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Research article

Vascular plant taxonomic and functional richness differentially affect non-vascular photoautotroph communities

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Despite their ecological significance, non-vascular photoautotrophs (NVPs) are frequently excluded from ecological experimental studies, leading to a limited comprehension of how their communities are affected by the ecosystem dynamics and an underestimation of their role in ecosystem functioning. We studied the impact of vascular plant taxonomic and functional diversity on three groups of ground NVPs (lichens, bryophytes, and cyanobacteria) within one of the longest-running plant biodiversity experiments (Biodiversity and Ecosystem Function at Cedar Creek Ecosystem Science Reserve). Utilizing the permanent plot framework of this experiment, we analyzed the effects of almost 30 years of treatment across various levels of vascular plant taxonomic and functional diversity on NVPs. For each diversity level we documented NVP cover and richness. Using generalized linear models we evaluated the effect of vascular plant taxonomic and functional diversity, as well as environmental factors affected by vascular diversity (such as vascular plant cover, light penetration, soil nutrient content, and microtopography) on NVP richness and cover. Using these models, we conducted structural equation modeling analyses (SEM) that allowed us to differentiate the direct and indirect impacts of vascular plant taxonomic and functional diversity on NVPs. Our results showed that both lichen and bryophyte richness and cover decreased with higher vascular plant taxonomic and functional diversity, while cyanobacteria cover increased as a function of the same parameters. We also showed that microtopography serves as better predictor for lichens and bryophytes, while nutrient-related factors perform better as predictors for cyanobacteria. Additionally, our findings indicate that NVP cover ranged from 0.001% to 100% (mean 15%) in the surveyed plots, representing a major, still ignored, component of the experimental plots. This study shows that vascular plant diversity directly and indirectly affects NVP communities, but the consequences of these effects at community and ecosystem levels are still to be explored.

Keywords: bryophytes, cyanobacteria, effects of plant diversity, lichens, long-term ecological research, prairie ecosystem

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Introduction

Non-vascular photoautotrophs (NVPs), such as lichens, bryophytes, and cyanobacteria (Porada et al. 2023) are key components of terrestrial ecosystems (Longton 1992, Belnap et al. 2001, Evans and Lange 2001, Warren 2001). These organisms are particularly important in environments that are limiting for vascular plants, such as landscapes undergoing primary succession or drylands. Very often the colonization of NVPs in these areas represents the first step to turning a limiting environment into a suitable area for vascular plant colonization (Gavini et al. 2019, Havrilla et al. 2019). Despite these well-established effects on soil and other plants, NVPs are very often ignored or poorly sampled in studies of plant community ecology. Most experimental studies of plant functional diversity effects do not include any NVPs in their treatments, and it is often unclear whether or not they occur in the plots. In some cases ‘monoculture‘ treatments can include outright dominance by mosses or lichens (Fig. 1), but the interactions with vascular plants are rarely reported.

Although, in theory, NVPs can compete with vascular plants for common resources, such as light, water, and nutrients, they lack specialized structures for the intake and regulation of the internal content of water and nutrients (Büdel and Scheidegger 2008, Lakatos 2011, Porada et al. 2023). This lack of specialized structures limits NVPs’ abilities to exploit soil resources and therefore their growth rate (Green and Lange 1994, Honegger 2008), creating a feedback between both processes. The higher rates at which vascular plants produce biomass increase their ability to exploit resources, very often promoting the competitive exclusion of NVPs. This negative effect of vascular plants on NVPs can be crucial in the current scenario of climate change which makes vascular plants more frequent and abundant in areas where NVPs are often dominant, such as arctic or alpine environments, drylands, or during the early stages of primary succession (Longton 1992, Chapin et al. 1995, Bardgett and Walker 2004, Walther et al. 2005, Cornelissen et al. 2007, Cutler et al. 2008, Favero-Longo et al. 2012, Rodriguez-Caballero et al. 2018, Llambí et al. 2021). The consequences of these changes for NVP communities (and the possible consequences on ecosystem functioning after the exclusion of NVPs (Porada et al. 2023) are uncertain, because the specific effects of vascular plants on NVP communities are still poorly understood (Cornelissen et al. 2001, Büdel and Scheidegger 2008).

How vascular plants affect NVP communities is often related to their ability to modify abiotic conditions at the micro-environmental level through physical or chemical alterations. For instance, the presence of vascular plants can intercept light, increasing shading at the soil level and maintaining higher soil and air humidity, which changes the microenvironmental conditions for ground NVPs (Cornelissen et al. 2001). Some vascular plants can also modify the soil microtopography, increasing the irregularity of the surface and generating more space for colonization and water accumulation on the soil (Cammeraat 2002). In the same sense, soil nutrient content can change in the presence of vascular plants, depleting or increasing nutrient soil availability by modifying the quantity or the form in which these nutrients are found in the soil (Furey and Tilman 2021).

The magnitude of these modifications depends on vascular plant abundance and nutrient dynamics, which can be driven by vascular plant taxonomic and functional diversity (Cardinale et al. 2007, Tilman et al. 2014, Furey and Tilman 2021). Both vascular plant taxonomic and functional diversity can have independent and complementary effects

Figure 1. Example of a plot mainly colonized by non-vascular photoautotrophs (NVPs), dominated by the moss *Ceratodon purpureus*, in the Big Biodiversity Experiment (E120) at Cedar Creek Ecosystem Science Reserve. Credit: Daniel E. Stanton.

on ecosystem functioning and processes (Reich et al. 2004). Considering this, both vascular plant taxonomic and functional diversity can directly or indirectly affect NVP communities. However, the causes and consequences of increasing both vascular plant taxonomic and functional diversity on NVPs are poorly understood, and little is known about the response of different types of NVPs to vascular plant diversity patterns. Moreover, the specific mechanisms by which vascular plants can affect NVPs are critically understudied (Thompson et al. 2006, Ding and Eldridge 2020, Mallen-Cooper et al. 2022).

The goal of the present study is to assess how vascular plants affect three groups of NVP communities: lichens, bryophytes, and cyanobacteria. We resampled plots in one of the longest-running plant biodiversity experiments (Biodiversity and Ecosystem Function at Cedar Creek Ecosystem Science Reserve, Minnesota, US) for NVP cover and species richness. Despite being presented as plant biodiversity experiments, non-vascular plants have been entirely disregarded in the experimental design and diversity levels (Fig. 1). In this experiment, the richness and identity of vascular plants has been manipulated since 1994, and they have been carefully controlled every year since then (seasonal weeding and reseeding are applied every year). This presents a great opportunity to isolate the effect of vascular plant richness and identity on NVPs, removing the possible effects of NVPs on vascular plant communities. We explored how vascular plant taxonomic richness, functional group richness, and cover affected the richness and cover of lichens and bryophytes, as well as the cover of cyanobacteria, studying not only the direct effects of these factors in NVP communities but also the physical and chemical mechanisms by which vascular plants can affect NVP communities. We hypothesize that 1) NVPs represent a large, undocumented, component of study plots, 2) vascular plant richness and functional diversity will be negatively correlated with NVP cover and richness, 3) vascular plant impacts on NVPs are primarily driven by above-ground effects on microclimate (e.g. light availability), and 4) mosses, lichens, and cyanobacteria will respond differently to vascular plant diversity and identity.

Material and methods

Study area

This study took place in the E120-Biodiversity II experiment (hereafter E120, Supporting information) at Cedar Creek Ecosystem Science Reserve, Bethel, MN, USA (45°24'15.12"N, 93°11'13.1994"W), in an area that used to be a natural prairie. E120 represents an artificial set-up, consisting of 168 9 × 9 m plots with different levels of grasslands plant diversity (1, 2, 4, 8, 16 and 32 species) representing four functional groups: C3 grasses, C4 grasses, non-legume forbs, and legumes (Furey and Tilman 2021). This field experiment was first established in 1994 to understand the role of plant diversity on ecosystem processes (Tilman et al. 1997). The setup of this experiment required removing all vegetal cover (including lichens, bryophytes, and any other biocrust trace) and a series of burning events and soil removal that eliminated all vegetation and seed bank existent in the area. Because of the characteristics of the set-up of this experiment, this can be considered a primary successional process. Besides the annual burning in the plots (used to maintain the species composition in the experimental plots), NVP communities (lichens, bryophytes, and cyanobacteria) have not been disturbed or extracted since the beginning of the experiment (D. Tilman unpubl.). Taking this into consideration, this experiment represents almost 30 years of natural succession of NVPs, although NVP communities are also expected to be affected by the prescribed burning.

Sampling design

From the 168 experimental plots (9 × 9 m) in E120, we selected plots that represented different levels of plant taxonomic (1, 2, 4, 8 and 16 species) and functional diversity (1, 2, 3 and 4 functional groups). We selected only those in which non-woody plants were included. Since some of the experimental plots also serve as a platform for other experiments, we also excluded the plots with treatments additional to the diversity manipulation (e.g. N addition and artificially increased temperature). A total of 80 plots were selected and, in the early spring of 2021, we surveyed lichen, bryophyte, and cyanobacteria communities in each plot.

To characterize lichen, bryophyte, and cyanobacteria communities, each 9 × 9 m plot was sub-divided into a grid of 81 cells of 1 × 1 m (9 × 9 cells). Using this grid as a reference, we distributed uniformly 16 microplots of 0.5 × 0.5 m (for a total of 1280 sampling units in the study) inside each 9 × 9 m plot. The microplots were placed at 1 m from the edge of the 9 × 9 m plot to avoid the edge effect on NVP communities. Each microplot was separated from the others with 1.5–2 m between them (Supporting information).

In each plot, we identified each species of moss and lichenized fungi and estimated the cover (%) of each species. As it is not possible to recognize species of cyanobacteria in the field, we report only the cover of cyanobacterial crusts in each microplot, without differentiating between morphospecies.

To test the possible mechanisms driving the effect of vascular plant taxonomic and functional richness on NVP communities, we used pre-existent databases from E120 to determine the vascular richness, vascular plant functional group richness, vascular plant cover, functional group cover (Tilman 2020), and light penetration (Tilman 2018a) in each plot. We also extracted data on total C (Tilman 2021a), total P (Tilman 2021b), NO_2^- and NO_3^- and NH_4^+ soil content (Tilman 2018b) of each plot. Additionally, we determined the microtopography (mounds and depressions on the soil surface at millimeter and centimeter scale) of each plot with a semi-quantitative scale determining four categories according to the degree of irregularity observed in the surface: flat 1), semi-irregular 2), irregular 3), and very irregular 4). This microtopography is almost entirely generated by vascular plant and moss presence, as biological soil crusts, when present, are relatively thin.

Data analysis

Since lichens, bryophytes, and cyanobacteria have different physiological and ecological requirements, we analyzed the effect of each variable on each type of organism independently. First, using generalized linear models (GLMs), we tested if vascular plant taxonomic and functional diversity and vascular plant cover affected significantly both the cover and richness of lichens and bryophytes (and only cover in the case of cyanobacteria). We also explored the possible mechanisms by which vascular plants affect lichen, bryophyte, and cyanobacteria communities by running individual GLMs of all the variables that can be affected by vascular plants (light penetration, microtopography, total P, total C, total N, NO_2^- and NO_3^- and NH_4^+). For the GLMs, when analyzing cover of NVPs as response variable we used the Gaussian family, but when the response variable was richness, we used the Poisson family.

To reduce the complexity of the models we used the results of the individual GLMs to build models using only the factors that significantly affected lichen and bryophyte cover and richness, and cyanobacteria cover. However, we included vascular plant cover and taxonomic and functional richness, even when non-significant effects were found in the individual GLMs to detect possible indirect effects through other explanatory variables. We also included the cover of the different vascular plant functional groups (C3 grasses, C4 grasses, non-legume forbs, and legumes), since this has the potential of driving one or more of the physical or chemical variables. We used these models to run structural equation modeling analyses (SEM) that allowed us to explore the main variables and the combination of variables significantly affecting our response variables. Because the variables we explored in this study had different units of measurement and magnitude orders, we normalized the data to run the SEMs. We explored models with different levels of complexity, selecting the models using Fisher's C as a measurement of the goodness of fit. The final models only included variables showing statistically significant effects on the response variable or in the main explanatory variables affecting the response variable. The GLMs were conducted using base R, while the SEMs were conducted using the package 'piecewiseSEM' (Lefcheck 2016) in R Studio 2021. 09.01.

Additionally, to detect correlations among the predictive and the response variables, we built correlation matrices using the package 'corrplot' (Wei and Simko 2021) in R Studio 2021. 09.01 (Supporting information).

Results

On average, NVPs covered 14.8% of the 80 experimental plots of E120 surveyed for this study (ranging from 0.001% to 100%). Nearly 9% of the plots had an NVP cover of more than 40%, while 32% presented NVP covers between 10 and 40%. Bryophytes (represented only by mosses) were the NVP community with the highest abundance (10.4% cover on average) and highest richness (6 spp.), followed by Cyanobacteria (near 3.6% cover), and lichens (0.8% cover, 4 spp.). We recorded a total of 10 species including bryophytes and lichens. *Ceratodon purpureus*, *Cladonia* cf. *symphycarpia* and *Polytrichum pilliferum* were the most frequent species, found in 96%, 43%, and 12% of the surveyed plots. The other species were found only in 1 to 10% of the plots.

Effects of vascular plant cover, taxonomic and functional richness, on NVPs

In general, increasing vascular plant cover, as well as taxonomic and functional richness, significantly decreased the overall cover and richness of NVPs ($p < 0.05$ in all cases, Supporting information). However, due to a noticeable disparity in the abundance of the three components of NVPs considered in this study, we will subsequently analyze the three types of organisms separately.

Vascular plant taxonomic and functional richness, as well as vascular plant cover, showed a significant negative impact on bryophytes, while only vascular plant cover showed a significant negative impact on lichen cover. In contrast, cyanobacteria cover was significantly enhanced by both taxonomic and functional richness (Fig. 2). These effects were less evident on lichen and bryophyte richness, showing that bryophyte richness decreases significantly only in function of vascular plant richness, while lichen richness decreased significantly only with the increase of vascular plant cover (Fig. 3).

Physical mechanisms: light and microtopography effects on NVPs

The effects of light penetration on NVP cover were statistically significant in all the groups. Lichen and bryophyte cover increased significantly with the increase of light penetration, while cyanobacteria cover decreased significantly with this same factor (Supporting information). Increasing the irregularity of the soil surface (microtopography scale) significantly increased lichen and bryophyte cover, while it did not affect significantly cyanobacteria cover (Supporting information). Light penetration and microtopography did not affect significantly lichen and bryophyte richness (Supporting information).

Chemical mechanisms: nutrients

Increasing soil nutrient content in general negatively affected lichen, bryophyte, and cyanobacteria cover, although not all the nutrients studied showed significant effects (Supporting information). Bryophyte cover decreased significantly with higher soil content of NO_2^- and NO_3^-, NH_4^+ and C. Lichen and cyanobacteria cover decreased significantly with higher levels of N, although different forms of this nutrient affected

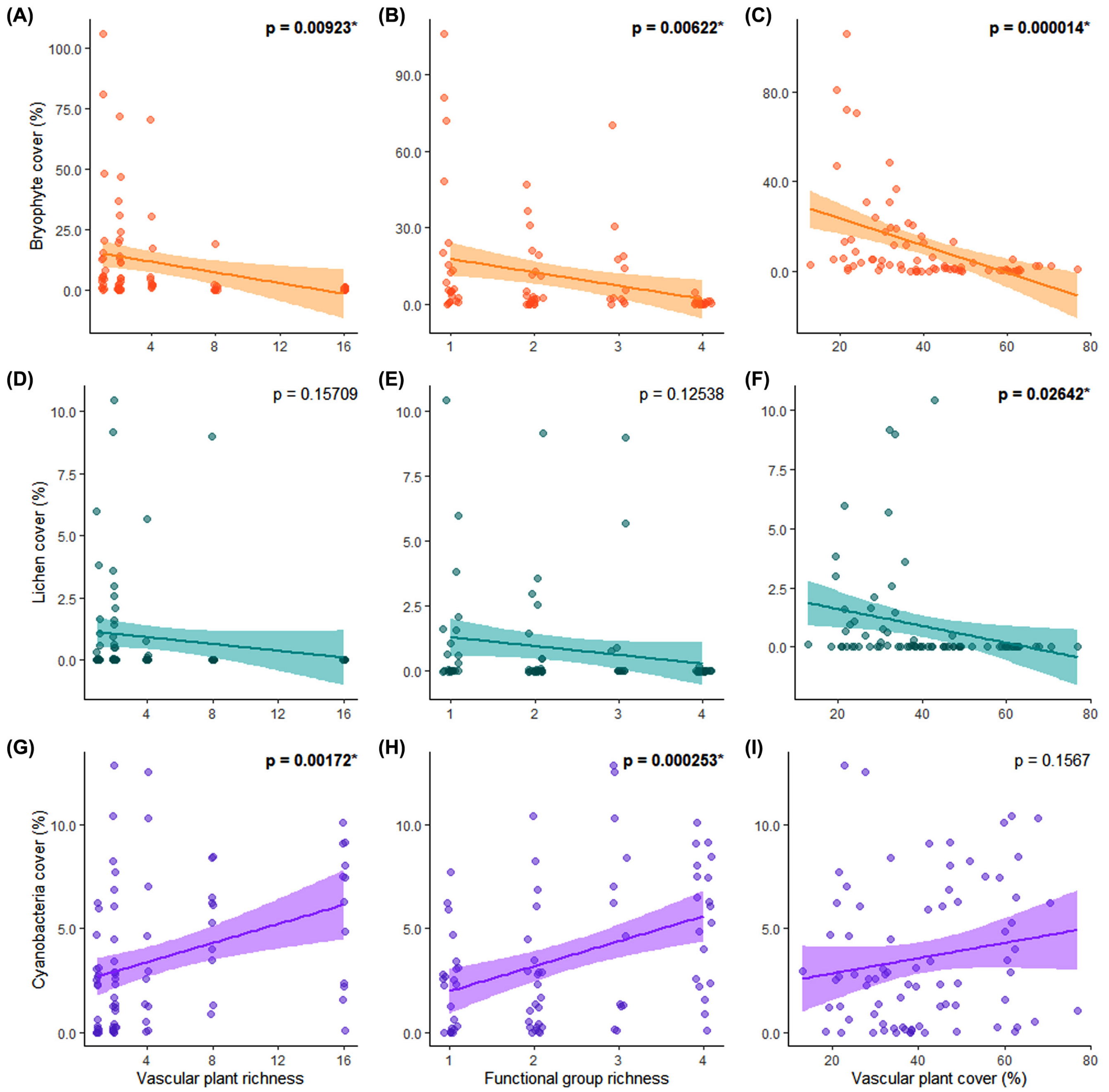

Figure 2. Effect of vascular plant taxonomic richness, functional richness, and cover on bryophyte, lichen, and cyanobacterium cover. The shading area around the lines represents the 95% confidence interval.

each group: lichen cover decreased significantly with the increase of NH_4^+, and cyanobacteria cover decreased significantly with high NO_2^- and NO_3^- soil content (Supporting information). P content was the only chemical factor that did not affect significantly the cover of any of the studied groups (Supporting information). Lichen and bryophyte richness did not respond significantly to increased levels of nutrients in the soil, with the exception of P soil content, which significantly decreased lichen richness (Supporting information).

Integrating the mechanisms

The results of the SEM analyses showed that physical factors were the main factors affecting lichens and bryophytes, while chemical factors were the main drivers of cyanobacteria cover.

Bryophytes – Microtopography (increased by the presence of C4 grasses and negatively affected by the presence of non-legume forbs) was the main factor affecting bryophytes, with more irregular surfaces increasing significantly cover and richness (Fig. 4). Bryophyte cover was also directly affected

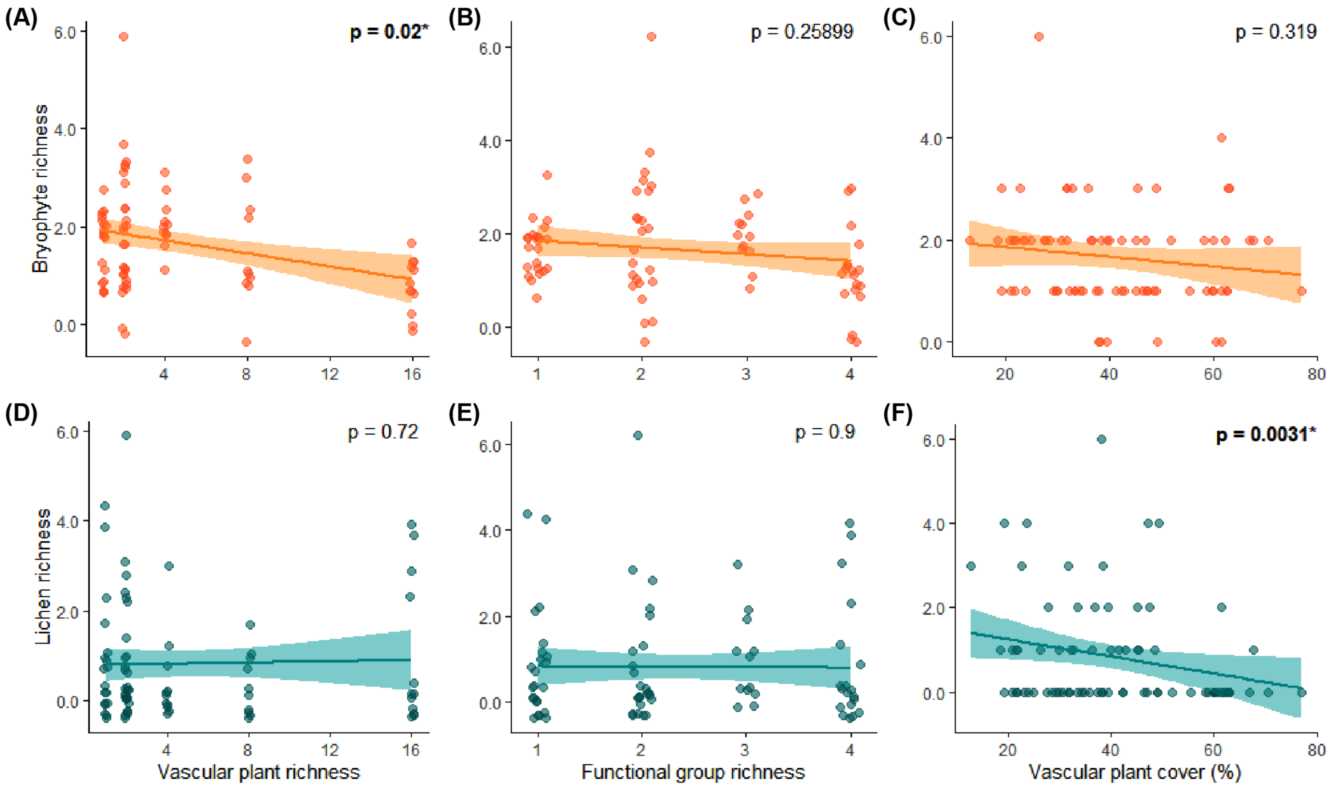

Figure 3. Effect of vascular plant taxonomic richness, functional richness, and cover on bryophyte and lichen richness. The shading area around the lines represents the 95% confidence interval.

by functional groups and the cover of legumes, presenting a significant decrease increasing both factors. The model for bryophyte cover showed the goodness of fit of Fisher's C=10.323 (p-value=0.243), while the model for bryophyte richness showed the goodness of fit of Fisher's C=1.345 with p-value=0.854.

Lichens – Similar to bryophytes, lichen was increased significantly by increasing irregularity on the substrate surface, although lichen cover was negatively affected by legume cover (Fig. 5). The goodness of fit for the model of lichen cover was Fisher's C=7.039 (p-value=0.317). None of the models explored to explain lichen richness showed significant relationships, although the model with better fit (Fisher's C=224.968 with p-value=0) included a positive but not significant relationship with microtopography.

Cyanobacteria – Cyanobacteria cover was negatively affected by increasing levels of NO_2^- and NO_3^- (Fig. 6). The levels of these forms of N in the soil of the plots are positively related to the increase of non-legume forbs, C3 grasses and legumes, which indicates that an increase of these functional groups (independently or in synergy) can cause a decrease in cyanobacteria cover. In contrast to to bryophytes,

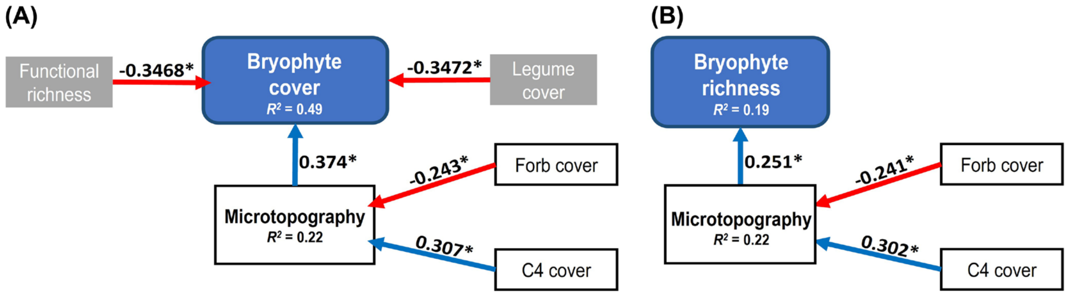

Figure 4. Models for bryophyte cover (A) and richness (B). Blue squares represent the response variable, white squares variables related to the physical effects of vascular plants, and gray squares variables that affect both physical and chemical mechanisms. Red arrows indicate negative effects and blue arrows represent positive effects. The numbers above the arrows indicate the coefficients. Only variables with statistically significant effects are included in the models. Abbreviations: functional richness (number of vascular plant functional types in the plot), C4 cover (C4 grass cover in the plot).

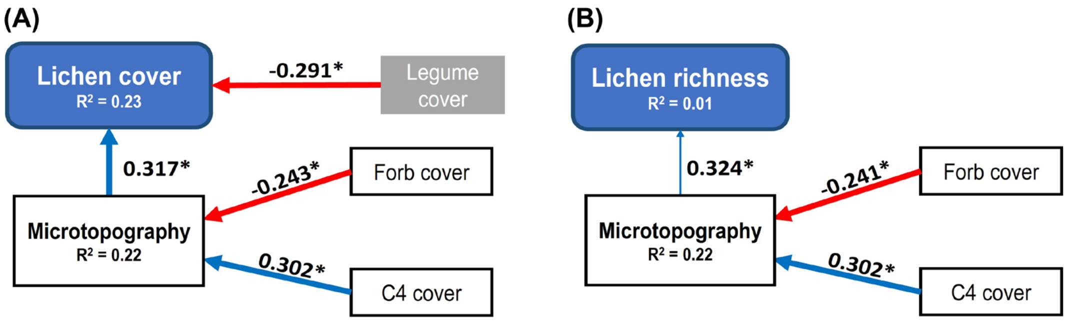

Figure 5. Model for lichen cover (A) and richness (B). Blue squares represent the response variables, white squares variables related to the physical effects of vascular plants, and gray squares variables that affect both physical and chemical mechanisms. Red arrows indicate negative effects, while blue arrows represent positive effects; bold arrows indicate significant effects, while thin arrows represent non-significant relationships. The numbers above the arrows indicate the coefficients. In the lichen cover model only variables with statistically significant effects are shown. Abbreviation: C4 cover (C4 grass cover in the plot).

cyanobacteria cover showed a significant positive association with vascular plant functional richness. The goodness of fit for this model was Fisher's C=7.164 (p-value=0.519).

Discussion

NVPs, such as lichens, bryophytes, and cyanobacteria, are often grouped in contrast to vascular plants mainly because of their lack of active control of water gain and loss, which gives them the ability to grow and dominate in water-limited ecosystems, where vascular plants are scarce or absent, but few competitive abilities when vascular plants are present, resulting in a exclusion of NVPs when vascular plants are abundant (Belnap 2003, Porada et al. 2023). As expected, our results showed that NVP cover and richness are negatively affected by increasing vascular plant taxonomic and functional richness, as well as plant cover (Supporting information). However, contrary to the expectation of a similar response from all the NVPs studied, our results showed two contrasting patterns in the effect of vascular plants on the NVPs studied: one group (lichens and bryophytes) was negatively affected by increasing cover and taxonomic and functional diversity of vascular plants, while cyanobacteria were positively related to the same parameters.

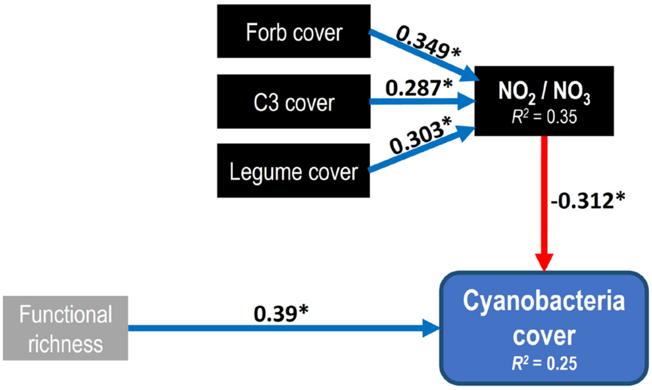

Figure 6. Model for cyanobacteria cover. Blue squares represent the response variable, black squares the chemical effects, and gray squares variables that affect both physical and chemical mechanisms. Red arrows indicate negative effects, while blue arrows represent positive effects. The numbers above the arrows indicate the coefficients. Only variables with statistically significant effects are shown in the model. Abbreviations: NO_2^-/NO_3^-: nitrate/nitrite soil content.

These findings suggest that these organisms are not only constrained by different physical or chemical factors specific to their physiological requirements, but also that they operate at different temporal and spatial scales. For instance, lichens and bryophytes are mostly perennial organisms that are present in the study area all year round. In consequence, they can be constrained by seasonal factors (e.g. a light-limited environment during the summer, low temperatures during the winter, and controlled fire during early spring burning treatment) which cumulatively affect their yearly growth rates and biomass accumulation. Contrastingly, cyanobacteria colonies show a seasonal peak, particularly during the spring, when the snow is melting and the accumulation of water on the warming soil surface promotes the rapid growth of these organisms (Bowker et al. 2002). The temporal scales at which these organisms operate seem to be key to understanding the detected patterns.

How vascular plants affect lichens and bryophytes

As expected, lichen and bryophyte cover was negatively affected by vascular plant taxonomic and functional richness, as well as vascular plant cover, while an increase in light penetration increased the cover by these organisms. These parameters are interrelated, as greater vascular plant richness promotes increased vascular plant cover/biomass (Cardinale et al. 2007, Tilman et al. 2014, Furey and Tilman 2021, Supporting information), reducing light penetration and potentially increasing humidity at ground level. Both lichen and bryophyte abundance and biomass accumulation depend on their photosynthetic rates, which are limited by light and water availability (Lange et al. 2001).

However, despite light being a key limiting factor for both bryophytes and lichens, the SEM analysis results revealed that microtopography is the primary factor influencing the cover and richness of these organisms (Fig. 4, 5), showing that increasing the irregularity of the soil surface significantly benefits lichen and bryophyte cover, as well as bryophyte richness. This microtopographical variation is present as mounds and depressions ranging from a few millimeters to several centimeters above or below the soil surface (Nash et al. 2003, Nippert et al. 2012). This irregularity on the soil surface results in a higher accumulation of water and nutrients in the depressions (Nash et al. 2003, Biederman and Whisenant 2011), generating a beneficial microenvironment for both lichens and bryophytes, which more often colonize these depressions (Cárdenas-Henao and Stanton unpubl.). However, since NVP communities in the experimental plots have not been disturbed since the beginning of the experiment, a feedback between microtopography and cover of NVPs (Rodríguez-Caballero et al. 2012) should be further explored in the study area.

Although we did not consider the direct effects of the different vascular plant functional groups (C3 grasses, C4 grasses, non-legume forbs, and legumes) on NVP cover and richness, the overall cover of each functional group in each plot was considered in the SEMs. Similar to other studies in prairies (Nash et al. 2003), the SEM analysis showed that high levels of irregularity on the soil surface are related to the higher cover of C4 grasses, which is related to their perennial nature and high production of root biomass (Nash et al. 2003). Additionally, legumes showed a direct negative effect on lichen and bryophyte cover. In our study system, an increase in legume cover modifies several aspects of productivity in the plots, such as increasing significantly vascular plant cover (data not shown), probably derived from the significantly increased levels of N (both NH_4^+ and NO_2^-/NO_3^-, Furey and Tilman 2021). If increasing vascular plant cover and overall biomass reduces light penetration, legumes can limit lichen and bryophyte biomass accumulation, promoting limiting factors such as vascular plant cover. These findings highlight the importance of considering vascular plant functional groups as important factors that can indirectly affect NVP communities.

How vascular plant communities affect cyanobacteria

Our findings revealed two linked primary trends concerning cyanobacteria. First, their cover was positively impacted by vascular plant functional and taxonomic richness, while negatively impacted by light penetration. However, it is essential to note that the results do not suggest a direct inhibition of cyanobacteria growth due to increased light penetration modulated by vascular plant cover.

Our sampling was conducted during the early spring, when the melting snow leads to soil saturation and vascular plant cover is still very low (Fig. 1). This timeframe corresponds to the peak of abundance of terrestrial cyanobacteria in the study area (authors' direct observation). However, the light penetration data used in this study represent its long-term dynamics in the study area, measured yearly at the peak of the vascular plant growth season, which makes this parameter a weak predicting factor for cyanobacteria cover. Other studies reported that cyanobacteria-dominated biocrusts depend on vascular plant productivity, since increasing vascular plant biomass reduces light penetration to the ground (She et al. 2022).

Even if light is necessary for photosynthesis, increasing light penetration can reduce humidity at soil level, another limiting factor in photosynthesis. Although terrestrial cyanobacteria are reported to be desiccation tolerant (Davey 1989, Scherer and Zhong 1991), a tradeoff between light penetration and surface soil humidity can regulate cyanobacteria abundance. It is necessary to conduct a seasonal assessment of cyanobacteria cover, light penetration, and soil level humidity, to understand the temporal relationship between these factors in the study area.

Our second key finding showed that increased values of NO_2^- and NO_3^- significantly decreased cyanobacteria cover. Cyanobacteria can fix atmospheric N (Cornelissen et al. 2007), but when N is not a limiting nutrient these organisms limit N fixation, a very energetically costly process (reviewed by Bhaya et al. 2002, Stal 2015). In these cases, they use nitrate, nitrite, or ammonium as an N source (Whitton 1992, Herrero et al. 2001). Similar to lichens, high levels of N deposition directly affect cyanobacteria growth, decreasing total chlorophyll content (Zhou et al. 2016), or indirectly increasing vascular plant productivity (She et al. 2022), which would outcompete cyanobacteria. According to our results, NO_2^- and NO_3^- deposition in the experimental plots is regulated by the abundance of legume and not legume forbs, as well as C3 grasses (Fig. 6), but it also can be related to the different levels of diversity in the experiment (Furey and Tilman 2021) or to aerial deposition from the agricultural matrix where the experiment is located.

Last, our results suggest a positive but not significant relationship between soil P content and cyanobacteria cover, although this nutrient is expected to be the most limiting nutrient for these organisms (Bhaya et al. 2002, Pentecost and Whitton 2012), given its importance for N fixation stimulation (Liengen 1999, Bhaya et al. 2002). This suggests two scenarios: first, the study plots are not particularly P limited enough to represent a constraint for cyanobacteria communities; and second, the absence of N limitation in the experimental plots makes P less limiting for N acquisition. However, since P seems to be depleting with time in the experimental plots while increasing vascular plant biomass (Furey and Tilman 2021), further analyses on the effects of different levels of P on cyanobacteria communities will provide another key element on the understanding of the long-term effects of increased vascular plant diversity on NVPs.

NVP richness and prescribed burning

It is notable that this study showed a very low richness of both lichens and bryophytes (two and four species reported in the experimental plots, respectively). Even areas in the surrounding prairies show higher richness (Johansson and

Reich (2005) reported up to 11 species of ground lichens at the prairies in Cedar Creek). However, prescribed burning is applied in the experimental plots once a year before the start of the growing season. Although fire can increase light availability on the soil surface by eliminating the shade produced by vascular plants, the recovery rate of both lichens and bryophytes after a fire event is thought to be relatively slow (given their low growth rates), and the recovery process can be slower than the disturbance frequency, reducing considerably the cover and richness of these organisms (Schulten 1985, Ray et al. 2015). It may be that the high frequency of burning used to maintain vascular plants constrains lichen and bryophyte communities to those species that can tolerate constant disturbances (Schulten 1985, Davies and Legg 2008, Ray et al. 2015, Calabria et al. 2016). We acknowledge that this is possibly one of the factors, together with vascular plant taxonomic and functional richness, affecting NVP cover and richness in the experimental plots. Further research is required in the research location to unveil the effects of prescribed burning on lichens, bryophytes, and cyanobacteria, and how this factor interacts with vascular plant diversity.

Reflecting on the importance of including NVPs in long-term plant diversity studies

Although the present study focused on understanding how vascular plant functional and taxonomic diversity affect NVP communities, our results on the abundance of these organisms in the experimental plots raised questions about the potential effects of NVPs on overall ecosystem functioning and, consequently, on the results generated in this long-term experiment year after year.

More often than not, NVPs are ignored as components in long-term ecological studies, either due to a lack of knowledge about their taxonomy and ecology or to the false assumption that, given the scale at which these organisms operate or respond, they are not relevant at larger spatiotemporal scales. Our results demonstrated that, on average, 14.8% of the surveyed plots are covered by various types of NVPs, and in nearly 10% of these plots, NVPs represent more than 40% of the area. Furthermore, NVPs are present in these plots year-round (even during winter months), having a peak of growth (lichens and bryophytes) and abundance (cyanobacteria) during the early spring, representing the main primary producers before vascular plants' main growing season. Moreover, some of them are well-known for improving soil fertility and releasing substances that inhibit or promote plant growth (reviewed by Singh et al. 2014).

Additionally, these experiments and all the associated data are specifically designed to measure vascular plant contribution to ecosystem functioning, making it even harder to study the contribution of NVPs to ecosystem dynamics together with vascular plants in a standardized way. One of the main barriers to including NVPs in these assessments is the phenological mismatch between these organisms and vascular plants. The peak of growth and/or abundance of NVPs occurs during early spring, even when temperatures are low, but water and light are not limiting factors. While it would pose a logistical challenge, we suggest monitoring these factors beyond the peak of vascular plant growth to comprehend their temporal dynamics. This approach would facilitate the inclusion of NVPs as part of long-term field experiments. We hope that this first assessment of NVP communities in this emblematic field experiment motivates this and other long-term ecological field experiments to include NVPs as integral parts of their long-term monitoring programs (a great example of this implementation is the International Tundra Experiment (ITEX), Henry et al. 2022), even in those ecosystems where vascular plants are dominant. If not, the role of NVPs in large-scale ecological processes will remain a mystery and the ecological story of these ecosystems will remain incomplete.

Conclusions

Vascular plant diversity has been widely studied as a key component of ecosystem functioning and an important factor influencing the diversity and abundance of other organisms. However, the mechanisms by which vascular plants influence other photoautotrophs are not fully understood, particularly in often overlooked organisms such as NVPs. This study showed that vascular plant diversity, both taxonomic and functional, affects NVPs directly and indirectly, mainly influencing physical and chemical factors that constrain NVPs in different spatial and temporal scales. Two consequences emerge from this: first, although NVPs have similar limitations, these limiting factors affect differently their ecology, and consequently, their contribution to spatial and temporal dynamics of ecosystem functioning. Second, the effect of vascular plants on NVPs is not uniform throughout the year and is likely asynchronous, varying seasonally depending on vascular plant productivity which regulates the specific factors limiting NVPs. Future studies of grassland diversity need to not only include the often extensive cover of NVPs that can be present, but also to account for the key phenological differences that have contributed to this important vegetation component being overlooked in the past.

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Author contributions

Mariana Cárdenas-Henao: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (equal). **Daniel E. Stanton**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the EDI Data Portal: https://doi.org/10.6073/pasta/2a3036e402a65e7db08098761db22f1d (Cárdenas-Henao 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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