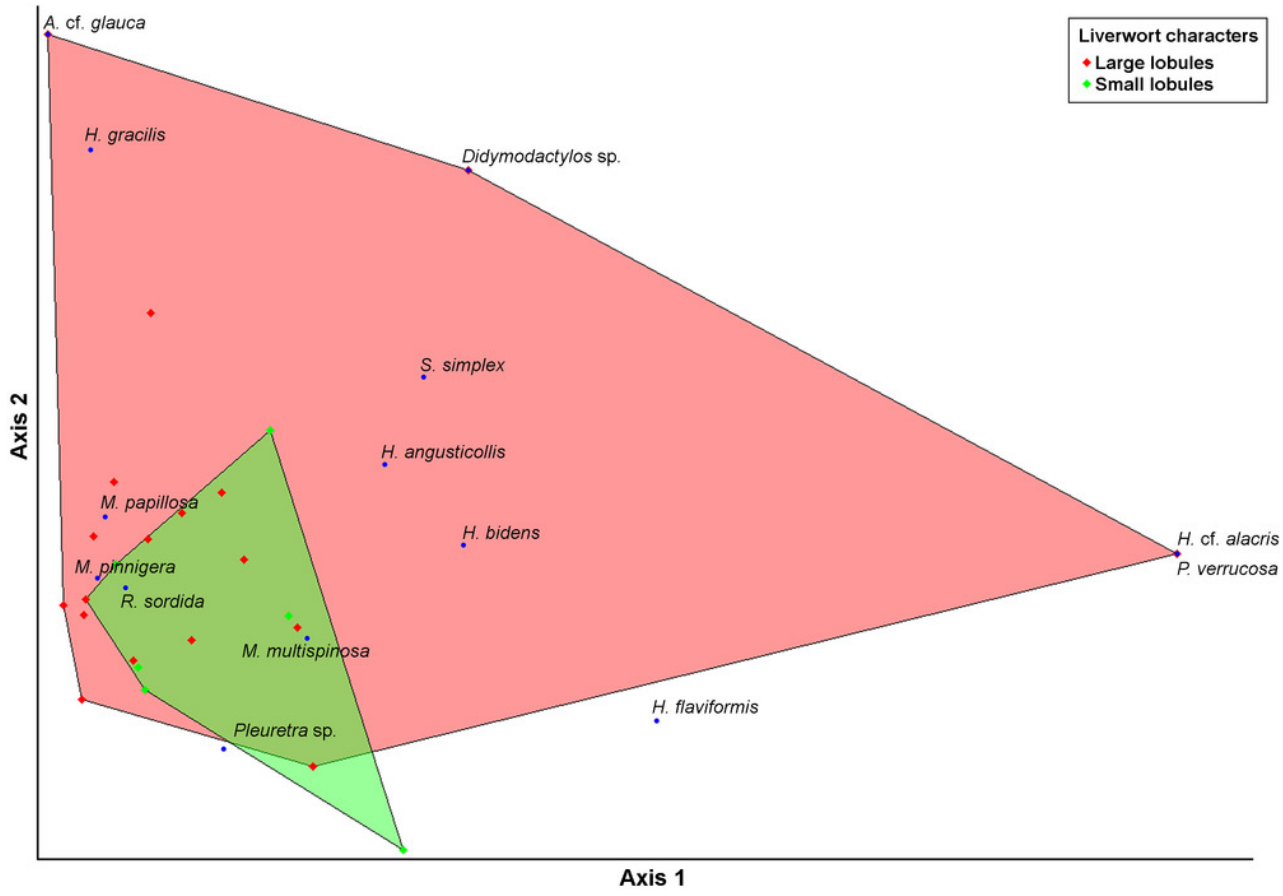

Figure 11

Principal Components Analysis (PCA) illustrates the distribution of bdelloid rotifers among seasons. The first two PCA axes explained 15.43% and 11.37% of the total variation, respectively. The polygons represent groups of seasons, differentiated by color

The first two PCA axes explained 15.43% and 11.37% of the total variation, respectively. The polygons represent groups of seasons, differentiated by color. Blue circles indicate bdelloid rotifer species.