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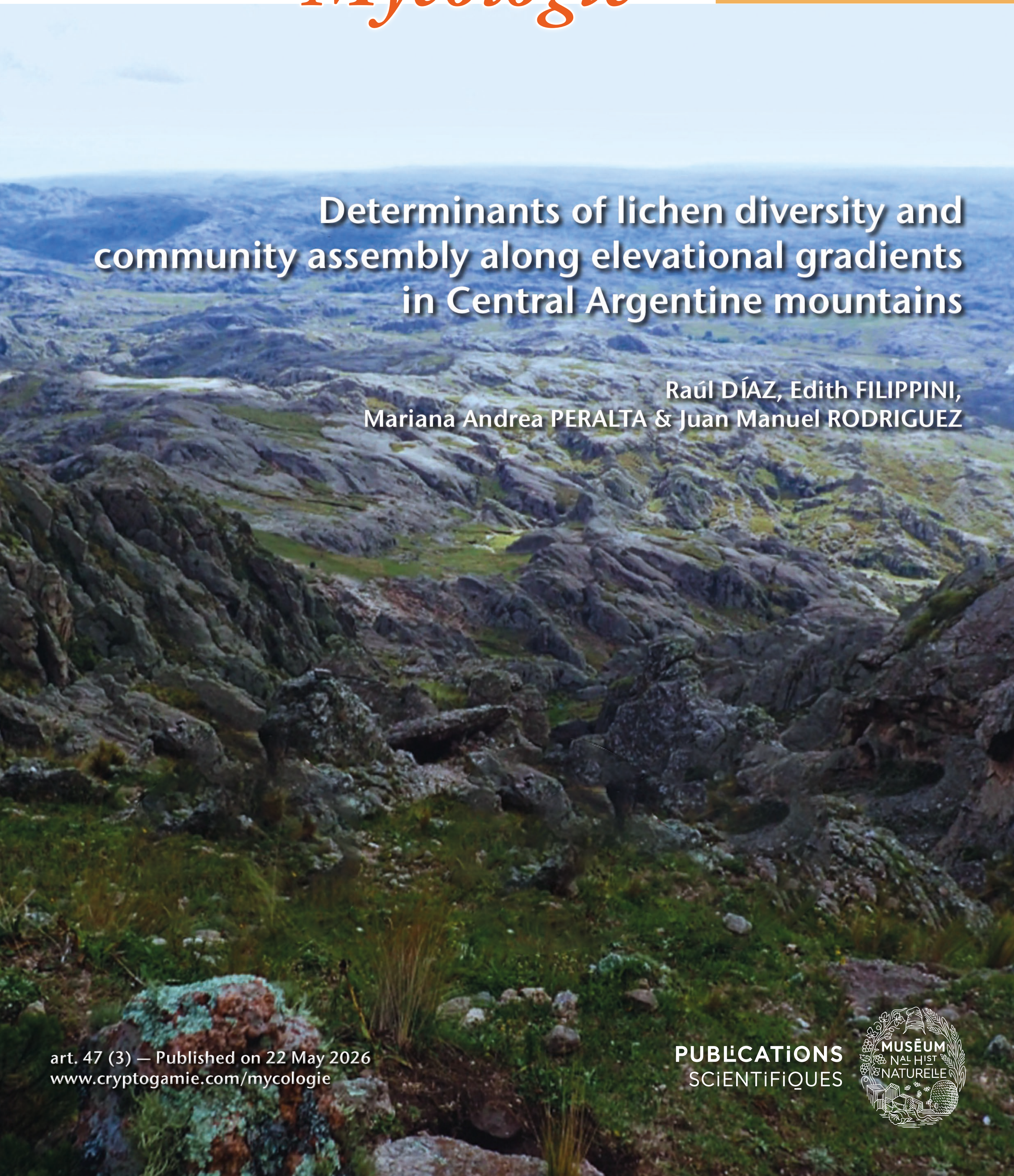

Determinants of lichen diversity and community assembly along elevational gradients in Central Argentine mountains

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Determinants of lichen diversity and community assembly along elevational gradients in Central Argentine mountains

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ABSTRACT

The distinctive features of alpine ecosystems, along with complex evolutionary and migration patterns, contribute significantly to the remarkable species richness found within these environments. This study aimed to investigate the environmental effects of elevation and microsite characteristics on the diversity and community structure of saxicolous lichens in mountain ecosystems. We also explored the hypothesis that lichen species may migrate to more sheltered microsites in response to climate change. We surveyed 406 plots across seven elevation levels (900 to 2700 m a.s.l.), documenting saxicolous lichen species richness and community composition. Microsite factors such as rock aspect, inclination, and sun exposure were recorded. Statistical analyses included generalized linear mixed models (GLMMs) for richness and community weighted mean trait (CWM) by growth form, as well as multivariate analyses (CCA and NMS) to assess the influence of environmental variables on lichen community composition. We identified 195 lichen species, with significantly lower richness at 900 m a.s.l. compared to higher elevations. Richness was also greater on steep and south-facing rocks. Crustose CWM varied significantly with rock aspect, while foliose and fruticose CWMs were influenced by rock inclination. Multivariate analyses indicated that elevation, rock inclination, rock aspect, and sun exposure significantly shaped the community structure. The study highlights the combined influence of macro- and micro-environmental factors on lichen diversity. Crustose species tolerate harsher conditions, while foliose and fruticose lichens prefer steeper, south-facing microsites. These findings underscore the importance of considering both scales of environmental variation when analyzing the assembly and biodiversity of lichen communities, especially under scenarios of climate change.

KEY WORDS
Climate change,
ecological niches,
endemism patterns,
environmental gradient,
lichen diversity,
microsite,
mountain ecosystems.

RÉSUMÉ

Déterminants de la diversité des lichens et de l'assemblage des communautés le long de gradients altitudinaux dans les montagnes du centre de l'Argentine.

Les caractéristiques distinctives des écosystèmes alpins, ainsi que les schémas complexes d'évolution et de migration, contribuent de manière significative à la richesse en espèces remarquable que l'on trouve dans ces environnements. Cette étude visait à examiner les effets environnementaux de l'altitude et des caractéristiques des microsites sur la diversité et la structure de la communauté des lichens saxicoles dans les écosystèmes de montagne. Nous avons également exploré l'hypothèse selon laquelle les espèces de lichens peuvent migrer vers des microsites plus abrités en réponse au changement climatique. Nous avons étudié 406 parcelles sur sept niveaux d'altitude (900 à 2700 m d'altitude), documentant la richesse en espèces de lichens saxicoles et la composition de la communauté. Des facteurs de microsite tels que l'aspect rocheux, l'inclinaison et l'exposition au soleil ont été enregistrés. Les analyses statistiques comprenaient des modèles mixtes linéaires généralisés (GLMM) pour la richesse et les moyennes pondérées de la communauté (CWM) par forme de croissance, ainsi que des analyses multivariées (CCA et NMS) pour évaluer l'influence des variables environnementales sur la composition de la communauté de lichens. Nous avons identifié 195 espèces de lichens, avec une richesse significativement plus faible à 900 m d'altitude par rapport aux altitudes plus élevées. La richesse était également plus importante sur les rochers abrupts et exposés au sud. Les CWM crustacés variaient significativement avec l'aspect du rocher, tandis que les CWM foliacés et fruticuleux étaient influencés par l'inclinaison du rocher. Des analyses multivariées ont indiqué que l'altitude, l'inclinaison du rocher, l'aspect du rocher et l'exposition au soleil façonnaient de manière significative la structure de la communauté. L'étude met en évidence l'influence combinée des facteurs macro- et micro-environnementaux sur la diversité des lichens. Les espèces crustacés tolèrent des conditions plus difficiles, tandis que les lichens foliacés et fruticuleux préfèrent les microsites plus abrupts et exposés au sud. Ces résultats soulignent l'importance de prendre en compte les deux échelles de variation environnementale lors de l'analyse de l'assemblage et de la biodiversité des communautés de lichens, en particulier dans le cadre de scénarios de changement climatique.

MOTS CLÉS
Changement climatique,
niches écologiques,
modèles d'endémisme,
gradient
environnemental,
diversité des lichens,
microsite,
écosystèmes de
montagne.

INTRODUCTION

Alpine ecosystems are characterized by various distinctive features, including geographic isolation, unique climatic conditions, tectonic uplift, and pronounced microclimatic variations (Scherrer & Körner 2011). These factors, along with the intricate evolutionary and migration patterns throughout history, contribute significantly to the remarkable species richness found within these ecosystems (Körner 1999). Collectively, these attributes, coupled with the steep gradients inherent to mountainous regions, render high-altitude areas as veritable hotspots, providing ideal habitats for endemic species (Merckx *et al.* 2015).

Ecological studies suggest that species richness in lichen communities of mountainous regions is predominantly shaped by elevation. Research has shown that lichen richness patterns along elevational gradients are not uniform and can vary significantly with altitude. In some instances, the number of lichen species increases with elevation (Bässler *et al.* 2016). While lichen diversity is often highest at mid-elevations, a decline in both diversity and richness may occur with bigger elevational gradients (Bruun *et al.* 2006; Baniya *et al.* 2010). Importantly, elevation is not the only abiotic factor influencing lichen community characteristics; microsite conditions such as slope and aspect also play a crucial role in determining lichen growth, community composition, and richness (Rutherford & Rebertus 2022).

Current research also underscores the pivotal role played by elevation in shaping the composition of lichen communities (Nanda *et al.* 2021). However, microsite conditions such as slope and aspect also impact the arrangement of lichen species. To some extent, microsite conditions such as micro-slope and microsite aspect have been found to be significant in determining lichen community composition (Rutherford & Rebertus 2022). The fundamental concepts of elevational gradient and microsite conditions are central to characterizing the lichen community composition in a mountainous system. Recent research suggests that microsites with steep inclinations offer more sheltered conditions to lichens, while those with low or flat inclinations expose lichens to varying conditions such as UV radiation and fluctuating temperatures (Díaz *et al.* 2022, 2023). Naturally, these distinct niches harbor populations adapted to their specific environmental conditions, whether in more sheltered or exposed microsites.

It is essential to consider that different niches support different species. Therefore, a comprehensive description of the community, accounting for all niches, is crucial for a nuanced interpretation of this ecological succession model. Previous research by Rodriguez *et al.* (2017) proposed that in a climate change scenario, lichen species may respond differently according to the habitat they occupy as a consequence of a warmer climate. This has strong implications for the species distribution in extra Andean mountains from Central Argentina. According to their prediction, species at lower altitudes occupying south-facing slopes will need to migrate upwards. However, at the mountain tops, most species might still find refuge through microsite segregation to compensate for climate change under a warming scenario.

In this study, we tested this hypothesis by including more transects with a narrower elevational range. This approach allowed us to describe the lichen community at various points in mountains from Central Argentina. If the prediction of Rodriguez *et al.* (2017) holds true, we expect that mountain species at the mountain top will not be present in the narrower transects, indicating their potential disappearance in a climate change scenario.

On the other hand, some ecology patterns are also related to morphological traits, such as water retention capabilities and lichen growth forms. Beyond describing the communities and considering the previous model proposed for the same study site, we aim to address broader ecological questions, like what limits species distributions? Why do species occur in some places but not in others?

It has been discussed that lichen occupy certain environmental niches depending on their different growth forms (Bässler *et al.* 2016). In this sense, traditionally, crustose lichens have been regarded as resilient to exposed conditions. However, this perception is largely based on findings from controlled experimental settings, and only a restricted number of studies have systematically evaluated, through controlled sampling methodologies, whether crustose species are adapted to better cope with exposed environments than foliose of fruticose ones (Nascimbene & Marini 2015). While the detailed aspects of lichen morphology have long been understood, a systematic understanding of how lichen morphological traits contribute to functional aspects in lichen community ecology remains elusive (Büdel & Scheidegger 2008).

Traditional classifications of lichen growth forms – particularly the fundamental categories of crustose, foliose, and fruticose with their detailed subdivisions (Grube & Hawksworth 2007) – have served as valuable frameworks in ecological research. While we recognize this tripartite classification represents a simplification of lichen morphological diversity, it remains a practical and ecologically meaningful perspective. However, emerging evidence of gradient-like trait variations (Wan & Ellis 2019), intraspecific morphological plasticity, and community assembly patterns across environmental gradients (Pérez-Ortega *et al.* 2012; Stanton 2015; Díaz *et al.* 2022) suggests these forms may better represent points along an ecological continuum rather than discrete categories. In this study, we aimed to evaluate the practical applicability of this categorical framework (crustose-foliose-fruticose) within our study site's environmental gradient, testing its effectiveness as an ecological indicator despite its inherent simplifications.

There have been studies assessing the role of competition in lichen community structure, yet scientific understanding of the scales at which competition influences these communities remains limited (Armstrong 2008). Other factors such as stressful environmental conditions, allelopathy of lichen substances, and more play significant roles in competition, but evidence suggests that morphology is the primary driver of competitive interactions. This includes morphology at very small scales; for example, species with wider and thicker lobes, or margins with greater height, are able to overgrow their competitors (Harris 1996; Armstrong & Welch 2007).

Studies have also identified specific communities occupying elevational and microsite niches, suggesting that species sharing growth types or even taxonomic relationships at the genus level tend to occupy similar niches. For instance, *Usnea* Dill. ex Adans. and *Parmotrema* A. Massal. species often form a wall or carpet on south-facing rocks (Rodriguez *et al.* 2017). This highlights the relevance of analyzing community assemblies at both the genus and species levels for a better understanding of these patterns. By doing so, we can gain deeper insights into the ecological and evolutionary processes shaping lichen communities.

In this study, we examine whether variables dependent on the altitudinal gradient influence the richness and composition of lichen species within communities. We propose that these patterns are modified by microhabitat variables, hypothesizing that the most stressful conditions (e.g., greater insolation, lesser slope, and north-facing orientation in the southern hemisphere) favor the colonization of more tolerant species. Additionally, we investigate how different lichen growth forms contribute to community assembly, exploring potential explanations for these observed patterns.

MATERIAL AND METHODS

ABBREVIATIONS

CCA	Canonical Correspondence Analysis;
CI	Confidence Intervals;
CWM	Community-Weighted Mean;
CWMs	Community-Weighted Means.

STUDY SITE

The "Sierras Grandes de Córdoba" are situated within the "Sierras Pampeanas" mountainous system, which ranks among the largest and highest systems after the "Los Andes" in South

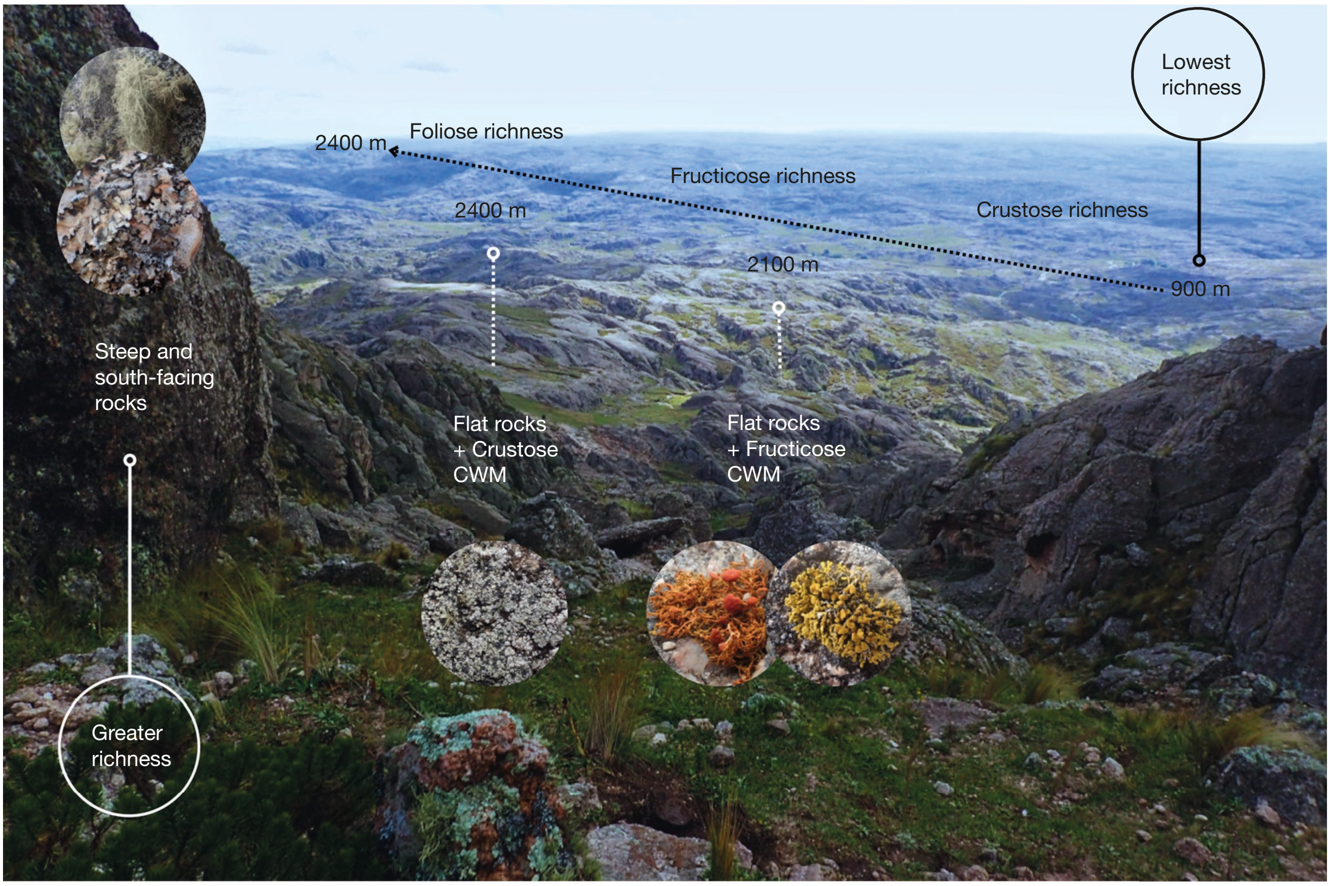

Fig. 1. — Graphical summary and representation of the main results. **White symbols** and **letters** depict the effect of elevation on lichen community composition and species richness, while **black symbols** and **letters** indicate the effect of microsite conditions (rock aspect and inclination). **Dotted black lines** connecting elevation and microsite illustrate interaction effects, showing specific responses to microsite conditions at particular elevations. Representative species from crustose, foliose, and fruticose communities are shown within their dominant niches. Abbreviations: See Material and methods. Photo credits: Raúl Díaz and Edith Filippini.

America (Cabido *et al.* 1998). These systems encompass a diverse landscape, characterized by a mosaic of grasslands, forests predominantly populated by *Polylepis australis* Bitter, and approximately 30% of the surface area occupied by rocky outcrops (Cingolani 2004; Cingolani *et al.* 2008). The weather in this region is temperate, with significant temperature fluctuations particularly noticeable during the winter months. Rainfall is concentrated in the warmer seasons, while frost occurs throughout much of the year, occasionally accompanied by snowfall (Cingolani *et al.* 2015).

Weather is typical of mountain-subtropics, in which winter is the dry season (June, July and August) and summer is rainy (December, January and February), however the dry season can be delayed until November. Also, snow occasionally occurs in winter (Cingolani *et al.* 2015). Temperature variations correspond closely with seasonal changes, resulting in a distinct thermal winter and a brief, cool summer. Temperature changes with elevation and microsite, data collected over 2 years by Díaz *et al.* (2022) revealed median temperatures of 17 ± 5°C (900 m a.s.l.), 15 ± 4°C (1800 m a.s.l.), and 10 ± 3°C (2700 m a.s.l.) in north-facing microsites, whereas temperatures in south-facing microsites were recorded as 16 ± 6°C (900 m a.s.l.), 13 ± 5°C (1800 m a.s.l.), and 8 ± 5°C (2700 m a.s.l.). Rainfall also changes seasonally and along elevation. Over a 20-year data series, average rainfall reached 127 ± 14.52 mm for rainiest months, and 7 ± 0.83 mm for the driest months, and 68.5 ± 55 mm/year, average values ± s.d. were calculated from Colladon (2014).

SAMPLING DESIGN

Sampling was conducted along four transects (Fig. 2), all originating at 900 meters above sea level (m), with distinct upper elevations, the two narrower at 2100 m (Los Gigantes) 2400 m (Parque Nacional Quebrada del Condorito), and 2700 m, and two broader which share the same upper limit of 2700 m a.s.l. (Cerro Champaquí and Cerro Linderos). The different heights depend on the highest peak of each sector. Transects were selected to encompass the latitudinal heterogeneity of Las Sierras. At intervals of 300 ± 100 m along each transect, rocks measuring three meters or larger were selected, with a minimum separation distance of 10 meters between each rock. To address microsite variability, rock inclination and aspect were considered as microsite variables. Assessment was carried out on three rocks for each specified rock inclination within north and south aspect conditions, categorized as flat (0° to 20°), low (35° to 55°), and steep (<80°) relative to the

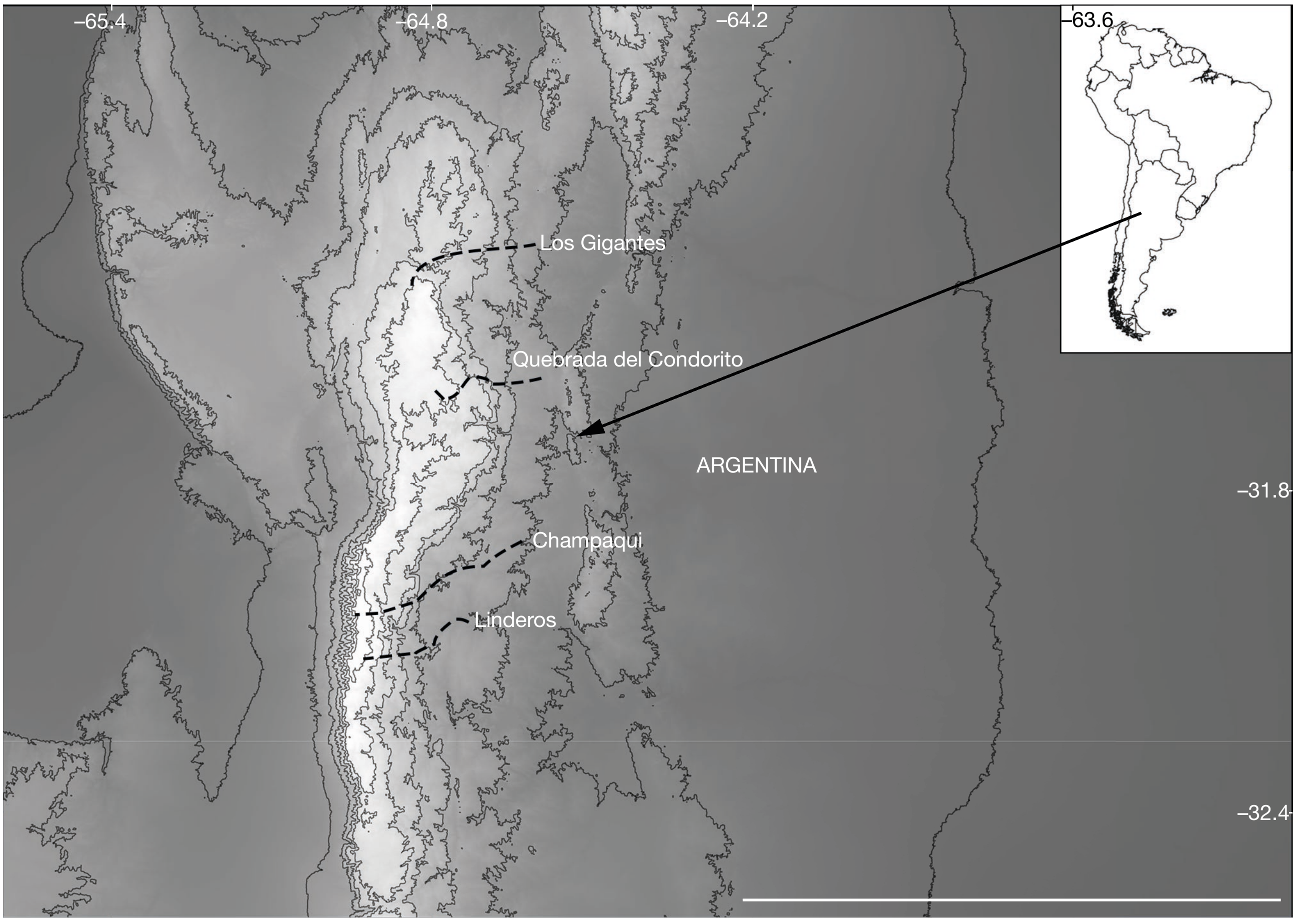

Fig. 2. — Study site and sampling points. Scale bar: 68 kilometers.

ground, resulting in a total of 18 rocks per elevation interval. In this paper, the term "sites" will be used to refer to these specific intervals. A total of 424 rock outcrops were measured.

Over each of the 424 rocks, five grids were applied equidistantly to each rock under investigation, with each grid measuring 20 × 20 cm and further subdivided into 25 sub-squares, each measuring 16 cm^2. Frequency was determined by quantifying the instances in which a particular lichen species occupied a sub-square, while richness was defined as the total number of distinct species observed within a given grid. Other descriptive environmental data like solar exposure, length and width of the rock surface and surrounding vegetation were recorded, however they were excluded from the models because they lacked significant statistical data according to the model selection criteria (Inchausti 2023). Solar exposure was measured according to the procedure used by Renison *et al.* (2006).

Species identification

Routine methods for lichen species identification were followed. This involved thin-layer chromatography (Tønsberg 2002), microscopic, macroscopic and anatomic observation, that subsequently were subjected to dichotomous keys specific to their respective taxonomic (Estrabou 1999; Nash *et al.* 2004; Rodriguez *et al.* 2011; Knudsen *et al.* 2012; Spielmann & Marcelli 2020). Voucher species were deposited in the LUTI herbaria.

Statistical modeling

To test the richness dependency on elevation, microsite inclination and aspect, we conducted a model selection from a GLMM, assuming lichen richness followed a Poisson distribution given that richness are count values and it showed the best probability distribution (Inchausti 2023). Richness was modeled as the response variable, while environmental variables (elevation, rock aspect, rock slope) were treated as fixed effects. Sites were modeled as random effects, with rocks nested within sites (Inchausti 2023). For flat rocks, the aspect was categorized as "flat", and no directional aspect was considered, as this was supported by model selection, including checks for multicollinearity using VIF and other model fitness indicators (see Appendices 3 and 4). Interaction effects between elevation, aspect, and slope were also evaluated.

Community-weighted mean trait (CWM) of growth form values were calculated. In order to calculate the CWM for each growth form, a frequency matrix of crustose, foliose, and fruticose species was constructed. Following this process, the CWM weighted by their relative abundance for growth form

Table 1. — Generalized Mixed Linear Models (GLMM) of the species richness and crustose, foliose and fruticose species richness. Only the fixed effects or their interaction with significant differences are informed. **Bold values** indicate statistically significative differences.

	Richness			Crustose Richness			Foliose Richness			Fruticose Richness		
Fixed effects	**Chisq**	***df***	**Pr (>*Chi*)**	**Chisq**	***df***	**Pr(>*Chi*)**	**Chisq**	***df***	**Pr(>*Chi*)**	**Chisq**	***df***	**Pr(>*Chi*)**
Elevation	78.866	6	**<0.001**	60.3259	6	**<0.001**	**48.436**	6	**<0.001**	62.325	6	**<0.001**
Rock aspect	6.65	2	**0.03**	1.681	2	**0.431**	–	–	–	14.497	2	**<0.001**
Rock inclination	20.368	2	**<0.001**	–	–	–	**38.51**	2	**<0.001**	10.616	2	**0.005**
Elevation × Rock aspect	–	–	–	25.381	12	**0.01**	–	–	–	–	–	–
Elevation × Rock inclination	–	–	–	–	–	–	22.429	12	0.032	–	–	–
Observations		1212			1212			1212			1212	
Random effects (sites)		4			4			4			4	

was done through the "FD" package (Laliberté & Legendre 2010). Finally, to establish whether the CWM of each morphotype changes along elevation and microsite, beta regression GLMs were performed, in which CWMs were modeled as response variables, while elevation, rock aspect, and rock inclination were modeled as fixed effects. As for the univariate analysis, significant terms were calculated and plotted with the "car" (Fox & Weisberg 2019), the "ggeffects" (Lüdecke 2018), and the "GGplot" (Wickham 2016) packages of the R software (R Core Team 2020).

The significant terms were calculated with the type II Wald chisquare test through the "car" package (Fox & Weisberg 2019) and plotted using the "ggeffect" package (Lüdecke 2018). Post hoc tests were applied to the GLM and the GLMMs for identify differences between explanatory variable levels using the "emmeans" package.

Species with less than 10% occurrence were excluded from the multivariate analyses to reduce noise and improve interpretability (McCune & Grace 2003). Canonical Correspondence Analysis (CCA) was performed to examine the relationship between community structure and the environmental variables: elevation, rock inclination, solar exposure, and rock aspect. Additionally, a permutational test under a reduced model was conducted to assess the significance of the CCA. The CCA plot enabled us to evaluate the influence of these environmental variables on the lichen community and their interrelationships. We identified species strongly associated with each environmental variable by calculating their angular alignment in the CCA ordination space. For each environmental vector, the five species with the smallest angular difference relative to the vector's direction were selected as representative. This approach prioritizes species whose distributions align most closely with the environmental gradient, as visualized in the biplot (Fig. 8).

Finally, a Non-metric Multidimensional Scaling (NMS) analysis was performed to visualize the relationship between species distribution and environmental variables. The NMS was based on a Bray-Curtis distance matrix and ran for 100 iterations, with stress levels stabilizing at iteration 40. The optimal solution was achieved with a three-axis configuration. However, there was no clear pattern between the third and the second axis, nor between the third and the first axis; therefore, we excluded the third axis from the plots to simplify pattern interpretation. Subsequently, canonical correlation analyses were conducted between the NMS axes and environmental variables to assess the relation between these variables and the first two axes of the analysis. NMS was done using the PC-ORD software (McCune & Mefford 2011) and the "vegan" package of the R software (Okasen *et al.* 2022; R Core Team 2020). Results were plotted with the "ggplot2" package (Wickham 2016). Rock inclination was also treated as a quantitative variable for this analysis.

RESULTS

A number of 195 species were distinguished throughout the sampling (a list of the species is found in Appendix 1). Species richness varied significantly with elevation, rock aspect and rock inclination. Specifically, total richness and richness of fruticose lichens showed significant differences based on rock aspect (p = 0.03 and p <0.001; Table 1), while total, foliose, and fruticose richness varied significantly with rock inclination (p <0.001; Table 1). Notably, significant interactions were found between elevation and rock aspect for crustose richness (p = 0.01; Table 1) and between elevation and rock inclination for foliose richness (p = 0.032; Table 1).

Examining specific elevations, richness was notably lower at 900 m compared to the other elevations (1500, 1800, 2100, 2400, and 2700 m a.s.l., see Fig. 3A). Additionally, richness tended to be greater on steep rocks compared to flat and low-inclination rocks (Fig. 3A, B), and south-facing rocks exhibited higher richness compared to flat rocks (Fig. 3C, D).

Crustose lichen richness was lower at 900 m a.s.l. compared to other elevations (Fig. 4A). For flat rocks, the highest crustose richness was observed at 2400 and 2700 m a.s.l., while north-facing rocks showed higher richness at 1500 m a.s.l. compared to 900 m a.s.l. Moreover, crustose richness at south-facing rocks was consistently higher from 1800 to 2700 m a.s.l. compared to 900 m a.s.l. (Fig. 4B).

Foliose lichen richness exhibited variations across elevations, with lower richness noted at 2400 and 2700 m a.s.l. compared to lower elevations (Fig. 5A). Specifically, on flat rocks, greater richness was observed at 1800 m a.s.l. compared to elevations of 2400 and 2700 m a.s.l. Conversely, for low inclined rocks, lower richness was recorded at 2700 m a.s.l. compared to 1500 and 1800 m a.s.l. Meanwhile, steep rocks showed stable richness with no changes along elevation (Fig. 5B).

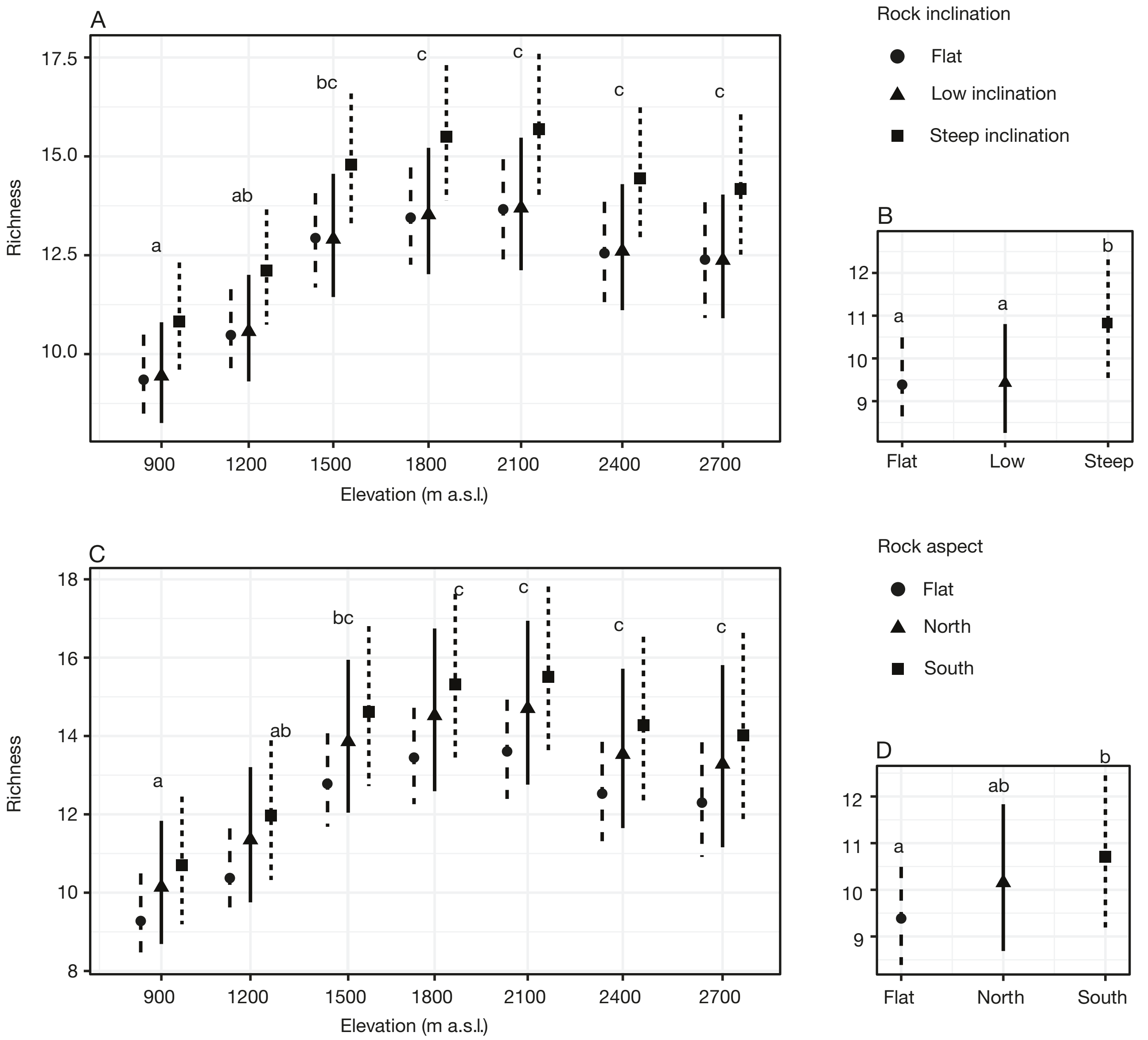

Fig. 3. — Predicted richness: **A**, in elevation and rock inclination; **B**, rock inclination only; **C**, elevation and rock aspect; **D**, and rock aspect only. Predicted values were calculated from the Generalized Mixed Linear Model (GLMM) with their corresponding 95% CI. Groups with the same lowercase letters indicate statistical similarities.

In the case of fruticose species, the greatest richness was observed at 2100 m a.s.l. compared all the other elevations (with the exception of 2700 m a.s.l.; Fig. 6A). Additionally, rocks with steep inclination exhibited greater richness of fruticose species compared to rocks with low inclination (Fig. 6B). Conversely, microsite analysis revealed higher richness on south-facing rocks compared to north-facing rocks (Fig. 6C, D).

The GLMs of the CWM showed that crustose, foliose, and fruticose communities respond to elevation ($p < 0.001$; Table 2). At microsite level, rock aspect influenced significatively to crustose and fruticose communities ($p = 0.01$ and $p = 0.08$ respectively; Table 2), foliose and fruticose communities changed significantly with rock inclination ($p < 0.01$ and $p = 0.01$ respectively; Table 2). Also, a significant interaction between rock inclination and elevation was detected for foliose, and fruticose communities ($p < 0.01$, $p = 0.02$, and $p = 0.003$ respectively; Table 2). Similarly, a significant interaction between rock aspect and elevation was observed for crustose, foliose, and fruticose communities ($p = 0.05$, $p < 0.001$, $p = 0.04$ for each case; Table 2).

The GLM analysis of crustose CWM revealed an overall increase in crustose communities with elevation. However, this elevation-driven increase varied across different rock aspects, with the most pronounced increase observed in communities from flat rocks (Fig. 7A). Conversely, foliose CWM exhibited a more drastic decrease in flat rocks and rocks with low inclination compared to those with steep inclination (Fig. 7B). Moreover, fruticose CWM from both north and south-facing rocks exhibited an increase with elevation (Fig. 7C), whereas those from flat rocks showed no significant change along the elevation gradient (Fig. 7D).

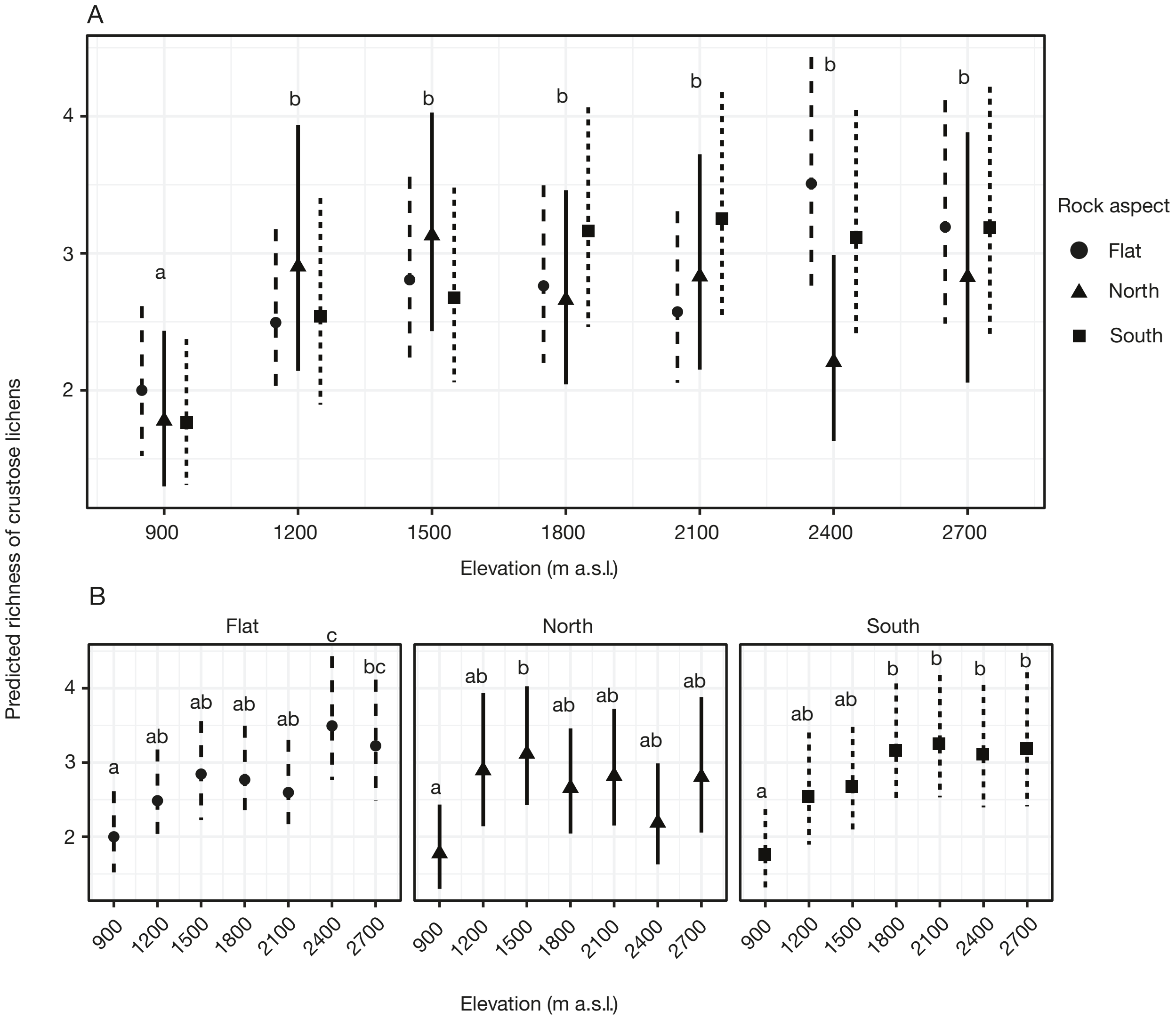

Fig. 4. — Crustose predicted richness: **A**, in elevation; **B**, in microsite. Predicted values were calculated from the Generalized Mixed Linear Model (GLMM) with their corresponding 95% CI. Groups with the same lowercase letters indicate statistical similarities.

Table 2. — Generalized Linear Model (**GLM**) of the Community Weighted Means (**CWM**) for each morphotype. The table includes the Chi-Square statistic (**Chisq**), degrees of freedom (**df**), and the P-value, denoted as **Pr(>Chisq)**, indicating the significance of the Chi-Square statistic. **Bold** values indicate statistically significative differences.

Fixed effects	**Crustose (CWM)**			**Foliose (CWM)**			**Fruticose (CWM)**		
	Chisq	***df***	**Pr(>*Chi*)**	**Chisq**	***df***	**Pr(>*Chi*)**	**Chisq**	***df***	**Pr(>*Chi*)**
Elevation	49.188	1	**<0.001**	99.807	1	**<0.001**	41.11	1	**<0.001**
Rock aspect	7.22	2	**0.01**	–	–	–	5	2	**0.08**
Rock inclination	–	–	–	16.096	2	**<0.001**	8.76	2	**0.01**
Rock inclination × elevation	–	–	–	16.074	2	**<0.001**	11.55	2	**0.003**
Rock aspect × elevation	5.85	2	**0.05**	16.074	2	**<0.001**	6.34	2	**0.04**
Observations		406			406			406	

MULTIVARIATE ANALYSIS

The permutational test for the CCA under a reduced model showed a significant relation between the lichen community and the modeled environmental variables (F = 4.01; p <0.001). The first two axes explained the 72.6% of the variability. The permutational test showed that all the variables were significantly relevant for the model (p <0.001 for rock inclination, elevation, rock aspect, and p = 0.02 for sun exposure). Also, elevation and microsite slope are the most important environmental variables that explain species distribution, while

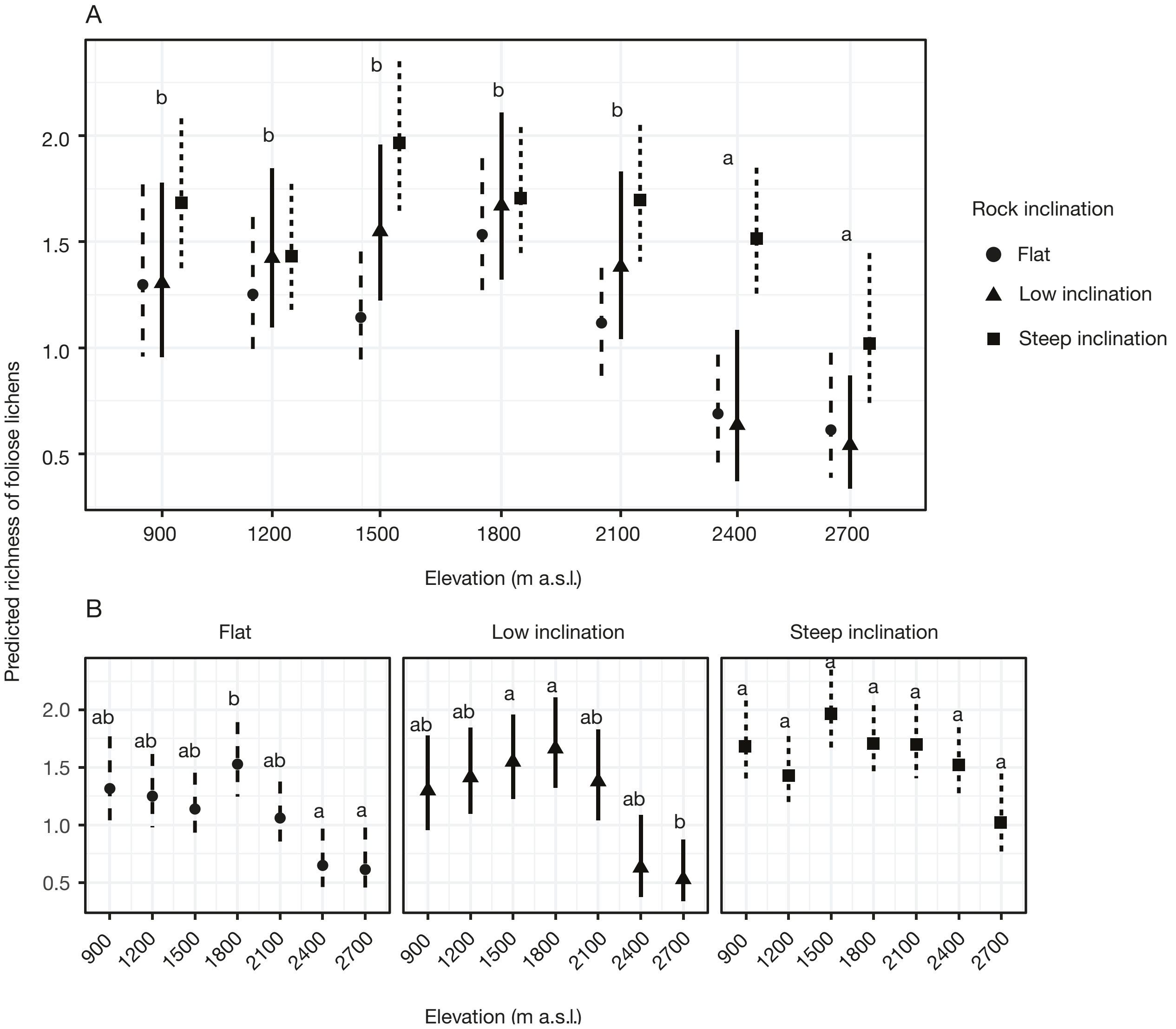

FIG. 5. — Foliose predicted richness: **A**, in elevation; **B**, in microsite. Predicted values were calculated from the Generalized Mixed Linear Model (GLMM) with their corresponding 95% CI. Groups with the same lowercase letters indicate statistical similarities.

exposure and southern aspect explain less of the community distribution (Fig. 8).

The Non-Metric Multidimensional Scaling (NMS) analysis yielded its optimal solution as a three-axis configuration with a stress value of 18. The NMS cumulative R^2 was 95%. The model that best describes the axis 1 of the NMDS includes elevation ($p > 0.001$), rock inclination ($p > 0.001$) and their interaction ($p = 0.02$, Fig. 9B). The resulting NMS plot distinctly revealed a pattern of groupings corresponding to varying elevations (Fig. 9). Notably, the biplot illustrated a community composed of species such as *Acarospora lorentzii* (Müll. Arg.) Hue, *Cladonia* sp., *Diploschistes scruposus* (Schreb.) Norman, *Leptogium* sp., *Parmotrema reticulatum* (Taylor) M. Choisy, *Punctelia perreticulata* (Räsänen) G. Wilh. & Ladd, *Punctelia punctilla* (Hale) Krog, *Xanthoparmelia cordillerana* (Gyeln.) Hale, *Xanthoparmelia farinose* (Vain.) T.H. Nash, Elix & J. Johnst., *Xanthoparmelia microspore* (Müll. Arg.) Hale, *Xanthoparmelia plittii* (Gyeln.) Hale, and *Xanthoparmelia wrightiana* T.H. Nash, Elix & J. Johnst., predominantly clustered at elevations of 900, 1200, and 1500 m a.s.l.

The middle-elevation community is more complicated to define from the plot, given that many species inhabit both the lower and upper elevations. However, the species grouped within the 1800 m a.s.l. could be considered the most representative of this community. Some of these species are *Heterodermia leucomelos* (L.) Kalb, *Hypotrachyna revoluta* (Flörke) Hale, *Hypotrachyna rhabdiformis* (Kurok.) Divakar & A. Crespo, *Phaeophyscia* sp., *Pertusaria* sp., *Punctelia perreticulata* (Räsänen) G. Wilh. & Ladd, *P. stictica* (Delise ex Duby) Krog, *Stereocaulon ramulosum* Raeusch., *Xanthoparmelia cordillerana* (Gyeln.) Hale, *Xanthoparmelia microspora* (Müll. Arg.) Hale, and *Xanthoparmelia punctulata* (Gyeln.) Hale.

A more restricted high-elevation community, identified through the NMS plot, comprises species such as *Buellia aethalea* (Ach.) Th. Fr., *Buellia aff. aethalea, Buellia sulphurea* Malme, *Diploschistes diacapsis* (Ach.) Lumbsch, *Lecanora*

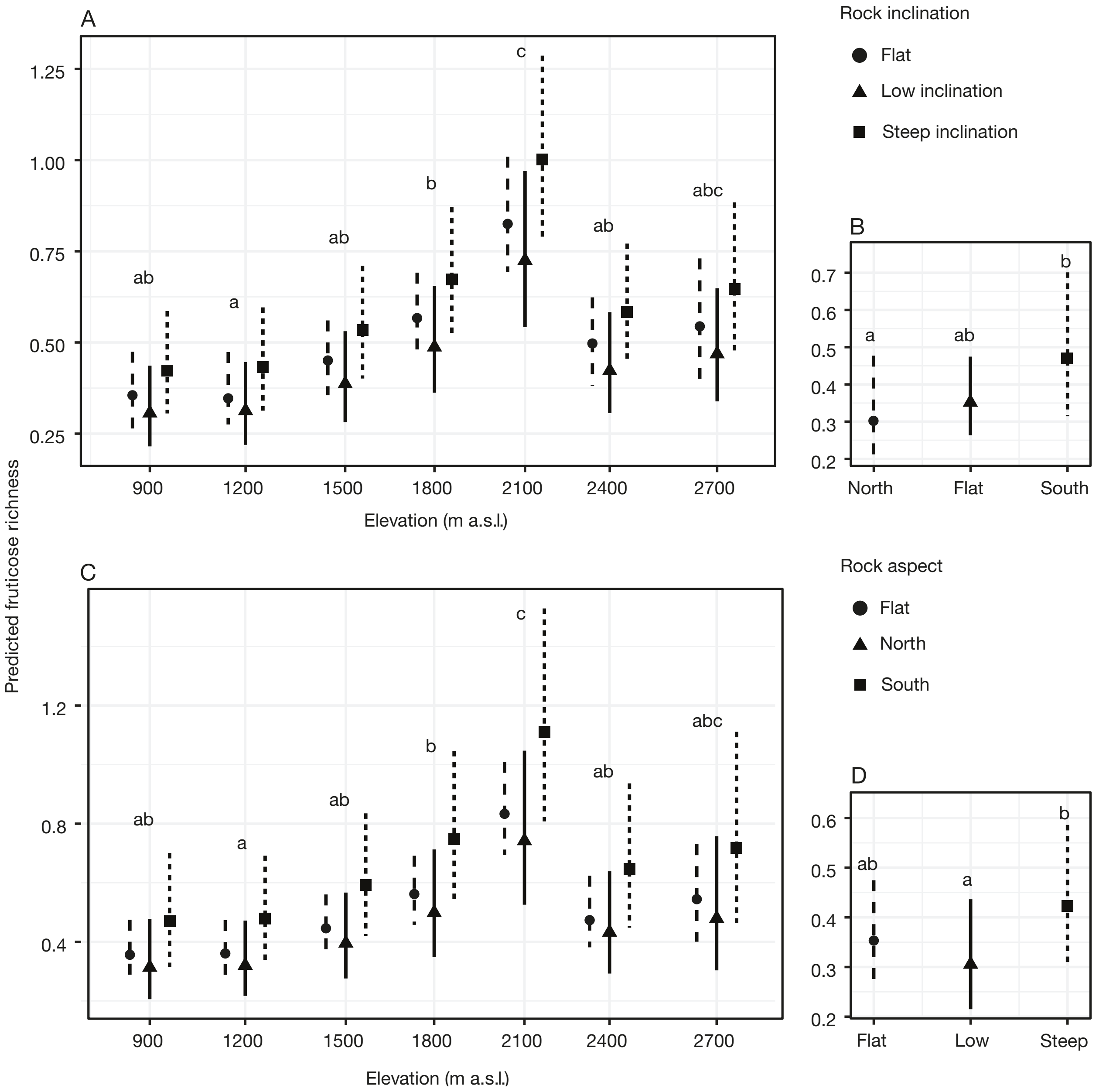

FIG. 6. — Fruticose predicted richness along the elevation: **A**, **C**, in elevation; **B**, **D**, in microsite. Predicted values were calculated from the Generalized Mixed Linear Model (GLMM) with their corresponding 95% CI. Groups with the same lowercase letters indicate statistical similarities.

rupicola (L.) Zahlbr., *Neobrownliella cinnabarina* (Ach.) S.Y. Kondr., Upreti & A. Thell, *Ochrolechia parella* (L.) A. Massal., *Parmotrema warmingii* (Vain.) A.A. Spielm. & Marcelli, *Phaeophyscia* sp., *Rhizocarpon geographicum* (L.) DC., *Rhizocarpon inorense* (Vain.) Vain., *Rhizocarpon* sp., *Rhizocarpon disporum* (Nägeli ex Hepp) Müll. Arg., *Teloschistes nodulifer* (Nyl.) Hillmann, *Usnea luti* J.M. Rodr. & P. Clerc, *Usnea saxidilatata* J.M. Rodr. & P. Clerc, *Xanthoparmelia imitatrix* (Taylor) O. Blanco A. Crespo, Elix D. Hawksw. & Lumbsch and *Xanthoparmelia punctulata* (Gyeln.) Hale, among others. This community predominantly inhabits the higher elevations, around 2100, 2400, and 2700 m a.s.l.

DISCUSSION

RICHNESS PATTERNS

One unanticipated result was that species richness varied with elevation, contrary to the findings of Rodriguez *et al.* (2017). Conversely, this result aligns partially with observations of Costas *et al.* (2021), who found differences in species richness across low, medium, and high elevations along a longer gradient (2895-4500 m a.s.l.) in northern Argentina. The discrepancy between our findings and the results of Rodriguez *et al.* (2017) may be attributed to our substantially increased sampling effort, achieved through replication across four transects.

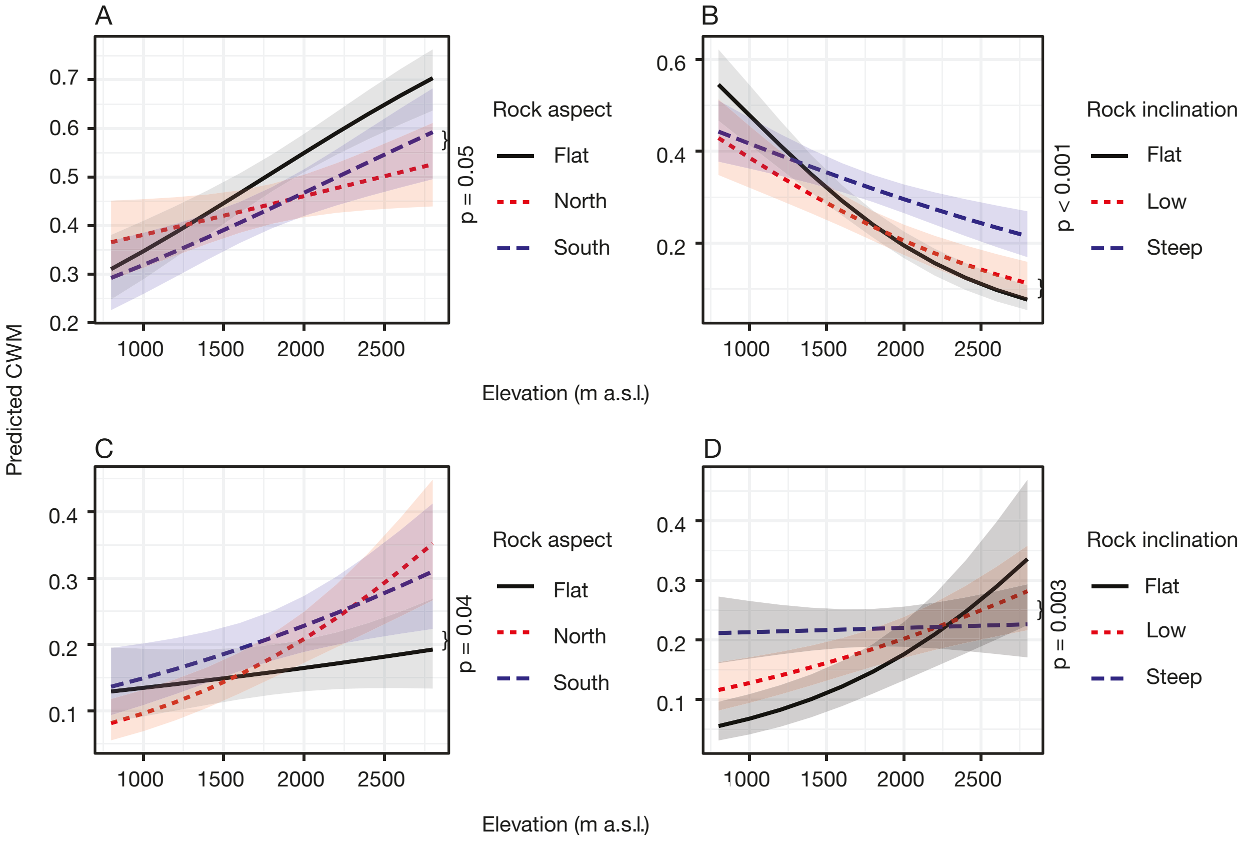

FIG. 7. — Predicted community weighted means (**CWM**) of: **A**, crustose; **B**, foliose; **C**, fruticose in elevation and rock aspect; **D**, fruticose in elevation and rock inclination. Predicted values were calculated from the Generalized Mixed Linear Model (GLMM) with their corresponding 95% CI (shaded areas).

Similar to the work by Costas *et al.* (2021), previous studies by Baniya *et al.* (2010) and Pinokiyo *et al.* (2008) also found changes in species richness of lichens with changes in elevation, with a pattern of increasing species numbers along low and middle elevations, followed by a decrease at higher elevations. Here, we did not detect a significant difference between lichen richness at middle and high elevations. A possible explanation might be that our gradient was not long enough to affect lichen richness at its highest elevation (Nanda *et al.* 2021). A similar pattern has been reported by other authors, where species richness increased at middle elevations but did not decrease at higher elevations (Grytnes *et al.* 2006; Bässler *et al.* 2016). Higher richness at steeper slopes (without considering the aspect) is consistent with the pattern reported by Rodriguez *et al.* (2017) who reported lowest richness on flat boulder tops.

The observed increase in crustose species richness of lichens with elevation aligns with findings reported by (Blinkova & Urbanavichus 2005), who noted an increase in the percentage of crustose lichens along their study gradient from low to high altitude. Conversely, the concentration of fruticose lichens peaking at 2100 m a.s.l. agrees with a similar pattern identified by (Baniya *et al.* 2010). These researchers observed that species richness of fruticose lichens tends to reach its apex slightly above other growth forms, attributing this phenomenon to the advantage of fruticose lichens in being able to utilize light from all directions, in open sites whereas foliose and flat lichens maximize the harvest of more or less unidirectional light in more shaded positions.

The predominance of foliose and fruticose lichen on vertical substrates aligns with previous findings (Rodriguez *et al.* 2017; Rutherford & Rebertus 2022). Rutherford & Rebertus (2022) demonstrated that microslope significantly influences where lichen grow, with *Umbilicaria* species (foliose-like umbilicate morphotypes) predominantly occupying steeper slopes. Their study also identified a particular group of species to be associated with rock overhangs, a microhabitat whose formation obviously correlates strongly with micro-slope angle and micro-aspect. Our supplementary data support these observations, showing that highly inclined rock surfaces (>45°) generally experience reduced solar exposure (see Appendices 1; 2; 3; 4; 5; 6). While this pattern requires more targeted investigation (Díaz *et al.* 2022), it suggests that microtopography-mediated light and moisture regimes drive lichen occurrence patterns.

Additionally, biotic interactions likely contribute to foliose lichen dominance on vertical surfaces. As Rodriguez *et al.* (2017) noted, foliose and fruticose species frequently overgrow crustose lichens on steeper slopes, potentially through competitive exclusion. This combination of abiotic filtering (slope-induced microclimate) and biotic interactions may collectively explain the morphotype occurrence patterns we observed.

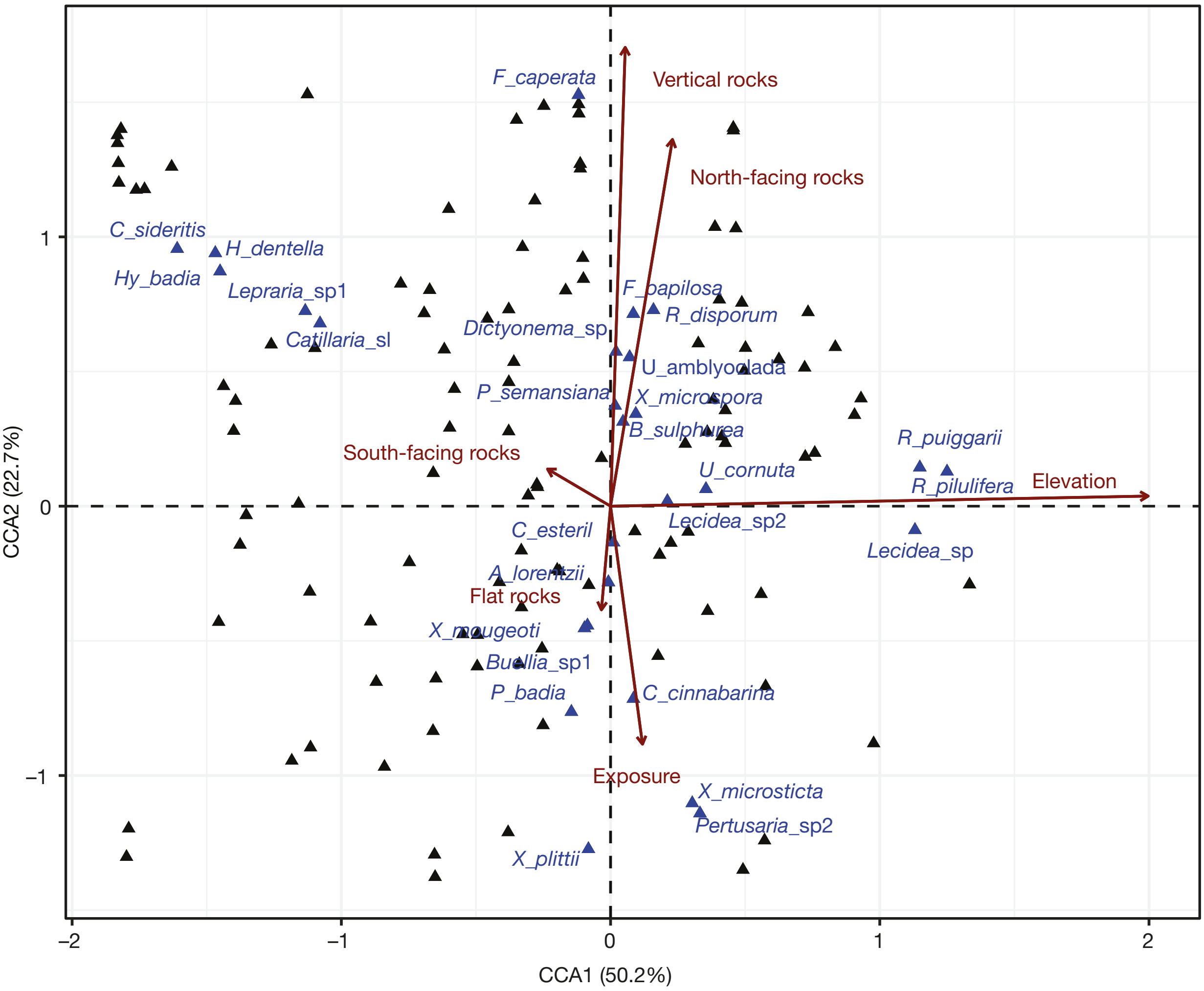

Fig. 8. — Canonical Correspondence Analysis (**CCA**) of lichen community composition and environmental variables. Species are represented by **triangles**, with labels showing the five species most strongly correlated. For each environmental vector, the five species with the smallest angular difference relative to the vector's direction were selected as representative. **Arrows** indicate the direction and relative strength of environmental variable influences.

Nascimbene & Marini (2015) observed distinct elevational occurrence patterns among lichen growth forms, noting crustose species were particularly abundant in exposed high-elevation sites. While they suggested this may be a result of a desiccation-tolerance, we propose that these growth form dynamics also are influenced by microhabitat availability. The vertical rock surfaces in our study area offer sheltered microsites, thus buffering environmental extremes through reduced direct solar exposure (as evidenced by our supplementary solar exposure measurements), enhanced moisture retention in microtopographic features, and protection from wind abrasion. These conditions particularly benefit foliose and fruticose growth forms, while flat-exposed microsites remain dominated by crustose species. This micro-refugium hypothesis reinterprets Nascimbene & Marini's (2015) "elevational preferences" as microhabitat filtering along the gradient. Specifically, crustose dominance at high elevations (>1800 m) likely reflects priority effects (early colonization of exposed surfaces with sheltered microsites), facultative stress tolerance (exploitation of flat microsites where other growth forms cannot establish), and niche partitioning (vertical surfaces remain available for stress-sensitive taxa). Thus, crustose communities may capitalize on abiotic exclusion of competitors in extreme flat microsites, while vertical refugia maintain growth-form diversity at lower stress levels (Armstrong & Bradwell 2010; Gauslaa 2014; Weidlich *et al.* 2021).

COMMUNITY WEIGHTED MEANS (CWM) OF THE GROWTH FORMS

An increase in crustose Community Weighted Mean (CWM) with elevation has been observed in previous studies (Nascimbene & Marini 2015). However, our results reveal a particularly striking increase in crustose CWM at higher elevations, especially on flat rocks. As mentioned before, this pattern may be due to the lower surface-to-volume ratio of crustose lichens, which enhances their tolerance to exposed environments (Nascimbene & Marini 2015). Additionally, crustose lichens are more resilient to drought, unlike foliose and fruticose growth forms, which are more sensitive to desiccation (Merinero *et al.* 2014). This resilience allows crustose

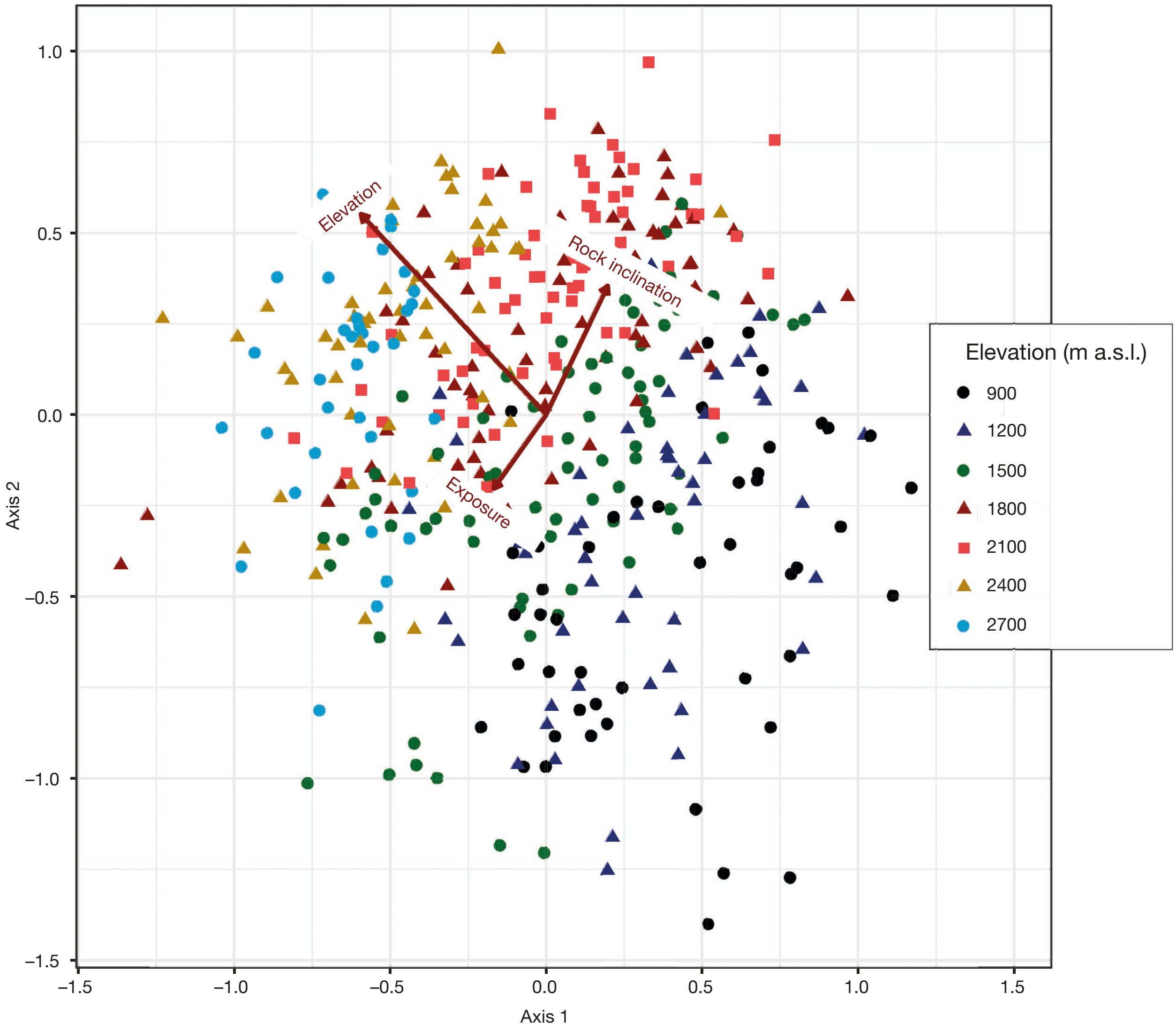

Fig. 9. — Non-metric multidimensional scaling (NMS) ordination biplot of lichen community composition. **Points** represent sampling sites, with colors and shapes indicating different elevations. **Arrows** show environmental vectors significantly associated with community structure.

lichens to thrive in flat, exposed microsites. Conversely, the decrease in foliose CWM with elevation could be attributed to their sensitivity to harsh conditions. However, this decrease is less pronounced on high, steep rocks that offer sheltered microsites, which likely support the persistence of foliose lichens (Díaz *et al.* 2022). Furthermore, their evolutionary strategy prioritizes stress tolerance over competitive growth, making them particularly suited to high-stress environments (Wan & Ellis 2019).

The notably higher community-weighted mean (CWM) of fruticose lichens on flat rocks presents an intriguing ecological pattern. This trend appears largely driven by the strong presence of *Teloschistes nodulifer*, a species demonstrating both clear substrate preference for flat rock surfaces (as discussed ahead), and photoprotective adaptations through anthraquinone production (Nguyen *et al.* 2013). While this occurrence pattern might initially seem paradoxical for well-lit habitats, transplant experiments provide mechanistic insights (Gauslaa *et al.* 2009). Their work revealed that fruticose growth forms possess competitive advantages in three-dimensional light harvesting, including omnidirectional photon capture capability and unique dispersal strategies (e.g., direct branch-to-branch colonization bypassing juvenile stages). These features, combined with chemical photoprotection, may explain fruticose lichens' CWM increase in exposed microhabitats despite high radiation stress in our system.

Competition may also play a crucial role in structuring lichen communities. Previous studies have suggested that foliose species often have a competitive advantage over crustose growth types (Armstrong & Welch 2007). In our results, crustose communities predominantly occupy upper elevations, coinciding with a decrease in the foliose community. Additionally, crustose lichens tend to inhabit microsites where other growth forms are less represented based on their weighted means. This pattern aligns with current understandings of lichen competition, suggesting that competition does not necessarily lead

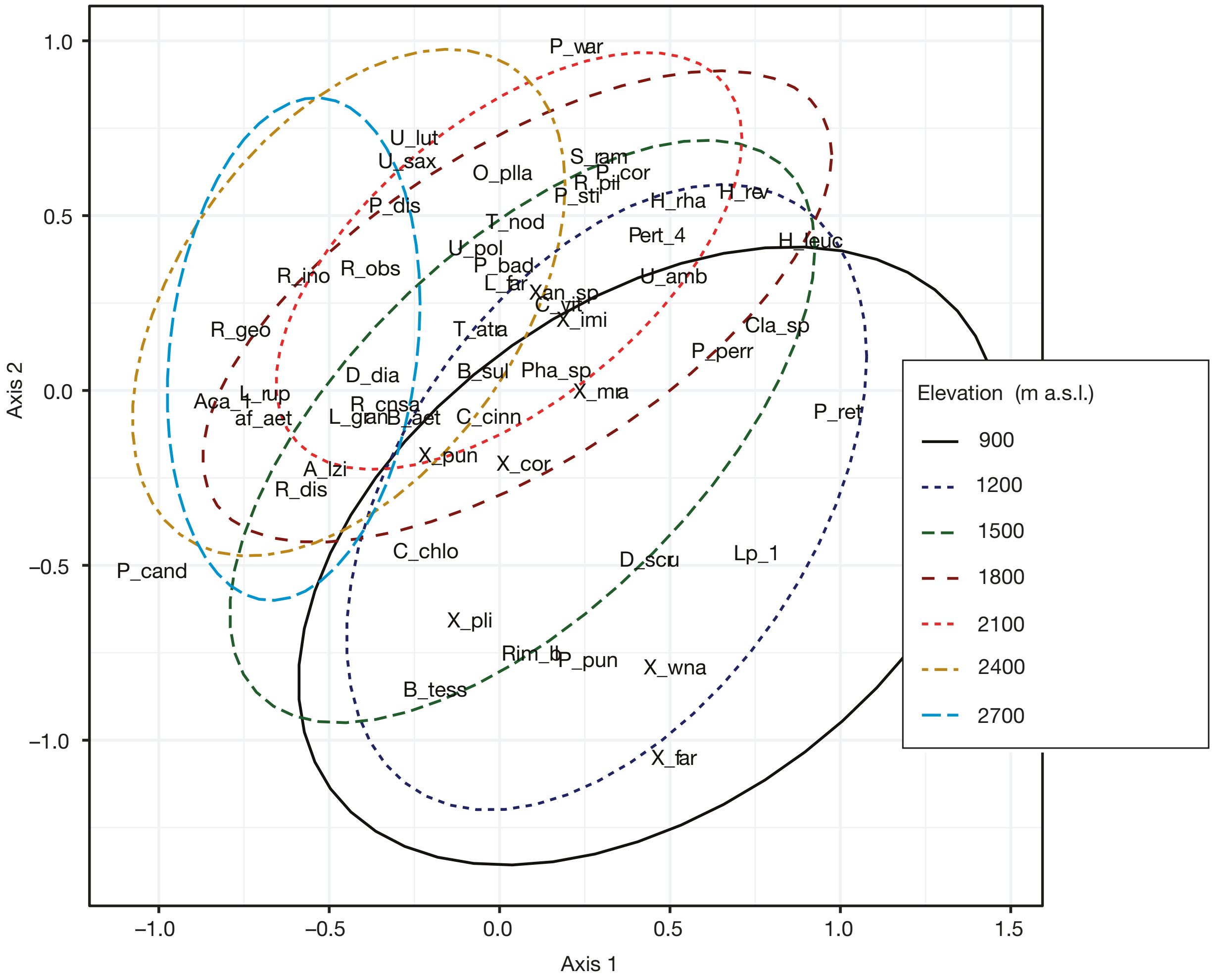

FIG. 10. — Non-metric multidimensional scaling (NMS) ordination of lichen species composition, corresponding to the analysis shown in Fig. 9. Sampling sites are omitted to highlight species grouped by elevation. **Colored polygons** enclose species associated with each elevation category.

to the exclusion of less competitive species but significantly influences community structure (Armstrong & Welch 2007).

Although fruticose lichens' architectural advantages in light harvesting might suggest they would dominate exposed microsites, our elevational analysis reveals distinct species turnover patterns. The data suggest a transition zone around 1500 m where flat-exposed rocks shift from competition-mediated to stress-dominated systems, favoring crustose species. Importantly, this broad pattern coexists with taxon-specific exceptions: although rock inclination explains decreasing variance in overall community composition with elevation, vertical microsites still support foliose lichens at high elevations. These findings align with multi-scale filtering theory discussed by Ellis *et al.* (2021), where elevation drives community turnover while microtopography maintains niche space for fruticose species.

THE COMMUNITY ASSEMBLY

With respect to our studies on community analysis, the occurrence of some genera exhibited distinct correlation with specific environmental conditions. For instance, genera such as *Xanthoria* (Fr.) Th. Fr., *Protoparmelia* M. Choisy and *Teloschistes* Norman were predominantly linked with flat, exposed microsites. Conversely, genera like *Rhizocarpon* Ramond ex DC., *Buellia* De Not. and *Acarospora* A. Massal. showed a modest association with elevation. Interestingly, *Lecanora* Ach., *Usnea* Dill. ex Adans., *Rinodina* (Ach.) Gray, *Placomaronea* Räsänen and *Parmotrema* A. Massal. were notably correlated with microsite slope (see Figure 10 for graphical representation)

Xanthoria (Fr.) Th. Fr. and *Teloschistes* Norman belong to distinct genera within the Teloschistaceae Zahlbr. family. Despite this taxonomic difference, *Xanthoria* (Fr.) Th. is classified as a foliose genus while *Teloschistes* Norman is categorized as fruticose. Consequently, the morphological distinction between foliose and fruticose does not entirely account for why these two groups exhibit similarities in microsite preferences. However, their shared membership in the Teloschistaceae Zahlbr. is relevant. This family is characterized by the presence of parietin, an orange pigment found principally in the cortex and apothecial discs of the species. Extensive research, including ecological studies and controlled laboratory experiments, has demonstrated the reductive oxidative stress and photoprotective functions of parietin

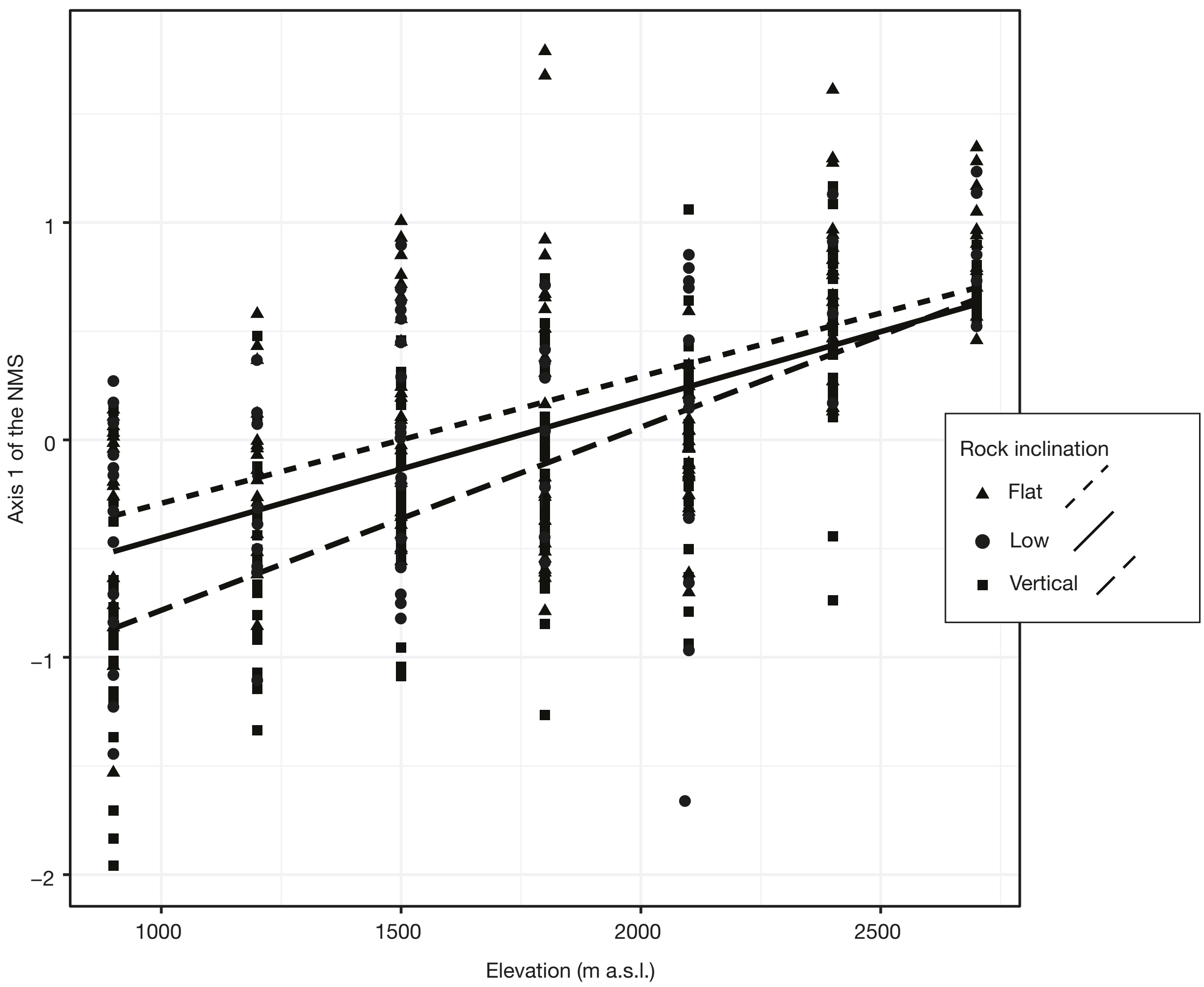

Fig. 11. Relationship between non-metric multidimensional scaling (NMS) axis 1 site scores and elevation, displayed separately by rock inclination category. **Point shapes** indicate inclination levels: flat, low, and vertical. **Fitted trend lines** illustrate the correlation within each category, with **line types** distinguishing levels (**dotted** = flat; **continuous** = low; **widely dashed** = vertical).

(Solhaug & Gauslaa 2004; Nguyen *et al.* 2013). Therefore, the presence of parietin may provide a plausible explanation for the observed similarities in microsite preferences between *Xanthoria* (Fr.) Th. Fr. and *Teloschistes* Norman , despite their morphological differences.

The correlation between elevation and the presence of *Rhizocarpon* Ramond ex DC., *Buellia* De Not. and *Acarospora* A. Massal. is likely due to the altitudinal specialization observed in species within each of these genera, as proposed by Rodriguez *et al.* (2017). Additionally, these authors also observed an increase of foliose and fruticose species such as *Usnea* Dill. ex Adans. and *Parmotrema* A. Massal. on high-inclination rocks.

A noteworthy transition in community composition emerged above 1800 m a.s.l., characterized by a gradual species turnover where low-elevation specialists disappeared and were progressively replaced by mid- and high-elevation specialists. This transitional zone represented an ecotone where species with broader elevation ranges (e.g., *Parmotrema reticulatum* (Taylor) M. Choisy, *Usnea amblyoclada* (Müll. Arg.) Zahlbr. coexist with true high-elevation specialists, creating a peak in species richness. The community includes both cold-adapted species with wide distributions (e.g., *Rhizocarpon geographicum* (L.) DC.) and high-mountain endemics (e.g., *Usnea luti* J.M. Rodr. & P. Clerc, *Usnea saxidilatata* J.M. Rodr. & P. Clerc, Rodriguez *et al.* 2011, 2018). This pattern reflects classic elevational zonation, where species replacement occurs along the gradient rather than simple accumulation of species from lower elevations.

A distinct community organization corresponding to elevation is evident (Fig. 11), with a well-defined transition occurring above intermediate elevations. This pattern aligns classic turnover patterns (Baniya *et al.* 2010; Rodriguez *et al.* 2017; Nanda *et al.* 2021) the high-elevation communities (>2400 m a.s.l.) are compositionally distinct, being dominated by cold-adapted species rather than representing random mixtures across elevations. This replacement pattern reflects environmental filtering along the elevational gradient.

The species-level community analysis underscores the predominant specialization of communities primarily along elevation, followed by microsite slope and aspect – a finding consistent with previous studies by Rodriguez *et al.* (2017) and Rutherford & Rebertus (2022). Notably, the significance of microsite over community composition diminishes with increasing elevation, as evidenced by the significant interaction effect between elevation and rock inclination. This trend mirrors the observations of Rodriguez *et al.* (2017) and Costas *et al.* (2021).

However, vertical rock faces retain ecological relevance as microrefugia for stress-sensitive taxa like fruticose lichens. Crucially, while lichen species composition shifts along the elevational gradient (e.g., *Usnea amblyoclada* (Müll. Arg.) Zahlbr. at mid-elevations transitioning to *Usnea saxidilatata* J.M. Rodr. & P. Clerc at higher zones), the occurrence of fruticose growth forms remains constant. This consistency highlights the fruticose growth form-mediated adaptation to vertical microhabitats. Concurrently, species turnover within this growth form reflects fruticose growth form-mediated specialization to elevation-specific conditions, a pattern supported by Armstrong (2017), who emphasizes growth forms as key adaptive strategies for extreme environments.

CONCLUSIONS

This study aimed to determine whether the lichen community of the studied environmental gradient was primarily shaped by elevation or microsite conditions and whether lichen growth forms were reliable predictors of community composition along this gradient. The results confirmed that lichen richness, community composition and growth forms are significantly influenced by both elevation and microsite conditions. Moreover, the findings highlight the strong interaction between macro- and micro-environmental factors, which collectively affect diversity and community composition.

Importantly we found that true high-elevation specialist species were restricted to the highest portions of our transects that reached summit areas (>2400 m), and absent from lower-elevation transects that didn't extend into these extreme habitats. Consequently, these specialist species are vulnerable to displacement as their narrow elevational ranges leave no room for upward migration with changes predicted as a result of climate change.

Mountain top species were predominantly present at the top of the broader transects. This outcome underscores the vulnerability of these species and the risk they face of disappearing, emphasizing the importance of understanding these dynamics in the context of climate change and environmental stressors (a graphical example is found in Appendix 2).

These findings are particularly significant as they support a model in which lichen communities are shaped not only by elevation but also by microsite conditions. This interaction between elevation and microsite factors creates specific niches, potentially harboring and supporting species restricted to specific microsites, thus limited in their capacity to establish and consequently narrowly distributed. Another notable result is that lichen community patterns can be described based on the niches occupied by different growth forms.

Taken together, the findings of this study provide valuable insights for delimiting ecological niches of lichens, assessing how patterns of species occurrences differ, potentially limiting distribution, thus resulting in endemism, helping to explaingeneral ecological patterns within the context of microsite variation. They underscore the importance of considering both macro- and micro-environmental variables in understanding the complex dynamics of lichen community assembly and biodiversity.

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Statements & Declarations

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Author contributions

Juan Manuel Rodriguez and Mariana Peralta contributed to the study conception and design. Material preparation, data collection and analysis were performed by Raúl Díaz, Juan Manuel Rodriguez, and Edith Filippini. The first draft of the manuscript was written by Raúl Díaz and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability

The datasets generated during and/or analysed during the current study will be available in the CONICET public data repository after they pass the curatory process. Dataset and the R script are also available from the corresponding author on request (raulenriquedd@hotmail.com).

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APPENDICES

Appendix 1. — List of species and the locations where they were found. Note: *Taxa not identified due to a lack of visible taxonomic characters. **Species excluded from multivariate analyses due to their rarity in the sampling process. Transect references are as follows: **CL** for "Cerro Linderos"; **CH** for "Cerro Champaquí"; **LG**, for "Los Gigantes"; and **PNQ**, for "Quebrada del Condorito". MFT refers to species morphotype. The "Abbreviations" column indicates the shorthand used for species in the multivariate analyses.

Species	Family	Morpho-type	CL	CH	PNQ	LG	Abbreviation
Acarospora altoandina H. Magn.	Acarosporaceae Zahlbr.	C	x			x	A_dna
Acarospora lorentzii (Müll. Arg.) Hue	Acarosporaceae Zahlbr.	C	x	x	x	x	A_lzi
Acarospora sp. 1	Acarosporaceae Zahlbr.	C	x	x	x	x	Aca_1
Acarospora sp. 2	Acarosporaceae Zahlbr.	C	x	x	x	x	Aca_2
Buellia aethalea (Ach.) Th. Fr.	Caliciaceae Chevall.	C	x	x	x	x	B_aet
Buellia aff. aethalea	Caliciaceae Chevall.	C	x	x	x	x	af_aet
Buellia dispersa (A. Massal.) A. Massal.	Caliciaceae Chevall.	C	x	x	x		B_dis
Buellia sp. 1	Caliciaceae Chevall.	C	x		x	x	B_sp1**
Buellia sulphurea Malme	Caliciaceae Chevall.	C	x	x	x	x	B_sul
Buellia stellulata (Taylor) Mudd	Caliciaceae Chevall.	C				x	B_tel**
Buellia tesserata Körb.	Caliciaceae Chevall.	C	x	x	x	x	B_tess
Buellia umbrina Malme	Caliciaceae Chevall.	C		x		x	B_umb**
Caloplaca chlorina (Flot.) H. Olivier	Teloschistaceae Zahlbr.	C	x	x	x	x	C_chlo**
Caloplaca sideritis (Tuck.) Zahlbr.	Teloschistaceae Zahlbr.	C	x	x	x	x	C_sid**
Caloplaca cinnabarina (Ach.) Zahlbr.	Teloschistaceae Zahlbr.	C	x	x	x	x	C_cinn
Candelariella vitellina (Hoffm.) Müll. Arg.	Candelariaceae Hakul.	C	x	x	x	x	C_vit
Canoparmelia rupicola (Lynge) Elix	Parmeliaceae Bercht. & J. Presl	F	x	x		x	P_rup**
Catillaria s.l.	Catillariaceae Hafellner	C	x	x		x	C_s.l**
*Cladonia esteril**	Cladoniaceae Zenker	D		x			Cla_es**
Cladonia fimbriata (L.) Fr.	Cladoniaceae Zenker	D	x		x	x	C_fim**
Cladonia melanopoda Ahti	Cladoniaceae Zenker	D	x	x			C_mel**
*Cladonia esteril**	Cladoniaceae Zenker	D	x	x	x		C_pyx**
Cladonia sp.	Cladoniaceae Zenker	D	x	x	x	x	C_sp.**
Cladonia symphycarpa (Ehrh. ex Schrad.) Fr.	Cladoniaceae Zenker	D	x	x			C_sym**
Cora pavonia (Weber & D. Mohr) Mont.	Hygrophoraceae Lotsy	Fi	x			x	D_pav**
Crespoa carneopruinata (Zahlbr.) Lendemer & B.P. Hodk.	Parmeliaceae Bercht. & J. Presl	F				x	C_car**
Dimelaena oreina (Ach.) Norman	Caliciaceae Chevall.	F	x				D_ore**
Diploschistes diacapsis (Ach.) Lumbsch	Graphidaceae Dumort.	C	x	x	x	x	D_dia
Diploschistes scruposus (Schreb.) Norman	Graphidaceae Dumort.	C	x	x	x	x	D_scru
Diploschistes muscorum (Scop.) R. Sant.	Graphidaceae Dumort.	C	x	x	x	x	D_mus**
Flavoparmelia caperata (L.) Hale	Parmeliaceae Bercht. & J. Presl	F		x			F_cap**
Flavoparmelia haysomii (C.W. Dodge) Hale	Parmeliaceae Bercht. & J. Presl	F	x	x			F_hay**
Flavoparmelia papillosa (Lynge ex Gyeln.) Hale	Parmeliaceae Bercht. & J. Presl	F	x	x			F_pap**
Haematomma fenzlianum A. Massal.	Haematommataceae Hafellner	C				x	H_fen**
Heterodermia badia Moberg	Physciaceae Zahlbr.	F	x				H_bad**
Heterodermia obscurata (Nyl.) Trevis.	Physciaceae Zahlbr.	F			x	x	H_obs**
Heterodermia speciosa (Wulfen) Trevis.	Physciaceae Zahlbr.	F				x	H_spec**
Hypotrachyna dentella (Hale & Kurok.) Hale	Parmeliaceae Bercht. & J. Presl	F	x				H_dent**
Hypotrachyna intercalanda (Vain.) Hale	Parmeliaceae Bercht. & J. Presl	F			x		H_inte**
Hypotrachyna longiloba (H. Magn.) Hale	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	H_long**
Hypotrachyna sp. 2	Parmeliaceae Bercht. & J. Presl	F		x			Hy_ba**
Hypotrachyna brevirhiza (Kurok.) Hale	Parmeliaceae Bercht. & J. Presl	F	x		x		H_brev**
Hypotrachyna revoluta (Flörke) Hale	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	H_rev
Hypotrachyna sp.	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	Para_sp**
Hypotrachyna afrorevoluta (Krog & Swinscow) Krog & Swinscow	Parmeliaceae Bercht. & J. Presl	F	x				Par_afr**
Ingvariella bispora (Bagl.) Guderley & Lumbsch	Graphidaceae Dumort.	C	x		x		D_bis**
Lecanora labiosa Stizenb.	Lecanoraceae Körb.	C	x				L_lab**
Lecanora rupicola (L.) Zahlbr.	Lecanoraceae Körb.	C	x	x	x	x	L_rup
Lecanora farinosa (Flörke) Nyl.	Lecanoraceae Körb.	C	x	x	x	x	L_far
Lecidea sp.	Lecideaceae Chevall.	C	x	x	x	x	Lec_sp**
Lecidea sp. 2	Lecideaceae Chevall.	C	x				Lec_sp2**
Lecidea granulosula Nyl.	Lecideaceae Chevall.	C	x	x	x	x	L_gran
Lepraria sp.	Stereocaulaceae Chevall.	C		x	x		Lp_1
Lepraria sp. 2	Stereocaulaceae Chevall.	C	x	x			Lp_2
Lepraria sp. 3	Stereocaulaceae Chevall.	C	x	x	x	x	Lp_3
Leptogium sp.	Collemataceae Zenker	F	x			x	Lep_sp
Leucodermia leucomelos (L.) Kalb	Physciaceae Zahlbr.	F	x	x	x	x	H_leuc
Ochrolechia austroamericana (Räsänen) Räsänen	Ochrolechiaceae R.C. Harris ex Lumbsch & I. Schmitt	C	x	x	x	x	O_aus**

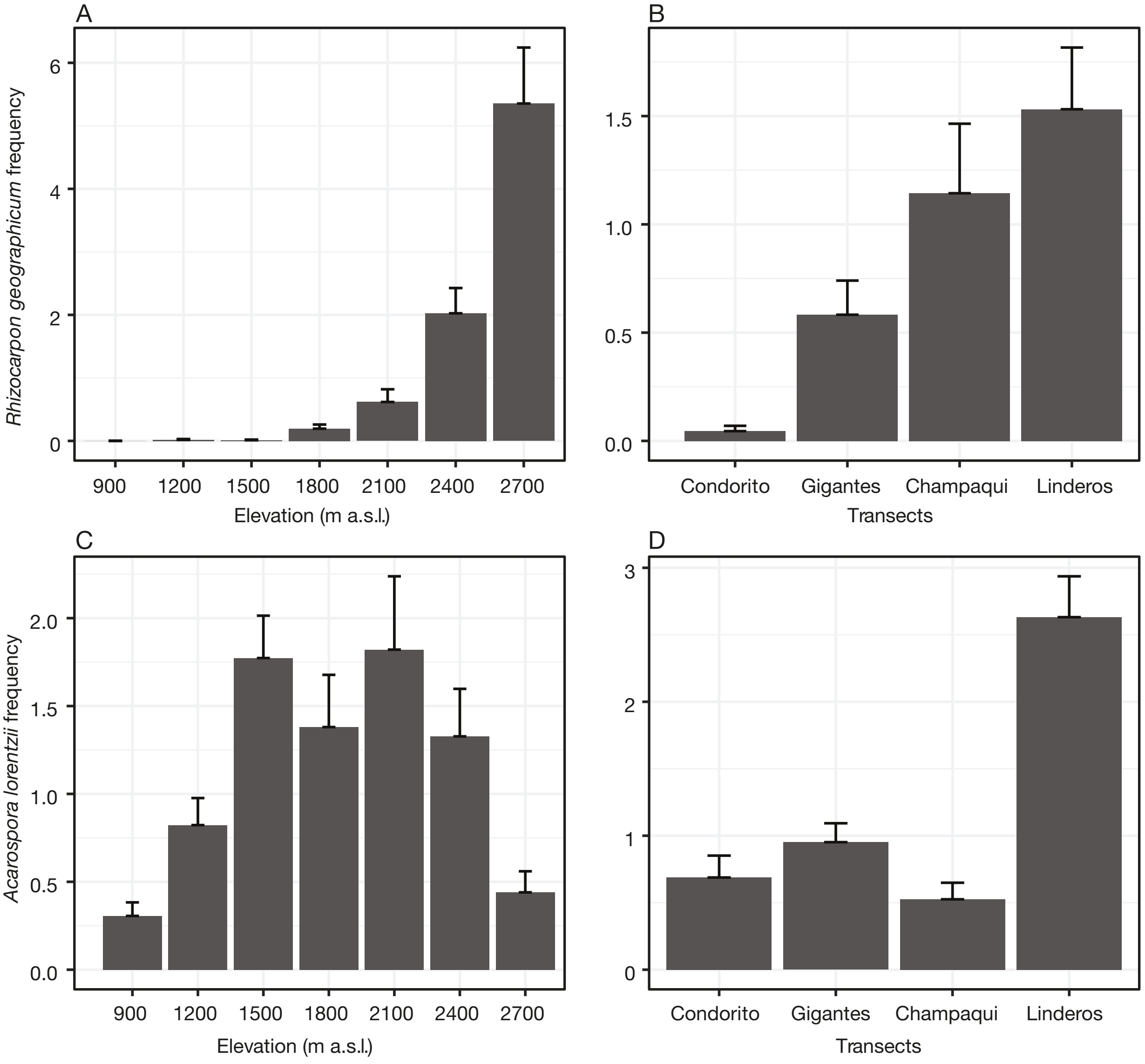
Appendix 1. — Continuation.

Species	**Family**	**Morpho-type**	**CL**	**CH**	**PNQ**	**LG**	**Abbreviation**
Ochrolechia parella (L.) A. Massal.	Ochrolechiaceae R.C. Harris ex Lumbsch & I. Schmitt	C	x				O_plla
Parmotrema tandilense (Adler & Elix) O. Blanco A. Crespo, Divakar, Elix & Lumbsch	Parmeliaceae Bercht. & J. Presl	F		x			P_bona**
Parmotrema hababianum (Gyeln.) Hale	Parmeliaceae Bercht. & J. Presl	F			x	x	P_hab**
Parmotrema reticulatum (Taylor) M. Choisy	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	P_ret
Parmotrema warmingii (Vain.) A.A. Spielm. & Marcelli	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	P_war
Peltigera dydactila (With.) J.R. Laundon	Peltigeraceae Dumort.	F		x			P_dyda**
Pertusaria sp.	Pertusariaceae Körb.	C	x			x	Pert_4
Pertusaria coriacea (Th. Fr.) Th. Fr.	Pertusariaceae Körb.	C	x	x	x	x	P_cor
Pertusaria sp. 2	Pertusariaceae Körb.	C	x	x	x	x	Pert_2**
Phaeophyscia sp.	Physciaceae Zahlbr.	F	x	x	x	x	Pha_sp
Physcia dubia (Hoffm.) Lettau	Physciaceae Zahlbr.	F		x		x	Ph_dub**
Physcia tribacia (Ach.) Nyl.	Physciaceae Zahlbr.	F	x	x	x	x	Ph_trib**
Physcia mobergii Bungartz	Physciaceae Zahlbr.	F				x	Ph_lob**
Placidium sp.	Verrucariaceae Eschw.	E	x				Plac_sp**
Placomaronea candelarioides Räsänen	Candelariaceae Hakul.	Fr	x	x	x	x	P_cand
Protoparmelia badia (Hoffm.) Hafellner	Parmeliaceae Bercht. & J. Presl	C	x	x	x	x	P_bad
Psiloparmelia distincta (Nyl.) Hale	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	P_dis
Psiloparmelia pustulata Elix & T.H. Nash	Parmeliaceae Bercht. & J. Presl	F	x		x		Ps_pus**
Psora sp.	Psoraceae Zahlbr.	E				x	Ps_sp**
Punctelia hypoleucites (Nyl.) Krog	Parmeliaceae Bercht. & J. Presl	F		x	x	x	Pu_hyp**
Punctelia semansiana (W.L. Culb. & C.F. Culb.) Krog	Parmeliaceae Bercht. & J. Presl	F		x	x	x	Pu_sem**
Punctelia colombiana Sérus.	Parmeliaceae Bercht. & J. Presl	F	x	x	x		Pu_col**
Punctelia perreticulata (Räsänen) G. Wilh. & Ladd	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	P_perr
Punctelia punctilla (Hale) Krog	Parmeliaceae Bercht. & J. Presl	F	x	x		x	P_pun
Punctelia stictica (Delise ex Duby) Krog	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	P_sti
Punctelia microsticta (Müll. Arg.) Krog	Parmeliaceae Bercht. & J. Presl	F		x	x		X_mic**
Ramalina celastri (Spreng.) A. Massal.	Ramalinaceae C. Agardh	Fr	x		x	x	Ra_cel**
Ramalina pilulifera Taylor	Ramalinaceae C. Agardh	Fr	x	x	x	x	R_pil
Ramalina puiggarii Müll. Arg.	Ramalinaceae C. Agardh	Fr			x		Ra_pui**
Remototrachyna rhabdiformis (Kurok.) Divakar & A. Crespo	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	H_rha
Rhizocarpon inarense (Vain.) Vain.	Rhizocarpaceae M. Choisy ex Hafellner	C	x		x		R_ino
Rhizocarpon disporum (Nägeli ex Hepp) Müll. Arg.	Rhizocarpaceae M. Choisy ex Hafellner	C	x	x	x	x	R_dis
Rhizocarpon geographicum (L.) DC.	Rhizocarpaceae M. Choisy ex Hafellner	C	x	x	x	x	R_geo
Rhizocarpon sp. *	Rhizocarpaceae M. Choisy ex Hafellner	C	x	x	x	x	Rh_gri**
Rhizocarpon obscuratum (Ach.) A. Massal.	Rhizocarpaceae M. Choisy ex Hafellner	C	x	x		x	R_obs
Rhizocarpon sp. 2	Rhizocarpaceae M. Choisy ex Hafellner	C	x	x		x	Rh_pro**
Rinodina confragosula (Nyl.) Müll.Arg.	Physciaceae Zahlbr.	C		x		x	Ri_con**
Rinodina confragosa (Ach.) Körb.	Physciaceae Zahlbr.	C	x			x	R_cnsa
Stereocaulon ramulosum Raeusch.	Stereocaulaceae Chevall.	D	x	x	x	x	S_ram
Teloschistes nodulifer (Nyl.) Hillmann	Teloschistaceae Zahlbr.	Fr	x	x	x	x	T_nod
Tephromela atra (Huds.) Hafellner	Tephromelataceae Hafellner	C	x	x	x	x	T_atra
Tetramelas concinnus (Th. Fr.) Giralt	Caliciaceae Chevall.	C	x	x	x	x	B_con**
Umbilicaria africana (Jatta) Krog & Swinscow	Umbilicariaceae Chevall.	F	x		x	x	U_afr**
Umbilicaria polyrrhiza (L.) Fr.	Umbilicariaceae Chevall.	F	x	x	x	x	U_pol
Usnea amblyoclada (Müll. Arg.) Zahlbr.	Parmeliaceae Bercht. & J. Presl	Fr	x	x	x	x	U_amb
Usnea cornuta Körb.	Parmeliaceae Bercht. & J. Presl	Fr		x			U_corn**
Usnea diuretzii Motyka	Parmeliaceae Bercht. & J. Presl	Fr	x	x		x	U_diur**
Usnea hieronymi Kremp.	Parmeliaceae Bercht. & J. Presl	Fr		x		x	U_hier**
Usnea krogiana P. Clerc	Parmeliaceae Bercht. & J. Presl	Fr		x			U_krog**
Usnea luti J.M. Rodr. & P. Clerc	Parmeliaceae Bercht. & J. Presl	Fr	x	x	x	x	U_lut
Usnea saxidilatata J.M. Rodr. & P. Clerc	Parmeliaceae Bercht. & J. Presl	Fr	x	x	x	x	U_sax
Xanthoparmelia imitatrix (Taylor) O. Blanco A. Crespo, Elix D. Hawksw. & Lumbsch	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	X_imi
Xanthoparmelia cordillerana (Gyeln.) Hale	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	X_cor
Xanthoparmelia cotopaxiensis T.H. Nash, Elix & J. Johnst.	Parmeliaceae Bercht. & J. Presl	F	x		x	x	X_cot**
Xanthoparmelia farinosa (Vain.) T.H. Nash, Elix & J. Johnst.	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	X_far
Xanthoparmelia hypopsila (Müll. Arg.) Hale	Parmeliaceae Bercht. & J. Presl	F		x		x	H_hyp**
Xanthoparmelia microspora (Müll. Arg.) Hale	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	X_mra
Xanthoparmelia mougeoti (Schaer. ex D. Dietr.) Hale	Parmeliaceae Bercht. & J. Presl	F	x		x		X_mou**
Xanthoparmelia plittii (Gyeln.) Hale	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	X_pli
Xanthoparmelia punctulata (Gyeln.) Hale	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	X_pun

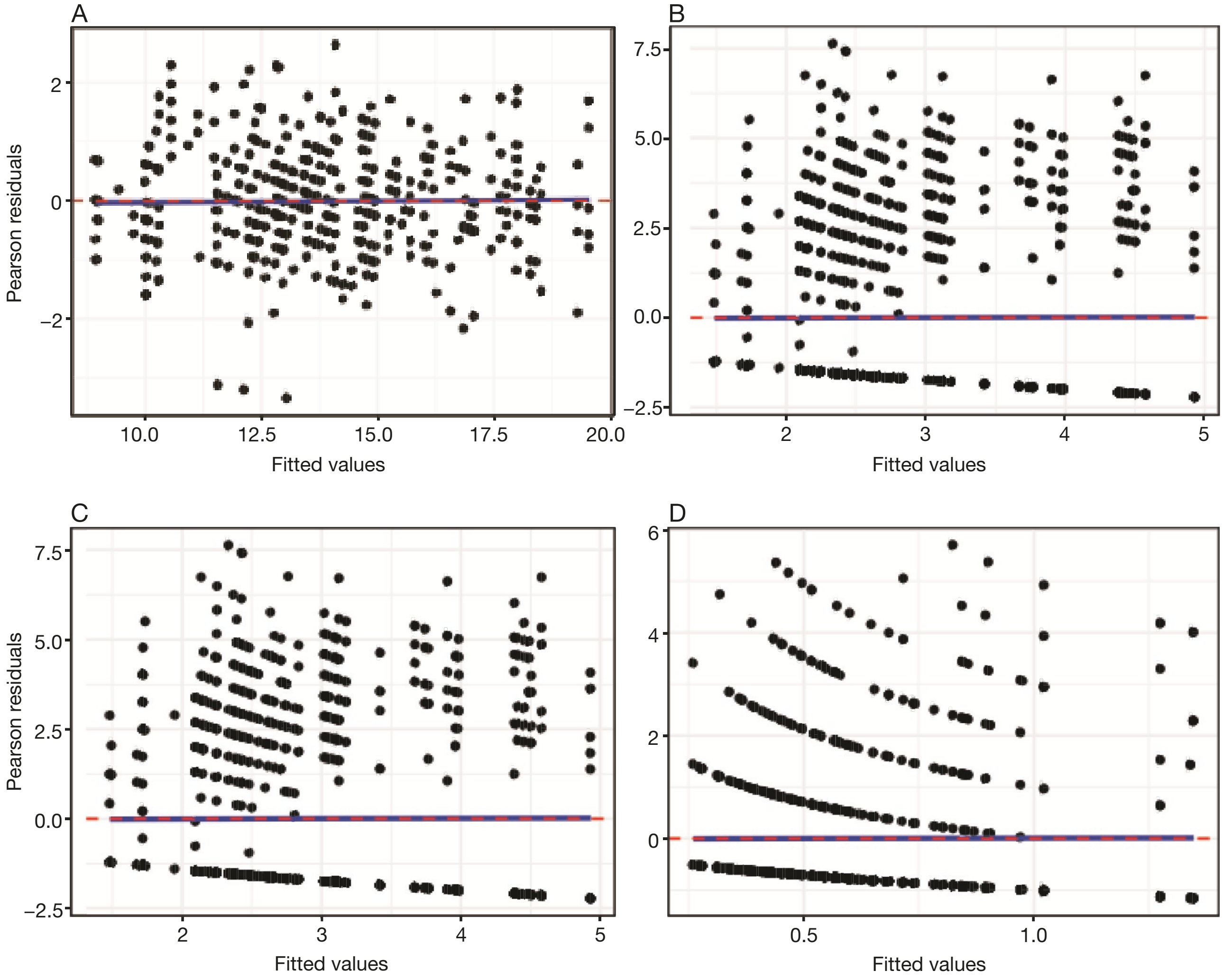
Appendix 1. — Continuation.

Species	Family	Morpho-type	CL	CH	PNQ	LG	Abbreviation
Xanthoparmelia santessonii T.H. Nash & Elix	Parmeliaceae Bercht. & J. Presl	F		x			X_san**
Xanthoparmelia scabrosa (Taylor) Hale	Parmeliaceae Bercht. & J. Presl	F			x		X_sca**
Xanthoparmelia sp.	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	X_sp
Xanthoparmelia sp. 2	Parmeliaceae Bercht. & J. Presl	F					X_sp2**
Xanthoparmelia submougeotii Hale	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	X_subm**
Xanthoparmelia subtinctina T.H. Nash & Elix	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	X_subt**
Xanthoparmelia subulcerosa T.H. Nash & Elix	Parmeliaceae Bercht. & J. Presl	F			x	x	X_subu**
Xanthoparmelia taractica (Kremp.) Hale	Parmeliaceae Bercht. & J. Presl	F		x		x	X_tar**
Xanthoparmelia ulcerosa (Zahlbr.) Hale	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	X_ulce**
Xanthoparmelia wrightiana T.H. Nash, Elix & J. Johnst.	Parmeliaceae Bercht. & J. Presl	F	x	x	x	x	X_wna
Xanthoria parietina (L.) Th. Fr.	Parmeliaceae Bercht. & J. Presl	F			x		X_par**

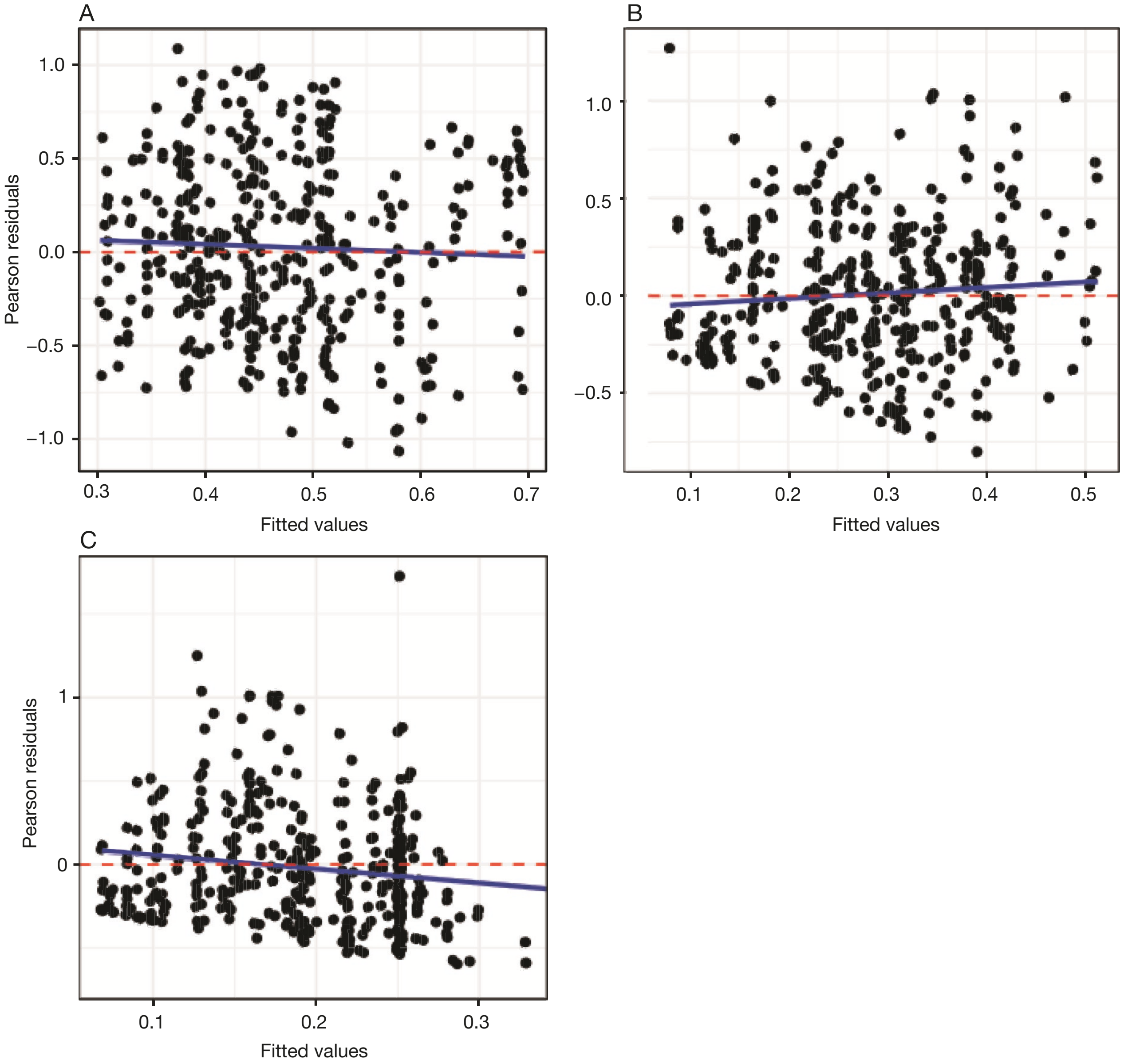
Appendix 2. — Frequency of a mountain top species across: **A**, elevation gradients; **B**, different transects; **C**, frequency of a cosmopolitan species across elevation gradients; **D**, different transects.



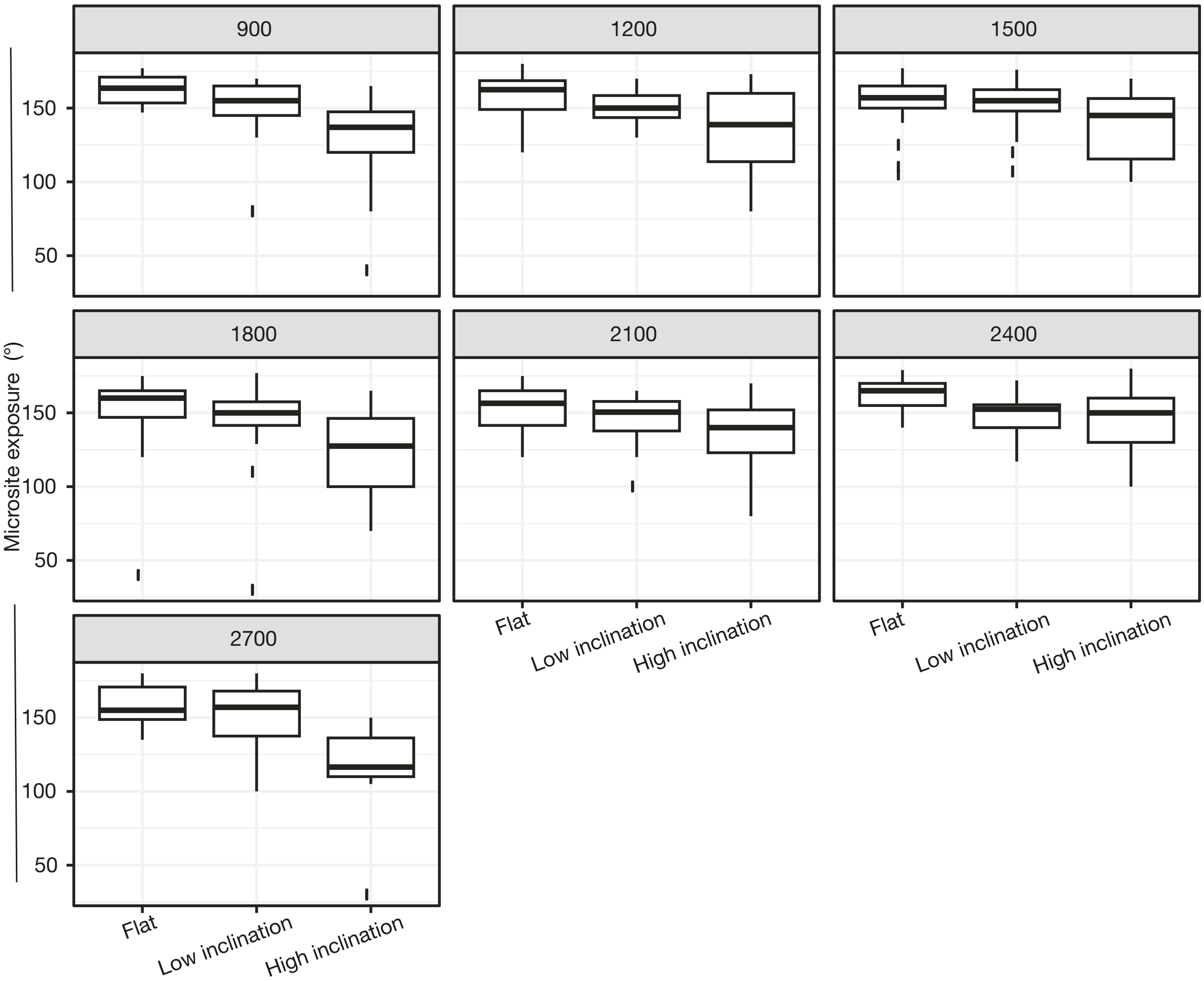
Appendix 3. — Model validation for Generalized Mixed Linear Models (GLMMs) carried for total richness: **A**, total richness; **B**, crustose richness; **C**, foliose richness; **D**, fruticose richness.



Appendix 4. — Top five representative species per Environmental variable of the performed Canonical Correlation Analysis (CCA).



Appendix 5. — Microsite inclination and exposure among the elevational gradient of the study site.



Appendix 6. — Top five representative species per Environmental variable of the performed CCA.

Species	Angle Difference	Environmental Variable	CCA1 Score	CCA2 Score	Abbreviation
Xanthoparmelia plittii (Gyeln.) Hale	1.3413	Flat rocks	–0.0822	–1.2732	X_plittii
Acarospora lorentzii (Müll. Arg.) Hue	3.4142	Flat rocks	–0.0080	–0.2824	A_lorentzii
Protoparmelia badia (Hoffm.) Hafellner	5.7529	Flat rocks	–0.1455	–0.7636	P_badia
Xanthoparmelia mougeotii (Schaer. ex D. Dietr.) Hale	5.9201	Flat rocks	–0.0858	–0.4430	X_mougeoti
Buellia sp.	7.0382	Flat rocks	–0.0969	–0.4528	Buellia_sp1
Cora pavonia (Weber & D. Mohr) Mont.	0.1846	Vertical rocks	0.0202	0.5736	Dictyonema_sp
Punctelia semansiana (W.L. Culb. & C.F. Culb.) Krog	0.7291	Vertical rocks	0.0167	0.3734	P_semansiana
Flavoparmelia papillosa (Lynge ex Gyeln.) Hale	4.9077	Vertical rocks	0.0844	0.7145	F_papilosa
Usnea amblyoclada (Müll. Arg.) Zahlbr.	5.4653	Vertical rocks	0.0709	0.5535	U_amblyoclada
Flavoparmelia caperata (L.) Hale	6.2970	Vertical rocks	–0.1193	1.5271	F_caperata
Lecidea sp. 2	4.0669	Elevation	0.2111	0.0190	Lecidea_sp2
Ramalina pilulifera Taylor	4.7986	Elevation	1.2498	0.1286	R_pilulifera
Lecidea sp. 1	5.5405	Elevation	1.1307	–0.0883	Lecidea_sp
Ramalina puiggarii Müll. Arg.	6.0624	Elevation	1.1487	0.1439	R_puiggarii
Usnea cornuta Körb.	9.1342	Elevation	0.3543	0.0638	U_cornuta
Buellia sulphurea Malme	1.2027	North-facing rocks	0.0463	0.3138	B_sulphurea
Usnea amblyoclada (Müll. Arg.) Zahlbr.	2.2926	North-facing rocks	0.0709	0.5535	U_amblyoclada
Rhizocarpon disporum (Nägeli ex Hepp) Müll. Arg.	2.7509	North-facing rocks	0.1594	0.7286	R_disporum
Flavoparmelia papillosa (Lynge ex Gyeln.) Hale	2.8501	North-facing rocks	0.0844	0.7145	F_papilosa
Xanthoparmelia microspora (Müll. Arg.) Hale	5.6805	North-facing rocks	0.0936	0.3430	X_microspora
Caloplaca sideritis (Tuck.) Zahlbr.	0.1917	South-facing rocks	–1.6098	0.9557	C_sideritis
Hypotrachyna sp.	0.5084	South-facing rocks	–1.4505	0.8720	Hy_badia
Catillaria sp.	1.6682	South-facing rocks	–1.0792	0.6789	Catillaria_sl
Lepraria sp.	2.0941	South-facing rocks	–1.1341	0.7253	Lepraria_sp1
Hypotrachyna dentella (Hale & Kurok.) Hale	2.1207	South-facing rocks	–1.4682	0.9399	H_dentella
Caloplaca cinnabarina (Ach.) Zahlbr.	0.8727	Exposition	0.0848	–0.7148	C_cinnabarina
Cladonia sp.	2.8990	Exposition	0.0112	–0.1346	C_esteril
Xanthoparmelia microspora (Müll. Arg.) Hale	7.7443	Exposition	0.3035	–1.1028	X_microsticta
Pertusaria sp. 2	8.5928	Exposition	0.3321	–1.1406	Pertusaria_sp2
Acarospora lorentzii (Müll. Arg.) Hue	9.2623	Exposition	–0.0080	–0.2824	A_lorentzii