https://doi.org/10.59893/abud.23(1).005

Acta Biol. Univ. Daugavp. 23 (1) 2023
ISSN 1407 - 8953

REVIEW OF BRYOPHYTE FUNCTIONAL TRAITS IN ECOLOGICAL STUDIES

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Oļehnoviča E., Pastare-Skutele A., Mežaka A. 2023. Review of bryophyte functional traits in ecological studies. *Acta Biol. Univ. Daugavp., 23(1): 59–67.*

Abstract
Functional traits are increasingly being used in ecological studies. The aim of our review paper is to compile published studies about bryophyte functional traits to clarify their current use for various ecological studies and identify their further application in bryophyte studies. Possible challenges in applying bryophyte functional traits in ecological studies are the selection of the representative traits, which would be typical for the target bryophyte species and communities. Functional traits should also be specific, depending on the study objective and experimental design.

Keywords: bryophytes, functional traits

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INTRODUCTION

Functional diversity is the amount and range of functional traits of organisms in an ecosystem (Diaz & Cabido 2001). A set of organisms that have a similar response to the environment and a similar effect on the ecosystem form functional groups (Keddy 1992, Diaz et al. 2001, Cadotte et al. 2011). Functional trait is any morphological, biochemical, physiological or structural feature that can be measured individually, from the cell to the organism level (Violle et al. 2007). Functional traits play an important role in functional ecology. These traits are used to better understand ecological patterns and relate functional group composition to ecosystem-level processes (Calow 1987, Keddy 1992). Functional trait-based systems are increasingly being used to understand the consequences of environmental change and studying, how species respond to environmental changes and how these changes affect overall ecosystem processes (Lavorel & Garnier 2002, Violle et al. 2007, Lavorel 2013, Gladstone-Gallagher et al. 2019).

Bryophytes make an important part in species diversity in ecosystems (Kraus & Krumm 2013). They represent a very important component of ecosystem functioning, especially in humid European forest and wetland ecosystems, where vegetation is often dominated by bryophytes (Cornelissen et al. 2007). Bryophytes contribute to ecosystem functioning by many different roles, for example, they significantly promote aboveground productive biomass (Wolf 1993), carbon sequestration (Yu 2012) or control soil and vegetation hydrology and temperature (Beringer et al. 2001).

Each bryophyte species is connected to a specific ecological niche, where it is most often found and best adapted. Bryophytes can be used as indicators for habitats (Abolin 1968). All organisms respond to habitat changes at local and landscape levels. Small organisms like bryophytes can be particularly sensitive to environmental variation (Gustafsson & Hallingbäck 1988, Frisvoll & Prestø 1997). Bryophyte functional traits are ecologically relevant and can provide an understanding of various environmental processes and ecosystem functioning (Cornelissen et al. 2007, Hill et al. 2007, Lett et al. 2017).

The considerable diversity of bryophyte species is a challenge in ecological studies. Traditional research of each species would be time-consuming, but studies using species functional traits may increase our knowledge in bryophyte ecology faster. Generalizations, which allow to bridge across taxonomic diversity by emphasizing shared functional traits, can be used in ecological studies (Lavorel & Garnier 2002).

The number of ecological studies, where bryophyte functional traits are included, have increased considerably during the last years. Most of these studies are focused on particular habitat or ecological variable. However, overview of the ecological studies about bryophyte functional traits are needed that could serve not only as a summary of the current knowledge, but also can reveal further study directions (Stanton & Coe 2021).

The aim of this work is to compile fundamental and recently published contributions about bryophyte functional traits and evaluate their applications in further bryophyte ecological studies.

MATERIALS AND METHODS

For a more convenient look at many functional traits, databases are created, which organize and group traits for bryophyte species (Bernhardt-Römermann et al. 2018, van Zuijlen et al. 2023). BryForTrait database contains information for 35 traits, containing more than 23 000 trait values (Bernhardt-Römermann et al. 2018). Bryophytes of Europe Traits (BET) dataset includes values for 65 traits and 25 bioclimatic variables, containing more than 135 000 trait values. In this dataset, there is available information about biological traits, ecological traits and bioclimatic variables based on the species European range (van Zuijlen et al. 2023).

In this work, we compiled the knowledge about bryophyte functional trait studies and databases. We reviewed ecological studies to clarify the importance and application of bryophyte functional traits in further research.

RESULTS AND DISCUSSION

Functional trait databases are an invaluable resource for various ecological studies. Online species databases offer great opportunity to understand species traits and species responses to environmental change at large spatial scales (Löbel et al. 2018). Plant trait composition that correctly reflects the ecosystem processes can reflect ecosystem functioning (Lavorel & Garnier 2002).

For this review we divided bryophyte functional traits into two large groups: biological and ecological traits (Tab. 1) following van Zuijlen et al. (2023). Also other large groups can be distinguished, like sexual traits (Bernhardt-Römermann et al. 2018), bioclimatical traits and status (important for rare species) (van Zuijlen et al. 2023).

Functional characteristics of bryophytes are divided into groups and often studied individually, but data (Bernhardt-Römermann et al. 2018, van Zuijlen et al. 2023) show that the functional characteristics are closely related to each other. Each species has developed a complex of characteristics, which increases the chances of survival in specific conditions. As a result, species adapted to similar conditions may be from different functional groups (Fig. 1).

Table 1. Overview of main bryophyte functional traits according to van Zuijlen et al. (2023).

Biological traits	Ecological traits
generation length	aquatic species
growth form	epiphytic species or not
life form	how strong species are bound to forest habitats
life strategy	major habitat class "Artificial/Terrestrial"
peristome	major habitat class "Forest"
permanent protonema	major habitat class "Grassland"
rhizoids	major habitat class "Rocky areas"
r or K strategy	major habitat class "Shrubland"
length of the seta	major habitat class "Wetlands"
sexual condition	indicator value – moisture
sporophyte frequency	indicator value – heavy metal tolerance
shoot size	indicator value – continentality
spore size	indicator value – light
deciduous branches or stem tips	indicator value – nutrients
bulbils	indicator value – salt tolerance
gemmae	indicator value – temperature
deciduous leaves or leave fragments	substrate class: dead animal carcass or dung
tubers	substrate class: bark of living phanerophyte
size of vegetative propagule	substrate class: epiphytic on non-woody living substrate
	substrate class: rock
	substrate class: soil
	substrate class: deadwood

Figure 1. Example of two bryophyte species *Radula complanata* (L.) Dumort., 1831) and *Dicranum viride* (Lindberg, 1863) with different life strategies (*D. viride:* perennial stayer; *Radula complanata*: perennial shuttle species) and life forms (*D. viride:* cushion; *R. complamata*: turf), which share the same substrate affinity trait: bark (Bernhardt-Römermann et al. 2018). Photo: Anna Pastare-Skutele.

Bryophyte functional traits in ecological studies are frequently used to characterize general functional diversity in particular ecosystem or along the environmental gradient. For example, Asplund et al. (2022) studied changes in bryophyte, lichen and vascular plant functional diversity along elevation gradient and found different responses to environmental gradient among these organism groups, suggesting that bryophytes should be considered in community-level studies.

Biological traits

Biological traits include morphological traits and reproduction traits (van Zuijlen et al. 2023). The morphology of bryophytes has been studied extensively and for a long time (Watson 1964, Goffinet & Shaw 2009, Sabovljević et al. 2014). Morphological traits are complex, because they examine the bryophyte from the cellular to population level. The morphological characteristics include, for example, plant size, growth form, life form (Bernhardt-Römermann et al. 2018). Morphological traits are used to describe new species and consequently are used in species identification. In the field conditions, macro characteristics are used, such as leaf shape and shoot size. In laboratory conditions, more attention is dedicated to the morphological features at a cell level: cell size, and cell number. However, all these traits are functionally related to ecology. For example, Fernández-Martínez et al. (2021) found that the bryophyte size is related to nitrogen and phosphorous concentration in the plant.

Life strategy is the functional trait that shows how species adapt to various environmental conditions by differences in their life cycles. The general system of bryophyte life strategies distinguishes six main categories: annual shuttle species, colonists, fugitives, perennial shuttle species, perennial stayers and short–lived shuttle species (During 1979), where the main characteristics are: life span, reproductive system, sexual or asexual reproduction, spore size and their dispersal (During 1979, Kürschner & Frey 2012). Recent study by Širka et al. (2019) revealed that colonist bryophytes are more common in open and warmer places in spoil heap of Central Slovakia.

Growth form is the functional trait that characterizes individual shoot structure, including direction of growth, branch length, frequency and location (Henriques et al. 2017). Bernhardt-Römermann et al. (2018) recognized two growth forms: 1) orthotrop: stems stand up vertically from the substrate 2) plagiotrop: shoots are close to the substrate, differentiation into main and lateral shoots, including thalloid bryophytes. The study by Wang et al. (2015) revealed that erect bryophyte species have a higher photosynthetic capacity than prostate species. Erect bryophyte species invest more nitrogen in chloroplast to collect more light. The structure of prostrate species allows for more efficient light capture and bryophytes could be good models for studying the carbon economy and nutrient distribution (Wang et al. 2015).

Bryophyte life strategy and life form are biological traits that are widely used in ecological studies (Oishi 2009, Stehn et al. 2010, Ezer et al. 2019, Żarnowiec et al. 2021). Bryophyte life strategies and life forms were successfully used to study habitat succession in Moricsala Strict Nature Reserve in Latvia (Strazdiņa et al. 2013) and these biological traits were used to characterize the bryophyte diversity in broad-leaved forests in Latvia (Gerra-Inohosa & Strazdiņa 2021). Bryophyte life strategy was an important predictor in epiphytic bryophyte occurrence on trees in Lūznava manor park (Mežaka & Kirillova 2019). A study in Italy showed that bryophyte life form models can be predicted in different land cover types. This indicates the importance of bryophyte response in landscape scale (Spitale et al. 2020). However, research between life forms and different environmental traits, like moisture availability and light intensity, is important in contributing to the knowledge about bryophyte ecology (Bates 1998, Vieira et al. 2012).

In the BryForTrait database reproduction traits are distinguished as a separate functional trait group, but many of the reproduction traits are characterized by morphological features, for example, spore size, spore number and length of seta (Bernhardt-Römermannet al. 2018). Reproduction traits, such as sporophyte frequency or spore size were used to characterize both functional diversity and the role of each trait in different aspects of bryophyte ecology, e.g., the ability of species to spread as a result of climate change (Löbel et al. 2018, Sulavik et al. 2021). Reproduction traits have also been recognized as a useful tool in metapopulation studies (Söderström & During 2013).

Ecological traits

Bryophytes have developed various adaptations, which make them resistant to various environmental stresses. Ecological studies can contribute to understanding the bryophyte species, by observing environmentally influenced expressions of physiological and morphological traits depending on habitat (Glime 2017). Bryophytes can serve as indicators for various environmental variables: temperature, moisture, light, salinity (Dull 1991, Gignac 2001, van Zuijlen et al. 2023). In study by Vitt and House (2021) bryophytes were considered as one of the most significant indicators for wetland site-type classification that uses bryophyte abundances across water level, nutrient and salinity gradients.

Bryophytes can also serve as indicators of anthropogenic impact. Several studies show, how forestry affects bryophyte species richness (Horvat et al. 2017, Bernhardt-Römermann et al. 2018). Bryophyte species, for example, *Geocalyx graveolens* and *Syzygiella autumnalis*, which are sensitive to anthropogenic impact, can be used as natural environmental indicators (Bernhardt-Römermann et al. 2018).

Figure 2. Bryophyte species complex on log in black alder swamp forest habitat. Photo: Anna Pastare-Skutele.

Substrate-related functional traits show the typical substrate that species colonizes, and they can be divided in six substrate classes: bark, deadwood, soil, rock, epiphytic on non-woody living substrate, dead animal carcass or dung (van Zuijlen et al. 2023). Substrate functional trait is often used to study the effect of human disturbance, such as logging and hydrological alterations in relation to forest bryophyte communities (Hylander et al. 2005). A study in Slovenia concluded that functional traits and their ecological indicator values were significantly influenced by bedrock and soil, but much less by the composition of tree species (Kutnar et al. 2023). A study in the Alpine region in Italy showed that bryophyte preference to specific substrate is important in their distribution in changing climate. For instance, epigeic bryophytes will be less influenced by changing climate than epiphytes and epixylls (Spitale 2016).

CONCLUSIONS

Functional traits are actively used in various ecological studies. Possible challenges in applying bryophyte functional traits in ecological studies are the selection of the representative traits which would be typical for the target bryophyte species or communities. Functional traits should be also specific that fit well with the study objective and experimental design.

ACKNOWLEDGEMENTS

This work was financially supported by the ESF Project "Strengthening of Professional Competence of Daugavpils University Academic Personnel of Strategic Specialization Branches 3rd Call" (No. 8.2.2.0/20/I/003).

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Received: 20.03.2023.
Accepted: 30.06.2023.