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

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It has been hypothesised that small organisms tend to be widely distributed because of their small size and specific capabilities. However, evidence shows that bdelloid rotifers living in bryophytes exhibit habitat specialisation, as the species composition varies among microhabitats. Therefore, the distribution pattern of small animals seems to occur in a complex scenario of ecological processes, which requires further research to explain the effects on species composition, especially at the microscale. Consequently, we aimed to test whether there were differences in species richness and composition across bryophyte species, forms and characteristics, as well as seasons, to understand the distribution patterns and habitat preferences of bdelloid rotifers in this semiterrestrial habitat. To answer these questions, bdelloid rotifers were sorted, identified and counted from 173 bryophyte samples collected in April, August and December 2022 in Bang Berd Beach Forest, Chumphon Province, Thailand. A total of 22 bdelloid species were discovered, including 14 new records, increasing Thailand’s total number of bdelloid species to 30. In addition, the present results report a broader distribution range for *Habrotrocha flaviformis*, *Philodina verrucosa*, and *Scepanotrocha simplex*, which were discovered for the first time in Oriental region. It was found that species richness was not significantly different among bryophyte species ($p = 0.43$) and that it was higher in liverwort than in moss. Bryophytes with mat forms and large lobules contain more species than other forms and characteristics. However, the similarities in species composition between bryophyte groups, species, life forms, characteristics and seasons are low. Only two species, *Rotaria sordida* and *Macrotrachela multispinosa*, were distributed in more than 50% of the samples, which could be explained by their high desiccation tolerance. Moreover, the results revealed no specificity between bdelloid species and bryophytes, except for *Scepanotrocha simplex* and *Habrotrocha* cf. *alacris*, which were found in only one species of liverwort. However, their specificity cannot be confirmed until more studies are carried out. Nevertheless, these results indicate a narrow distribution at the small scale in this semiterrestrial habitat, which may be due to several factors. Therefore, to better understand the distribution pattern and habitat preference of bdelloid rotifers in this type of habitat, more research is needed. Furthermore, most of these animals can be expected to change along with their habitats. As a result, to maintain the high species richness and diverse composition of bdelloid rotifers in bryophytes in beach forests, it is recommended to keep this habitat as close to its natural state as possible under changing conditions while avoiding severe management interventions.

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## Abstract

It has been hypothesised that small organisms tend to be widely distributed because of their small size and specific capabilities. However, evidence shows that bdelloid rotifers living in bryophytes exhibit habitat specialisation, as the species composition varies among microhabitats. Therefore, the distribution pattern of small animals seems to occur in a complex scenario of ecological processes, which requires further research to explain the effects on species composition, especially at the microscale. Consequently, we aimed to test whether there were differences in species richness and composition across bryophyte species, forms and characteristics, as well as seasons, to understand the distribution patterns and habitat preferences of bdelloid rotifers in this semiterrestrial habitat. To answer these questions, bdelloid rotifers were ~~sorted~~, identified and counted from 173 bryophyte samples collected in April, August and December 2022 in Bang Berd Beach Forest, Chumphon Province, Thailand. A total of 22 bdelloid species were ~~discovered~~, including 14 new records, increasing Thailand’s total number of bdelloid species to 30. In addition, ~~the present results~~ report a broader distribution range for *Habrotrocha flaviformis*, *Philodina verrucosa*, and ~~*Scepanotrocha*~~ *simplex*, ~~which were discovered for the first time in Oriental region~~. ~~It was found that~~ species richness was not significantly different among bryophyte species ~~(p = 0.43)~~ ~~and that it was higher~~ in liverwort

than in moss. Bryophytes with mat forms and large lobules contain more species than other forms and characteristics. However, the similarities in species composition between bryophyte groups, species, life forms, characteristics and seasons are low. Only two species, *Rotaria sordida* and *Macrotrachela multispinosa*, were distributed in more than 50% of the samples, which could be explained by their high desiccation tolerance. Moreover, the results revealed no specificity between bdelloid species and bryophytes, except for *Scepanotrocha simplex* and *Habrotrocha* cf. *alacris*, which were found in only one species of liverwort. However, their specificity cannot be confirmed until more studies are carried out. Nevertheless, these results indicate a narrow distribution at the small scale in this semiterrestrial habitat, which may be due to several factors. Therefore, to better understand the distribution pattern and habitat preference of bdelloid rotifers in this type of habitat, more research is needed. Furthermore, most of these animals can be expected to change along with their habitats. As a result, to maintain the high species richness and diverse composition of bdelloid rotifers in bryophytes in beach forests, it is recommended to keep this habitat as close to its natural state as possible under changing conditions while avoiding severe management interventions.

## Introduction

Over the years, there has been increasing research on the distribution of small organisms, as it has been questioned whether they are distributed like large organisms (Fontaneto et al., 2008; Segers & De Smet, 2008; Kaya & Erdoğan, 2015; Zawierucha et al., 2023). It has been hypothesised that small organisms tend to be more widely distributed because they are small enough to be passively dispersed by wind over long distances. In addition, in some cases, such as rotifers, they have efficient resting stages that allow them to survive for long periods while dormant, and their asexual and parthenogenetic reproduction makes it possible for them to rapidly colonise any suitable habitats. This implies that they can be considered cosmopolitan (Fontaneto, 2011). Moreover, Fontaneto, Westberg & Hortal (2011) confirmed that microscopic organisms, such as bdelloid rotifers, have a lower degree of habitat specialisation than larger organisms. However, this seems to occur in 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 and bdelloid rotifers, in bryophytes has been studied (Kaya, De Smet & Fontaneto, 2010; Dražina et al., 2013; Kaya & Erdoğan, 2015). Bryophytes have ecological associations with microorganisms, such as protozoans and rotifers, and many other invertebrates, plants and fungi (Gerson, 1982), because they provide food, shelter and nesting material for small animals and invertebrates and indirectly serve as a matrix for a variety of interactions among all the organisms (Bahuguna et al., 2013). Several studies have illustrated greatly enhanced invertebrate densities in bryophytes when compared with unstable gravels (Suren, 1991; Suren, 1993). In addition, it was reported that the species richness and composition of bdelloid rotifers living in bryophytes were significantly different among microhabitats, showing evidence of habitat specialisation (Kaya & Erdoğan, 2015). In contrast, there are no relationships between bdelloids and moss species (Burger, 1948; Kaya, De Smet & Fontaneto, 2010). Therefore, it seems that organisms that inhabit bryophytes may change over time, or there may be some species that coexist in a specific way.

Bdelloid rotifers are small organisms that can reproduce without fertilisation and resist dry conditions, allowing bdelloid rotifers to disperse in a variety of terrestrial and aquatic habitats (Ricci & Caprioli, 2005). Currently, approximately 460 species of bdelloid rotifers have been reported worldwide (Segers, 2007). Although there are few studies in terrestrial habitats, a considerable number of species have been recorded (Fontaneto et al., 2007; Zeng et al., 2020).

Like other areas, there have also been more studies on bdelloids from freshwater habitats than terrestrial ones, with 16 species of bdelloid rotifers reported in Thailand (Sa-Ardrit, Pholpunthin & Segers, 2013; Maiphae, 2017; Jaturapruek et al., 2018; Jaturapruek et al., 2021). While there have been attempts to define the niche preference and distribution pattern of bdelloids in freshwater habitats (Jaturapruek et al., 2021), there are still gaps in knowledge regarding the distribution of this animal in semi-terrestrial or terrestrial habitats.

Consequently, this study aims to answer the question of whether bdelloids have a distribution pattern related to bryophyte species, forms and characteristics by studying the Bang Berd Beach Forest, the largest beach forest on sand dunes in Thailand. The characteristics of this forest differ from other beach forests because the plant community ranges from climbers to trees that have adapted to areas with sandy soil, strong sunlight, high wind, dryness and continual seawater spray (Inuthai, 2007). A previous study reported a high diversity of bryophytes (mosses and liverworts) in this area, with 16 species (Inuthai, 2007), implying a high diversity of microhabitats for invertebrates (Budke et al., 2018). Therefore, in the present study, we aimed to test whether there were differences in species richness and composition due to differences in bryophyte species and different bryophyte forms and characteristics in order to understand the habitat preferences of bdelloid rotifers.

## Materials & Methods

### Sampling site

Bang Berd Beach Forest, Chumphon Province, Thailand is located close to the coast (10.987531700278218, 99.49570988282339). This forest is characterized by sand dunes and scattered patches of plants. Around the forest is dry and sunny, whereas it is more humid inside. The plant community consists of shrubs, trees, and climbers, which are the habitats for bryophytes (Fig. 1).

### Sample collection, species identification and count

A total of 173 bryophyte samples were collected in April 2022 (low rainy season), August 2022 (mid rainy season) and December 2022 (high rainy season). All samples were stored in a zip-lock plastic bag. Each sample was divided for 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 characters.

Mosses are classified into two characters including leave curl when dry and leave does not curl when dry) 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 which mixed bryophytes species were excluded from the analysis (Table S1), therefore a total of 52 samples were used for data analysis.

In the laboratory, a 3x3 $cm^2$ of each sample was soaked in mineral water for 24 hours and then shaken well before taken all water samples for further bdelloid rotifer identification and counting. Bdelloid rotifers in each water sample were sorted with a stereomicroscope (Olympus SZ51). The morphological characteristics of each specimen were examined with a light microscope (Olympus CH2) while they were still alive. All the taxonomical characters were photographed, and video recorded. The identifications using the morphological characters were followed Donner (1965) and Ricci & Melone (2000).

**Data analysis**

**Species richness**

Shannon diversity and species evenness index was used to compare species diversity of bdelloid rotifers among bryophyte species, among seasons (low rainy season, mid rainy season and high rainy season), among bryophyte forms (cushion, turf, mat) and among bryophyte characters (mosses: leaves curl when dry and leaves do not curl when dry; liverworts: large lobule and small lobule). These analyses used the Microsoft Excel program (Microsoft 365). Boxplot in R studio version 4.3.3 was used to visualize the range of bdelloid rotifer among bryophyte species and among seasons.

**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, a Two-Way Cluster Analysis was performed using PC-ORD program version 7.11 (McCune & Mefford, 2016). 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**

In 83 of the 173 bryophyte samples we collected, we found a total of 22 bdelloid species (Table 2), 14 of which were 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 only in mixed bryophyte species samples (Table 2), making it difficult to determine the exact species of bryophytes they inhabited. Moreover, it was found that 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. This was followed by *Habrotrocha angusticollis* (25.30%) and *Habrotrocha bidens* (19.28%), which were relatively widespread, whereas most other species were found in only 1–8 samples (Fig. 4). The species richness of bdelloid rotifers found in each bryophyte species ranged from 1 to 8 and did not differ significantly across species (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 3).

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 significant (t-test, p = 0.11) (Table 4). Moreover, the highest species richness was found in bryophytes with a mat life form (14 species), followed by turf (8 species) and cushion (3 species). This result mostly agrees with the trend in the diversity index, except for the evenness of the cushion life form, which showed the highest value. In addition, large-lobule bryophytes showed the highest richness (14 species), followed by bryophytes whose leaves curl when dry (9 species). However, the highest diversity index was found in large-lobule bryophytes (1.93), followed by small-lobule bryophytes (1.68) (Table 4). Furthermore, the low rainy season showed both the highest species richness and diversity index (14 species, 1.85), followed by the high rainy season (9 species, 1.67) and the mid rainy season (8 species, 1.52) (Table 4). This result agrees with the boxplot graph; the highest range was in the low rainy season, while the mid and high rainy seasons were quite similar, centred around the median. The mid rainy season seems to have a left-skewed distribution, while the other seasons seem to have a right-skewed distribution (Fig. 5).

**Bdelloid rotifer community in bryophytes**

The similarity of most bdelloid rotifer groups, life forms, and characteristics was less than 50%. Bdelloid rotifer species found in mosses and liverworts showed 41% similarity (Table S2). Even at the species level, bryophytes showed similarities of only 0–45%. For example, one species of moss (*Frullania ericoides*) and one species of liverwort (*Taxithelium instratum*) host the same bdelloid rotifer species (Table S3). Furthermore, species composition among life forms showed the lowest similarity, with the cushion form being the most dissimilar from the others, showing only 10% similarity with turf and 21% similarity with mat forms (Fig. 6, Table S4). *Macrotrachela pinnigera* and *Pleuretra* sp. are the two species that are highly abundant in the cushion form of bryophytes. Moreover, the species composition similarities for each characteristic of mosses and liverworts were only 40% and 57%, respectively (Fig. 7, Tables S4 and S5). In addition, species found in the low rainy season are more than 50% different from those found in other seasons (Fig. 8, Table S5). Notably, *Adineta* was detected only in the low rainy season.

**Ind indices and Habitat preference degree**

All bdelloid rotifer species had an indicator value for bryophyte groups (mosses and liverworts) of less than 30%. Therefore, all recorded bdelloid rotifer species are low indicators of mosses and liverworts. Even though most of them showed less specific habitat preferences for bryophyte species, *Scepanotrocha simplex* and *Habrotrocha* cf. *alacris* exhibited strong habitat preferences (IndVal ≥ 50%) for the liverwort species *Cheilolejeunea ceylanica* and *Schiffneriolejeunea tumida* var. *haskarliana*, respectively (Table 5).

## Discussion

**Species diversity**

A total of 22 taxa were found in the present study, which is three times higher than previous records and accounts for about 4% of bdelloids worldwide (Murray, 1906; Jakubski, 1914; Donner, 1965; Segers, 2007; Birky et al., 2011; Iakovenko et al., 2013; Iakovenko et al., 2015; Song & Min, 2015; Örstan & Plewka, 2017; Song & Lee, 2017; Jaturapruek et al., 2018; Örstan, 2018; Song & Lee, 2019; Song & Lee, 2020; Örstan, 2021; Örstan, 2022). 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, even in harsh environments (Song & Kim, 2000; Fontaneto et al., 2007; Kaya, De Smet & Fontaneto, 2010; Zeng et al., 2020; Wang et al., 2023).

These results reveal that *Habrotrocha flaviformis*, *Philodina verrucosa* and *Scepanotrocha simplex*, which were found for the first time in Asia, have a wider distribution range than the other species. Moreover, most species found in the present study were first reported 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. Their widespread presence is likely due to their thick integuments, a characteristic of species living in dry environments (Kutikova, 2003). In particular, *Rotaria sordida* has been recorded as a successful anhydrobiotic species (Eyres et al., 2015). Another possibility is that these two species may have first colonised this area before spreading out and becoming widespread (Fontaneto, Melone & Ricci, 2003). 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. This might be 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 have specialised structures, such as underleaves, imbricate leaves or lobules, that can 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 characterised as a sac (Puterbaugh, Skinner & Miller, 2004; Hess, Frahm & Theisen, 2005; Parsons et al., 2007) 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*, which has small lobules and a simple lobule shape, also hosts a high number of bdelloid rotifer species. Thus, it is possible that other factors, such as phytochemicals, determine habitat suitability (Puterbaugh, Skinner & Miller, 2004; Xie & Lou, 2009). In addition, liverworts were frequently found in areas protected by trees, which helped slow down 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, which 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). It has also 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 a variety of invertebrates that feed on them or use them as a resource. Some invertebrates directly consume liverwort tissues or utilise 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 or other invertebrates is needed.

However, surprisingly, in the mid and high rainy seasons, which are characterised by high humidity, fewer species were found. One possible reason 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; Fontaneto, Iakovenko & De Smet, 2015). However, this hypothesis should be further tested in tropical ecosystems.

Another possible reason is that bdelloid rotifers themselves 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 characteristic, which is often 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 found 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). Therefore, this temporal variation can enhance species diversity by supporting a succession of bdelloid rotifer species adapted to different ecological conditions throughout the dry season.

**Species community and habitat preference**

The similarities in species composition between bryophyte groups, life forms and bryophyte characteristics are low. These results confirm the narrow distribution of bdelloid rotifers in this semi-terrestrial habitat, which may be due to several factors, such as habitat characteristics or the species' capacities for surviving desiccation, achieving long-term colonisation 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. It is possible that 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 specialised species and leading to distinct bdelloid communities. In this study, only *Macrotrachela pinnigera* and *Pleuretra* sp. were highly abundant in cushion form. It has been reported that both species can distribute well in moss. Therefore, it is possible that the cushion form, which is the form most likely to have high internal moisture, is a suitable habitat for the growth of these two species (Donner, 1965; Ricci & Melone, 2000; Glime, 2017c). In addition, we detected *Adineta* only in the low rainy season, although with low abundance. This common genus, which is highly desiccation-tolerant, may prefer to avoid competition and predation in the high rainy season and to distribute more in the low rainy season (Donner, 1965; 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, previously, neither species has 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, because low abundance was observed in both species, it cannot be concluded that they are specific to these two species of liverworts unless additional studies are carried out. Therefore, to better understand the impact of these factors on the species composition of bdelloid rotifers, more research is needed.

**Diversity and ecology of bdelloid rotifers for supporting the conservation of beach forests along sand dunes**

Sand dunes provide a range of ecological benefits, including shore protection, erosion control, water purification and high biological diversity. The Bang Berd Beach Forest along the sand dunes on the eastern coast of Thailand is relatively rich in bryophytes (Inuthai, 2007) and bdelloid rotifers, as indicated by 14 new records from the present study. This diversity highlights the unique ecological roles of different organisms, with some being widely distributed, while others are rare. It was hypothesised that higher habitat heterogeneity would lead to higher diversity, which in turn would increase the habitat's resilience to changing environmental conditions. However, at present, several factors affect the biodiversity of organisms in this type of habitat, especially climate change and human activities.

The former factor might have less effect on the bdelloids because these small invertebrates have anhydrobiotic capability, which is in agreement with the present result that there is more richness in low rainy seasons than in other seasons. However, bryophytes are highly sensitive to elevated temperatures in their hydrated state. As a consequence of global warming, significant losses in bryophyte diversity are expected and will lead to ecosystem alterations (He, He & Hyvönen, 2016). Therefore, it is expected that the population of most small invertebrates and the plants they inhabit will decrease (Cock et al., 2011; Kutnar, Kermavnar & Sabovljević, 2023). In addition, the decline in bryophyte habitat is due not only to climate change but also to human activities. Changes in the conditions of sand dunes will affect tree composition, the main habitat of bryophytes in beach forests. Host tree species composition has been reported to be an important driver of bryophyte species diversity and composition (Gosselin et al., 2017). Thus, the loss of species with unique roles can have drastic ecological effects that lead to the long-term deterioration of ecosystem capacity.

Therefore, to maintain the high species richness and diverse composition of bryophytes and organisms that inhabit sand dunes, it is recommended to keep beach forests as close to their natural state as possible under changing conditions and to avoid intensive management interventions and silvicultural practices.

## Conclusions

The distribution pattern of small animals on a small scale is still debatable. The results of the present study on bdelloid rotifers in bryophytes confirm their restricted distribution across microhabitats and seasons. Most bdelloid rotifers found in this study are predominantly found in bryophytes with mat life forms, especially in liverworts, regardless of whether they have large or small lobules, whereas mosses show high diversity only in species with leaves that curl when dry. In addition, there is a higher bdelloid species diversity in the low rainy season than in the other seasons, likely due to the desiccation tolerance that allows bdelloid rotifers to survive through competition. Bdelloid rotifers exhibited low similarity in terms of species composition across bryophyte species, forms, characteristics and seasons and mostly showed no specific relationship between bdelloid and bryophyte species, except for a few species. Therefore, additional studies are required to fully assess their effectiveness as indicators.

While more research is needed, the present results indicate a relationship between bdelloid rotifer species and bryophyte characteristics. To maintain the high species richness and diverse composition of organisms that inhabit bryophytes in sand dunes, it is necessary to keep beach forests as close to their natural state as possible under changing conditions.

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## Table 1(on next page)

Bryophyte species that were used for data analysis

**Table 1:**

**Bryophyte species that were used for data analysis.**

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

## Table 2 (on next page)

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

* = new records in Thailand

**Table 2:**

**Bdelloid rotifer species found in the present study and their distribution in mosses and liverworts.**

*** = new records in Thailand**

| | **Mosses** | | | | | | **Liverworts** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Bdelloid rotifer species** | ***Brachymenium* sp.** | ***Calymperes erosum*** | ***Calymperes tenerum*** | ***Octoblepharum benitotanii*** | ***Octoblepharum poscii*** | ***Taxithelium instratum*** | ***Cheilolejeunea ceylanica*** | ***Acrolejeunea recurvata*** | ***Cheilolejeunea* cf. *intertexa*** | ***Cololejeunea planissima*** | ***Frullania ericoides*** | ***Lejeunea adpressa*** | ***Lejeunea cocoes*** | ***Microlejeunea punctiformis*** | ***Schiffneriolejeunea cumingiana*** | ***Schiffneriolejeunea tumida* var. *haskarliana*** | **mixed bryophyte species sample** |
| **Adineta* cf. *glauca* Murray, 1911 | | | | | | | | | + | | | | | | | | |
| **A. vaga* (Davis, 1873) | | | | | | | | | | | | | | | | | + |
| *Adineta* sp.1 | | | + | | | | | | | | | | | | | | |
| *Adineta* sp.2 | | | | | | | | | | | | | | | | | + |
| *Didymodactylos* sp. | | | | | | | | | | | | | | + | | | |
| *Habrotrocha angusticollis* (Murray, 1905) | | + | | + | | + | | | | + | + | + | | + | | + | + |
| **H.* cf. *alacris* Milne, 1916 | | | | | | | | | | | | | | | | + | |
| **H. bidens* (Gosse, 1851) | | + | + | + | | | | | + | + | | + | | + | | + | + |
| **H.* cf. *brocklehursti* Murray, 1911 | | | | | | | | | | | | | | | | | + |
| **H. flaviformis* | | | | | | | | | | + | | + | | | | + | + |

| | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| De Koning, 1947 | | | | | | | | | | | | | | | | | |
| **H. gracilis* Montet, 1915 | | | | | | | + | | + | | | | | | | | |
| *Habrotrocha* sp. | | + | | | | | | | | | | | | | | | |
| **Macrotrachela multispinosa* Thompson, 1892 | | + | + | + | + | + | + | | | + | + | + | + | + | | + | + |
| **M. papillosa* Thompson, 1892 | | | | | | | + | | | + | | | | + | | + | + |
| *M. pinnigera* (Murray, 1908) | + | | | | | | | + | | | | + | | | | | + |
| **M.* cf. *plicata* (Bryce, 1892) | | | | | | | | | | | | | | | | | + |
| *Macrotrachela* sp. | | | | + | | | | | | | | | | | | | |
| **Philodina rugosa* Bryce, 1903 | | | | | | | | | | | | | | | | | + |
| **P. verrucosa* Song & Lee, 2020 | | | + | | | | | | | | | | | | | + | + |
| *Pleuretra* sp. | + | | | | | | | | | + | | + | + | | | | + |
| **Rotaria sordida* (Western, 1893) | + | | + | | + | + | + | + | + | + | + | + | + | + | + | | + |
| **Scepanotrocha simplex* De Koning, 1947 | | | | | | | + | | | | | + | | + | | + | |

## Table 3(on next page)

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

**Table 3:**

**Shannon Diversity of bdelloid rotifer species that 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 4(on next page)

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

**Table 4:**
**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 rainy season | **14** | **1.85** | 0.70 |
| mid rainy season | 8 | 1.52 | 0.73 |
| high rainy season | 9 | 1.67 | **0.76** |

# Table 5(on next page)

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

**Table 5:**

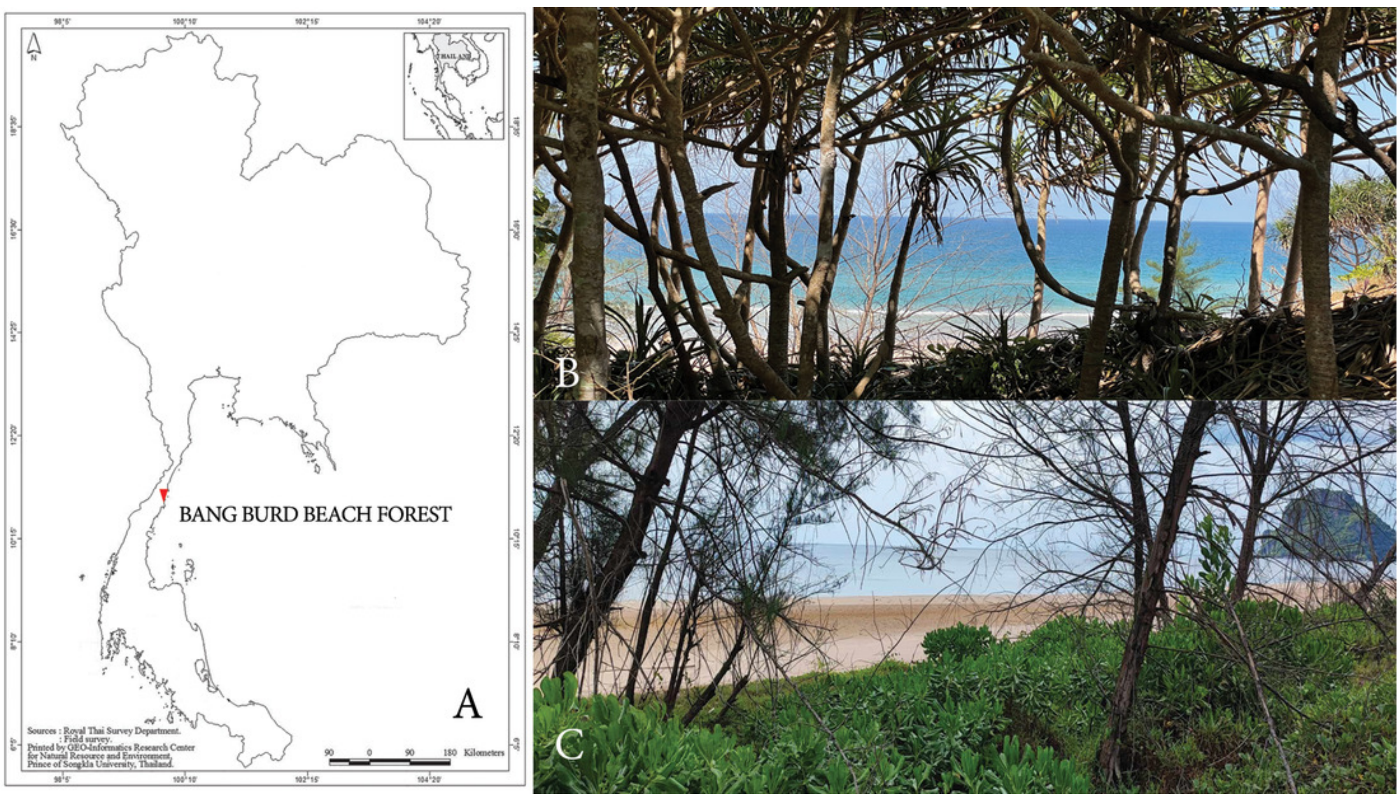
**IndVal value and habitat preferences of species found in bryophyte species.**

| **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 | **medium** |
| *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 | **medium** |
| *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 | **medium** |
| *M. multispinosa* | 33.33 | 11.19 | 29.56 | 24.06 | without preference | **low** |
| *M. papillosa* | 0 | 2.45 | 16.67 | 35.61 | without preference | **medium** |
| *M. pinnigera* | 2.38 | 19.58 | 2.95 | 32.74 | without preference | **medium** |
| *Macrotrachela* sp. | 1.59 | 0 | 4.55 | 33.33 | without preference | **medium** |
| *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** |

# Figure 1

Sampling site

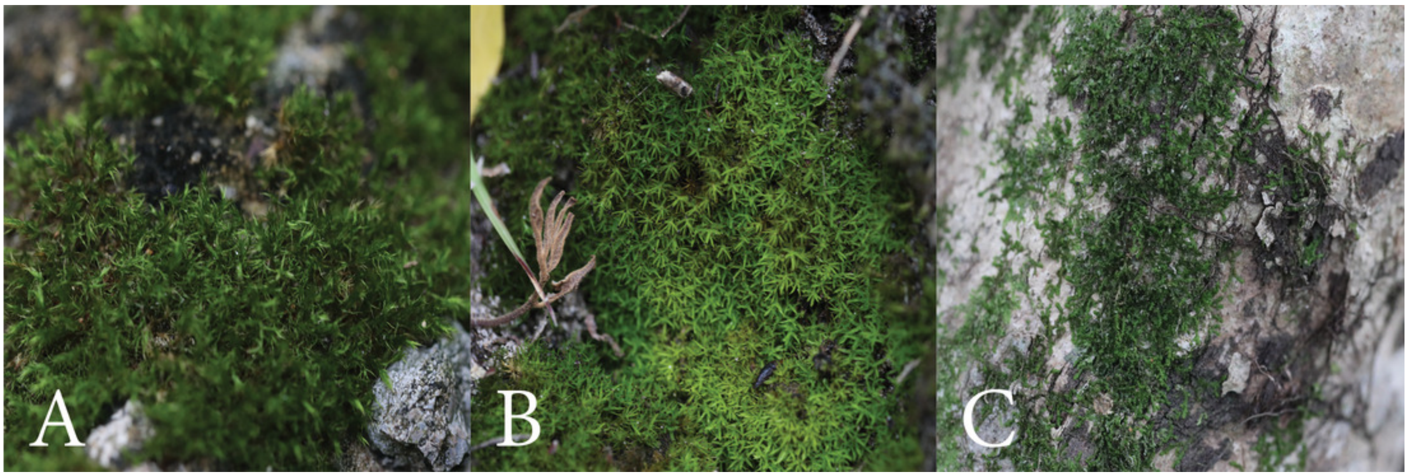
(A) Sampling site at Bang Berd Beach Forest, Chumphon Province, Thailand and (B-C) Bang Berd Beach Forest environment area.



# Figure 2

Bryophyte life forms

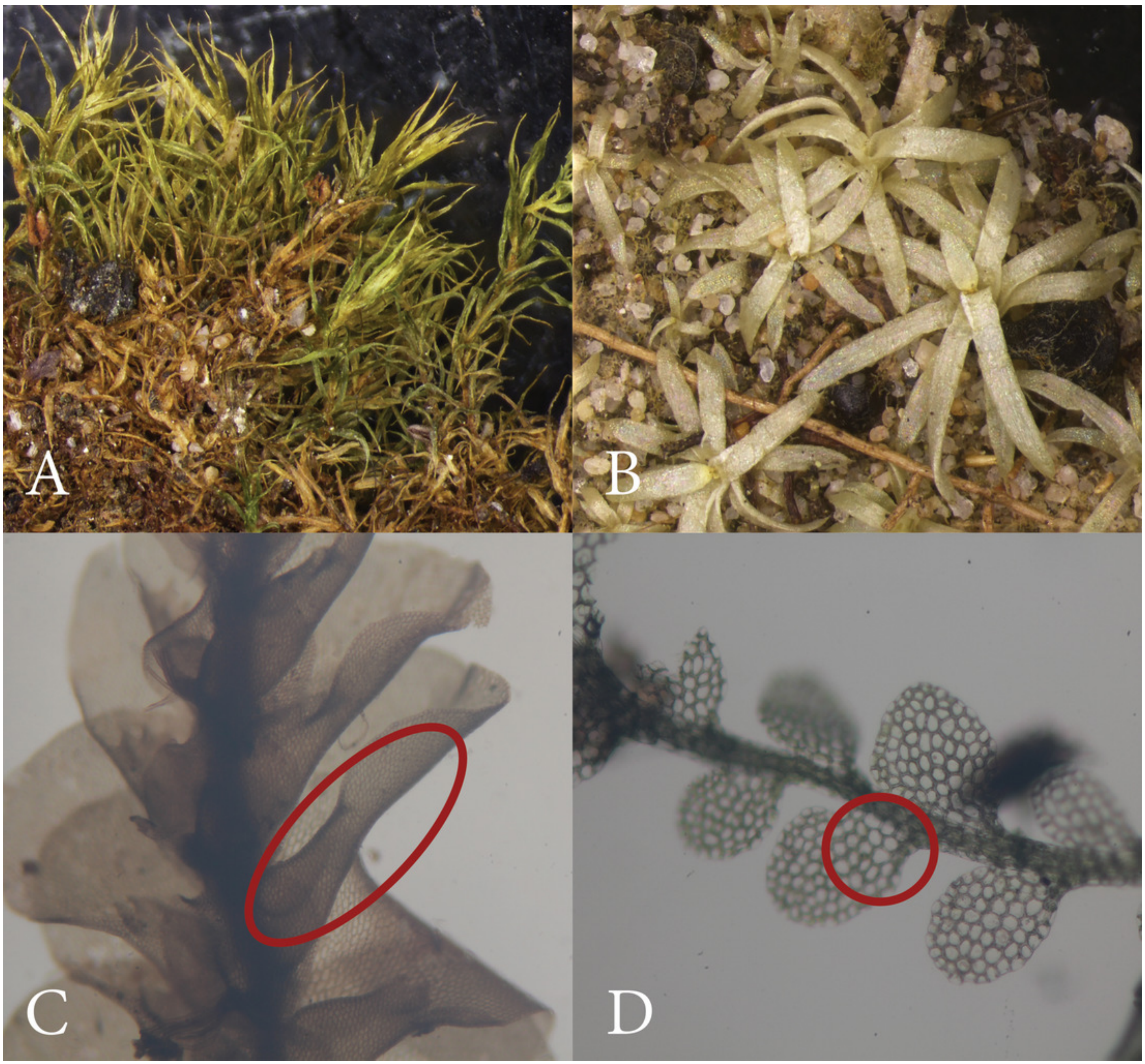
(A) cushion (*Brachymenium* sp.). (B) turf (*Calymperes erosum*). (C) mat (*Frullania ericoides*).



# Figure 3

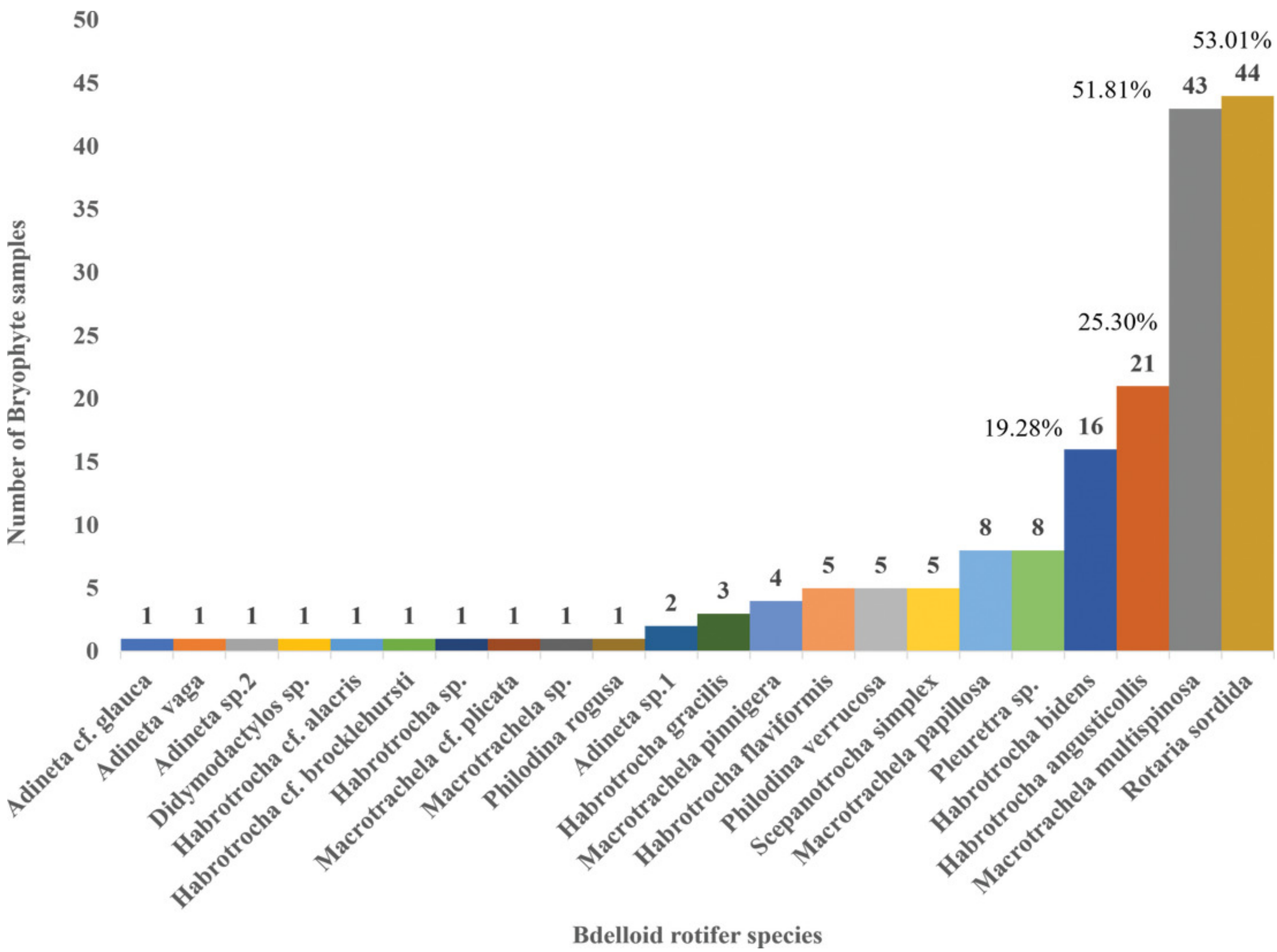
Bryophyte characters

(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.



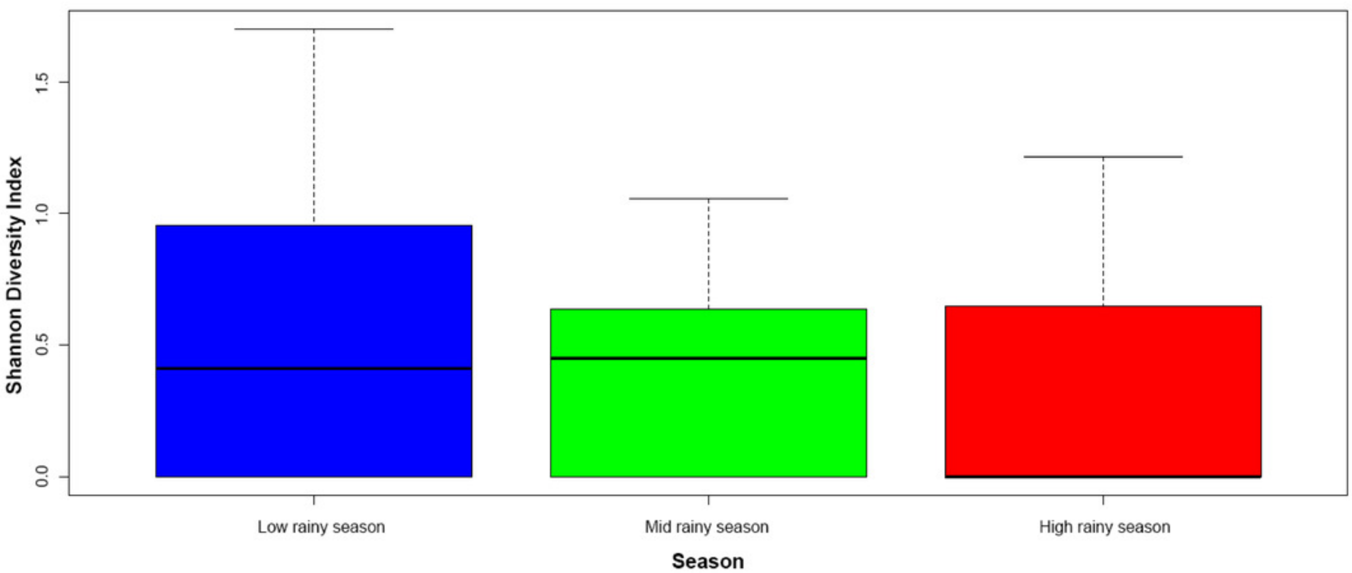
# Figure 4

The number of bryophyte samples found for each bdelloid rotifer taxon



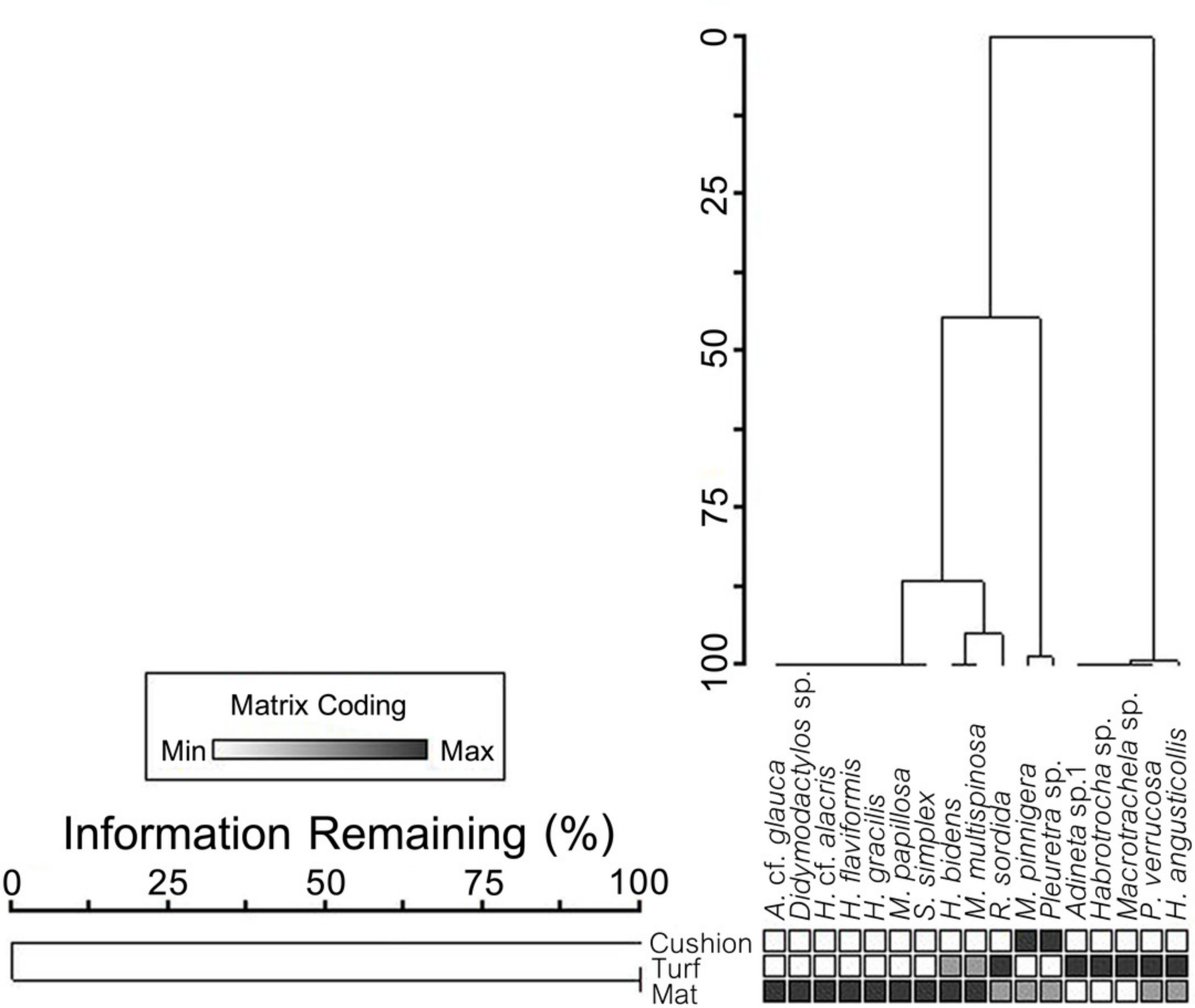
# Figure 5

Boxplot of the Shannon diversity index of bdelloid rotifer species found in each season



# Figure 6

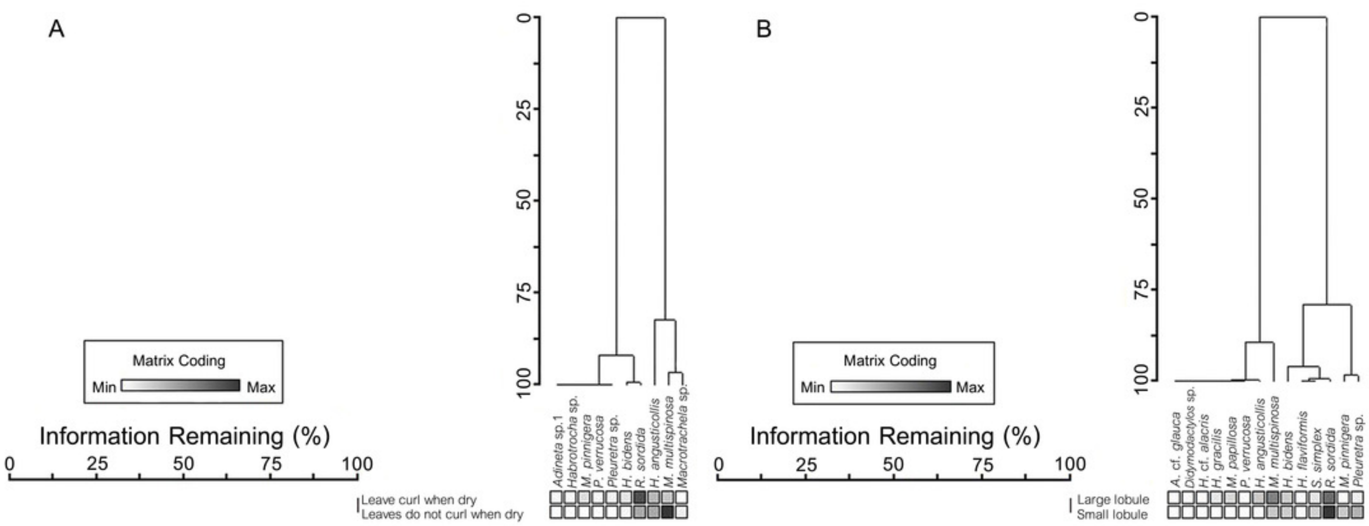
Habitat preferences of bdelloids reported as a two-way cluster plot with species and habitat life forms ordered according to their similarity in species occurrence and abundance



# Figure 7

Habitat preferences of bdelloids reported as a two-way cluster plot

(A) with species and moss characteristics and (B) with species and liverwort characteristics, ordered according to their similarities in species occurrence and abundance.



# Figure 8

Habitat preferences of bdelloids reported as a two-way cluster plot with species and seasons ordered according to their similarities in species occurrence and abundance