Microhabitat structure predicts eye presence in bryophyte-dwelling tardigrade communities

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Abstract: Microscopic invertebrates often exhibit variation in eye presence within closely related taxa, yet the ecological correlates of this variation remain poorly understood. In tardigrades, eyes may occur or be absent even among species inhabiting similar environments. Because structures that enable seeing are frequently linked to environmental conditions, we investigated which factors influence eye occurrence in bryophyte-dwelling tardigrade communities. We tested whether eye presence is primarily associated with broad-scale light conditions or with fine-scale microhabitat characteristics related to bryophyte structure. Bryophyte samples were collected from shaded and sun-exposed alpine sites, and eye presence was analyzed at the individual level using mixed-effects models incorporating bryophyte light preference and its morphological complexity. The probability of eye presence decreased significantly with increasing structural complexity of bryophyte mats, whereas direct effects of site exposition were not supported. Association with bryophyte light preference was weaker but directionally consistent. These results indicate that microhabitat structure, rather than coarse environmental light availability, is a factor associated with vision in limno-terrestrial tardigrade communities. Therefore, our study indicates the role of fine-scale environmental filtering in structuring sensory trait variation in microscopic animals.

Keywords: eye spots; Tardigrada; microhabitat filtering; bryophytes; microfauna;

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Highlights

- Microhabitat characteristics of bryophytes significantly predict eye presence in tardigrade communities
- Bryophyte architecture modulates effective light availability within moss microhabitats
- Eyeless tardigrade taxa show strong fine-scale spatial clustering among samples
- Stochastic and neutral processes dominate community-level variation in eye occurrence

1. Introduction

Light is one of the most pervasive and ecologically relevant environmental factors shaping animal behaviour, physiology, and evolution (Cronin et al., 2014). Across metazoans, visual and light-sensitive systems translate ambient illumination into information guiding circadian rhythms, habitat choice, predator avoidance, and foraging, thereby functioning as a primary interface between organisms and their environment (Land & Nilsson, 2012). Because the development and maintenance of visual structures are energetically costly, their presence and complexity are tightly linked to local light conditions. For example, in persistently dim environments, visual systems are often reduced, simplified, or lost altogether (Porter, 2025). Importantly, light availability not only varies across broad habitat types such as forests, soils, caves, or aquatic systems, but also across fine spatial scales (Wainwright et al., 2025). Microhabitat structure, substrate composition, and biological cover strongly modify illumination, enhancing moisture retention, biofilm formation, and generating steep and persistent light gradients even within centimeters (e.g., Irving & Connell, 2002; Glime, 2017; Bustos et al., 2022; Kaniewska & Sampayo, 2022). Such micro-scale variation can impose strong selective and filtering pressures on small-bodied invertebrates, whose sensory traits often reflect vertical and structural stratification within habitats, as documented for terrestrial and aquatic ecosystems (e.g., Lythgoe & Partridge, 1989; Cummings & Partridge, 2001; Seehausen et al., 2008; Salmon & Ponge, 2012). Consequently, sensory systems in microscopic organisms are expected to be particularly sensitive indicators of habitat filtering along light-related environmental gradients (Wangpraseurt et al., 2014).

In this context, tardigrades provide a suitable model for examining how micro-scale light environments shape sensory traits in microscopic animals. These microfaunal invertebrates (typically about 200-500 µm in body length) depend on a surrounding water film for activity and occur in aquatic and limno-terrestrial habitats such as mosses, lichens, and soils, where light availability varies strongly over small spatial scales. More than 1,500 species have been described, including approximately 960 limno-terrestrial taxa (Degma & Guidetti, 2025). Their behaviour is primarily expressed through taxis and kinesis and relies on multiple sensory modalities, including chemo- and mechanoreception and photoreception mediated by simple eyes (Beasley, 2001; Nelson et al., 2015, 2019), making them an ideal system for studying sensory trait filtering along microhabitat light gradients.

Despite the recognized importance of sensory perception for tardigrade behavior, current knowledge of their visual system remains limited and fragmented. Two main types of photoreceptive structures have been described: lipid-based eyes in some marine Heterotardigrada (Kristensen, 1978) and inverse pigmented eye cups or pigmented eye spots, first reported by Marcus (1929). The latter are typically located in the head region and associated with the dorso-lateral lobes of the brain and occur primarily in terrestrial Eutardigrada and some Arthrotardigrada. However, not all tardigrades possess visible pigmented eyes, and species lacking these structures are sometimes referred to as “blind” in the literature (Greven, 2007). Despite this terminology, eyeless species have rarely been studied explicitly, and

nothing is known about their sensory ecology. Moreover, the presence of pigmented eye spots may vary among closely related species and even within genera, where it often serves as a taxonomic character (e.g., Guidetti et al., 2022; Vecci, 2024; Kayastha et al., 2025).

Available evidence on light-related behavior in tardigrades is inconsistent. Species possessing pigmented eye spots (hereafter referred to as "eyes" for brevity) have been reported to exhibit both positive and negative responses to light, but these reactions appear to be taxon- and age-specific, and remain difficult to interpret functionally (Marcus, 1929; Baumann, 1961; Ramazzotti and Maucci, 1983; Beasley, 2001). In particular, it is still unresolved whether these responses represent true phototaxis or rather photokinesis. Most existing observations have been conducted under artificial laboratory conditions and without standardized experimental designs, limiting their ecological relevance. Consequently, reliable conclusions about the role of vision in natural tardigrade habitats remain scarce, and the ecological significance of eye presence is still poorly understood.

At the same time, sensory traits have rarely been incorporated into community-level analyses of tardigrades and other microscopic invertebrates (Martínez et al. 2025). In limno-terrestrial systems, tardigrade functional traits that can be reliably quantified across large numbers of samples and species remain scarce (Surmacz et al., 2025a), constraining efforts to link community composition to environmental gradients. The presence or absence of pigmented eyes represents one of the few readily observable and taxonomically stable traits in tardigrades and may therefore serve as a functional indicator of habitat filtering related to light availability and microhabitat structure. Rather than reflecting short-term behavioral plasticity, this trait primarily captures how environmental conditions shape tardigrade communities.

In this study, we hypothesized that the relative occurrence of eyed and eyeless taxa in natural assemblages is structured by light-related microhabitat conditions, mediated by bryophyte species morphology and growth architecture. Specifically, we predicted that communities associated with light-demanding and structurally compact bryophytes would differ in the proportion of eyeless taxa from those occurring in more shaded or structurally complex, multilayered microhabitats. To test it, we analyzed tardigrade assemblages collected from bryophyte samples spanning contrasting exposure conditions and structural traits and quantified eye presence at the individual level. By integrating microhabitat characteristics with community-level trait distributions, our study aims to evaluate whether eye presence functions as an ecologically meaningful trait reflecting habitat filtering in limno-terrestrial tardigrade communities.

2. Materials and Methods

2.1. Samples

To test our hypothesis, we used the collection of 546 bryophyte samples from the Italian Alps analyzed in Surmacz et al. (2025a). Each sample was identified to bryophyte species and included information on whether it was collected from an exposed or shaded site. Samples were classified as shaded if collected beneath a tree, shrub, or rock overhang that obstructed direct sunlight and open-space exposure; otherwise, they were scored as exposed. Because many exposed samples in the original dataset came from higher elevations, and samples were distributed across seven transects, we selected a balanced subset of 112 samples to ensure equal representation of transects and altitudes. This subset was obtained by randomly sampling within each transect and exposition category in R v4.3.3 (R Core Team, 2024), so that shaded and exposed sites were equally represented and their altitude distributions remained comparable. To include microhabitat variables in our analyses, we also extracted the following traits for each bryophyte sample (species) from the Bryophytes of Europe Traits (BET) dataset (van Zuijlen et al., 2023): mean shoot (gametophyte) size, life form (cushion, dendroid, mat, turf, or weft), growth form (acrocarpous or pleurocarpous), and light indicator value (indL, which scores bryophyte light preference from 1 = deep shade to 9 = full light). A detailed list of the samples used in this study is provided in Supplementary Materials (SM.1).

2.2. Tardigrade extraction and eyes scoring

Each analyzed sample was stored as sieved, frozen sediment in Falcon tubes (Surmacz et al., 2025a). Prior to eye scoring, samples were thawed at room temperature, mixed, and a portion of sediment (about 1 ml) from each Falcon tube was transferred to a Petri dish (O 7 cm) using a plastic Pasteur pipette and diluted with distilled water if necessary and examined under a stereomicroscope. The aim was to extract the first 30–40 individuals of the class Eutardigrada. The class Heterotardigrada was excluded due to its low frequency in the samples (Surmacz et al., 2025a) and because some taxa exhibit reddish eyes that are difficult to distinguish from body pigmentation (Greven 2007). Deformed or broken individuals were also discarded. Suitable specimens were picked using a homemade Irwin loop and transferred to glass cubes with distilled water. If fewer than 30 tardigrades were obtained from one Petri dish, the procedure was repeated; if enough were not reached after examining six consecutive Petri dishes, the sample was excluded from further analysis. Extracted animals were subsequently checked for the presence of eyes using an Olympus BX 60 microscope. Each specimen was placed in a drop of water, covered with a coverslip, and examined at 1000× magnification with oil immersion. Eye presence and absence were scored as 1 and 0, respectively. We did not mount specimens on permanent slides using standard preparation media, as the associated chemicals can dissolve eyes (e.g., Stec et al., 2018). The total number of tardigrades examined per sample is provided in Supplementary Materials (SM.01).

2.3. Statistical analyses

All statistical analyses were conducted in R v4.3.3 (R Core Team, 2024). To characterize the structural properties of each bryophyte sample, we performed a Factor Analysis of Mixed Data (FAMD) using *FactoMineR* (Lê et al., 2008), integrating shoot size (continuous), life form (categorical), and growth

form (categorical). We used the first principal axis (PC1) as an index of "morphological complexity," understood operationally as a structural gradient describing how open, horizontally spreading, and multi-layered a bryophyte mat is relative to organized cushion-like forms. Because PC1 reflects a combination of architectural traits rather than any single feature, it should be interpreted as a general structural axis influencing the microhabitat topology experienced by tardigrades.

The presence/absence of eyes in individual tardigrades was analyzed with generalized linear mixed-effects models (GLMMs) implemented in *lme4* package (Bates et al., 2015), with a binomial error distribution with logit link. Equal representation across transects was ensured by design (eight exposed and eight shaded samples from each transect), and altitude did not differ between exposed and shaded groups (Supplementary Materials (SM.02: Figure S1); hence, transect and altitude were not included in modelling. Fixed effects included sample exposition (exposed vs. shaded), bryophyte light indicator (indL), and morphological complexity (PC1). Samples with indL value recorded as 0 ("indifferent"; 13 samples) were excluded from GLMMs because this value does not represent a valid position on the 1–9 light-preference scale and therefore cannot be interpreted as part of the indL intensity gradient. The sample was fitted as a random intercept to account for the non-independence of individuals. Because sample exposition was non-significant in the full model and showed moderate correlation with the bryophyte light indicator Supplementary Materials (SM.02: Figure S2), it was excluded from the final model reported in the results, which included only indL and PC1. Competing model structures were compared using likelihood ratio tests (LRT) and AIC values Supplementary Materials (SM.02: Table S1). Significance of fixed effects was evaluated with type-III Wald χ^2 tests (Anova function, *car* package). Model assumptions were evaluated with residual diagnostics using the *DHARMa* package (Hartig 2026), checks for overdispersion with package *performance* (Lüdecke et al., 2021), and variance inflation factors for collinearity. Model fit was summarized with marginal and conditional R^2 (*performance*). Predictions with 95% confidence intervals were generated using *ggeffects* (Lüdecke et al., 2018) and visualized in *ggplot2* (Wickham 2016).

To further explore relationships among bryophyte traits and to characterize fine-scale variation in eye occurrence, we conducted additional exploratory analyses at the sample level. First, the association between bryophyte light indicator values (indL) and morphological complexity (PC1) was tested using Spearman's rank correlation. Second, differences in indL between pleurocarpous and acrocarpous growth forms were assessed using Wilcoxon rank-sum tests, with rank-biserial correlation as an effect size. Finally, to evaluate the degree of spatial heterogeneity in the occurrence of eyeless taxa, individual-level data were aggregated at the sample level, and the proportion and absolute number of eyeless individuals were calculated for each sample. The concentration of eyeless individuals among samples was summarized using cumulative contribution metrics (e.g. the proportion of individuals occurring in the most enriched samples). The R code and entry data are provided in Supplementary Materials (SM.03).

3. Results

After excluding low-abundance samples, 88 bryophyte samples entered the analysis. Samples with undefined bryophyte light indicator values (indL = 0) were then excluded, resulting in the removal of 13 samples and yielding a final dataset of 75 samples with 2,778 eutardigrade individuals. Individuals were distributed evenly between exposed (n = 1,412) and shaded (n = 1,366) sites. Across all samples, eyes were present in 2,459 individuals (88.5%) and absent in 319 individuals (11.5%).

Bryophyte traits (shoot size, life form, growth form) produced a first principal axis (PC1) that explained ~40% of the variance. PC1 reflected a structural gradient linking larger shoot size with pleurocarpous and weft-forming species, and smaller, more compact shoots with cushion and acrocarpous forms. Higher PC1 values, therefore, corresponded to more open, horizontally spreading and multi-layered growth architectures, whereas lower values reflected vertical growth forms. Contributions of the three traits were broadly balanced, indicating that PC1 captured a composite architectural gradient rather than being dominated by a single variable (Supplementary Materials SM.02: Figure S3).

Both bryophyte light indicator values (indL) and morphological complexity (PC1) significantly predicted the presence of eyes in tardigrades, with both variables showing negative effects (indL: χ^2 = 4.68, p = 0.031; PC1: χ^2 = 4.13, p = 0.042). The model explained a substantial proportion of variance at the community level (conditional R^2 = 0.535), but fixed effects accounted for a fraction of the total variance (marginal R^2 = 0.062). Residual diagnostics indicated no evidence of overdispersion or systematic deviations from model assumptions, and collinearity among predictors was low. Predicted probabilities from the final model showed that eye presence decreased with increasing bryophyte light indicator values and increasing morphological complexity (Figure 1).

Additional exploratory analyses revealed structured relationships among bryophyte traits and pronounced fine-scale heterogeneity in the occurrence of eyeless taxa. Bryophyte light indicator values were moderately negatively correlated with morphological complexity (Spearman's $\rho = -0.36$, $p < 0.001$), indicating that light-demanding species tended to form more compact growth forms (Supplementary Materials SM.02: Figure S4). Consistently, acrocarpous and pleurocarpous bryophytes differed significantly in their light preferences, with acrocarpous species exhibiting higher indL values (Wilcoxon rank-sum test: W = 1422, p < 0.001; rank-biserial r = 0.49) (Supplementary Materials SM.02: Figure S5). Furthermore, the distribution of eyeless individuals across samples was highly uneven. More than half of all eyeless specimens (52%) were concentrated in only ten samples, and over 70% occurred in the top 20% of samples with the highest number of eyeless individuals, indicating strong patchiness in the occurrence of eyeless taxa at the microhabitat scale.

4. Discussion

Our results indicate that the occurrence of pigmented eyes in limno-terrestrial tardigrade communities is structured primarily by microhabitat characteristics rather than by broad-scale environmental factors. Because eye presence represents a species-specific and taxonomically stable trait, variation in its frequency across samples reflects differences in community composition rather than short-term phenotypic plasticity. Consequently, patterns detected in our experiment can be interpreted as evidence of habitat filtering acting on assemblages of eyed and eyeless taxa.

4.1. Microhabitat structure outweighs macroenvironmental conditions

Previous studies have shown that communities of microscopic invertebrates may be influenced by both macroenvironmental factors and fine-scale habitat characteristics. For example, Klarenberg et al. (2025) demonstrated that microarthropod communities associated with cryptogams are structured by species-specific traits such as nitrogen and moisture content, and that the strength of these effects depends on local environmental context. Similarly, Martínez et al. (2025) demonstrated that harsh hydrodynamic regimes on sandy beaches filter meiofaunal communities according to species traits, leading to distinct functional assemblages across beach microhabitats. In tardigrades, community composition has been shown to be shaped by both macro- and microhabitat-related filters (Guil et al., 2009a; Surmacz et al. 2025a,b; Guidetti et al. 2024). At the same time, increasing evidence indicates that microhabitat structure plays a dominant role in shaping communities of microscopic organisms (Ramsay et al. 2021; Surmacz et al. 2025a; Mäenpää et al. 2025). Environmental conditions experienced by organisms living in water films may differ substantially over millimeter scales, even within closely adjacent substrates. In bryophyte-associated systems, mosses and liverworts regulate moisture retention, aeration, and light penetration (Proctor, 2000; Michel et al., 2012; Jaroszynska et al., 2023), thereby defining the effective habitat available to microfauna, depending on water. Consistent with this view, differentiation in bdelloid rotifer communities has been linked to substrate type and cryptogam species identity (Fontaneto et al., 2011; Wang et al., 2023). In tardigrades, biodiversity patterns have also been reported to correlate with microhabitat formed by specific cryptogams but also substrate on which cryptogamic vegetation grows (Guil et al., 2009b; Surmacz et al. 2025 a,b; Guidetti et al. 2024). In our study, macro-scale exposition did not exert a detectable independent effect on eye occurrence, whereas bryophyte light preferences and growth architecture were significant predictors. These findings indicate that local structural conditions within habitats created by bryophytes are more relevant for shaping community-level distributions of eyed and eyeless taxa than broad-scale exposure to sunlight.

4.2. Bryophyte architecture and effective light availability

Both bryophyte light indicator values and morphological complexity were negatively associated with the probability of eye presence. These two variables were moderately correlated, reflecting an ecological syndrome in which light-demanding species tend to form compact, cushion-like growth forms, whereas shade-tolerant species are more often horizontally spreading and multilayered (Glime, 2017). This pattern suggests that effective light availability experienced by tardigrades is strongly mediated by

bryophyte architecture. Dense cushions composed of small, closely packed shoots may strongly attenuate light within the moss interior, even when externally exposed. Conversely, more open and horizontally spreading forms may also reduce internal illumination through multilayered shading. As tardigrades are typically active only when embedded in a continuous water film (Møbjerg & Neves, 2021), they are likely to spend most of their active life within these internal microhabitats rather than on exposed surfaces. Consequently, external light conditions may provide only a coarse approximation of the sensory environment experienced by individuals. Under such circumstances, the selective advantage of possessing pigmented eye spots may be reduced, as reliable light cues may be limited or absent within structurally complex bryophyte microhabitats. Our results therefore support the hypothesis that bryophyte-mediated modification of microhabitat light regimes plays a role in shaping the distribution of vision in tardigrade communities. Importantly, a prominent feature of our data was the highly uneven distribution of eyeless individuals among samples. More than half of all eyeless specimens were concentrated in a small subset of samples, and over 70% occurred in the top 20% of samples with the highest number of eyeless individuals. This pronounced patchiness explains the high proportion of variance captured by sample-level random effects and the relatively low marginal R^2 values of fixed predictors. Together, these patterns indicate that, although bryophyte-related microhabitat characteristics impose some ecological filters, most community variation is shaped by stochastic and neutral processes (Meyer 2006; Surmacz et al. 2025a,b, Matsko et al. in press; Mäenpää et al. 2025).

4.3. Eye loss and sensory evolution in microscopic taxa

Most tardigrade individuals examined in this study possessed pigmented eye spots, indicating that eye absence is restricted to a limited subset of lineages. Nevertheless, the occurrence of eyeless taxa raises questions about the evolutionary and functional significance of eye loss in this group. Comparative evidence from other taxa suggests that reduction or loss of visual structures is a recurrent outcome in low-light environments. In onychophorans, simple eyes are generally present, but several species lack them entirely, and in some cases, rudimentary structures indicate gradual reduction rather than abrupt loss (Ruhberg et al., 2001; Martin et al., 2017). In flatworms, independent losses of pigmented eyes have been accompanied by the evolution of alternative sensory organs, such as ciliated pits, which may partially compensate for reduced photosensitivity (Gąsiorowski et al., 2023). In rotifers, variation in eye pigmentation demonstrates that the external visibility of photoreceptive structures may be influenced by physiological and environmental factors, including nutritional constraints (Clément & Wurdak, 1984; Kim et al., 2014). These examples indicate that eye absence does not necessarily reflect a single evolutionary pathway but may result from multiple processes, including gradual degeneration, functional replacement, or shifts in selective regimes. In tardigrades, the limited phylogenetic and developmental data currently available preclude strong conclusions about the mechanisms underlying eye loss. However, our community-level results are consistent with the view that eyeless lineages are preferentially associated with structurally complex and internally dark microhabitats, where visual cues may provide a limited adaptive advantage.

4.4. Conclusions

Our results demonstrate that variation in eye presence among tardigrade assemblages is structured more by bryophyte-associated microhabitat characteristics rather than by broad-scale exposure to light. Bryophyte growth form and light preferences jointly shape internal light regimes, which in turn influence the relative occurrence of eyed and eyeless taxa. At the same time, the pronounced fine-scale patchiness observed across samples indicates that stochastic and historically contingent processes play a substantial role in modulating these patterns. By treating eye presence as a functional trait reflecting sensory investment, this study provides a community-level perspective on how microhabitat structure contributes to trait filtering in limno-terrestrial tardigrades. Because eye presence is taxonomically stable and readily quantifiable, it represents a rare example of an accessible functional trait in microscopic invertebrates, a group that remains underrepresented in trait-based ecological research (Martínez et al., 2025). More broadly, our findings highlight that even simple morphological traits may reveal complex interactions between structural habitat filters and stochastic assembly processes operating at minute spatial scales.

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CRediT authorship contribution statement:

Yelyzaveta Matsko: Investigation, Conceptualization, Formal analysis, Writing – review & editing; Methodology, Data curation, Project administration, Visualization; **Krzysztof Miler**: Investigation, Writing – review & editing, Methodology, Data curation; **Izabela Poprawa**: Writing – review & editing, Methodology, Resources; **Daniel Stec**: Conceptualization, Writing – review & editing, Supervision, Resources, Methodology, Validation, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

The dataset underlying the analyses in this study is available in the FigShare repository: https://doi.org/10.6084/m9.figshare.31655233

Declaration of competing interests

We have nothing to declare

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work, the authors used ChatGPT in order to improve the readability and language of the manuscript. After using this tool, the authors reviewed and edited the content as needed and took full responsibility for the content of the published article.

References

Baumann, H. (1961) 'Der Lebenslauf von *Hypsibius (H.) convergens* Urbanowicz (Tardigrada)', *Zoologischer Anzeiger*, 165, pp. 123–128.

Bates, D., Mächler, M., Bolker, B. and Walker, S. (2015) 'Fitting linear mixed-effects models using lme4', *Journal of Statistical Software*, 67, pp. 1–48. https://doi.org/10.18637/jss.v067.i01

Beasley, C.W. (2001) 'Photokinesis of *Macrobiotus hufelandi* (Tardigrada, Eutardigrada)', *Zoologischer Anzeiger*, 240, pp. 233–236. https://doi.org/10.1078/0044-5231-00030

Bustos, M.J., Garibotti, I.A., Cech, N., Navarro, M.C., Gonzalez Polo, M. and Satti, P. (2022) 'Microhabitat-specific differences on the composition and function of biological soil crust communities', *Plant and Soil*, 479, pp. 663–677. https://doi.org/10.1007/s11104-022-05556-5

Clément, P. and Wurdak, E. (1984) 'Photoreceptors and photoreception in rotifers', in Ali, M.A. (ed.) *Photoreception and vision in invertebrates*. Boston, MA: Springer, pp. 99–112. https://doi.org/10.1007/978-1-4613-2743-1_8

Cronin, T.W., Johnsen, S., Marshall, N.J. and Warrant, E.J. (2014) *Visual Ecology*. Princeton: Princeton University Press.

Cummings, M.E. and Partridge, J. (2001) 'Visual pigments and optical habitats of surfperch (*Embiotocidae*) in the California kelp forest', *Journal of Comparative Physiology A*, 187, pp. 875–889. https://doi.org/10.1007/s00359-001-0258-6

Degma, P. and Guidetti, R. (2025) *Actual checklist of Tardigrada species (2009–2025, 44th Edition: 10-06-2025)*. Online checklist. Available at: https://doi.org/10.25431/11380_1178608

Fontaneto, D., Westberg, M. and Hortal, J. (2011) 'Evidence of weak habitat specialisation in microscopic animals', *PLoS ONE*, 6, e23969. https://doi.org/10.1371/journal.pone.0023969

Gąsiorowski, L., Dittmann, I.L., Brand, J.N., Ruhwedel, T., Möbius, W., Egger, B. and Rink, J.C. (2023) 'Convergent evolution of the sensory pits in and within flatworms', *BMC Biology*, 21, 266. https://doi.org/10.1186/s12915-023-01768-y

Glime, J.M. (2017) *Light: The Shade Plants. Chapter 9-1*, in Glime, J.M. (ed.) *Bryophyte Ecology*, vol. 1: Physiological Ecology. Michigan Technological University and the International Association of Bryologists. Updated 17 July 2020. Available at: http://digitalcommons.mtu.edu/bryophyte-ecology/

Greven, H. (2007) 'Comments on the eyes of tardigrades', *Arthropod Structure & Development*, 36, pp. 401–407. https://doi.org/10.1016/j.asd.2007.06.003

Guidetti, R., Cesari, M., Giovannini, I., Ebel, C., Förschler, M.I., Rebecchi, L. and Schill, R.O. (2022) 'Morphology and taxonomy of the genus *Ramazzottius* (Eutardigrada; Ramazzottiidae) with the integrative description of *Ramazzottius kretschmanni* sp. nov.', *European Zoological Journal*, 89, pp. 346–370. https://doi.org/10.1080/24750263.2022.2043468

Guil, N., Hortal, J., Sánchez-Moreno, S. and Machordom, A. (2009a) 'Effects of macro- and micro-environmental factors on the species richness of terrestrial tardigrade assemblages in an Iberian mountain environment', *Landscape Ecology*, 24, pp. 375–390. https://doi.org/10.1007/s10980-008-9312-x

Guil, N., Sánchez-Moreno, S. and Machordom, A. (2009b) 'Local biodiversity patterns in micrometazoans: Are tardigrades everywhere?', *Systematics and Biodiversity*, 7, pp. 259–268. https://doi.org/10.1017/S1477200009003016

Hartig, F. (2026) *DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression models*. R package version 0.5.0. Available at: https://github.com/florianhartig/dharma

Irving, A. and Connell, S. (2002) 'Sedimentation and light penetration interact to maintain heterogeneity of subtidal habitats: algal versus invertebrate dominated assemblages', *Marine Ecology Progress Series*, 245, pp. 83–91. https://doi.org/10.3354/meps245083

Jaroszynska, F., Althuizen, I., Halbritter, A.H., Klanderud, K., Lee, H., Telford, R.J. and Vandvik, V. (2023) 'Bryophytes dominate plant regulation of soil microclimate in alpine grasslands', *Oikos*, 2023, e10091. https://doi.org/10.1111/oik.10091

Kaniewska, P. and Sampayo, E.M. (2022) 'Macro- and micro-scale adaptations allow distinct *Stylophora pistillata-Symbiodiniaceae* holobionts to optimize performance across a broad light habitat', *Journal of Phycology*, 58, pp. 55–70. https://doi.org/10.1111/jpy.13215

Kayastha, P., Warguła, J., Bartylak, T., Mioduchowska, M., Gawlak, M., Kaczmarek, Ł. (2025) 'Integrative description of two new *Milnesium* species (Apochela: Milnesiidae) from Canada and Nepal', *European Zoological Journal*, 92, pp. 1358–1382. https://doi.org/10.1080/24750263.2025.2562907

Kim, H.-J., Sawada, C., Rhee, J.-S., Lee, J.-S., Suga, K. and Hagiwara, A. (2014) 'Nutritional effects on the visual system of the rotifer *Brachionus plicatilis* sensu stricto (Rotifera: Monogononta)', *Journal of Experimental Marine Biology and Ecology*, 460, pp. 177–183. https://doi.org/10.1016/j.jembe.2014.07.005

Klarenberg, I., Liu, R., Convey, P., Cornelissen, J. and Bokhorst, S. (2025) 'How the small host the small: Cryptogam trait-mediated structuring of Antarctic microarthropod communities'. https://doi.org/10.22541/au.174678850.01347224/v1

Kristensen, R.M. (1978) 'Notes on marine heterotardigrades. 1. Description of two new *Batillipes* species, using the electron microscope', *Zoologischer Anzeiger*, 200, pp. 1–17.

Land, M.F. and Nilsson, D.-E. (2012) *Animal Eyes*. Oxford: Oxford University Press.

Lê, S., Josse, J. and Husson, F. (2008) 'FactoMineR: An R package for multivariate analysis', *Journal of Statistical Software*, 25, pp. 1–18. https://doi.org/10.18637/jss.v025.i01

Lüdecke, D. (2018) 'ggeffects: Tidy data frames of marginal effects from regression models', *Journal of Open Source Software*, 3, 772. https://doi.org/10.21105/joss.00772

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P. and Makowski, D. (2021) 'performance: An R package for assessment, comparison and testing of statistical models', *Journal of Open Source Software*, 6, 3139. https://doi.org/10.21105/joss.03139

Lythgoe, J.N. and Partridge, J.C. (1989) 'Visual pigments and the acquisition of visual information', *Journal of Experimental Biology*, 146, pp. 1–8. https://doi.org/10.1242/jeb.146.1.1

Marcus, E. (1929) 'Tardigrada', in Bronn, H.G. (ed.) *Klassen und Ordnungen des Tierreichs*, vol. 5, Abtlg IV, Buch 3. Leipzig: Akademische Verlagsgesellschaft, pp. 1–808.

Mäenpää, H., Elo, M. and Calhim, S. (2024) 'A first look into moss living tardigrades in boreal peatlands', *Ecology and Evolution*, 14, e70045. https://doi.org/10.1002/ece3.70045

Martin, C., Gross, V., Hering, L., Tepper, B., Jahn, H., De Sena Oliveira, I., Stevenson, P.A. and Mayer, G. (2017) 'The nervous and visual systems of onychophorans and tardigrades', *Journal of Comparative Physiology A*, 203, pp. 565–590. https://doi.org/10.1007/s00359-017-1186-4

Martínez, A., Fontaneto, D. and Curini-Galletti, M. (2025) 'The swash zone selects functionally specialized assemblages of beach interstitial meiofauna', *Ecography*, 2025, e07179. https://doi.org/10.1111/ecog.07179

Meyer, H.A. (2006) 'Small-scale spatial distribution variability in terrestrial tardigrade populations', *Hydrobiologia*, 558, pp. 133–139. https://doi.org/10.1007/s10750-005-1412-x

Michel, P., Lee, W.G., During, H.J. and Cornelissen, J.H.C. (2012) 'Species traits and their non-additive interactions control the water economy of bryophyte cushions', *Journal of Ecology*, 100, pp. 222–231. https://doi.org/10.2307/41333101

Møbjerg, N. and Neves, R.C. (2021) 'New insights into survival strategies of tardigrades', *Comparative Biochemistry and Physiology Part A*, 254, 110890. https://doi.org/10.1016/j.cbpa.2020.110890

Nelson, D., Guidetti, R. and Rebecchi, L. (2015) 'Phylum Tardigrada', in Thorp, J. and Rogers, D.C. (eds.) *Thorp and Covich's Freshwater Invertebrates*, vol. 1. Academic Press, pp. 347–350. https://doi.org/10.1016/B978-0-12-385026-3.00017-6

Porter, M.L. (2025) 'At the edge of darkness: A framework for the evolution of visual systems in dim light', *Functional Ecology*, 39, pp. 2626–2636. https://doi.org/10.1111/1365-2435.70107

Proctor, M.C.F. (2000) 'Physiological ecology', in Shaw, A.J. and Goffinet, B. (eds.) *Bryophyte Biology*. Cambridge: Cambridge University Press, pp. 225–247. http://dx.doi.org/10.1017/CBO9781139171304.009

Ramazzotti, G. and Maucci, W. (1983) *Il Phylum Tardigrada*. Memorie dell'Istituto Italiano di Idrobiologia, 41, pp. 1–1012.

Ramsay, B.P.L., Marley, N.J., Bilton, D.T., Rundle, S.D. and Ramsay, P.M. (2021) 'The structure of tardigrade communities at fine spatial scales in an Andean *Polylepis* forest', *Neotropical Biodiversity*, 7, pp. 443–454. https://doi.org/10.1080/23766808.2021.1943216

R Core Team (2024) *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available at: https://www.r-project.org/

Ruhberg, H., Tiemann, H., Mette, A. and Rhode, B. (2001) 'Evolutionäre Aspekte der Augen-Rückbildung beim hemiedaphischen Onychophoren *Tasmanipatus anophthalmus*', *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 98, pp. 31–50.

Salmon, S., Ponge, J.F., Gachet, S., Deharveng, L., Lefebvre, N. and Delabrosse, F. (2014) 'Linking species, traits and habitat characteristics of Collembola at European scale', *Soil Biology and Biochemistry*, 75, pp. 73–85. https://doi.org/10.1016/j.soilbio.2014.04.002

Seehausen, O., Terai, Y., Magalhaes, I.S., Carleton, K.L., Mrosso, H.D.J., Miyagi, R., van der Sluijs, I., Schneider, M.V., Maan, M.E., Tachida, H., Imai, H. and Okada, N. (2008) 'Speciation through sensory drive in cichlid fish', *Nature*, 455, pp. 620–627. https://doi.org/10.1038/nature07285

Stec, D., Kristensen, R.M. and Michalczyk, Ł. (2018) 'Integrative taxonomy identifies *Macrobiotus papei*, a new tardigrade species of the *Macrobiotus hufelandi* complex (Eutardigrada: Macrobiotidae) from the Udzungwa Mountains National Park (Tanzania)', *Zootaxa*, 4446, pp. 273–291. https://doi.org/10.11646/zootaxa.4446.2.7

Surmacz, B., Fontaneto, D., Vončina, G. and Stec, D. (2025a) 'Deciphering the patterns and drivers of tardigrade diversity along altitudinal gradients', *Molecular Ecology*, 34, e70196. https://doi.org/10.1111/mec.70196

Surmacz, B., Budzik, K., Matsko, Y. and Stec, D. (2025b) 'Human impact on microinvertebrate diversity and distributions: Questioning the resilience of tardigrades', *Global Ecology and Biogeography*, 34, e70167. https://doi.org/10.1111/geb.70167

van Zuijlen, K., Nobis, M.P., Hedenäs, L., Hodgetts, N., Calleja Alarcón, J.A., Albertos, B. et al. (2023) 'Bryophytes of Europe Traits (BET) data set', *Journal of Vegetation Science*, 34, e13179. https://doi.org/10.1111/jvs.13179

Vecchi, M. (2024) 'A new leaf litter dwelling *Adropion* species', *Folia Biologica (Kraków)*, 72, pp. 109–117. https://doi.org/10.3409/fb_72-3.11

Wainwright, J.B., Loupasaki, T., Ramírez, F., Penry-Williams, I.L., England, S.J., Barker, A., Meier, J.I., How, M.J., Roberts, N.W., Troscianko, J., Montgomery, S.H. (2025) 'Mutualisms within light microhabitats are associated with sensory convergence', *Proceedings of the National Academy of Sciences of the USA*, 122, e2422397122. https://doi.org/10.1073/pnas.2422397122

Wang, W., Yang, Y., Cui, Z., Chen, M., Ma, X., Wang, Q. (2023) 'High diversity and strong habitat preference of bdelloid rotifers', *Biodiversity and Conservation*, 32, pp. 2769–2789. https://doi.org/10.1007/s10531-023-02630-x

Wangpraseurt, D., Polerecky, L., Larkum, A.W.D., Ralph, P.J., Nielsen, D.A., Pernice, M. and Köhl, M. (2014) 'The in situ light microenvironment of corals', *Limnology and Oceanography*, 59, pp. 917–926. https://doi.org/10.4319/lo.2014.59.3.0917

Wickham, H. (2016) *ggplot2: Elegant graphics for data analysis*. New York: Springer-Verlag. Available at: https://ggplot2.tidyverse.org

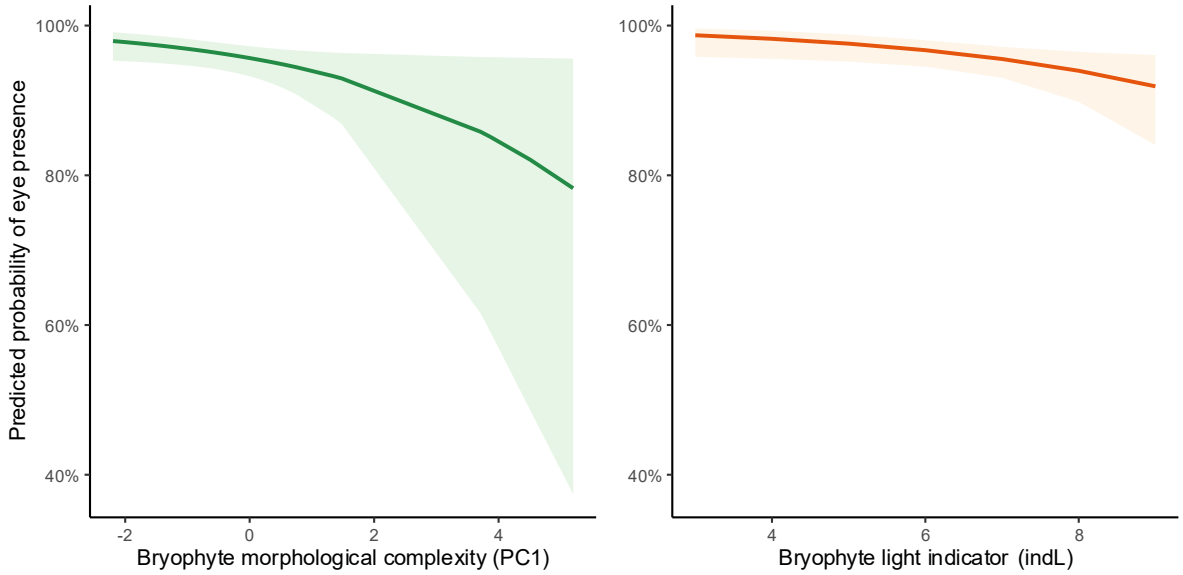

Figure 1. Predicted probability of eye presence in tardigrades as a function of bryophyte morphological complexity (left panel) and bryophyte light indicator values (right panel), based on generalized linear mixed-effects models. Solid lines represent model predictions, and shaded areas denote 95% confidence intervals.

Supplementary Materials

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Supplementary Materials SM.01. Information about the samples, predictors and tardigrade eyes counts.

Supplementary Materials SM.02. Supplementary figures and tables.

Supplementary Materials SM.03. Raw data and script for statistical analysis and visualizations.