

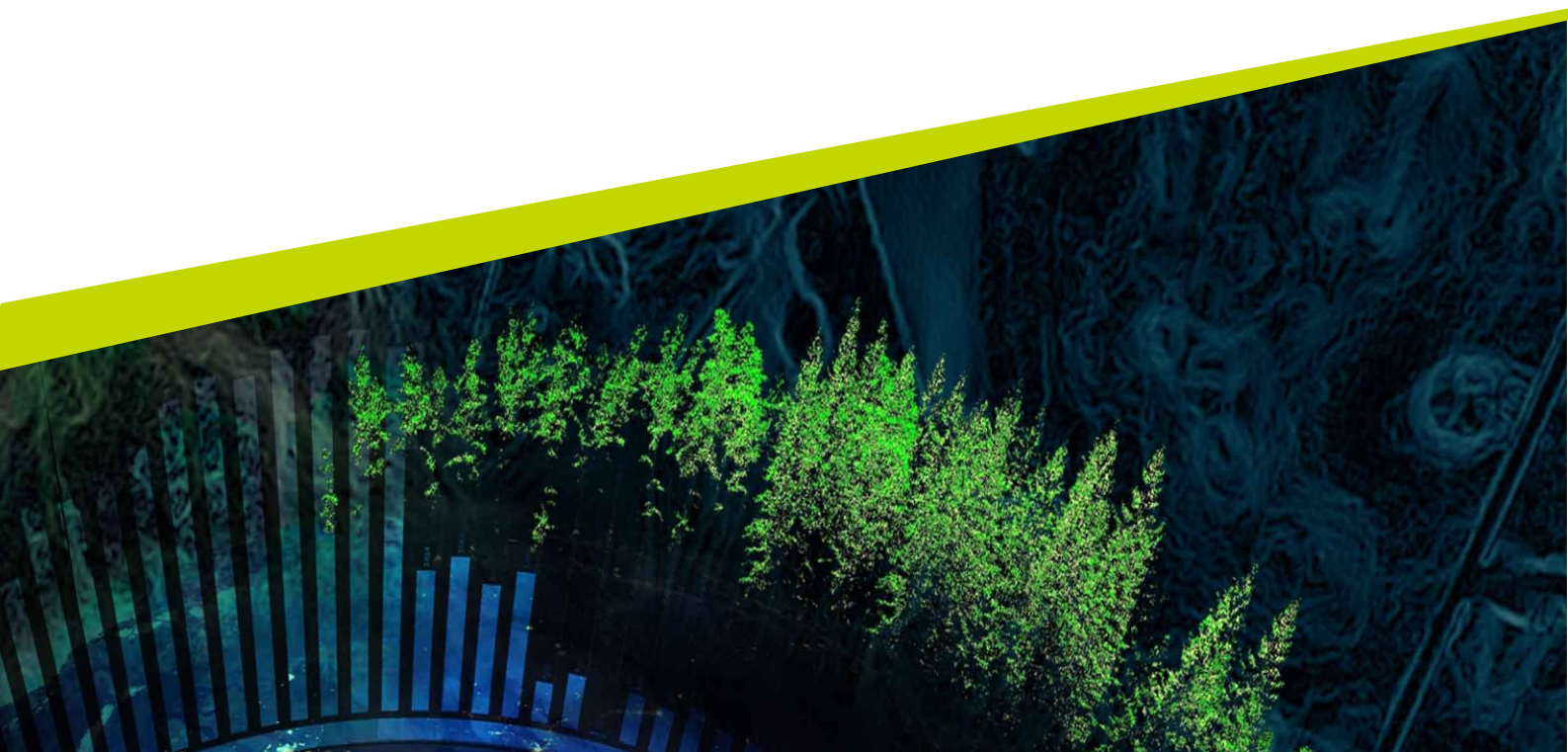


Microclimate as a Driver of Understory Plant Community Composition in Riparian Zones

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Mikroklimat som drivkraft för undervegetationens artsammansättning i ripariska zoner

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Sammanfattning

Ripariska zoner, övergången mellan land och vatten, är områden där akvatiska och terrestra förhållanden och organismgrupper möts. Samspelet mellan olika mikroklimatvariabler och rumsliga variationer i landskapet leder till ett unikt mikroklimat som ger upphov till hög biodiversitet. I denna studie undersöktes hur avståndet till bäckar påverkar artsammansättningen och artrikedomen mellan tre taxonomiska artgrupper (landväxter, mossor och kärlväxter), samt i vilken grad mikroklimatet kan förklara eventuella skillnader. Fältdatamaterialet är insamlat i Dalarna och Örebro län i Sverige under 2025. Analyser genomfördes sedan i Rstudio med NMDS, PERMANOVA och regressionsanalyser (LMER och GLMM) för att identifiera eventuella skillnader i artsammansättning och artrikedom mellan respektive grupp med avseende på avståndet till bäcken. Artrikedomen skiljde sig inte avsevärt mellan de taxonomiska grupperna, med undantag för kärlväxterna, som visade en signifikant minskning på 25%. Detta, tillsammans med PERMANOVA-resultaten, tyder på att kärlväxter förlorade arter med ökat avstånd till bäcken utan ny artetablering. Landväxter och mossor behöll däremot samma artrikedom när avståndet från bäcken ökade och visade ett artutbyte enligt PERMANOVA-resultaten. Markfuktighet och krontäckningsgrad korrelerade signifikant med samtliga taxonomiska grupper, vilket delvis kan förklara skillnaderna i gruppernas artsammansättning längst med miljögradienten. Låga R^2 -värden tyder däremot på att en stor del av variationen i artsammansättningen kan förklaras av ytterligare faktorer, såsom topografi, feedbackcykler och skogshistoria. Sammantaget visar studien att artsamhällen 0 m från bäcken skiljer sig från artsamhällen 10 m från bäcken och därför bör hänsyn tas vid avverkning för att bevara biologisk mångfald.

Nyckelord: Riparisk zon, riparisk buffert, artsammansättning, mikroklimat, bäckar

Abstract

Riparian zones, the transition between land and water, are areas where aquatic and terrestrial conditions and groups of organisms meet. The interplay among microclimatic variables and spatial variations in the landscape creates a unique microclimate that supports biodiversity. This study investigated how distance to streams affects species composition and richness across three taxonomic groups (embryophytes, bryophytes, and tracheophytes), and to what extent microclimate can explain any observed differences. Field data were collected in Dalarna and Örebro counties in 2025 and analyzed in RStudio using NMDS, PERMANOVA, and regression analyses (LMER and GLMM). Species richness did not differ substantially among taxonomic groups, except for tracheophytes, which showed a significant 25% decline with increasing distance. Together with the PERMANOVA results, this suggests that tracheophytes lost species without new ones establishing. Embryophytes and bryophytes, in contrast, retained the same species richness as distance from the stream increased, implying that species were replaced across the stream-distance gradient. This is also supported by the PERMANOVA results. Soil moisture and canopy cover were significantly correlated with all taxonomic groups, which may partly explain differences in species composition among groups along the environmental gradient. Low R^2 values, however, suggest that a large proportion of the variation in species composition can be explained by additional factors, such as topography, feedback cycles, and forest history. Overall, the study demonstrates that species communities at 0 m from the stream differ from those at 10 m, and that consideration should therefore be given during logging operations to preserve biodiversity.

Keywords: Riparian zone, riparian buffer, species communities, microclimate, headwaters

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1. Introduction

Buffer retention was introduced to Swedish forestry in the 1990s (Skogssällskapet n.d.) and provides several ecological functions. The riparian buffer zone is functional only if several criteria are fulfilled – one of which is biodiversity. (Skogforsk 2022). Characteristics of the riparian buffer zone that affect its functionality include tree species and age distributions, canopy layering, and buffer width (Skogforsk 2022). Headwater streams, which generally have a higher canopy-shading ratio, show a greater need for buffer retentions, especially since they receive minimal protection from forestry (Jyväsjärvi et al. 2020). Today, buffer retention is recommended to Swedish forest owners by the Forest Management Act, the forestry sector's objectives for good environmental consideration, and the Forest Stewardship Council (FSC) and Program for the Endorsement of Forest Certification (PEFC) certification standards (Skogforsk 2021). Studies have shown that riparian buffer zones need to be 10-30 m wide to provide desired functions (Broadmeadow 2004). However, a report from Skogstyrelsen (2025) shows that a third of all waterways in Swedish production forests lack riparian buffers, and another study indicates that Swedish riparian zones often have widths of less than 5 meters (Kuglerová et al. 2020). European Union (EU) regulations and policies have put pressure on Sweden, among other countries, to protect more forests to sustain biodiversity following the climate crisis. Implementing riparian buffers can be a key strategy to achieve these management goals. However, the relationship between understory plant community composition, microclimate, and distance to headwater streams have received relatively little attention. More knowledge of this subject could alter the design of future buffer retention to better serve as climate refugia for plant and animal species.

1.1 Aim and research questions

This study aims to investigate whether community composition and species richness of understory plants in riparian zones differ across a stream-distance gradient, and to explore whether these differences can be explained by microclimatic variation. In this study, we ask:

1. Does species richness of understory plants differ across a stream-distance gradient?
2. Do species richness of tracheophytes and bryophytes vary differently across a stream-distance gradient?
3. Does microclimatic variation explain differences in understory plant community composition across a stream-distance gradient?

We hypothesize that increased distance to streams will result in a loss of total species richness. However, we predict that differences along the stream-distance gradient will be greater among taxonomic groups. Specifically, we expect to see a turnover between bryophytes and tracheophytes. Furthermore, we hypothesize that microclimatic variation, particularly in soil moisture and light availability, will be strongly correlated with community composition across a stream-distance gradient.

1.2 Background

1.2.1 Microclimate in riparian zones

Riparian zones are areas between land and water, where aquatic and terrestrial conditions and communities meet. These zones typically provide unique microclimatic conditions with cooler temperatures, higher humidity, and more stable light availability than surrounding areas (Kemppinen et al. 2024). The unique conditions in riparian zones suggest a distinctive and more diverse set of plant species (Gregory et al. 1991). The distance to the water is therefore a critical factor, as it influences spatial variation in soil moisture, relative humidity, and temperature.

Spatial variation in soil moisture, relative humidity, and temperature are intricately connected and shaped by structural variation in the landscape (Gregory et al. 1991). Canopy cover determines the amount of incoming solar radiation (Liang et al. 2021), thereby influencing vegetation growth in the riparian zone. In addition, their findings suggest that riparian vegetation regulates local microclimate conditions by providing shade, modifying the airflow, and releasing water vapor through evapotranspiration. Taken together, these processes contribute to higher relative humidity and lower temperatures near the stream (Moore et al. 2005).

Water availability is essential for plant transpiration, supporting their seedling establishment (Ter Heerdt et al. 2016) and photosynthesis (Kimberley et al. 1997). The spatial variation in soil moisture along riverbanks is linked to distance from the stream. Under cooler conditions, dense vegetation, which reduces wind speed, can

decrease evaporation from the ground, thereby preventing moisture loss through latent heat flux (Reidy 2023). These environmental conditions enable specific niches to form and sustain key functions for riparian vegetation survival (Ter Heerdt et al. 2016).

1.2.2 Plant Physiology

Water availability is crucial for plant survival because it serves several essential physiological functions. It acts as a transport medium, facilitates the movement of organic metabolites, and distributes nutrients from the soil, making water availability essential for plant growth and organ development (Lambers & Oliveira 2019). The same study also describes how water uptake is controlled by the root system and driven by transpiration. Transpiration builds up the turgor pressure, which supports structural stability and temperature regulation within vascular plants (Lambers & Oliveira 2019).

In contrast to vascular plants, bryophytes are poikilohydric, meaning they lack roots and cannot regulate their internal water content (Gril et al. 2024). Instead, they rely on passive diffusion (Büdel et al. 2024). The authors further describe how this physiological mechanism enables the absorption of water vapor and, water liquid water across the vegetative thallus surface. Taken together, Büdel et al. (2024) illustrate how this evolutionary strategy allows bryophytes to successfully adapt to various environments, provided that suitable living conditions regarding light, soil moisture, nutrients, and relative humidity are available.

Light availability, which is determined by the amount of canopy cover (Liang, Xie & Che 2021) and expressed as irradiance (energy per unit area), plays a significant role for plants by regulating photosynthesis. Reduced light availability may cause physiological stress in plants by reducing photosynthetic performance, leading to reduced carbon assimilation and growth (Lambers & Oliveira 2019). However, in the same study, the authors also noted how few plant species affected by decreased light availability have evolved optimized irradiance capture, thereby supporting enhanced photosynthetic efficiency. This reflects the degree to which plant communities are adapted to their environments.

2. Method

2.1 Data collection

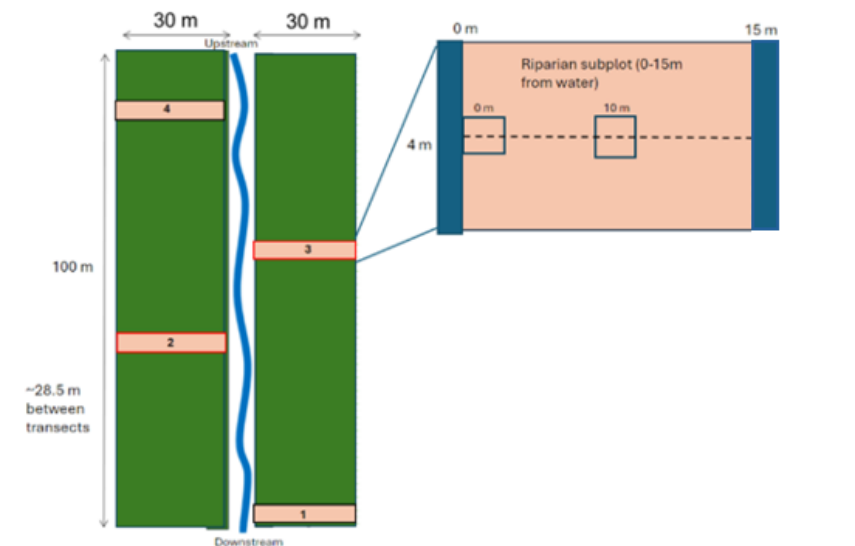


Figure 1. Schematic overview of the study design. The left panel shows the layout of a single site, with four transects distributed along 100 m of riparian zone on each side of the stream, each side extending 30 m from the stream channel, and transects spaced approximately 28.5 m apart. The right panel shows the structure of an individual transect, comprising a 4 m wide transect with two 1×1 m subplots positioned at 0 m and 10 m from the stream within a 15 m long riparian subplot.

Data was collected in Dalarna and Örebro counties in Sweden in 2025. In July 2025, field inventories were conducted across 10 sites, each covering between 100 and 300 m of riparian zone. Along each site, twelve transects were established approximately 28.5 m apart on both riparian margins, extending 30 m from the stream. Within each transect, two 1×1 m plots were positioned at 0 m and 10 m from the stream, within a riparian subplot spanning 0–15 m from the water (Figure 1). In each plot, terrestrial abiotic and biotic variables were recorded. During 2025, abiotic terrestrial variables were recorded continuously, which included air temperature, air humidity, soil temperature, and soil moisture. All abiotic variables were measured using sensors. Air temperature and relative humidity were recorded

with easyloggers (EL-USB-2). Soil moisture was measured using TMS 4 probes and presented as raw unitless values. Because no soil-specific calibration curve was available, the raw sensor output could not be converted into volumetric water content (m^3/m^3) and is therefore reported as a soil-moisture index. Canopy cover was estimated via a densitometer. In our models, we used vapor pressure deficit (VPD) as a metric for air humidity, derived from air temperature and Dew Point. Biotic terrestrial variables were assessed through vegetation inventories, in which the abundance of vascular plants and bryophytes was recorded through the relative abundance of all species present in the plot.

2.2 R analysis

We created three data frames representing different groups of species, defined by their physiological functions: (1) Tracheophyta, (2) Bryophyta, and (3) Embryophyta. Tracheophyta and Bryophyta are subgroups of Embryophyta. Abundance data were then converted to binary presence/absence values for all taxonomic groups in separate new data frames, keeping the abundance data intact. The binary presence/absence values were subsequently used to derive species richness per plot. Species richness of tracheophyte, bryophyte, and embryophyte was then calculated by summing presence across all plots for both 0 and 10 meters. To assess whether species richness significantly differs with stream distance, Generalized Linear Mixed-effects Models (GLMMs) were used separately for tracheophyte, bryophyte, and embryophyte species richness. Stream distance was included as a fixed effect and site as a random effect to account for the nested structure of the data. The GLMMs were fitted using the Poisson distribution.

Non-metric Multidimensional Scaling (NMDS) was used to visualize potential differences among taxonomic groups at 0- and 10-meter distances from the stream. Three dimensions were used for all taxonomic groups, and Bray-Curtis was chosen as the distance matrix, since the data frame contains abundance data. Microclimatic vectors with p -values < 0.05 were plotted on the NMDS model to visualize significant correlations between microclimatic factors and species composition. Microclimatic variables that proved significant were subsequently modeled against stream distance using Linear Mixed-Effects Regression (LMER) to assess whether microclimate varied with stream distance. In this case, the models did not need to be generalized as in previous models, since they were fitted using the Gaussian distribution. After performing NMDS, a Permutational Multivariate Analysis of Variance (PERMANOVA) was conducted to test whether there are significant differences in species communities among taxonomic groups compared to stream distance. 999 permutations were used.

3. Results

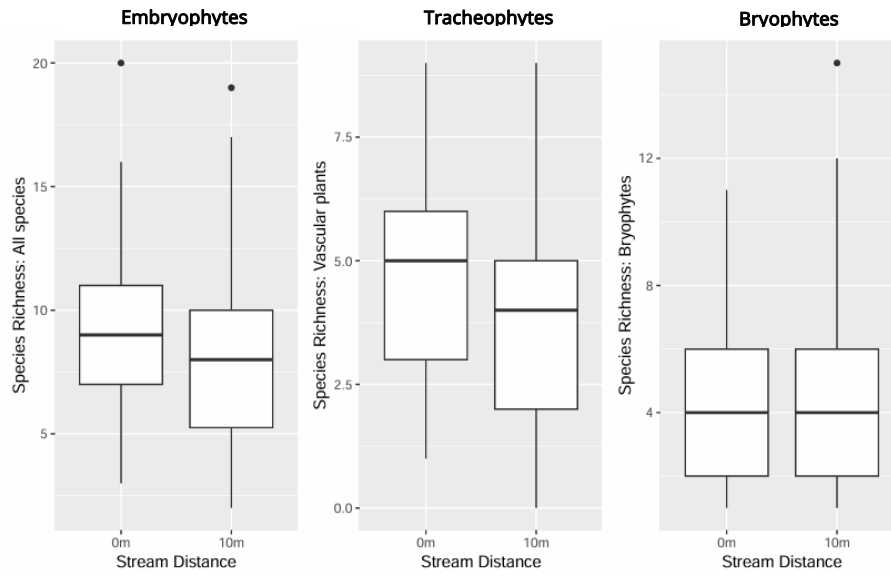


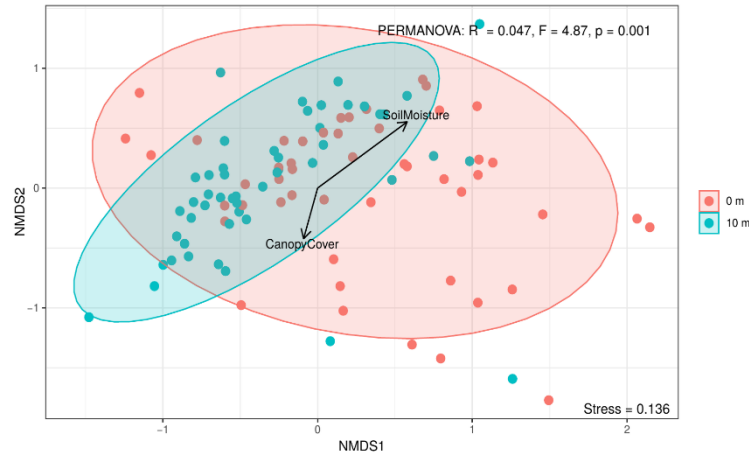
Figure 2. Boxplots illustrating how species richness for different taxonomical groups differs depending on the distance from the stream.

We found weak evidence of a difference in embryophyte species richness (Figure 2), but no evidence of a difference in bryophyte species richness (Table 1). Plots 10 meters from the stream have significantly lower tracheophyte species richness ($p=0.004$) (Table 1), which resembles the result of Annala et al. (2022), who found that plant species richness declined with increasing distance from the stream. Figure 2 illustrates differences in species richness among taxonomic groups across the stream-distance gradient.

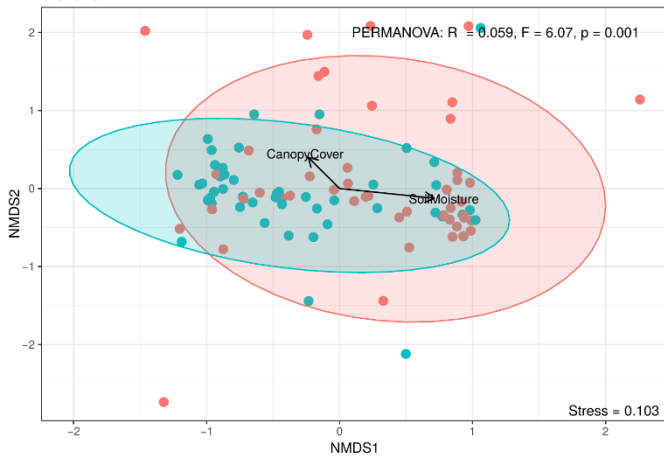
Table 1. Species richness at 0 m and 10 m distance from the stream, presented for each taxonomical group, alongside the relative change in species richness (%) at 10 m. p -values derived from GLMM are presented for each taxonomical group.

	Species richness at 0 meters	Species richness at 10 meters	Effect of 10 meters on species richness	p -value
Embryophyta	9.12	8.12	-10%	0.095
Tracheophyta	4.80	3.56	-25%	0.004**
Bryophyta	4.14	4.39	+6%	0.562

(1) Embryophyte communities and microclimate



(2) Bryophyte communities and microclimate



(3) Tracheophyte communities and microclimate

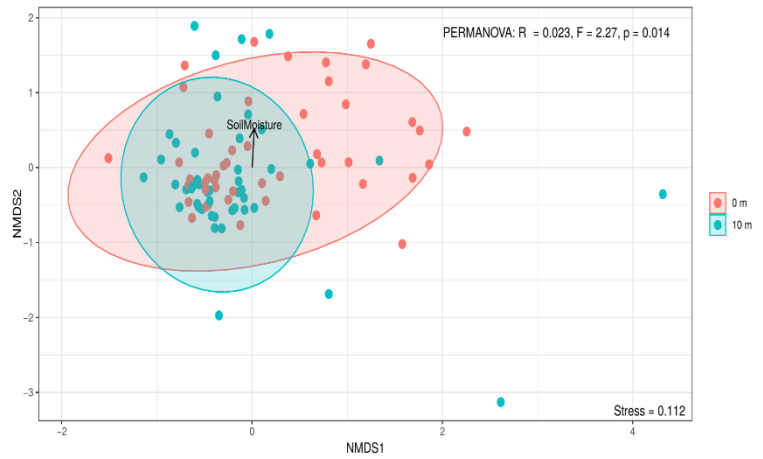


Figure 3. NMDS plots illustrating, for each taxonomical group: (1) embryophytes, (2) bryophytes and (3) tracheophytes, how communities within each plot are related to each other. The closer two points are to each other, the more similar their community composition. The distance from the stream is either coloured red (0 meters from the stream) or blue (10 meters from the stream), with the 95% prediction interval of those distances from the stream marked by an ellipse of the same colour. Microclimate vectors that significantly correlate with the distribution of the points are illustrated with black arrows (p -value < 0,05).

The NMDS plots (Figure 3) show that the 10-meter centroid is nested within the 0-meter centroid, regardless of the taxonomic group. However, PERMANOVA results show a significant difference in species composition between 0 and 10 meters from the stream across all taxonomic groups (Table 2). Annala et al. (2022) found that plant communities changed from herbaceous-dominated to shrub-dominated with increasing distance from the stream, indicating a shift in species composition, which our results also suggest. The stress values for the NMDS models – 0.136 for embryophytes, 0.103 for bryophytes, and 0.112 for tracheophytes- indicate a reliable fit of the two-dimensional ordination in the NMDS. We also found that soil moisture and canopy cover significantly correlate with the species composition of embryophytes and bryophytes ($p < 0,05$). For

tracheophytes, only soil moisture significantly correlated with the species composition ($p < 0,05$). In boreal riparian ecosystems, soil moisture has been identified as a key factor influencing plant species richness (Kuglerová et al. 2014; Jansson et al. 2007), a pattern our results also suggest.

Although all taxonomical groups differ significantly in community composition in relation to stream distance (Table 2), stream distance explains little of the variation within each species group. 5,9% of the variation in bryophyte communities, 4,7% of the variation in embryophytes, and 2,3% of the variation in tracheophytes is explained by stream distance (Table 2). The community composition of bryophytes shows the strongest separation between the 0 m and 10 m plots ($F = 6.07$). Community composition of embryophytes has an intermediate separation between the 0 m and 10 m plots compared to the other species groups ($F=4.87$), and the community composition of tracheophytes has the weakest separation between the 0 m and 10 m plots ($F=2.27$) (Table 2).

Table 2. R^2 -values, F -values, and p -values derived from PERMANOVA are presented for each taxonomical group.

	R^2	F	p -value
Embryophyta	0.047	4.87	0.001***
Tracheophyta	0.023	2.27	0.014*
Bryophyta	0.059	6.07	0.001***

LMER tests indicate no significant difference in microclimatic variables over stream distance (Table 3). This, however, does not fully align with previous research, which has found clear patterns of microclimatic gradients over stream distance (Kimberley et al. 1997).

Table 3. Soil moisture, air humidity, and canopy cover at 0 m and 10 m distance from the stream are presented for each species group, along with the relative change (%) at 10 m. p -values derived from LMER are presented for each species group.

	0 m	10 m	Effect of 10 m	p -value
Soil Moisture (raw value)	2370	2177	-8.14 %	0.125
VPD Annual Mean (kPa)	0.217	0.246	+13.36 %	0.435
Canopy cover (%)	79.67	81.03	+1.7 %	0.601

4. Analysis and discussion

Buffer retention is a vital management option for the Swedish forestry sector to comply with the regulations and policies of the EU, yet relatively little research has been conducted on the relationship between species community composition of understory plants, microclimate and distance to headwater streams. We investigated whether stream distance gradients drive differences in species richness or community composition of embryophytes, bryophytes, and tracheophytes, and if microclimatic variation can explain these differences. Our results suggest that embryophyte species richness does not change across a stream-distance gradient ($p = 0.095$), which is inconsistent with our hypothesis. However, when split into taxonomical groups (bryophytes and tracheophytes), tracheophytes significantly decreased in species richness ($p = 0.004$), while bryophytes experienced no significant change ($p = 0.562$). This fails to confirm our hypothesis, which predicted species replacement within each taxonomic group due to differing ecological strategies and environmental requirements.

However, the observed pattern aligns with known physiological differences. Vascular plants rely on their root systems for water and nutrient uptake (Lambers & Oliveira 2019). Water availability is essential for reproduction (Ter Heerdt et al. 2016), supports photosynthesis (Kimberley et al. 1997), and maintains plant growth by distributing nutrients (Lambers & Oliveira 2019). Our results show that soil moisture was 8.14% higher at 0 meters than at 10 meters from the stream ($p = 0.125$). This further aligns with previous research regarding the soil moisture gradient (Reidy 2023). Taken together, this supports a significant 25% decline of tracheophyte species richness between distances of 0 and 10 meters ($p = 0.004$), as reduced soil moisture suggests more constrained living conditions for tracheophytes.

Bryophytes, in contrast, are poikilohydric and can absorb water in forms of vapor and liquid across their vegetative thallus (Büdel et al. 2024). The slight, nonsignificant increase in bryophyte species richness between 0 and 10 meters ($p = 0.562$) is therefore ecologically reasonable and supported by our results, which showed a small decline in soil moisture ($p = 0.125$) and no significant change in VPD ($p = 0.435$). Because bryophytes can survive on either relative humidity or

soil moisture, their species richness remains unaffected even as soil moisture content decreases.

As expected, soil moisture and canopy cover both significantly correlated with species composition across taxonomic groups. Yet LMER tests showed no significant difference over the stream-distance gradient. This suggests that soil moisture and canopy cover explain some of the differences in community composition across taxonomic groups, a pattern supported by previous research (Kuglerová et al. 2014; Jansson et al. 2007), despite not changing significantly across the stream-distance gradient ($p = 0.125$). This might be due to the sampling pots being too near the stream to reveal any patterns.

Furthermore, NMDS plots show that 10-meter species composition is visually nested within 0-meter species composition across all taxonomic groups (Figure 3). However, our PERMANOVA results indicate that the species composition of all taxonomic groups differs significantly (Table 2), supporting our hypothesis. This could be because NMDS plots are a 2D-structure and the third dimension in the model becomes invisible. Hence, the two centroids may differ along the z-axis, explaining why PERMANOVA results can be significant despite visual overlap. Given the non-significant change in embryophyte species richness with stream distance ($p = 0.095$), one interpretation of our result is that embryophyte species composition is altered by the loss and subsequent gain of species as distance to the stream increases.

For bryophytes, our results imply that the community composition is structured similarly to that of embryophytes. Species are subsequently replaced as the distance from the stream increases. This is supported by our PERMANOVA results ($p = 0.001$) and the non-significant change in species richness over stream distance (Table 1). An interpretation of this pattern could be explained by their poikilohydric strategy, which allows them to tolerate a wide range of moisture conditions (Büdel et al. 2024). In contrast, tracheophytes show a significant decline in species richness ($p = 0.004$), and, together with significant PERMANOVA results ($p = 0.014$), these findings suggest that the shift in community composition is driven by this decline. In practice, this means that tracheophyte species near streams, adapted to wet conditions, are lost within 10 meters, since water is essential for their survival (Lambers & Oliveira 2019).

4.1 Other confounding variables

Although several microclimatic variables were included in our model, other factors may contribute to the variance in understory plant community composition across the stream distance gradient, as indicated by our low R^2 -values. The topography of the different sites, including slope and aspect, locally affects the amount of incoming solar radiation, drainage capacity, and soil nutrient availability, possibly influencing microclimatic gradients and community composition (Annala et al. 2022), which our models could not fully capture. Including a topographic wetness index and soil chemistry data in future studies could help separate topographical from hydrological drivers and nutrient availability from other microclimatic factors in the community composition of understory plants.

It should also be noted that variables in our model may not be independent and may interact through feedback cycles. For example, canopy cover and nutrient availability. Dense canopy cover promotes litter accumulation, which can alter soil chemistry over time, affecting which species can establish at the site and progressively altering canopy composition and cover (Majasalmi & Rautiainen 2020). The variation explained by canopy cover in our model may therefore reflect not only an abiotic effect but also the cumulative outcome of vegetation and soil shaping each other over time. Unravelling these feedback cycles would go beyond the scope of this study, but could be an important area for further research on conserving the community composition of understory plants along stream-distance gradients.

Disturbance history represents another potentially important source of unexplained variation in our results. Sweden's extensive forestry has drastically altered forest structure. For example, logging or thinning the riparian zone resets successional patterns and, rather than reflecting natural abiotic conditions, is affected by anthropogenic disturbance (Kuglerová et al. 2023). In our study, variables such as canopy cover and soil moisture, which influence the understory microclimate (Majasalmi & Rautiainen 2020), may be affected by this. Taken together, these indirect effects of disturbance history are likely to be reflected in measurements of canopy cover and soil moisture. This, combined with the possibility that the sampling point was too close to the stream, may help explain the absence of significant differences in microclimate variables between 0 and 10 meters (Table 3), despite significant correlations with community composition across all taxonomic groups (Figure 3).

4.2 Limitations

Our sample comprised about 100 observations across 10 sites. Even if we found statistically significant results, our R^2 values were low, suggesting that other important variables we did not measure may be important and that a larger sample size may be needed to detect smaller effects. Furthermore, across the statistical tests, we incorrectly applied the random-effects structure, namely, the nestedness structure of plots within transects within sites was not considered. Our analyses currently include just plots within sites, as a transect variable could not be created due to time constraints. However, significant results were obtained with site as the only random effect, and in future analyses, including transect within site as a random effect would produce more reliable results by better accounting for the nested structure of the data.

4.3 Conclusion

Buffer retention is a key management option for the Swedish forestry sector to comply with EU regulations and policies. Our study provides insight into how species communities across different taxonomic groups vary across a stream-distance gradient and whether microclimate correlates with these changes. We show that species communities differ significantly between 0 and 10 meters from the stream, and that soil moisture and canopy cover are potential explanatory factors. This means that species communities in the forest differ from the communities adjacent to streams. These results can provide the forestry sector with a solid basis for decision-making on the buffer width of the riparian zone during thinning and logging. However, additional factors such as topography and nutrient gradients should also be considered, as they play a major role in understory plant community composition in riparian zones. Thus, more research is needed on this topic to further develop and establish management strategies that will protect biodiversity adjacent to riparian buffers.

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