EFFECTS OF SOIL FACTORS ON PIONEER BRYOPHYTE SPECIES COMPOSITION

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Abstract

Bryophytes play a significant role in various ecological processes, including soil succession and colonization after disturbances. Although they are commonly believed to take up nutrients from soil solutions rather than the soil itself, the influence of soil on their growth and distribution is evident from previous studies. In order to examine the impact of soil conditions on bryophyte species composition and abundance, samples of soil and vegetation were collected from industrially disturbed sites in Skåne. pH and phosphate concentrations were measured and compared with the identified bryophyte species and their coverage. Both pH and phosphate were found to be important factors influencing bryophyte diversity. Most species were associated with high pH and low phosphate conditions. Moreover, total species richness exhibited a decline with rising phosphate levels. Certain species were restricted to very specific conditions. The results indicate the potential benefits of maintaining neutral to high pH and low phosphate levels to aid bryophyte conservation efforts.

1. Introduction

Bryophytes occur in almost every ecosystem on Earth and tend to have a greater distribution than tracheophytes (Vanderpoorten & Goffinet, 2009). They play a substantial role in various ecological processes, such as soil formation, long-term carbon storage, nutrient cycling and buffering of soil temperature and moisture. In certain instances, they can even be considered “ecosystem engineers” (e.g. formation of peatland, soil formation on bare substrates). They are able to take up nutrients from weak solutions and require lower concentrations than vascular plants (Glime, 2021). This allows them to colonize disturbed soil early, making them a significant factor in ecological succession.

A common cause of soil perturbation is urban development. Various vehicles and equipment used in construction cause compaction and poor drainage, causing a lack of oxygen, nutrient leaching and reduced microbial activity (Brady & Weil, 2016). The removal of topsoil and vegetation eliminates most of the organic matter and nutrients present in the soil and leads to erosion. The introduction of foreign materials can also have various effects on soil chemistry. For instance, the use of concrete and cement can result in increased soil alkalinity, whereas various other construction materials can reduce the pH levels. The combined effect of these disturbances is the disruption of nutrient cycles.

Bryophytes, being poikilohydric plants, absorb water through their entire surface, which often lacks a protective cuticle and stomata (Vanderpoorten & Goffinet, 2009). It is generally considered that bryophytes obtain most of their nutrients from precipitation by absorbing it through cation exchange from water solutions, rather than the soil, due to their lack of roots and a vascular system (Glime, 2021). During dry periods, it has been found that water limitation can considerably hinder nutrient uptake (Bates, 1997). Rhizoids, the root-like structures, don’t take up water or nutrients. However, it has been established that different species have different soil pH preferences (Tyler & Olsson, 2016; Virtanen et al., 2000; Waldheim, 1947) and that they can take up soil nitrogen (Ayres et al., 2006), clearly indicating that soil composition does influence their nutrient uptake. Binkley and Graham (1981) suggest that some of the N could be taken from soil as only 75% comes from precipitation. Still, little is known about their nutrient uptake, especially anion uptake.

Topsoil pH has been shown to be the primary environmental factor in determining species composition and richness (Tyler et al., 2018). Lower pH values enhance the process of weathering, which releases various minerals into the soil solution. Soil microorganisms, which play vital roles in organic matter decomposition, nutrient release, symbiotic relationships with plant roots, and nutrient cycling, are sensitive to pH levels (Paul, 2015). Furthermore, pH affects the water solubility of nutrients, and thus their availability for plants to absorb with water (Tyler & Olsson, 2001, 2002). Most mineral nutrients exhibit optimal availability within pH ranges of 4.5 to 6.5, becoming less soluble below or above this range (Taiz et al., 2023). Strong acidity can result in deficiencies of macronutrients (e.g., Ca, Mg, K, P, N, and S), while some nutrients may become excessively available, reaching toxic levels (Brady & Weil, 2016). A common case is aluminum toxicity, where aluminum is taken up by plants instead of calcium. The uptake of Al or heavy metal like cadmium and arsenic leads to the buildup of reactive oxygen species (ROS), inducing oxidative stress that damages cellular structures and interferes with photosynthesis and enzymatic reactions (Taiz et al., 2023). In highly acidic conditions, hydrogen ions can also become toxic, damaging cell membranes and disrupting biochemical processes.

Most bryophyte species in southern Sweden have been found to be restricted to the pH range of 4.7-7.2 (Tyler & Olsson, 2016). Virtanen et al. (2000) showed that bryophytes on the Park Grass Experiment have a more limited pH range than vascular plants of the same habitat and observed almost no mosses found below pH 4.5. A greater number of bryophyte species tend to be found on alkaline soils in many habitats, such as grasslands (Tyler & Tyler, 2005).

Phosphorus is crucial for synthesizing proteins, DNA, and ATP, but is usually the limiting factor for most bryophytes, along with nitrogen (Arróniz-Crespo et al., 2008; Phuyal et al., 2007). This is because it is predominantly found in soil in the form of very insoluble compounds, making it inaccessible to plants (Brady & Weil, 2016; Taiz et al., 2023). The solubility and ionization of phosphate, the plant available form of phosphorus, is directly impacted by pH (Taiz et al., 2023). Specifically, soil pH appears to be inversely proportional to plant available phosphorus concentrations (Hydbom et al., 2012; Tyler et al., 2018). Barrow & Hartemink (2023) show that pH influences both the rate of desorption and uptake by plant roots. Tooren et al. (1990) observed that the concentrations of nitrogen, phosphorus, and potassium were influenced by soil type and further enhanced by the application of fertilizers. Tyler et al. (1995) showed that higher phosphate availability led to accelerated colonization and influenced bryophyte species diversity. However, response to nutrient input can be affected by water availability as greater moisture leads to greater nutrient absorption (Bates, 1987).

Due to the aforementioned physiological traits, bryophytes are highly susceptible to environmental changes. Habitat modifications, climate change, changes in forestry and agriculture and pollution are the most significant environmental changes impacting bryophytes (Hodgetts et al., 2019). Despite their important ecosystem roles and being the second largest group of land plants after angiosperms, bryophytes' low visibility and limited economic value often result in them being overlooked in environmental research. Compared to vascular plants, understanding of bryophyte ecology and distribution is limited. Therefore, it is important to study how different environmental conditions impact bryophytes to protect their abundance and diversity, especially in ecosystems where human activity causes major disturbance.

Most studies have focused on the effects of P input on already established bryophyte populations, with few studies showing its impact on colonization. The aim of this project is to determine: (i) how do pH and phosphate availability individually affect the species composition and abundance; (ii) do these factors have a combined effect and (iii) what are the implications of these findings for conservation efforts?

2. Materials and methods

2.1. Sample collection

A total of 120 soil and bryophyte samples were collected from six sites located in Skåne, Sweden (Fig. 1). Specifically, two sites were taken from Malmö (55° 37' 04.4"N, 12° 58' 48.1"E and 55° 36' 18.9"N, 13° 02' 19.1"E), two from Höör (55° 57' 27.9"N, 13° 33' 60.0"E and 55° 56' 27.3"N, 13° 33' 16.6"E), one from Osby (56° 23' 11.0"N; 14° 00' 43.5"E), and one from Hässleholm (56° 10' 12.1"N, 13° 48' 43.5"E). The region of Skåne has a temperate climate characterized by mild winters (average temperatures of 0-5 °C) and cool summers (average temperatures of 15-20 °C) and the yearly precipitation typically ranges between 600 to 800 mm. The sampling was done during the months of February and March (2023). The sampled sites were chosen specifically for having exposed, flat, well-drained mineral soils with a recent history of industrial disturbance, mainly due to construction work. The sites were expected to have highly variable soil chemistry due to differences in bedrock mineral composition and past industrial activities. Collecting the soil samples involved placing a 26 cm diameter ring onto the ground and removing 2 cm of topsoil along with the vegetation cover within the ring. At each site, a total of 20 samples were randomly taken from various distances along a transect, to ensure representative sampling.

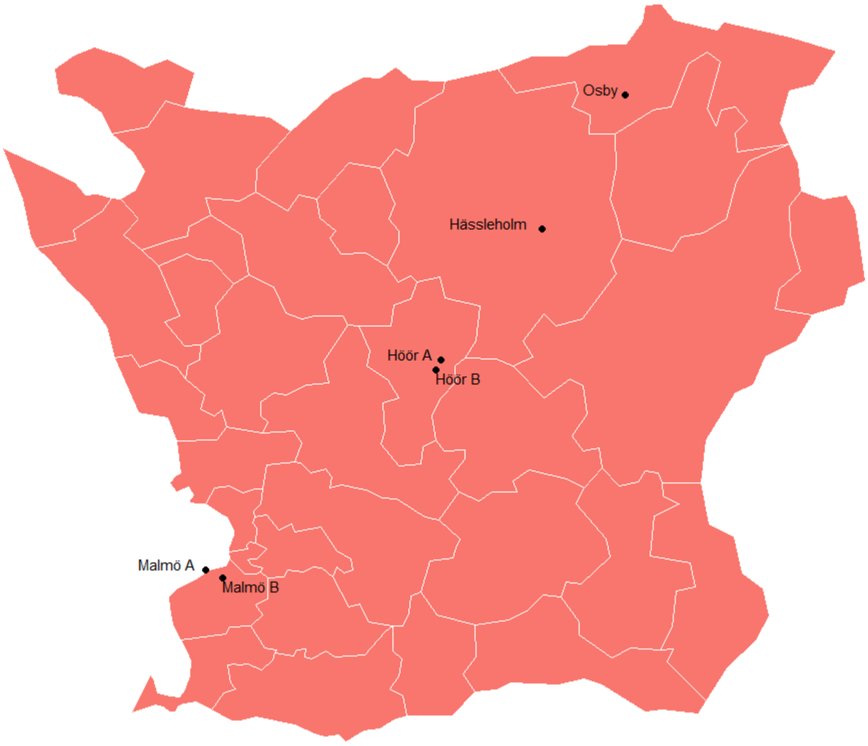

Figure 1. Map of Skåne showing the study sites

2.2 Chemical analysis

To prepare for the chemical analysis, samples were taken from the topsoil and combined with twice the volume of distilled water. The mixture was shaken and allowed to stabilize for 12-15 hours, after which pH and phosphate were measured in the supernatant. Soil pH was determined using a pH electrode. Concentrations of water-soluble phosphate were measured using a spectrophotometric method. A reagent (potassium disulfate) was added to the soil-water mixture and the solution was then tested using a phosphate photometer (Milwaukee MW12) using the Adaptation of the Ascorbic Acid Method. The reaction results in a blue tinted solution after which the photometer measures the amount of light absorbed by the solution and calculates the concentration of phosphate present in the sample.

Table 1. The Braun-Blanquet scale

Scale	% of plot covered
1	single individual
2	<1%
3	<5% (few individuals)
4	<5% (numerous individuals)
5	5-25%
6	25-50%
7	50-75%
8	75-100%

2.3. Species analysis

The vegetation covers collected from the sites were subsequently examined, and species identification was performed based on their morphological characteristics, with the help of identification keys (Hallingbäck, 2006; Hallingbäck et al., 2008; Hedenäs et al., 2014; Holyoak, 2021). The abundance of each species was estimated using the Braun-Blanquet scale, by assigning a numerical value representing the percentage of cover of each species (Table 1).

2.4. Statistical analysis

A Generalized Linear Model (GLM) was used to assess the relationship between vegetation cover and soil pH and phosphate concentrations for each species independently. Due to a large number of plots containing very low concentrations of phosphate, a separate analysis was conducted to investigate the effect of pH on plots containing <0.01 ppm phosphate. Furthermore, a GLM analysis was employed to examine the individual effects of pH and phosphate on overall species richness (number of species per plot).

Additionally, a Canonical Correspondence Analysis (CCA) was conducted to explore the relationship between the environmental variables (soil pH and phosphate concentrations) and the species composition and abundance in the study area. All data processing, transformation, statistical analyses, and visualization were performed using R (R Core Team, 2022) and RStudio (Rstudio Team, 2022).

Table 2. Frequency of all the species observed in the study

Species	**Frequency (%)**
Ceratodon purpureus	73.3
Barbula convoluta	59.2
Pseudocrossidium hornschuchianum	48.3
Brachythecium albicans	47.5
Barbula unguiculata	42.5
Bryum dichotomum	40
Bryum argenteum	36.7
Dicranella varia	30.8
Bryum creberrimum	30
Syntrichia ruraliformis	25
Didymodon fallax	20
Dicranella staphylina	18.3
Funaria hygrometrica	18.3
Bryum rubens	16.7
Bryum gemmiferum	15
Bryum ruderale	15
Ditrichum cylindricum	14.2
Hypnum cupressiforme	14.2
Racomitrium elongatum	13.3
Bryum subapiculatum	11.7
Polytrichum piliferum	10.8
Bryum violaceum	10
Rhynchostegium megapolitanum	10
Tortula acaulon	7.5
Rhytidiadelphus squarrosus	6.7
Syntrichia ruralis	6.7
Pseudoscleropodium purum	5.8
Calliergonella cuspidata	5
Riccia sorocarpa	5
Polytrichum juniperum	4.2
Tortula truncata	3.3
Lophocolea bidentata	2.5
Pohlia nutans	2.5
Bryum klinggraeffii	1.7
Brachythecium rutabulum	1.7
Dicranella heteromalla	1.7
Pohlia annotina	1.7
Tortula modica	1.7
Dicranum scoparium	0.8
Pogonatum urnigerum	0.8
Pohlia wahlbergii	0.8

3. Results

The results of the CCA indicate a significant relationship between the species composition and the environmental variables ($p < 0.001$). The constrained axes, CCA1 and CCA2, accounted for 15% of the total variation, while the unconstrained axes represented 85% of the variation. The CCA1 axis showed a strong positive correlation with phosphate and a negative correlation with pH. The biplot shows that most species are associated with higher pH values and lower phosphate values (Fig. 2). Species like *Brachythecium albicans*, *Syntrichia ruraliformis* and *Rhynchostegium megapolitanum* favor soil with higher availability of phosphate, while *Dicranella varia*, *Hypnum cupressiforme*, *Dicranella staphylina* and most *Bryum* species were found almost exclusively on low phosphate plots. Species of the *Polytrichum* genus, *Lophocolea bidentata* and *Dicranella heteromalla* appeared only in acidic plots, while *Pseudocrossidium hornschuchianum*, *Barbula convoluta*, *Barbula unguiculata* and *D. varia* were associated with higher pH values.

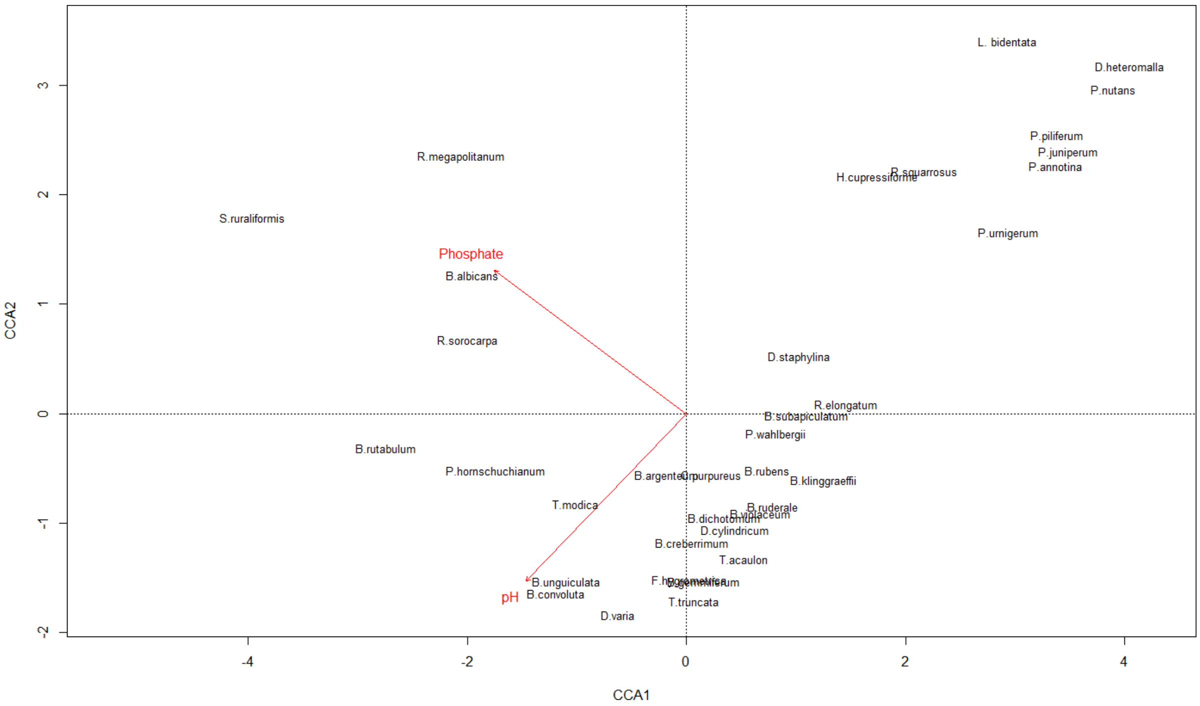

Figure 2. CCA biplot showing the relationship between the bryophyte species and the environmental variables, pH and phosphate. The arrows represent the environmental variables, with species positioned closer to the tip of an arrow are more strongly influenced by that variable, while the ones positioned away from it are less associated with the variable. Species closer to each other have similar responses to environmental gradients. For complete species names, refer to Table 2.

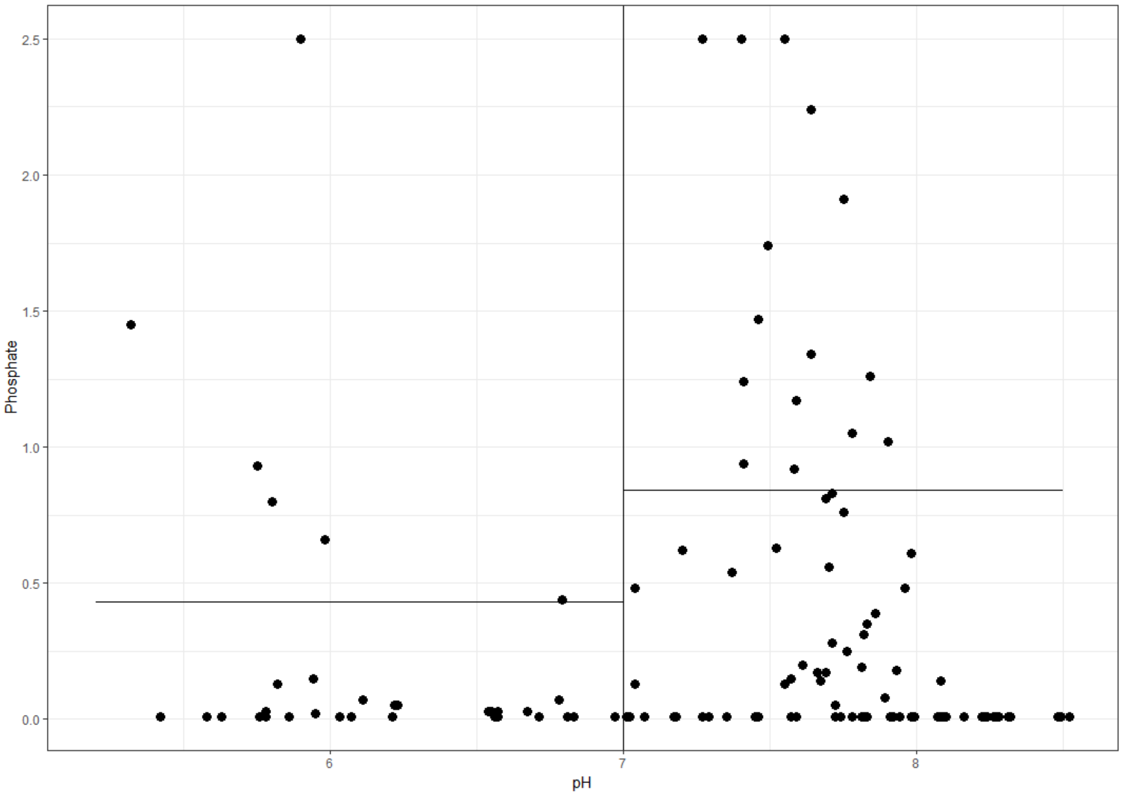

Figure 3. Distribution of all sampled plots with regards to their pH and phosphate levels. The horizontal lines represent the median values of phosphate concentrations for acidic and alkaline soils, respectively. Phosphate concentrations below these lines are considered low.

The GLM analyses revealed significant results regarding the area covered by specific species in relation to soil pH and phosphate concentrations. Specifically, *Didymodon fallax* and *Bryum subapiculatum* exhibited significant increases in cover with higher pH, whereas *Ceratodon purpureus, H. cupressiforme,* and *Polytrichum piliferum* decreased with increasing pH (Fig. 4). Conversely, *B. albicans* and *S. ruraliformis* became more abundant as phosphate concentrations increased, while *Bryum dichotomum* and *Bryum creberrimum* declined with higher phosphate levels (Fig. 5). In plots containing <0.01 ppm phosphate, both *B. convoluta* and *D. fallax* displayed significant increases with increasing pH, while *H. cupressiforme, Funaria hygrometrica,* and *P. piliferum* exhibited significant decreases. Furthermore, a significant decline in total species richness with increasing phosphate levels was revealed (p = 0.0115). Although the highest species richness was observed in mostly neutral soils, there was no significant relationship found between species richness and pH.

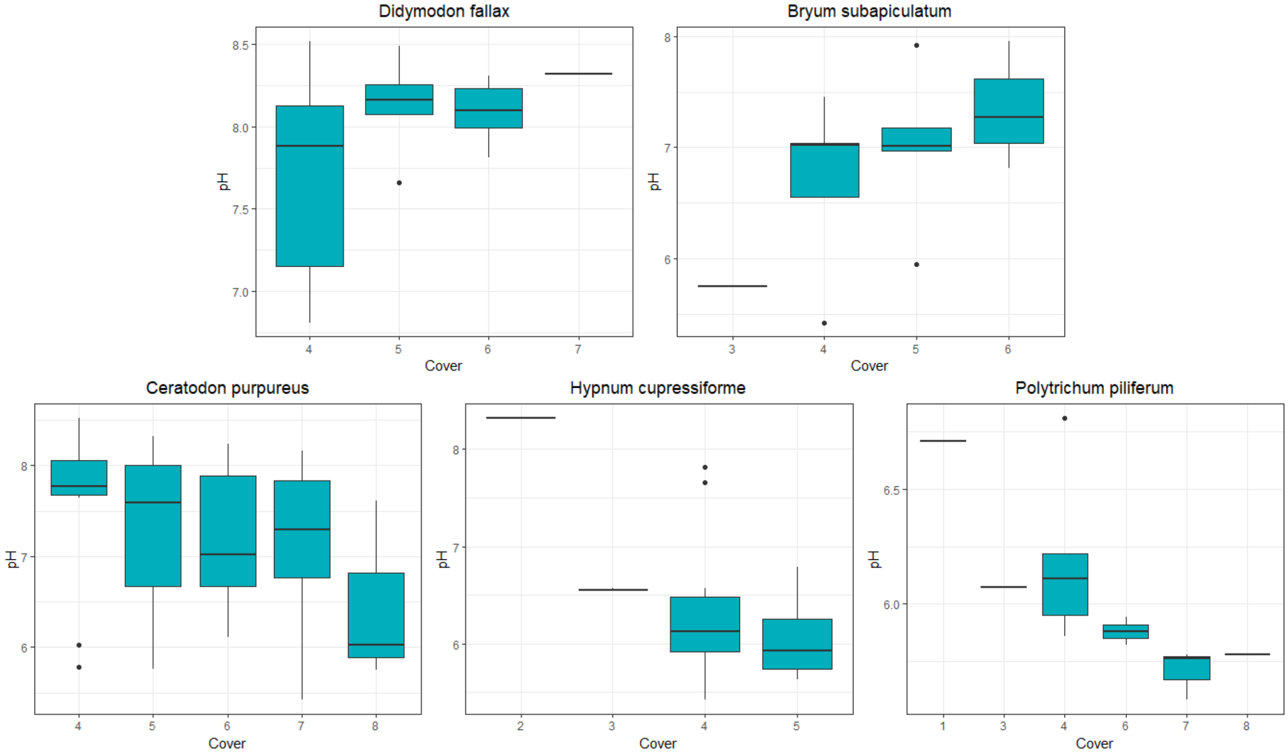

Figure 4. Effects of pH on vegetation cover on individual species

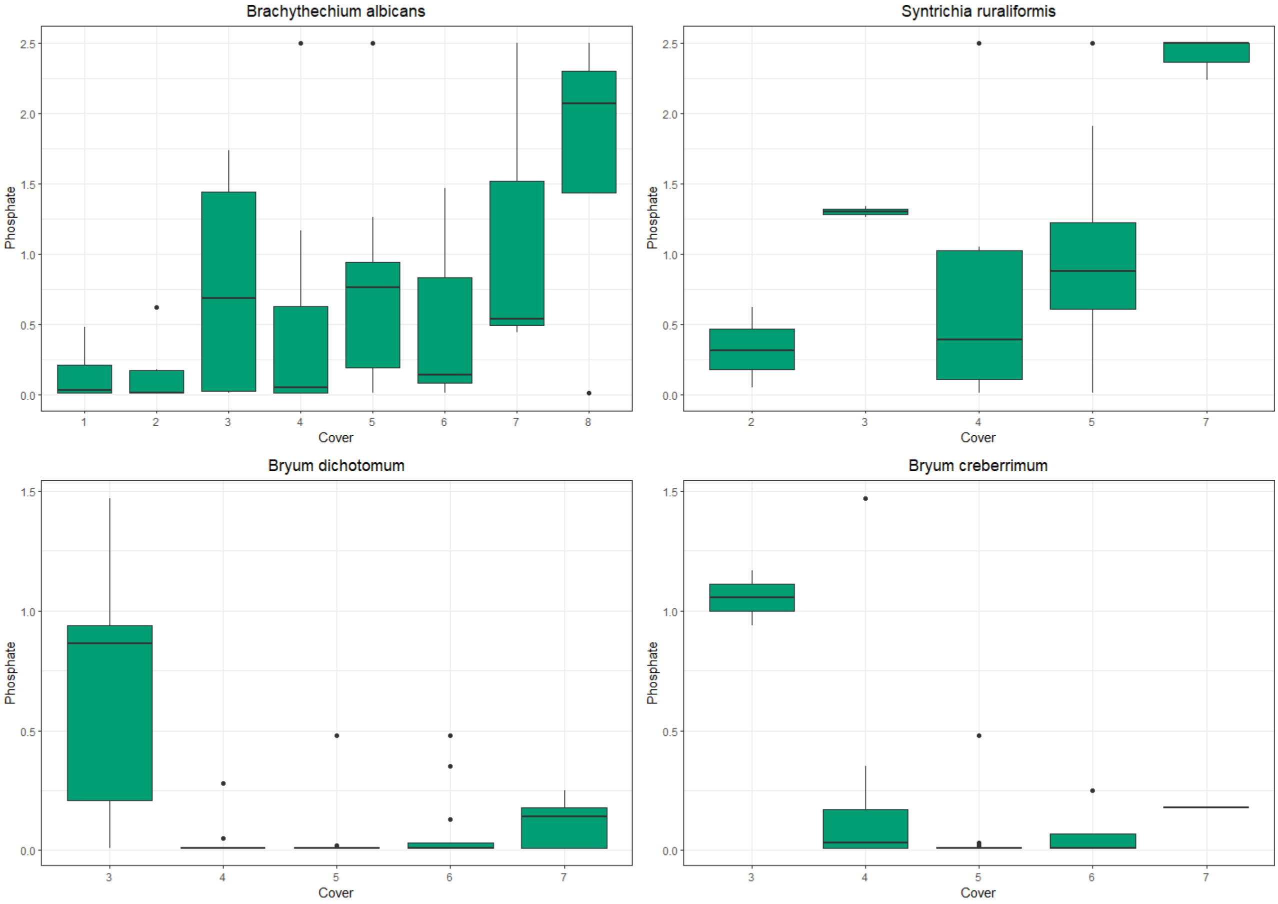

Figure 5. Effects of phosphate concentrations on vegetation cover of individual species

P. piliferum was exclusively found in plots characterized by low phosphate and low pH, while *D. fallax*, *F. hygrometrica*, and *Bryum gemmiferum* were solely found in plots with high pH and low phosphate levels (Fig. 7). Regarding specific conditions, *B. albicans and S. ruraliformis* had the greatest cover (>75%) in plots with high pH and high phosphate concentrations, whereas *P. hornschuchianum* and *B. dichotomum* exhibited their greatest cover in plots with high pH and low phosphate levels (Fig. 6).

In acidic conditions, both *C. purpureus* and *R. megapolitanum* showed significant increases as phosphate concentrations increased. *Bryum argenteum*, although predominantly found in alkaline soil, significantly decreased with increasing phosphate when in acidic soil. Additionally, *B. albicans* cover increased with phosphate in alkaline soils. The interaction between phosphate and pH appeared to have an influence on the cover of *C. purpureus*, *Bryum rubens*, and *H. cupressiforme*.

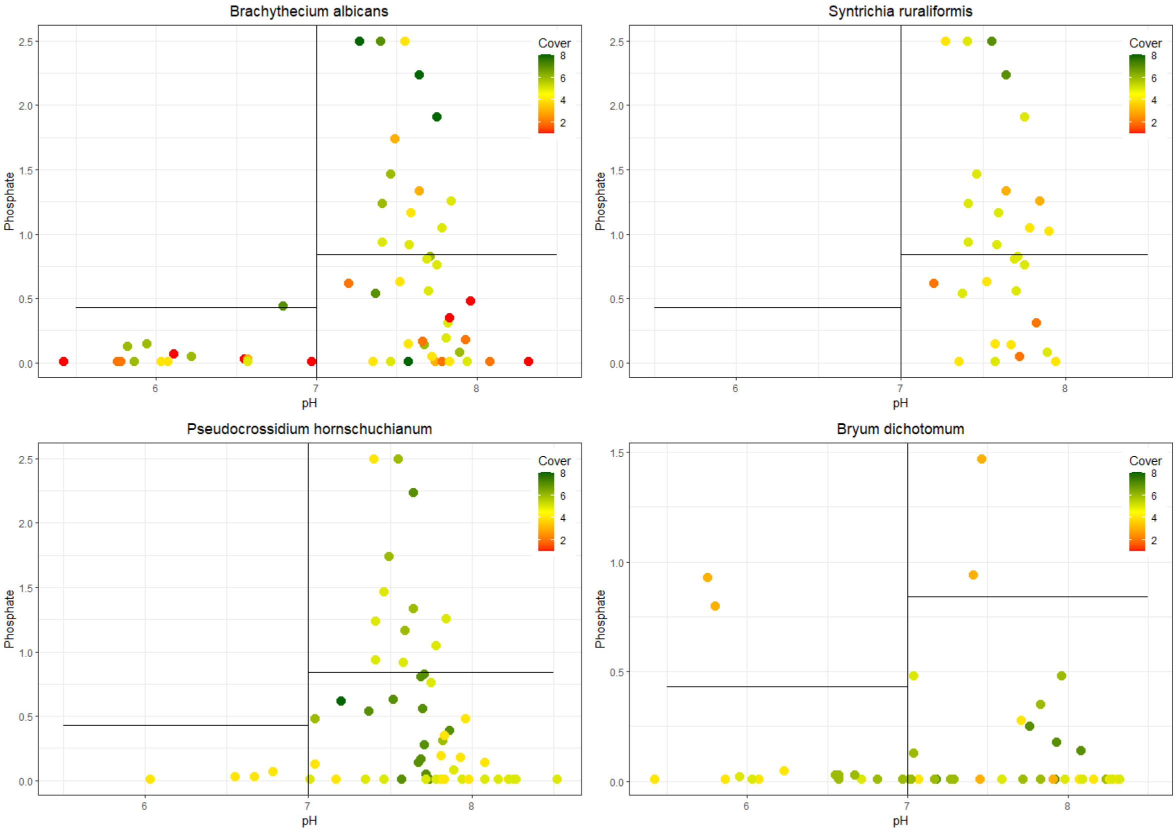

Figure 6. Combined effects of phosphate concentrations and pH on vegetation cover. The horizontal lines represent the median values of phosphate concentrations for acidic and alkaline soils, respectively. Phosphate concentrations below these lines are considered low.

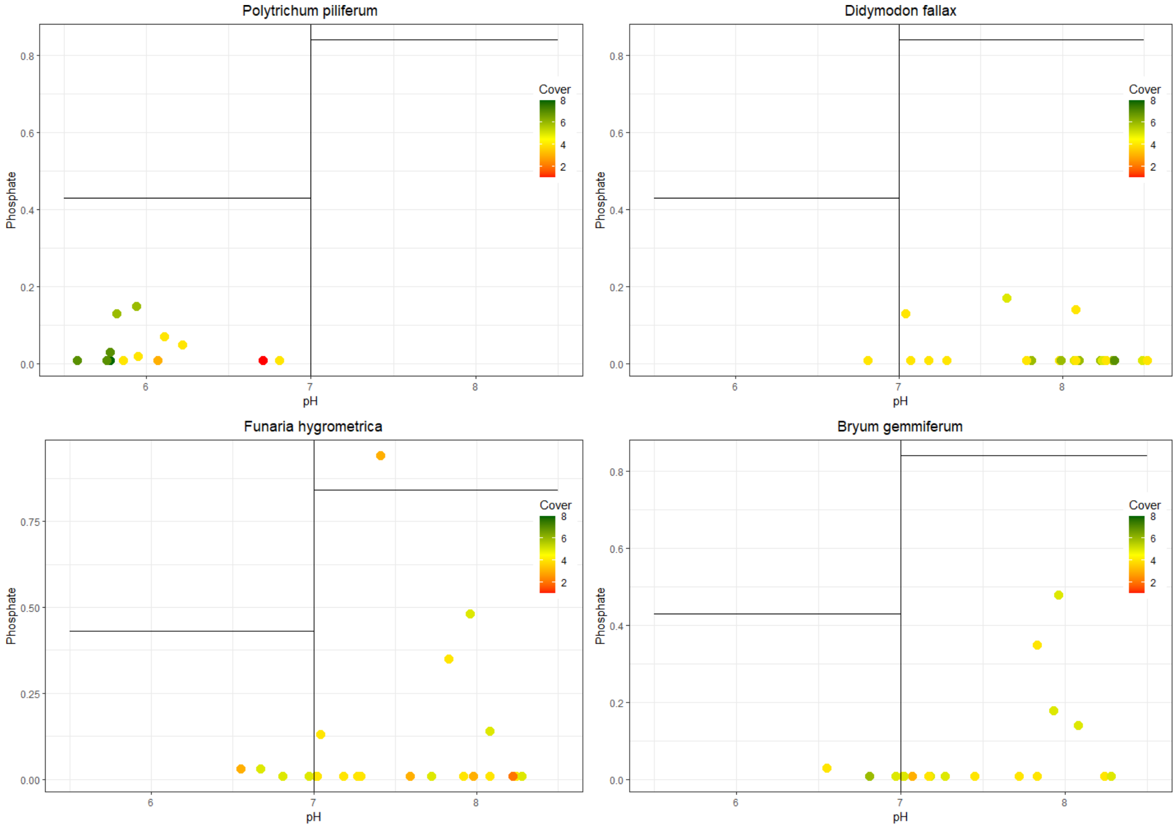

Figure 7. Species predominantly found in, or limited to, specific soil conditions. The horizontal lines represent the median values of phosphate concentrations for acidic and alkaline soils, respectively. Phosphate concentrations below these lines are considered low.

4. Discussion

4.1. Effects of phosphate availability

This study found that a greater number of species were associated with lower phosphate availability compared to higher phosphate levels (Fig. 2). This could be attributed to the fact that vascular plants often require higher nutrient concentrations than bryophytes, therefore, in more nutrient-poor soils, the competition is reduced. As a result, bryophytes can thrive and exhibit increased species richness under such circumstances. The negative correlation between species composition and cover and phosphate availability observed aligns with previous research demonstrating that high phosphate availability resulted in lower total species richness (T. Tyler, 2005; Hydbom et al., 2012), which was most likely due to out-competition by vascular plants and large pleurocarps in nutrient-rich environments.

Species like *B. albicans, S. ruraliformis,* and *R. megapolitanum* were associated with higher phosphate levels (Fig. 6), which aligns with findings from other studies. For instance, a study on sand-steppes in Skåne demonstrated that B. albicans was more frequently found and *R. megapolitanum* was restricted to plots with high phosphate (T. Tyler, 2005). Similarly, a study on the Great Alvar of Öland revealed that *S. ruraliformis* was linked to high pH values and high phosphate concentrations (T. Tyler et al., 2018). It is possible that *B. albicans* and *R. megapolitanum*, as larger, fast-growing pleurocarps, could have outcompeted other species and were thus able to dominate and cover more than 75% of a specific plot.

4.2. Effects of soil pH

Although it was not found to be statistically significant, more species were associated with higher pH values (Fig. 2), suggesting that most bryophytes thrive in more alkaline conditions, which is in alignment with research indicating that total species richness of bryophytes is associated with higher pH values and that topsoil pH significantly influences species composition (Hydbom et al., 2012; T. Tyler, 2005; Virtanen et al., 2000). It is also consistent with the findings of T. Tyler & Olsson (2016), which indicate that species growing on mineral soils tend to prefer high pH environments. This could be due to higher pH levels creating more favorable conditions for growth by reducing competition from vascular plants and promoting a lack of toxicity. Another possibility is that the presence of limestone bedrock in certain areas

Skåne contributes to generally more alkaline soils and as a result, more species found there may be better adapted to higher pH values.

4.3. Combined effects of pH and phosphate

Despite extremely low phosphate concentrations (<0.01 ppm) in some plots, pH still had a significant influence on vegetation, suggesting that this impact is independent of phosphate levels. Nevertheless, the data revealed an interactive effect of pH and phosphate on the area covered by *C. purpureus, B. rubens,* and *H. cupressiforme,* respectively. The data also revealed that certain species were limited to or had the widest distribution in highly specific conditions. This indicates a complex relationship between pH and phosphate in shaping the distribution of bryophytes. In general, the majority of species in the study displayed a preference for high pH and low phosphate conditions. An additional trend noted was that certain species, when deviating from their expected pH preferences, compensated by favoring higher phosphate conditions.

C. purpureus was the most frequent species in the study (Table 2). Although it typically appears in acidic to neutral soils, it was frequently found in alkaline plots, but its cover decreased with increasing pH (Fig. 4). In acidic conditions, it showed an increase in cover with increased phosphate. In alkaline conditions, it appeared more often in higher phosphate soils compared to acidic plots, however this was not shown to be statistically significant. This could be a compensation mechanism, where the increased preference for phosphate might mitigate the limitations of high pH. Its widespread presence could be attributed to its characteristics as a generalist species with high dispersibility (Glime, 2021).

Similarly, *H. cupressiforme* exhibited a decline in abundance with increasing pH (Fig. 4). Although this species has been reported to have a broad pH range in previous studies (Hydbom et al., 2012; T. Tyler et al., 2018), T. Tyler (2005) found it exclusively on acidic pH soils. Additionally, T. Tyler et al. (2018) associated it with relatively high phosphate levels. The results of this study further highlighted a significant interaction between pH and phosphate, suggesting that the combined influence of these factors contributes to the distribution patterns of *H. cupressiforme*. It was most often found in acidic plots with low concentrations of phosphate. The reduced occurrence in alkaline soils could be attributed to the scarcity of phosphate, as this species might have higher nutrient requirements in suboptimal (alkaline) conditions.

In contrast, *B. argenteum* was predominantly found in alkaline plots, however, in acidic plots, its abundance decreased in response to higher phosphate. When bryophytes growing on limestone soil were treated with phosphate, *B. argenteum* initially increased, but later declined as it was outcompeted by other species (G. Tyler et al., 1995). It is thus plausible that, in acidic conditions, *B. argenteum* was more susceptible to being outcompeted by species better able to utilize the increased phosphate levels.

T. Tyler et al. (2018) revealed a general trend of species on alkaline soil exhibiting a preference for low phosphate concentrations, a trend that is further supported by the results of this study. Particularly, species such as *D. fallax, F. hygrometrica,* and *B. gemmiferum* were almost exclusively found in plots with high pH levels and low phosphate concentrations (Fig. 7). The discovery of *F. hygrometrica* in low phosphate conditions, contrary to its usual occurrence in nutrient-rich soils, could point to other nutrients, such as nitrogen, having a greater impact on its growth. In this study, it consistently maintained plot cover below 25%, indicating its ability to tolerate low nutrient conditions, while its optimal performance is probably in habitats with higher nutrient availability. *P. piliferum*, however, was only found in plots with low pH and low phosphate concentrations (Fig. 7). These results show that certain species thrive in very specific soil conditions, demonstrating the importance of pH and phosphate as factors influencing the distribution of bryophytes.

With these findings, it is important to note that this study only considered two environmental variables, meaning other unmeasured environmental factors could have had a potential influence on bryophyte vegetation. For example, T. Tyler et al. (2018) demonstrated that factors like substrate type and percentage of bare soil all had significant effects on vegetation cover. While the chosen sites were specifically selected to minimize variations in factors like moisture, inundation, and exposition, it is important to consider the potential influence of the different mineral composition of the bedrock between the sites. Li & Vitt (1994) also revealed that nitrogen availability had a greater effect on establishment than phosphorus. Additionally, Salemaa et al. (2008) suggested that the response to nutrients could depend on moisture conditions.

4.4. Implication for conservation strategies

The significant relationship between species composition and environmental variables revealed in the CCA emphasizes the importance of soil pH and plant available phosphate in shaping bryophyte populations. The presence of certain species in specific conditions further highlights the impact of soil chemistry on bryophyte distribution and abundance. Understanding the influence of these factors on species composition and abundance could be meaningful for conservation strategies.

The results of this study, supported by previous research (T. Tyler, 2005; T. Tyler et al., 2018), indicate that maintaining low phosphate concentrations and higher pH values is generally beneficial for most bryophyte species. pH has already been shown to be a crucial factor (Löbel et al., 2006). Maintaining a neutral to alkaline soil pH range could positively impact bryophyte conservation by generating greater species richness and diversity.

The presence of nutrient-rich conditions might negatively affect bryophytes, but this is likely due to competition from vascular plants rather than an “over-availability” of nutrients. For instance, with a continuous removal of vascular plants, G. Tyler et al. (1995) demonstrated that the addition of phosphate promoted bryophyte establishment. Fertilization and increased nutrient availability have also been shown to have adverse effects on species richness by Virtanen et al. (2000), Zechmeister et al. (2003), and Boch et al. (2018), as they promoted the growth of vascular plants and nitrophilous bryophytes, leading to a decline in bryophyte diversity. This shows how important a balance in soil nutrient levels is to the coexistence of plant populations, both vascular and bryophytes.

Moderate disturbances like low-intensity grazing have been found to aid bryophyte colonization (Boch et al., 2018). Such disturbances can create open patches and reduce competition, providing opportunities for bryophytes to establish and thrive. Managing such disturbances in the ecosystem can play a role in supporting bryophyte diversity. However, it's important to acknowledge that certain bryophyte species, like *R. megapolitanum*, have specific requirements and are restricted to high phosphate soils. Conservation efforts need to consider the needs of such specialized species, especially the rare and endangered species, to ensure their survival.

In conclusion, this study emphasizes the significant influence of phosphate availability and soil pH on bryophyte communities. While certain species may have distinct preferences for specific conditions, a general tendency towards favoring low phosphate and high pH environments was observed. Nonetheless, to gain a more comprehensive knowledge of bryophyte populations, additional factors such as competition, nutrient availability, and disturbance must be taken into account. Understanding these environmental variables and how they interact is crucial for creating management practices to conserve bryophyte diversity.

5. Literature

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