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REVIEW

A model species in focus: the silver-thread moss *Bryum argenteum* as a model for ecological and evolutionary studies

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Abstract
Model organisms are species selected for studies due to characteristics that make them ideal for research purposes. These species are chosen for their suitability for scientific investigations. For ecological and evolutionary studies, good model organisms typically exhibit the following characteristics: (1) small genome size; (2) rapid reproductive cycle; and (3) easy manipulation. A small genome size is important for quicker and easier gene sequencing. Rapid reproduction allows for the generation of offspring within a short period, facilitating the study of reproductive processes. Lastly, easy manipulability enables the establishment of colonies in laboratory and field settings for experimentation. In this regard, the moss *Bryum argenteum* stands out for possessing these three characteristics, along with others that make it a suitable model organism for ecological and evolutionary studies. Accordingly, a growing body of literature has already used B. argenteum in ecological and evolutionary research. Thus, we conducted a literature review and compiled all ecological and evolutionary studies using *B. argenteum* as a model species. Our review emphasized themes such as reproduction, environmental adaptation, genetics and biogeography, bioindicators, physiology, interactions, and soil crusts, encompassing a total of 80 studies. Additionally, we identified three important and timely topics for further research: tolerance to low temperatures, macroecology, and reproduction. We hope that this study aids researchers in gaining a deeper understanding of the ecology and evolution of *B. argenteum* and inspires further investigations into this model organism, which exhibits fascinating characteristics for elucidating plant ecology and evolution.

Keywords Bioindicators · Genetics · Interactions · Physiology · Soil crusts · Reproduction · Ecophysiology

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Introduction

Model organisms emerge as essential tools in scientific studies of ecology and evolution because they enable mechanistic inference under controlled conditions, linking genotype, phenotype, and ecological performance (Huey et al. 1983; Shine and Bonnet 2000). Organisms such as the fruit fly *Drosophila melanogaster* L. and the nematode *Caenorhabditis elegans* Hansen. have a long history of use as model systems (Golden and Riddle 1984; Adams et al. 2000; Lemaitre and Hoffmann 2007; Erkut et al. 2013). In these cases, they are used in experiments to investigate how key environmental drivers (e.g., temperature, humidity, and resource availability) influence performance, demography, and interactions (Golden and Riddle 1984; Adams et al. 2000; Lemaitre and Hoffmann 2007; Erkut et al. 2013). These controlled manipulations allow the investigation of ecological and evolutionary responses to environmental variation providing mechanistic insights into population dynamics and species interactions (Huey et al. 1983).

Model systems also serve as experimental platforms for genetic and genomic investigations in evolutionary research (Kellogg and Shaffer 1993). The plant *Arabidopsis thaliana* (L.) Heynh., is an established model system extensively used in developmental research. In addition to flowering plants, several non-flowering plant models have also been established, particularly among bryophytes, such as the moss *Physcomitrium patens* (Hedw.) Mitt. and the liverwort *Marchantia polymorpha* L., which are extensively used in molecular genetics, developmental biology, and genome evolution studies (Naramoto et al. 2022). These models offer advantages, such as short life cycles and ease of genetic manipulation, enabling the identification and characterization of genes involved in crucial evolutionary processes, including the response to selective pressures and adaptation to new environments (Paull et al. 2010; Lawrence et al. 2012; Postma and Ågren 2016). Its use facilitates systematic analysis of genetic mechanisms driving evolution (Van Eeden et al. 1996; Schmid et al. 2005). Therefore, model species play a central role in building a robust knowledge base for ecology and evolutionary biology and in improving our understanding of biological complexity (Kellogg and Shaffer 1993). However, reliance on a limited number of model taxa also highlights the importance of expanding the diversity of experimental systems, particularly within bryophytes.

Physcomitrium patens is the best established moss model for functional genomics and developmental genetics, supported by a high-quality genome, standardized cultivation, and efficient genetic tools (Rensing et al. 2020). However, its long-term laboratory domestication in the relatively narrow range of environmental contexts typically represented in experiments can limit direct inference about performance under complex, field realistic stress combinations (McDaniel et al. 2010; Klips 2015; de Keijzer et al. 2021; Eisenring et al. 2023). In contrast, *B. argenteum* complements established bryophyte models by combining experimental tractability with exceptional ecological breadth, thriving across natural and anthropogenic habitats and showing striking plasticity and tolerance to the multi-stressor environments. This combination positions *B. argenteum* as a particularly useful system for eco-evolutionary questions where genotype phenotype links must be interpreted in realistic environmental settings, and expanding cultivation resources across bryophyte lineages further facilitate comparative work (Müller et al. 2016; Božović et al. 2025).

Among terrestrial plants, bryophytes, a monophyletic group of plants that includes liverworts, hornworts and mosses, contribute to soil stabilization, water retention, and nutrient

cycling, thereby supporting multiple areas of ecological and evolutionary research (Oliver et al. 2000; Harris et al. 2020). Bryophytes remain underrepresented in ecological and evolutionary research, partly due to their small size and identification challenges (McDaniel 2021), even though they play important ecosystem roles such as soil formation and maintenance, nutrient cycling and water retention in the ecosystem (Eldridge and Tozer 1996; Bergamini and Pauli 2001; Carroll 2003; He et al. 2016). Furthermore, bryophytes are excellent organisms for carrying out experiments due to their small size and the ease of gametophyte regeneration, enabling cultivation in laboratories under different conditions (Beckert et al. 1999; Bisang and Hedenäs 2005; Proctor et al. 2007a; dos Santos et al. 2020; Santos et al. 2024b). Their morphological simplicity and short life cycle, with a well-defined alternation of generations, make bryophytes ideal for studies of genetics, physiology and evolutionary ecology, since their reproductive cycle is very marked between the haploid and diploid phases (gametophytic and sporophytic) (Maciel-Silva and Pôrto 2014). Thus, the use of bryophytes as study models provides valuable insights into fundamental processes, including organism development, responses to environmental stress, and the evolution of adaptive traits (Brown and Lemmon 1988; Horsley et al. 2011). Highlighting their ecological importance and utility as study models, bryophytes emerge as valuable organisms for a broader understanding of plant biology and terrestrial ecosystems (Slack 2011). Building on this broader perspective, and complementing recent broader syntheses on bryophytes as models (reviewed by Yadav et al. 2023), this review focuses on *Bryum argenteum* as a particularly promising model species for ecological and evolutionary research.

In this context, *Bryum argenteum* Hedw. is proposed not as a substitute for established bryophyte models, but as a complementary system, particularly suited for ecological and evolutionary studies. Unlike highly domesticated laboratory models, *B. argenteum* occurs across a wide range of natural and anthropogenic environments, exhibits extreme tolerance to multiple abiotic stresses, and maintains a dioicous sexual system, making it especially valuable for investigating ecological processes, reproductive strategies, and adaptation under realistic environmental conditions. Thus, this paper reviews ecological and evolutionary studies that use *B. argenteum*, evaluating the traits that make it experimentally tractable and ecologically relevant. By focusing on this experimentally tractable species, which occupies a broad range of habitats and tolerates multiple abiotic stresses, we can analyze ecological and evolutionary processes under controlled and field-relevant conditions. The review will encompass studies exploring various aspects of *B. argenteum* biology, providing a comprehensive overview to understand the intricate interactions governing its life cycle. By synthesizing and critically evaluating existing literature, this study seeks to assess the scope and limitations of *B. argenteum* as a model system for ecological and evolutionary studies, offering crucial insights for a deeper understanding of the evolutionary and ecological processes of this remarkable species.

Characteristics of the silver moss *Bryum argenteum*

Bryum argenteum is an acrocarpous moss in the family Bryaceae, widely distributed across terrestrial ecosystems worldwide and characterized by traits that facilitate experimental research (Bhatla and Chopra 1981; da Silva et al. 2010, p. 198; Zaccara et al. 2020; Zhuo et al. 2020). The species was described by Hedwig (1801), who named the moss for the silver color observed when dry (Tropicos. (n.d.). Missouri Botanical Garden. Retrieved January

31, 2024, from https://www.tropicos.org/home) (Fig. 1). This peculiarity results from the absence of chloroplasts at the apex of the leaves, providing a protective layer against solar radiation (Robinson and Waterman 2014). Commonly referred to as "silver moss" or "silvery thread moss", *B. argenteum* illustrates the link between leaf anatomy, hydration status, and optical properties. (Raudenbush et al. 2018; Castetter et al. 2019).

Beyond these morphological and physiological characteristics *B. argenteum* has a relatively small genome (308.8 Mbp) compared with many vascular plants, a feature widely recognized as advantageous for model organisms and one that facilitates genomic, comparative and functional studies (Pruthi 2022). Although a complete high-quality reference genome is not yet available for the species, its genome size, together with the growing availability of transcriptomic and population level genetic data highlights its strong potential for future genomic integration (Gao et al. 2015; Cannone et al. 2024). This includes applications such as genome editing and comparative evolutionary analysis, in a manner comparable to well-established bryophyte models such as *P. patens* and *M. polymorpha*.

This moss displays a dioicous sexual system, featuring separate male and female plants (dos Santos et al. 2024b; Santos et al. 2026) (Fig. 2A). In bryophytes, sexual condition is expressed in the haploid gametophyte; therefore, *dioicous* is the appropriate term for species with separate male and female gametophytes, whereas *dioecious* is typically used for seed plants (Maciel-Silva and Pôrto 2014). This haploid dominant life cycle provides a major advantage for genetic research because recessive mutations are immediately expressed at the gametophyte stage, enabling direct phenotype screening without requiring inbred lines or multiple generations. As a result genotype phenotype relationships can be assessed more directly in genetic analysis or simplified compared with diploid dominant systems (Cove et al. 1997). Reproduction occurs through both sexual and asexual mechanisms (Horsley et al. 2011). During sexual reproduction, in the presence of water, male plants release gametes, known as antherozoids, from mature male gametangia called antheridia (Fig. 2B) (Maciel-Silva and Pôrto 2014). The sperm cells swim to the female gamete, called the egg, located in the female gametangium called the archegonium (Fig. 2C), where they fertilize the egg,

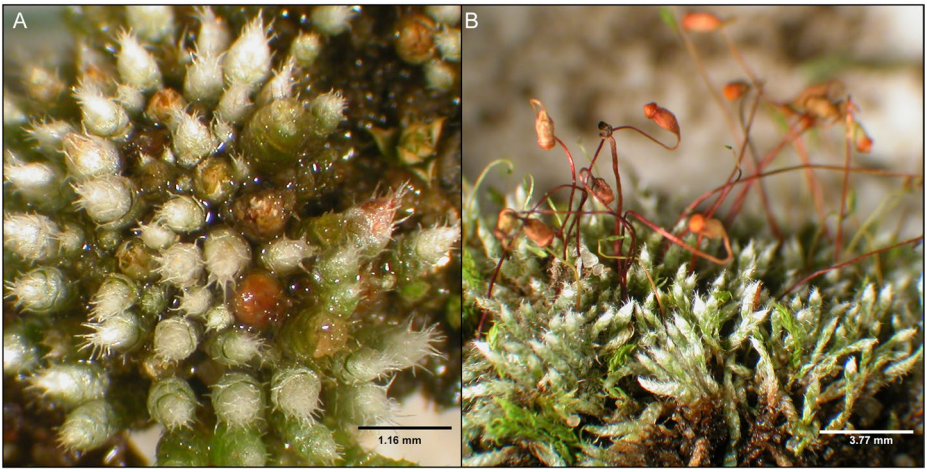

Fig. 1 Colony of *B. argenteum***A** Top view of hydrated colony with whitened shoot apices due to chloroplast deficiency. **B** Sporophytic colony of *B. argenteum*. All photographs were taken by Professor Lloyd R. Stark and are reproduced here with his permission

Fig. 2 Different ontogenetic stages of *B. argenteum*. **A** Male (two shoots on the right side) and female shoots (two shoots on the left side); **B** Male gametangia (antheridia); **C** Female gametangia (archegonia) indicated by the red arrow; **D** Embryo of B. argenteum indicated by the red arrow; **E** Sporophytic colony of B. argenteum; **F** Gemmae (indicated by the red arrow) attached to a shoot; **G** Germinating gemma with protonema at the base of the structure; **H** Protonemal gemmae; **I** Protonema formed from a spore placed in germination. All photographs were taken by Professor Lloyd R. Stark and are reproduced here with his permission

forming the embryo (Fig. 2D) that develops into the sporophyte (Fig. 3E) - the diploid phase of the reproductive cycle. From the sporophyte, spores (n) will be formed and dispersed into the environment. On the other hand, asexual reproduction occurs through the production of bulbils (Fig. 2F, G) and protonema gemmae (Fig. 2H), structures that detach from the main branch and give rise to new clones (Horsley et al. 2011). Additionally, *B. argenteum*

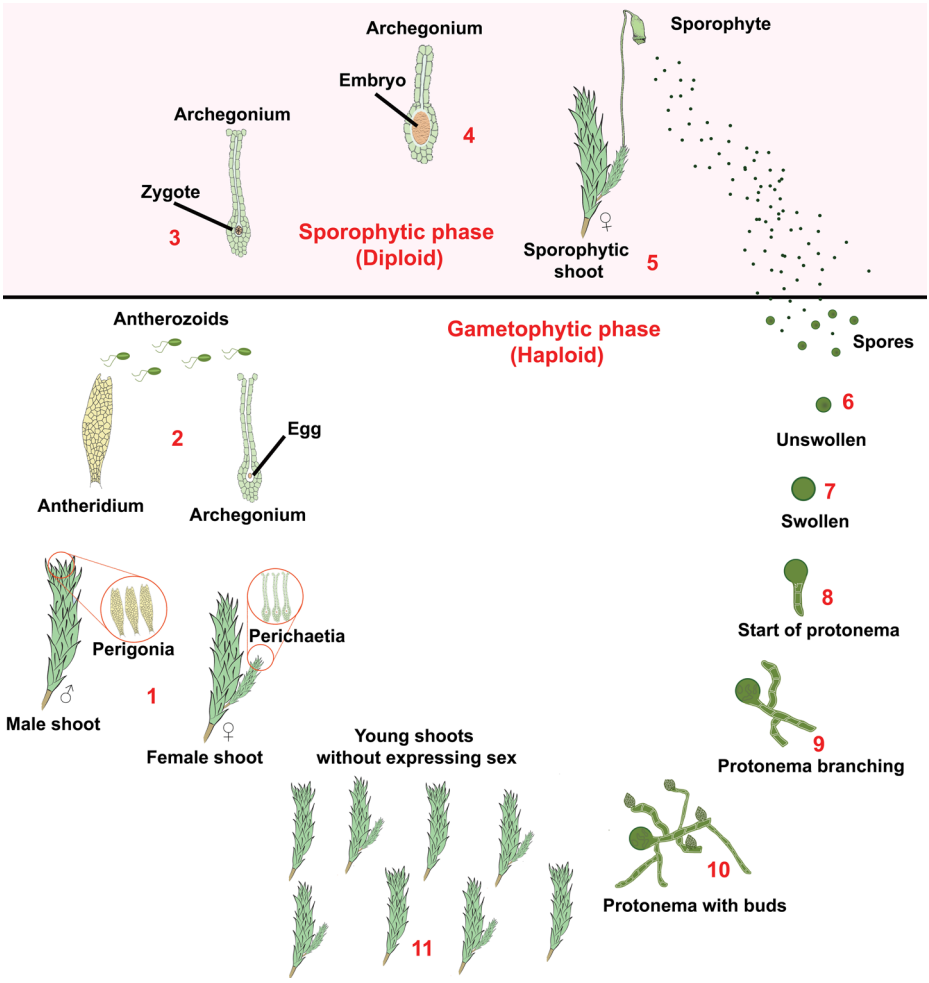

Fig. 3 Sexual reproduction in bryophytes. 1 - Male and female shoots expressing their respective gametangia (antheridia and archegonia); 2 - Male gametes (antherozoids) swimming towards the female egg for fertilization. 3 - Beginning of the diploid phase, when the male gamete fertilizes the egg and forms the zygote; 4 - Embryo; 5 - Sporophyte develops and releases spores; 6 - Beginning of the haploid phase, unswollen when the spore is dispersed into the environment; 7 - Swollen spores; 8 - Initiation of protonema, when the spore germinates; 9 - Protonema branching; 10 - Protonema with gametophyte buds; 11 - Shoots without sexual expression forming a new colony, these shoots will express sex and initiate the cycle in phase 1. Original illustration drawn by the author (Wagner Luiz dos Santos)

develops protonema buds during protonema formation, multicellular green filaments generated during spore germination (Fig. 2I) or branch regeneration. Together, dual reproductive modes and broad stress tolerance make *B. argenteum* suitable for testing hypotheses on reproductive allocation and life-history variation. The interaction between these reproductive strategies and the adaptability of the moss opens the possibility of exploring its role in ecological dynamics and broader biological contexts. The combination of reproductive flexibility and genomic tractability further strengthens its potential as a model organism for

integrating ecological, physiological, and evolutionary approaches. Furthermore, the clear distinction between haploid and diploid phases in bryophytes reproductive cycle (Fig. 3) enhances our understanding of plant evolution.

With a wide geographic distribution from the North Pole to the South Pole, a cosmopolitan species with records spanning polar to tropical regions (Fig. 4) GBIF.org (31 January 2024). Found in a variety of terrestrial ecosystems, this species thrives from cold, dry deserts to hot, humid tropical forests GBIF.org (31 January 2024). As a result, it stands out as a valuable model for studies on tolerance to abiotic stresses, such as water and heat. It's not surprising to discover that this species has been reported to tolerate short exposures up to 120 °C under desiccated conditions (Zhuo et al. 2020). This extreme tolerance, together with its wide distribution and emerging genomic resources, positions *B. argenteum* as a valuable system for studying plant responses to climate change and adaptation to harsh and fluctuating environments.

Taxonomic reliability and species delimitation in *Bryum argenteum*

The genus *Bryum* is widely recognized as taxonomically complex, characterized by high morphological similarity among species pronounced phenotypic plasticity and diagnostic characters that are often strongly influenced by environmental conditions (Holyoak and Pedersen 2007; Cannone et al. 2024). In this context *B. argenteum* has traditionally been treated as a cosmopolitan species with a broad geographic and ecological distribution (Zaccara et al. 2020). However its occurrence across highly contrasting environments together with the substantial morphological and physiological variation observed among populations raises the possibility that at least part of the material identified as *B. argenteum* may in fact correspond to distinct genetic lineages or to a complex of cryptic species (Pisa et al. 2013; Dhyani et al. 2025).

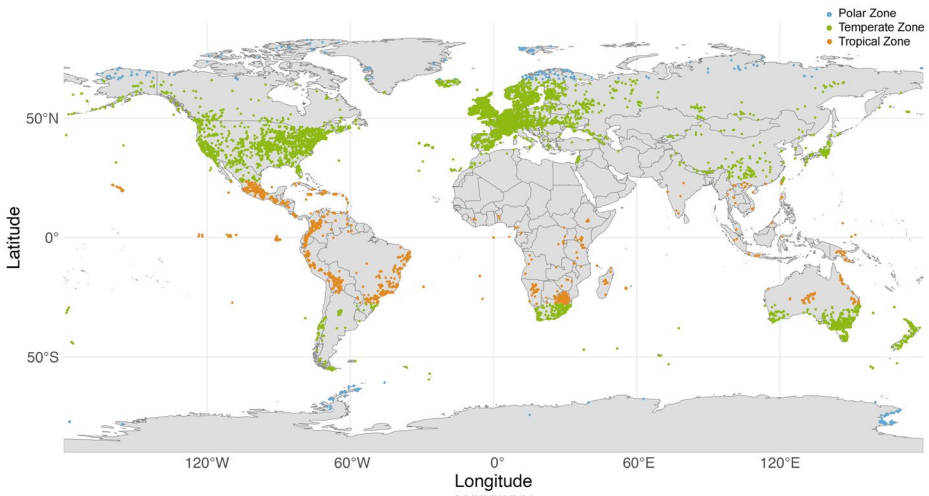

Fig. 4 Map displaying the locations where *B. argenteum* has been collected on Earth. The orange points represent samples taken in the tropics; the green points represent those collected in the temperate zone, and the blue ones in the polar zone. Data retrieved from GBIF. Please refer to the references to locate the data. The map was created using RStudio software and the ggplot2 package

A large proportion of ecological, physiological, and biogeographic studies using the *B. argenteum* implicitly assumed correct taxonomic identification, often relying exclusively on morphological characters (da Silva et al. 2010; Horsley et al. 2011; Raudenbush et al. 2018; dos Santos et al. 2023). Molecular confirmation remains relatively uncommon particularly in older studies or in those whose primary focus is not systematics (Wang and Zhao 2009). Although this does not invalidate the available results it calls for caution in the interpretation of spatial physiological and reproductive patterns as differences attributed to intraspecific variation may at least in part reflect unrecognized taxonomic structure or differential lineage composition among regions and populations (Hills et al. 2010; Zaccara et al. 2020).

This issue is especially relevant when *B. argenteum* is proposed as a model organism, since is requires taxonomic stability to ensure comparability across experiments populations and geographic scales (Pisa et al. 2015). The absence of such stability can compromise macroecological inferences evolutionary comparisons and generalizations about adaptive strategies. Thus, explicitly acknowledging the taxonomic challenges associated with *B. argenteum* does not weaken its use as a model rather, it underscores the need for integrative approaches that combined standardized morphological diagnosis, deposition of voucher specimens in herbaria, and, whenever possible, molecular confirmation, thereby strengthening the robustness and reproducibility of future studies (Pisa et al. 2015; Cannone et al. 2024).

Reproductive ecology of *Bryum argenteum*: patterns and processes

Bryum argenteum holds a remarkably significant role in reproductive biology. This moss has been pivotal in studies exploring theories aimed at elucidating patterns in the reproductive biology of dioicous species (Stark et al. 2010; dos Santos et al. 2023). As previously mentioned, *B. argenteum* is a dioicous moss, and it's noteworthy that over 90% of dioicous moss populations so far exhibit a female-biased sex ratio (Bowker et al. 2000; Bisang and Hedenäs 2005; Ekwealor et al. 2017; dos Santos et al. 2022), with few species showing populations with a male-biased sex ratio (Alvarenga et al. 2013; Holá et al. 2014). This phenomenon is particularly intriguing considering that spore formation in bryophytes occurs via meiosis, theoretically resulting in equal proportions of male and female spores (Haig 2016). However, this expectation is not reflected in the observed sexual distribution in natural populations. Thus, in order to further understand this pattern, Stark et al. (2010) utilized *B. argenteum* genotypes of USA as a model to test the shy male hypothesis. This hypothesis predicts that dioicous bryophyte species have a balanced sex ratio within populations, but due to male plants failing in sexual expression, populations appear to be biased towards the female sex when only sex-expressing branches are analyzed. However, in this study, the authors did not support the hypothesis, as after the regeneration of non-sex-expressing branches, there was no significant difference in the sex ratio. On the other hand, dos Santos et al. (2023) investigated the shy male hypothesis in populations from tropical dry and wet forests in Brazil. This study also did not fully support the hypothesis, as the sex ratio was biased towards the female sex in field plants and after regenerating sexless shoots. However, when the non-sex-expressing shoots were cultivated until they expressed sex, the sex ratio differed significantly from the field populations, showing a less female-biased ratio, with male shoots appearing in most populations. This demonstrates that differences within eco-

systems can be observed in the same species, suggesting divergent ecotypes may be found in different environments.

Other studies investigating variations in reproductive traits among different populations of *B. argenteum* have addressed a variety of reproductive characteristics, with sex ratio being the most studied trait. For instance, on a rocky outcrop in Brazil, colonies of *B. argenteum* displayed a diversity of sex ratios, including male-biased, female-biased, and unbiased ratios (Pôrto et al. 2017). Additionally, colonies without male plants but with sporophytes were found, suggesting spore transport might occur between colonies in the rocky outcrop. In populations studied in New Mexico, a higher rate of female sexual expression was observed compared to male expression, resulting in a female-biased sex ratio related by Castetter et al. (2019). However, the number of male plants in these populations may be influenced by light availability, as brighter locations tended to exhibit more male sexual expression. These variations in sex ratios and sexual expressions among different populations highlight the influence of the environment on reproductive traits, which can also be observed in the development of *B. argenteum* under different conditions. Regarding the development of *B. argenteum*, Raudenbush et al. (2018) reported that these mosses on golf courses are female only and grow and establish more quickly than in natural environments but produce fewer propagules (bulbils). This suggests that the well-manicured environment of golf courses has selected for traits that help them compete with grasses, with invasive plants adapting to compete better with grasses through the selection of specific characteristics or genetic types. On the other hand, Horsley et al. (2011) suggested that the reproduction of *B. argenteum*, whether sexual or asexual, seems to be controlled by genetic factors. In this study, Horsley et al. (2011) observed that ecotypes that grew more rapidly tended to reproduce more, both sexually and asexually, but when reproducing asexually, they did not produce as many shoots. No differences were found in growth or reproduction between male and female plants, except those females had longer shoots than male. However, in terms of reproductive allocation [proportion of resource allocate in reproduction (dos Santos et al. 2024a)], males allocated over 24 times more resources than females.

Reproductive aspects regarding the induction of gametangia have been investigated in some studies for the species *B. argenteum*. The studies by Bhatla and Chopra (1979), Chopra & Bhatla (1981a) on the influence of different substances on the inhibition and induction of sex in *B. argenteum* yielded significant findings. It was observed that the addition of 4% sucrose markedly reduces the sexual response in both male and female clones of this moss species. However, the inclusion of cyclic AMP 3',5' in the culture medium overcomes this inhibition, with optimal concentrations of $10-7$ μM and $10-5$ μM for male and female gametophytes, respectively. On the other hand, phytohormones such as auxins, cytokinins, gibberellins, and abscisic acid were observed to increase gametangial induction, resulting in greater expression in male clones and inhibition in female clones (Bhatla and Chopra 1981). Gibberellic acid (GA3) stood out as more effective than auxin (IAA) in this process. Additionally, the interaction between IAA and kinetin neutralized their individual inhibitory effects on male clones. Cyclic AMP also played an important role, nullifying the inhibitory effect of kinetin and stimulating the response in female clones (Bhatla and Chopra 1981). However, it acted as a general inhibitor of vegetative growth and gametangial induction, with greater inhibition in female clones. Subsequent studies supported these findings, highlighting the influence of temperature, light intensity, and photoperiod on gametangial formation in both sexes of this moss (Chopra and Bhatla 1981b). Furthermore, chelating

agents such as EDTA and EDDHA, along with gibberellic acid, were identified as significant stimulants of gametangial formation, especially in male clones (Bhatla and Chopra 1983). These results contribute to a deeper understanding of the mechanisms involved in the regulation of reproduction in *B. argenteum*.

Environmental adaptations of *Bryum argenteum*: a survival story

Adaptation is crucial for ecological processes as it enables organisms to modify themselves to enhance survival in diverse and challenging environments (Peck and Waxman 2018). This multifaceted concept integrates phenotypic, reproductive, physiological, and molecular characteristics that are commonly shared among species with similar lifestyles, collectively contributing to the organismal adjustment to specific environmental conditions (Tomasi et al. 2019; Lacoux et al. 2020; Cohen and Marron 2020). Figure 5 schematically illustrates this concept for *B. argenteum*, emphasizing how the species occurs under contrasting regimes of water availability, radiation, and temperature. By facilitating organismal development across varied living conditions, adaptation not only ensures their survival but also provides invaluable insights for effective biodiversity management strategies (Cohen and Marron 2020). Moreover, understanding how organisms respond to environmental pressures allows for informed inferences about ecosystem resilience and vulnerability, thereby illuminating the intricate interaction between adaptation and ecological dynamics (Mumby et al. 2014). The following sections synthesize evidence on relationship between ultraviolet radiation and tolerance to high temperature and drought in *B. argenteum*.

Responses to Ultraviolet radiation (UV) in Bryum argenteum

Ultraviolet radiation (UV) affects several vital processes in plants, especially in the photosynthetic system (Verdaguer et al. 2017). Additionally, high levels of UV can cause cellular damage and genetic mutations in plants, compromising their health and resilience (Rozema et al. 1997). *Bryum argenteum* has been a model in studies on the impact of UV radiation,

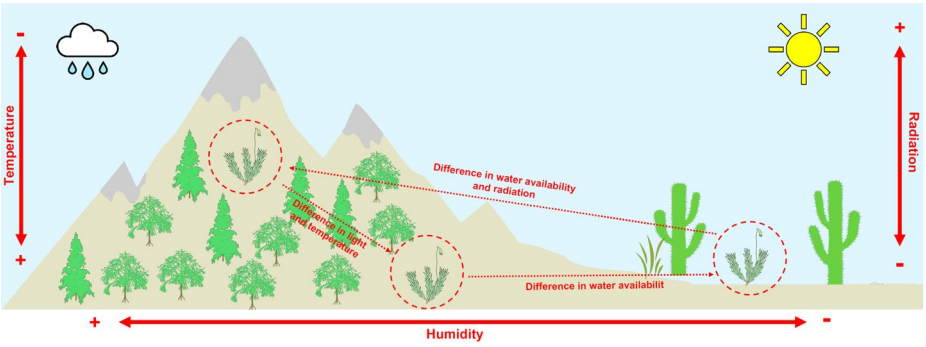

Fig. 5 Conceptual representation of the ecological breadth of *B. argenteum*. Landscape with environmental gradients of temperature, radiation, and humidity, demonstrating the abiotic influence on plant distribution and adaptations of *B. argenteum*. The moss *B. argenteum*, highlighted in red, shows adaptations that allow it to thrive in various environmental conditions. In dry and sunny environments, it becomes compact and silver-colored, minimizing water loss and reflecting intense sunlight. In humid and shaded locations, it becomes more elongated and greener, maximizing light absorption for photosynthesis. Original illustration created by the author Wagner Luiz dos Santos, using digital graphic software

with most of them focusing on polar genotypes. One of the pioneering studies to report the influence of ultraviolet radiation on *B. argenteum* was conducted by Smith (1999). In this research, aspects of growth, physiology, and survival of this species were investigated concerning environmental factors, including the effect of UV radiation. In a laboratory experiment, *B. argenteum* individuals were cultivated under three conditions - control, with UVB, and without UVB - for a period of 5 weeks. At the end of the experiment, it was observed that the average biomass of control colonies increased by 22%, while those under cloches showed increases of 93% and 137% in treatments with UVB and without UVB, respectively, indicating that UVB radiation can impair the growth of *B. argenteum* gametophytes. On the other hand, the findings of Singh et al. (2012), who also studied polar genotypes, showed that UVB can have different effects. Their findings indicated that the concentration of chlorophyll a and b increased during the 15 days in the treatment where plates were exposed to UV filters, while those not exposed decreased. Additionally, colonies exposed to UV increased carotenoid production, suggesting a defense mechanism against UV radiation.

Regarding soil crusts, which consist of associations between soil particles and cyanobacteria, algae, microfungal, lichens, and bryophytes (in different proportions) that live within or on top of the uppermost millimeters of soil, Hui et al. (2013) investigated the impact of UV-B radiation on soil crusts containing *B. argenteum*, focusing on its effects on photosynthesis and chloroplast ultrastructure. They note that while there is a better understanding of the UV-B effect on plants, cryptogamic organisms are less studied and require further research. Additionally, as observed by Hui et al. (2014), anticipating the consequences of increased UV-B radiation resulting from stratospheric ozone layer depletion in temperate desert ecosystems necessitates a deeper understanding of the eco-physiological response of common moss species. In *B. argenteum*, UV-B exposure significantly increases the content of malondialdehyde and reduces chlorophyll fluorescence parameters and chlorophyll content in response to the increase (Hui et al. 2015). Moreover, these alterations are correlated with changes in thylakoid protein and chloroplast structure. UV-B radiation can induce a decrease in photosynthetic rate due to damage to *B. argenteum* chloroplasts, highlighting the sensitivity of this species to UV-B radiation compared to other moss species (Hui et al. 2013). Overall, studies on UV radiation demonstrate various negative impacts on *B. argenteum*, which may affect its function in the ecosystem.

The effect of UV-B radiation related to lack of water has been reported in some studies on the moss *B. argenteum*. In an experiment conducted by Hui et al. (2016), it was reported that UV-B radiation caused a significant decrease in chlorophyll fluorescence parameters, carotenoid contents, total flavonoids, and a significant increase in malondialdehyde content. However, when investigating UV-B radiation in relation to water deficiency, it attenuated the negative effects of UV-B radiation, resulting in higher chlorophyll fluorescence parameters and pigment contents, along with a reduction in malondialdehyde content. Additionally, Hui et al. (2018a) conducted a study where they observed that water deficiency also alleviated the negative effects of UV-B radiation on UV-absorbing compounds and osmotic adjustment substances in *B. argenteum*. The sensitivity of *B. argenteum* to UV-B radiation and water deficiency was also highlighted by Hui et al. (2018b), suggesting that this moss species may be more affected by UV-B radiation than other species, such as the cyanobacteria *Microcoleus vaginatus* Gomont. These studies provide important insights into the effects of water on *B. argenteum* and its response to environmental conditions, emphasizing the importance of water in mitigating the stress caused by UV-B radiation.

Thermotolerance and drought tolerance in *B. argenteum*

Bryophytes are widely recognized for their ability to tolerate desiccation and recover metabolic activity after long dehydration periods a key trait in their terrestrial ecology (Proctor et al. 2007b). In *B. argenteum* studies on extreme heat tolerance have mainly focused on its combination with desiccation reflecting how these stresses occur together in nature. Mertens et al. (2008) investigated high-temperature tolerance in species of "Anhydrobiotes" (organisms capable of surviving extreme desiccation), including the moss *B. argenteum*. In this experiment, organisms were subjected to two heating speeds (slow and fast) and exposed to different heat levels (110, 120, 130, and 140 °C). The results indicated that the rate of warming influences survival only within specific temperature ranges, where branches subjected to slow temperature rise showed higher survival rates. Zhuo et al. (2020) conducted another study using *B. argenteum* as a model to investigate thermotolerance. In this study, they aimed to determine the lethal temperatures of dried *B. argenteum* shoots and to determine how this restoration species responds to extreme environments. Thus, *B. argenteum* was subjected to sudden thermal shock (control (20 °C), 80, 100, 110, or 120 °C), followed by heat exposure for an additional 10, 20, 30, or 60 min. The findings showed a new level of thermal tolerance for dried *B. argenteum* 120 °C for 20 min which was determined to be the highest temperature recorded for this moss, exceeding the previous study's 110 °C for 10 min. These results highlight that *B. argenteum* is evaluated under extreme thermal conditions rarely explored in classic model plants, reflecting ecologically realistic scenarios in which intense heat and desiccation occur in combination. Additionally, it was observed that nine genes (HSF3, HSP70, ERF, LEA, ELIP, LHCA, LHCB, Tr288, and DHN) had their expression induced in response to heat stress, as evaluated after 30 min of exposure. These gene families perform well established functions in the response to thermal and water stress including stabilization of denatured proteins (HSF3, HSP70), transcriptional regulation of the stress response (ERF), protection of membranes and cellular structures during desiccation (LEA, DHN, Tr288), and maintenance of the photosynthetic apparatus under conditions of excess light and heat (ELIP, LHCA, LHCB). These discoveries enhance our comprehension of how this species survives under thermal shock stress, while also assisting in the rehabilitation and rejuvenation of ecosystems that have suffered damage. It is important to highlight that these gene families are widely conserved among terrestrial plants, including *(A) thaliana* and *P. patens*, and that the uniqueness of *(B) argenteum* does not lie in the presence of exclusive genes, but in the magnitude of the physiological tolerance expressed and the extreme environmental context in which these responses are activated.

Research conducted thus far on heat tolerance in *B. argenteum* is closely linked to desiccation tolerance, as these studies involved drying the plants to subject them to high temperatures (Mertens et al. 2008; Zhuo et al. 2020). Overall, *B. argenteum* has been a remarkable species for desiccation tolerant (DT) studies, as several ontogenetic stages have been investigated (Proctor et al. 2007b; Shortlidge et al. 2012; Stark et al. 2016; Greenwood et al. 2019). However, overall, most studies have focused on investigating DT in the vegetative phase, primarily in the shoots. For instance Nabe et al. (2007) investigated the effects of air drying and hypertonic treatments in seven bryophyte species. Desiccation-tolerant mosses lost much of their photosynthetic capacity when electron transport was interrupted, while more sensitive mosses continued photosynthesis despite the interruption. Both protective

mechanisms against light and pH-induced damage play a crucial role in protect desiccation-tolerant mosses in this study.

The fluorescence of some moss types decreased when dried, indicating that photosynthetic performance was affected by desiccation. Among the mosses studied, *B. argenteum* was the species that recovered its photosynthetic system most rapidly and effectively. These results reinforce the idea that desiccation tolerance in *B. argenteum* involves not only structural survival but also rapid functional recovery of the photosynthetic apparatus, a key component of physiological resilience. Li et al. (2014a) also investigated DT in shoots of *B. argenteum*. However, Li et al. (2014b) focused not only on photosynthetic parameters but also on the thylakoid protein complex. It was reported that this protein complex decreased with shoot desiccation. However, during rehydration, there was a rapid increase in the amount of thylakoid protein complexes under light conditions, although this increase was slower and reached lower levels during rehydration in the dark. Similar to Li et al. (2014b), Gao et al. (2018) investigated desiccation-related proteins of *B. argenteum* in genotypes from Central Asia. They observed that some proteins increased while others decreased after rehydration. These proteins have various functions such as protecting against sun damage aiding recovery after stress and maintaining photosynthesis. Additionally, they noted that proteins do not always align with what is found in plant RNA, indicating there is still much about cellular functioning that we do not fully understand. This evidence suggests that post transcriptional mechanisms play a relevant role in desiccation tolerance, differentiating *B. argenteum* from model systems in which the stress response is often inferred only from transcriptional profiles. Other strategies have been observed in *B. argenteum*, as noted by Shibata et al. (2018), where they investigated genotypes from Antarctica and Japan and observed that this moss protects itself against drought by converting absorbed light energy into heat when it is dry. They also observed that when the moss runs out of water, some parts of it change color, and the energy it uses to grow and develop is affected.

In addition to studies on DT in the shoots of *B. argenteum*, this species has been a model for research with fascinating discoveries about different ontogeny phases of life cycle. Starting with gametes, *B. argenteum* pioneered the discovery that DT can be present even in gamete stages. Shortlidge et al. (2012) investigated DT in sperm in three moss species: *B.argenteum*, *Campylopus introflexus* (Hedw.) Brid., and *Ceratodon purpureus (Hedw.)* Brid. The findings showed that some of these sperm survived long periods in dry conditions, and DT does not vary among species. Furthermore, the presence of sucrose during the drying process increased DT in the sperm. A similar result was found by Stark et al. (2016), but in this study, the authors slowly dried the perigonia until reaching 50% atmospheric humidity equilibrium. They observed that rehydrating the dried antheridia for at least 3 h before immersing them in water made them function as if they had not been dried. On the other hand, prehydrating the antheridia did not help much in recovery after drying. Greenwood et al. (2019) analyzed how different life stages (protonema; juvenile, immature and mature shoots; and bulbils) of *B. argenteum* and the duration of desiccation affect its DT. Using a fluorometer to measure plant stress, they found that the faster the moss dries and the earlier life stage it is in, the more it is negatively affected by desiccation, with protonema most vulnerable and larger shoots and bulbils most protected. Additionally, they discovered that mosses from different locations have different ways of coping with desiccation, with some being more resilient than others. Regarding reproductive stages, dos Santos et al. (2024) found that the more developed the reproductive structures (gametangia) classified

as non-sex expressing, immature, mature, and postmature, the lower the desiccation tolerance, due to reproductive costs. Furthermore, the authors found differences between sexes, phenophases, and life phases (shoots and protonema), suggesting that adverse desiccation conditions may affect the population parameters of adult populations, as sexes exhibit differences in their tolerances. These results expand the value of *B. argenteum* as a model by demonstrating that desiccation, and heat stress tolerance varies systematically throughout the life cycle between sexes and among populations.

Studies investigating the effects of desiccation tolerance at the molecular level, through the analysis of gene transcriptomes during rehydration stages, have been crucial for advancing our understanding of bryophyte adaptations. Gao et al. (2015) represents the pioneering investigation of the transcriptome in *B. argenteum*. Gao et al. (2017) further expanded this approach by constructing a reference transcriptome across hydration, dehydration and rehydration stages, identifying hundreds of transcription factors and protein clusters associated with stress responses. Taken together, these studies indicate that, although the molecular components of the stress response are largely conserved among terrestrial plants, *B. argenteum* stands out for coordinating these responses under extreme and ecologically realistic conditions, reinforcing its role as an ecophysiological model of combined tolerance to heat and desiccation, in contrast to classic models such as *Arabidopsis thaliana* and *Physcomitrium patens*.

Bryum argenteum: a model for biogeographic and genetic diversity research

Although there have been few studies conducted with *B. argenteum* at a genetic level, it is already recognized that this organism is an excellent model for such investigation due to its relatively small genome, which is approximately 308.8 Mbp (Pruthi 2022). Regarding population genetics studies of *B. argenteum*, forerunner work was conducted in Antarctica. Selkirk et al. (1998 a) conducted a detailed study to investigate genetic diversity in *B. argenteum* in Antarctica. They used the RAPD technique to analyze over 30 populations of the species collected from five small glacier meltwater channels. Extensive genetic variation was observed, with each sample showing differences. Most populations showed internal variation, suggesting somatic mutation. Skotnicki et al. (1998 b) also used the RAPD technique to study the adaptation and dispersal of *B. argenteum* in Antarctica and temperate regions. They found that mosses from Antarctica had similar levels of genetic variation to those from warmer regions, even without observed sexual reproduction in Antarctic populations, suggesting that other genotypes could reach these colonies. Skotnicki et al. (1999) expanded the study to include samples from Ross Island and Southern Victoria Land, Antarctica. They found high genetic diversity both within and between moss colonies, with some spatial relationships observed in the drainage channels. Hills et al. (2010) investigated genetic variation in *B. argenteum* across different regions, including Antarctica, subantarctic, New Zealand, and Australia. They found disagreement between taxonomic delineations based on morphology and molecular markers, suggesting that all continental populations in Antarctica are associated to a specific variety of *B. argenteum*, while populations from other regions belong to another variety.

It is important to emphasize that the cited studies use molecular markers with very different mutation rates and resolutions, including RAPD, plastid markers, and, more recently, transcriptomic data (Zaccara et al. 2020; Cannone et al. 2024). Direct comparisons between

levels of genetic diversity obtained from these different types of markers should be interpreted with caution, since apparent patterns of greater polymorphism may reflect methodological bias. Differences in sampling effort or the temporal scale of the markers and not necessarily underlying evolutionary processes. Thus normalization of genetic diversity comparisons according to the type of marker used is essential to avoid distorted interpretations.

Genetic diversity and structure results obtained for *B. argenteum* populations from different origins shed light on the biogeography and evolution of this cosmopolitan moss, revealing patterns of adaptation and dispersal that transcend geographic and climatic boundaries. By collecting samples at various altitudes in the Sierra Nevada Mountains in Spain, Pisa et al. (2013) conducted a detailed DNA analysis to investigate its complex genetic relationships. The results of Pisa et al. (2013) unveiled that the genetic diversity of this moss is significantly higher at higher altitudes, indicating remarkable adaptation throughout the history of mountainous regions. Even when the area was covered by ice during the last glacial era, this resilient moss seems to have persisted, shedding light on its ability to survive in extreme conditions. These altitudinal patterns should be interpreted considering the type of molecular marker used in the sampling design, since different markers capture evolutionary processes at different temporal scales.

These findings provide crucial insights into plant adaptation mechanisms to different environments and their dispersal strategies worldwide. Furthermore, studies on the biogeography and evolution of the moss *B. argenteum* in Antarctica revealed an intriguing scenario (Pisa et al. 2014). Evidence points to multiple independent colonization events of the species in the region, with migration times ranging from four million to half a million years ago. This discovery suggests a remarkable in situ persistence of bryophytes in Antarctica over several previous glaciations, challenging expectations about the survival capacity of organisms in this extreme environment (Pisa et al. 2014). The analysis of the genetic structure of *B. argenteum* unveiled distribution patterns dating back to its origin, with additional dispersals and diversifications occurring during warming periods in the Pliocene and Pleistocene (Zaccara et al. 2020). These findings highlight the long-range dispersal and local diversification history of contemporary populations of *B. argenteum* in Antarctica, suggesting the presence of intra-Antarctic dispersal routes and unraveling the plant colonization in one of Earth's most challenging environments (Zaccara et al. 2020).

The role of *Bryum argenteum* as an environmental bioindicator

The growing concern about the presence of heavy metals and other pollutants in the environment highlights the potential negative impacts on human health and ecosystems (Briffa et al. 2020). To monitor the deposition of these pollutants, various bryophytes have been employed, with *B. argenteum* standing out as an effective bioindicator and bioremediation species (Lu et al. 2022). Its sensitivity to contamination and ability to accumulate heavy metals in its tissues have been well-documented. For instance, *B. argenteum* has shown remarkable sensitivity in detecting airborne pollutants such as Pb, Cu, Zn, and Cd, both in urban and rural areas, as observed in the Zurich region (Thoeni et al. 1986). Despite inhabiting diverse environments, including industrial and urban areas, no clear pattern of adaptation to these metals has been established, as noted by Shaw and Albright (1990) in populations in the USA. However, surprisingly, even with differences in population growth, the ability to resist metals has been consistent, suggesting greater flexibility than previously

assumed regarding tolerance to heavy metals. Comparative studies with other bryophytes have shown that *B. argenteum* exhibits higher sensitivity to cadmium (Gupta 1995). Similarly, in the Piedmont region of Italy, a significant correlation was found between the metal content in mosses and the level of pollution in the sampled areas (Aceto et al. 2003). In studies conducted in the Obrenovac region of Serbia, concentrations of heavy metals were analyzed in four types of mosses, including *B. argenteum*, focusing on elements such as Cu, Fe, Hg (Sabovljević et al. 2007), and Mn, Mo, Ni (Vukojević et al. 2009). The results of these studies were mapped, highlighting areas with higher contaminations. Furthermore, short and long-term atmospheric deposition was discussed and tabulated, revealing the potential of these mosses as effective bioindicators of pollution by heavy metals.

Although *B. argenteum* has been recurrently used in bioindicator studies like other bryophytes, it is crucial to establish simple rules for collecting and treating mosses, ensuring that the data are reliable and comparable (Thoni et al. 1993). Furthermore, the concept of setting legal limits for the amounts of heavy metals in mosses, along with the development of standardized methods, is a significant step in making this method more effective and useful (Thoni et al. 1993). These measures not only make it easier for everyone to adopt the moss method but also help complement more complex technologies, ensuring that resources are used as efficiently as possible for environmental monitoring. In summary, utilizing *B. argenteum* in environmental monitoring can assist us in making better decisions and taking proactive measures to mitigate the negative effects of heavy metal pollution on human health and nature.

Physiological insights from *Bryum argenteum*

The study of phytohormones is crucial for understanding plant growth and development processes (Drábková et al. 2015). In bryophytes, these compounds are less explored due to their lower economic relevance compared to vascular plants (Sabovljević 2010). Despite their limited production and economic interest, understanding their chlorophyll levels remains important for unraveling plant physiology in diverse ecosystems. *Bryum argenteum* has been a model organism in some studies relating to phytohormones and their functions (Sabovljević et al. 2004, 2010; Sabovljević 2010). The first study on the effect of phytohormones in *B. argenteum* revealed that increasing the concentration in the basal medium with phytohormones (AIB—indole-3-butyric acid, NAA—α-naphthaleneacetic acid, or BAP—6-benzylaminopurine) influenced its development (Sabovljević et al. 2004). A concentration of 0.1 μM of AIB promoted branch growth, but a slight decrease was observed at 1 μM and higher concentrations (Sabovljević et al. 2004). For NAA, the suggested optimal concentration is 1 μM for shoot growth. Protonemal patches treated with BAP showed a width three times greater than in other treatments (Sabovljević et al. 2004). However, BAP did not have a positive effect on the multiplication of *B. argenteum* shoots (Sabovljević et al. 2004). Gibberellins were not found in bryophytes, unlike other classes of phytohormones such as auxins, cytokinins, abscisic acid, and ethylene (Sabovljević et al. 2010). Tests on apical gametophyte buds of *B. argenteum* showed varied responses to growth regulators. Gibberellins GA(3) and GA(7) applied in vitro have positive effects on morphogenesis, while three growth retardants (ancymidol, BX-112, and chlorocholine chloride) negatively affect shoot multiplication, with less impact on protonema development (Sabovljević et al. 2010). Cytokinins had a variable positive effect on chlorophyll retention in both in vitro and natural

plant groups, with kinetin being the most effective. Kinetin application increases chlorophyll content in the concentration range of 0 to 10 µM. BAP yields similar results in both in vitro and natural losses, increasing chlorophyll content up to 1 µM and then significantly decreasing, with in vitro plants showing higher chlorophyll content. TDZ has a better effect on in vitro-cultivated moss shoots, but concentrations above 0.1 µM resulted in a decrease in total chlorophyll content (Sabovljević 2010).

Regarding developmental physiology, *B. argenteum* has been studied about the importance of abiotic factors (light availability and nutrients) on spore germination and moss protonema development (da Silva et al. 2010). *Bryum argenteum* showed positive photoblastic behavior, meaning they only germinated under light, regardless of the medium used (water or nutrient solution). In the dark, spores only swelled, becoming chlorophyllous likely through reserve breakdown. In nutrient solution, germination occurred more rapidly (within two days) compared to distilled water (over three days after cultivation) (da Silva et al. 2010). However, nutrients were required to complete the final phase of germination for most spores. Regarding differences in various ecosystems, *B. argenteum* clones responded similarly to cold and high-temperature stress, with a temperature regime of 22/15°C being most favorable for protonema growth and shoot production (Longton 1981). Although clones from Antarctic and tropical regions exhibited slow protonema growth and shoot production at 5–15 °C, Antarctic ones showed the most vigor in different environments, albeit displaying distinct morphological differences in shoot arrangement, protonema morphology, and leaf morphology (Longton 1981). Additionally, *B. argenteum* showed a strong, direct connection between its photosynthetic capacity and electron transport rate (Green et al. 1998). This finding was surprising, given that mosses are of the C3 type. Typically, such a direct correlation is not observed in larger plants. It appears that under bright conditions, moss respiration may decrease, which could potentially explain this phenomenon (Green et al. 1998).

In addition to phytohormones and abiotic factors like temperature and light intensity, sugars also had effects on the physiology of *B. argenteum*. Indeed, in this moss species, both sucrose, fructose, and glucose played a positive role in the development of protonema and the rate of shoot multiplication (Longton 1981; Green et al. 1998). In summary, despite the lower economic relevance of bryophytes compared to vascular plants, understanding the levels of chlorophyll, phytohormones, and other factors influencing the development of *B. argenteum* remains important for comprehending plant physiology across various ecosystems.

Ecological dynamics involving *Bryum argenteum*

Studying how mosses interact with other organisms is crucial for understanding their ecology and role in ecosystems (Alvarenga and Rousk 2022). This knowledge can guide conservation strategies and practical applications in various fields (Turetsky et al. 2012). While there is considerable research on interactions of *B. argenteum* with different organisms, there are still few specific studies on this. These interactions include associations with nematodes, bacteria, and fungi (El-Saadawi and Shabbara 1999; Kagoshima et al. 2012; Mitkowski and Chaves 2013). In a study led by El-Saadawi and Shabbara (1999) describes for the first time the association of *B. argenteum* with the fungus *Embellisia* sp. However, this study only observed the occurrence of this association without investigating its possible causes

and effects. On the other hand, Mitkowski and Chaves (2013) observed the fungus *Waitea circinate* (Warcup & Talbot) infecting moss on a golf course. They identified this fungus as a possible cause of moss mortality, capable of causing significant damage to grasses under certain temperature conditions. These results suggest that *W. circinata* could be a potential tool for controlling unwanted mosses on golf courses, although it is still unclear how common this ability of the fungus is in different locations (Mitkowski and Chaves 2013). Additionally, an interesting discovery was made by Bradner et al. (2000), who found a new species of microscopic fungus called *Embellisia* sp2 associated with the plant *B. argenteum* in Antarctica. This fungus only grew in samples of crushed moss tissue and sterilized leafy stems. The researchers also cultivated two other types of microscopic fungi, *Penicillium* sp. and *Trichoderma* sp., from a superficial wash of the moss.

Regarding interactions with bacteria, a very interesting finding was reported by Raymond (2016). Bacteria seem to play a crucial role in protecting *B. argenteum* in Antarctica. In this study, they discovered that *B. argenteum* employs a strategy to protect itself from freezing by creating cavities in the ice. These characteristics allow proteins produced by bacteria growing on the moss to enter, with these proteins being more common in polar bacteria than in bacteria from other plant regions (Raymond 2016). Thus, in this interaction, there is a beneficial exchange where the moss provides substrate and resources for the bacteria, and in return, the bacteria produce the protein to protect the moss. Interestingly, this same moss produces substances that act as bactericides, as reported by Sabovljevic et al. (2006) in a study where they extracted substances from *B. argenteum* that were able to inhibit four bacterial (*Escherichia coli*, *Bacillus subtilis*, *Micrococcus luteus*, and *Staphylococcus aureus*) and four fungal species (*Aspergillus niger*, *Penicillium ochrochloron*, *Candida albicans*, and *Trichophyton mentagrophytes*). Thus, it is evident that the relationship between this bacterium and *B. argenteum* is complex and requires further study.

Bryum argenteum's contribution to soil crust formation

Soil crusts are biological communities formed by microorganisms such as lichens, mosses, algae, and cyanobacteria that develop on the soil surface, playing a crucial role in soil stability, water retention, nutrient cycling, and erosion protection (Gao et al. 2020; Hashim et al. 2020). Their importance in the ecosystem is fundamental as they contribute to maintaining biodiversity, regulating the hydrological cycle, and promoting soil fertility (Gao et al. 2020; Hashim et al. 2020). Among the bryophytes found in soil crusts, *B. argenteum* stands out for its representativeness (Jia et al. 2012). These organisms play important roles in ecosystems, such as moisture retention and soil fertilization. In eastern Australia, *B. argenteum* is one of the predominant moss species in water runoff areas, suggesting an adaptation to soil erosion and highlighting its role in colonizing adverse soil conditions (Eldridge 1999). On the other hand, in the northern Great Basin of North America, the moss *B. argenteum* has shown that soil crusts dominated by it can hinder seed germination, reducing their quantity and delaying their growth (Serpe et al. 2006).

Bryum argenteum has shown excellent adaptation to the ecosystem related to soil crusts. For example, it recovers rapidly after prolonged periods of desiccation (approximately 1 year) (Li et al. 2014b). Furthermore, alterations in the micromorphology, ultrastructure, and chemical composition of moss cells, including increased lipid and carbohydrate contents, and changes in the secondary structure of proteins, evidence these important adaptations

to tolerate prolonged desiccation conditions (Li et al. 2014b). In addition to drought, *B. argenteum* can also survive burial by sand, presenting negative effects on moss growth, but they have also shown antagonistic effects on their physiological capacity, allowing them to overcome these challenges (Jia et al. 2012). This suggests that these mosses play an important role in maintaining biodiversity in arid sand ecosystems, such as hot and dry deserts (Jia et al. 2012). Another interesting adaptation observed in *B. argenteum* is its ability to thrive in stressful irrigation conditions on golf courses, especially when irrigation water contains moderate amounts of sodium and/or bicarbonates (Raudenbush et al. 2016). Additionally, adjusting the pH of irrigation water using acid injection systems can promote a significant increase in growth (Raudenbush et al. 2016).

Besides the aforementioned study conducted by Jia et al. (2012), Jia et al. (2018) investigated how *B. argenteum* survives in sandy deserts, facing adverse conditions like drought and sand burial. They simulated drought with varying levels of artificial rainfall and sand burial with different depths of sand. They found that the combination of these factors did not exacerbate the negative effects observed individually. Surprisingly, drought helped the moss cope better with sand burial, and sand burial helped the moss deal better with drought. This suggests that these stressors might aid the moss in growing better together. Additionally, when associated with soil crust, *B. argenteum* can assist in soil erosion resistance and hydrological functions, which has significant implications for managing severely burned landscapes (Grover et al. 2020). Overall, *B. argenteum* stands out in soil crust studies, being highly representative and multifunctional. Therefore, we can highlight three main aspects: first, its resilience and adaptation; second, its ecosystem function; and third its application in restoration processes. Thus, *B. argenteum* plays a fundamental role in the structure and function of soil crusts.

Research opportunities using *Bryum argenteum* as a model system

In this paper, we reviewed published articles that used *B. argenteum* as a model organism for ecological and evolutionary studies. These studies have shown that *B. argenteum* is a promising moss to be used as a model organism due to its ease of workability. Important gaps remain in the empirical literature on *B. argenteum*, and addressing them would expand the scope of this system as a model for ecology and evolution.

- Firstly, we highlight the lack of studies on thermotolerance. *Bryum argenteum* has been described as one of the most heat-tolerant bryophytes, as reported in scientific articles. However, despite heat being a stressful factor for this species in ecosystems like deserts and savannas, *B. argenteum* also faces challenges from low temperatures, occurring in cold regions such as polar and alpine areas. Therefore, it is important and necessary to investigate the effects of low temperatures.
- The second point we want to discuss, which lacks information, is the Macroecology of *B. argenteum*. Macroecology addresses ecological and evolutionary patterns at broad spatial and taxonomic scales. Studying the macroecology of *B. argenteum*, especially at the molecular level, is important to understand its dispersion, origin, and evolution. By understanding these processes, it becomes easier to understand how these species manage to be so successful in their dispersion and show this success in colonization and tolerance to environmental factors.

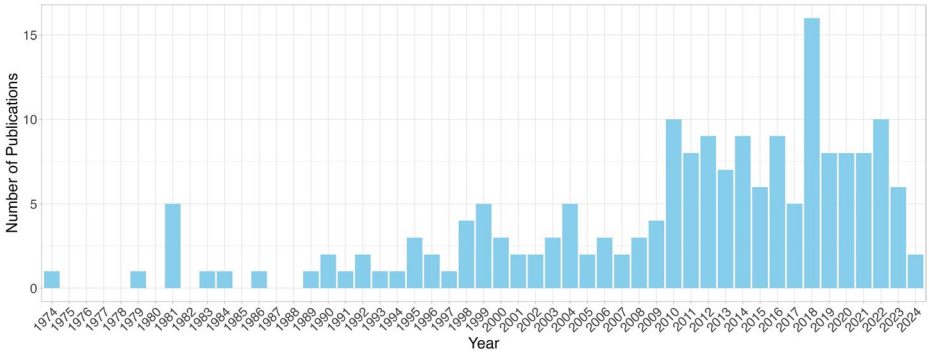

Fig. 6 Temporal distribution of published studies using *B. argenteum* in ecological and evolutionary research. Data were obtained through an advanced search in the web of science database using the terms "*Bryum argenteum*", "*B. argenteum*", "Silver moss" and "Silver thread moss" retrieved records were screened and studies focused primarily on taxonomy or species description were excluded only peer reviewed articles addressing ecological and evolutionary questions were retained for analysis the survey covered publications from 1974 to 2024

- The third point that we consider very important in future studies using *B. argenteum* as a model organism is reproduction. As mentioned in the reproduction section, Santos et al. (2023) found some genotypes expressing their sexual system as synoicous. Such cases provide an opportunity to test mechanisms proposed for transitions between sexual systems in bryophytes. The causes can be diverse, such as mutation, polyploidy, or even apomixis.

The three points mentioned are highly relevant topics for study in bryophytes, even highlighted in the study as priorities in bryology research.

Methodological limitations and research standards in studies of *Bryum argenteum*

The growing number of experimental studies using *B. argenteum* has contributed substantially to understanding of its ecology, physiology and reproductive biology (Fig. 6). However, the available literature still presents recurring methodological limitations that deserve explicit acknowledgement. Many studies rely on sampling restricted to a single population or a limited number of localities, often without detailed control or reporting of the environmental origin cultivation, life history, or ecological context of the material used (Smith 1999; Raudenbush et al. 2018; Castetter et al. 2019). Under these conditions responses observed in experimental settings may reflect locally specific characteristics making it difficult to extrapolate patterns to the species as a whole (Longton 1974).

Additional limitations are associated with the genetic and molecular approaches employed studies (Eisenring et al. 2023). Based on low-resolution markers, such as RAPD played an important historical role in initial exploration of genetic variability in *B. argenteum* but they have limited power to discriminate closely related lineages or to resolve fine scale genetic structure (Lynch and Milligan 1994). The lack of control for genetic lineage or ploidy level, or population composition can lead to the misinterpretation of physiological reproductive or ecological differences as general adaptations, when these patterns may instead reflect at least in part uncontrolled genetic variation among populations or individuals (Karunarathne

et al. 2018; Eisenring et al. 2023). Consequently, comparisons among studies conducted in different regions or under distinct experimental conditions should be interpreted with caution (Hein et al. 2021).

These issues become particularly relevant when *B. argenteum* is proposed as a model organism. The consolidation of a model system requires comparability reproducibility and methodological transparency allowing results to be integrated across time and among research groups (Leng et al. 2024). In this context future studies on *B. argenteum* would benefit from the adoption of minimum methodological standards, (1) including; one the use of multiple populations whenever possible (Pisa et al. 2013, 2015); (2) explicit documentation the geographic and environmental origin of the study material (Zaccara et al. 2020); (3) control reporting genetic lineage employe (Hills et al. 2010), and (4): careful selection of molecular markers appropriate the questions being addressed (Leng et al. 2024; Dhyani et al. 2025). Acknowledging and addressing these limitations does not weaken the existing literature, rather, it strengthens the use of *B. argenteum* as model systems by promoting more robust and generalizable inferences in ecological and evolutionary research.

Conclusion

The literature reviewed here supports *B. argenteum* as a useful complementary model system for ecological and evolutionary research. This becomes even more apparent when we observe that since 1974, when the first study using this species as a model organism was conducted, the number of research studies has only increased over the years (Fig. 6). Moreover, these studies cover a wide range of areas in ecology and evolution, including ecological adaptation, population genetics, macroecology, reproduction, among other topics. The findings from these studies are not limited to *B. argenteum* alone but are broadly applicable to other organisms as well. Many of these studies highlight the importance of using bryophytes as model organisms, further underscoring how *B. argenteum* is a complementary model system with particular strengths in field-relevant experiments and multi-stressor physiology.

In addition to summarizing its potential, the consolidation of the *B. argenteum* has a robust model organism will depend on addressing several research priorities and methodological challenges. the crucial step is the development of a high-quality reference genome, which would enable large scale comparative analysis, functional genomics, and the future integration of genome editing approaches. equally important as the adoption of standardized molecular and morphological criteria for species identification, given the taxonomic complexity of the genus Bryum, in order to ensure comparability between studies and regions.

At broader spatial scales, global and standardized sampling efforts are needed to strengthen macroecological and biogeographical inferences, reducing biases associated with uneven geographic coverage and marker selection. Finally, future research could benefit from greater integration between physiological experiments and transcriptomic and other omics approaches, allowing the establishment of mechanistic links between stress tolerance, life cycle variation, and ecological performance. by explicitly addressing these priorities, view. *B. argenteum* can move beyond being a complementary system and become a model for studying plant responses to complex environments with multiple stress factors within an evolutionary and ecological framework.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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