Original Paper The relative effect of altitude and aspect on saxicolous lichen communities at mountain summits from central-west of Argentina

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Abstract

The altitudinal patterns of lichen communities in altitudinal gradients are very variable. The changes that occur along the mountains depend on climatic factors but also on microsite variables such as substrate type and aspect. The effect of altitude and aspect on richness, cover and composition of saxicolous lichens communities along an elevation gradient in extra Andean mountains from the central-west of Argentina was studied. Rock outcrops on the north and south aspect of three mountain summits distributed between 2,500 and 4,500 m.a.s.l. were sampled. Lichen species present in a 20×20 cm square were identified and the relative cover was measured using digital photography. Richness, cover and composition were analyzed through linear models and multivariate analysis. Fifty-eight saxicolous lichen species were identified between the three sites. Richness and cover were maximum at middle altitude. Also compositional differences among communities of each mountain summit were found. Finally, the effect of the aspect was significant at lower altitudes for cover and composition.

Key words: diversity, elevation gradient, lichenized fungi, microsite, species composition.

Resumen

Los patrones de las comunidades de líquenes en gradientes altitudinales son muy variables. Los cambios que ocurren a lo largo de las montañas dependen de factores climáticos, pero también de variables de micrositio como el tipo de sustrato y la orientación. En este trabajo, se estudió el efecto de la altitud y la orientación sobre la riqueza, la cobertura y la composición de las comunidades de líquenes saxícolas a lo largo de un gradiente de elevación en las montañas extra andinas del centro-oeste de Argentina. Se tomaron muestras de afloramientos rocosos en las orientaciones norte y sur en tres cumbres de montañas distribuidas entre 2.500 y 4.500 msnm. Se identificaron las especies de líquenes presentes en un cuadrado de 20 × 20 cm y se midió la cobertura relativa mediante fotografía digital. La riqueza, cobertura y ocho especes de líquenes entre los tres sitios, La riqueza y la cobertura fueron máximas a media altitud, además, hubo diferencias en la composición de especies entre las comunidades de líquenes de cada cima. Por último, el efecto de la orientación de las comunidades de líquenes de cada cima. Por último, el efecto de la orientación fue significativo en altitudes más bajas para la cobertura y la composición.

Palabras clave: diversidad, gradiente altitudinal, hongos liquenizados, micrositio, composición.

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Introduction

Elevation gradients are considered one of the most important patterns in biogeography (Lomolino 2001). Environmental conditions change along the mountain ascension and, as a consequence, richness and species composition change too (Körner 2007).

It is well known that lichens, like the majority of organisms, respond to factors that change with elevation (Vetaas et al. 2019). Therefore, altitude is a strong variable that affects richness, species composition and diversity in lichen communities (Baniya et al. 2010; Vittoz et al. 2010; Bässler et al. 2016; Rodríguez et al. 2017; Cleavitt et al. 2019). Depending on the latitude, other important factors are aspect (principally N-S) and slope, because both determine the amount of solar radiation, which along with altitude, impact on incident solar radiation (insolation) and amount of evapotranspiration (Pentecost 1979; Kidron & Termina 2010; Rodríguez et al. 2017). Thus, south aspects are colder and more humid than north aspects (Körner 1995, 2007) in the southern hemisphere.

Many authors highlight the huge diversity of lichens in high mountain tops in Europe and Asia (Baniya et al. 2010; Vittoz et al. 2010), and this pattern is also observed in South America where many species of lichen have been found in mountain systems (Marcano et al. 1996;). In spite of this, the relationship between altitude and lichen communities is far from being completely understood. Previous works show different patterns such as lineal, unimodal or no relationship between diversity and altitude (Baniya et al. 2010; Bässler et al. 2016; Rodríguez et al. 2017). These studies differ in their altitudinal range, for example Rodríguez et al. (2017) use a gradient between 900 to 2,700 m.a.s.l., however Pinokiyo et al. (2008) use a range between 400 to 2,700 and Baniya et al. (2010) from 200 to 7,400 m.a.s.l. This may be the cause of such different results. In the same way Körner & Spehn (2002) highlight the importance of inquiring in particular characteristics of each study zone and their intrinsic heterogeneity.

On the other hand, lichens growing on rock outcrops could make a particularly good study system more isolated than other taxa from human disturbances such as agriculture, fires and livestock trampling (*i.e.* for plants: Sylvester *et al.* 2014).

We attempt to answer the question of how the saxicolous lichen communities changes with altitude and aspect in one of the highest gradients in an extra Andean mountain in Argentina. Thus, our hypothesis is that richness, cover and species composition of saxicolous lichen communities change not only with altitudinal gradient but also with the aspect.

Material and Methods

Study area

Famatina mountain is located in centralwest of Argentina, in La Rioja province between 28°40'S, 68°W and 29°20'S, 67°30'W. Famatina mountain belongs to the Famatina system (Toselli *et al.* 1996) which is isolated from the Andean mountain range and has an altitude to 6,097 m.a.s.l. Thus, exclusive ecosystems and huge biodiversity are present, allowing the convergence of Patagonian, Cuyana and NOA floras (Femenia 2011).

According to previous observations, Famatina mountain has many rocky outcrops. We selected three mountain tops that we called: "Gemelos" (GEM) with 2,581 m.a.s.l. (-28.868; -67.692), "Mirador del Ocre" (MDO) with 2,897 m.a.s.l. (-28.918; -67.680) and Arcoíris (ARC) with 4,500 m.a.s.l. (-29.013; -67.747). Therefore, an elevation gradient was settled between 2,581 m.a.s.l. and 4,500 m.a.s.l. We did not use mountain tops higher than 4,500 m.a.s.l because there were no lichens above this altitude in Famatina mountain (Rodríguez personal observations). As can be seen in Figure 1, GEM (lowest altitude) was the warmest top in the study with average temperature per month in summer up to fifteen degrees Celsius and in winter the average temperature goes down closer to eight degrees Celsius, while in MDO (middle altitude), average temperature was in general lower. In summer it is not warmer than fifteen degrees Celsius and in winter it is closer to five degrees Celsius. Finally, the coldest top was ARC (highest altitude), where average temperature in summer is less than eight degrees and in winter it is less than zero degrees Celsius (Fick & Hijams 2017).

Every summit lacked active volcanism, had to be exposed to the same local climate and had to be composed of similar bedrock, in order to exclude other possible factors which might influence the zonal communities of each summit (Pauli *et al.* 2015).



Figure 1 – Average monthly temperature. It corresponds to the period between 1970 and 2000, the information is given by Fick & Hijams (2017) in World Clime and it was obtained using Qgis (Qgis 2019), with the gps points of the tops.

Sampling

The study was carried out during March 2017. We selected 20 rocky outcrops in each summit, 10 on the north aspect and 10 on the south aspect. The rock outcrops were within 10 m contour line below the top's highest point and they were separated by at least 50 m from each other. The selected rock outcrops shared similar conditions: same aspect as the hillside and slope between 40 and 90 degrees in order to avoid the effect to the slope.

In the central part of each outcrop, we identified lichen species in a square of 20×20 cm. We measured the relative cover of each species in the square through the use of digital images of each square, a photography was taken per square and the total lichen cover and the cover of each species was calculated using the software Image J.

Species identification

Previously to taking the photography, we identified lichen species in the field, using hand magnifiers and michrochemical tests. When the field identification was difficult, we took samples and we analyzed them in the laboratory.

We analyzed morphological, anatomical and chemical characteristics following routine-techniques including macroscopic and microscopic observations of sections of thallus and identification of secondary metabolites by Thin Layer Chromatography (Orange *et al.* 2001).

A specimen of each identified species was deposited in CORD Herbaria. When the identification of some crustose specimens was impossible at the genus or species level due to the lack of reproductive structures or information about the taxa, these specimens were processed with artificial names.

Data analysis

Each square was the sample unit in all analysis. To assess total lichen cover we used General mixed model because the variable has normal error distribution (mean total lichen cover per summit and aspect). A parameter was added to account for heteroscedasticity. On the other hand the species richness was analyzed using generalized linear model with Poisson distribution (mean species richness per summit and aspect). For both models we used Fisher's least significant difference (LSD) in order to compare average treatments. Model selection was conducted using nonlinear fittings in R project software version 2.6.2 and INFOSTAT (Di Rienzo *et al.* 2017).

To analyze compositional differences of lichen communities according to altitude and aspect, we employed canonical correlation analysis

4 de 11

(CCA), using the cover species per units. The variable aspect was transformed throught cosine of slope aspect. So as to filter noise that could obscure the underlying structure of the data and to reduce the stochastic effects of rare species, we excluded lichen species present in three or less sample points (McCune *et al.* 2002).

As a Classification method, we used indicator species analysis (ISA) to detect and describe the species values in groups determined by altitude, aspect and both factors together. These last two analysis were conducted using PcOrd (McCune & Mefford 1999).

Results

Fifty-eight saxicolous lichen species were identified in 60 rocky outcrops (squares) analyzed between the three sites (Tab. 1). Five North rocky outcrops in ARC do not have any lichens. The 58 lichens recorded belong to 15 families and the best represented family was Parmeliaceae with 13 species. The most diverse genera were *Xanthoparmelia, Buellia, Caloplaca* (including *Polycauliona*). Among the species, 55% were crustose, 33% foliose, 9% squamulouse and 3% fruticose (Tab. 1).

Table 1 – Saxicolous lichen species from Famatina mountains (Argentina), their family, summits and growth form.
GEM = Gemelos 2,581 m.a.s.l; MDO = Mirador del Ocre 2,897 m.a.s.l.; ARC = Arcoíris 4,500 m.a.s.l.; 1 = presence;
0 = absence; $GF = $ growth form; $C = $ crustose; $F = $ foliose; $Fr = $ fruticulose; $S = $ squamulouse.

Species	Family	GEM	MDO	ARC	GF
Acarospora altoandina H. Magn.	Acarosporaceae	1	1	1	С
Acarospora boliviana H. Magn.	Acarosporaceae	1	1	1	С
Acarospora rouxii K. Knudsen, Elix & Reeb	Acarosporaceae	1	0	0	С
Acarospora sp. 1	Acarosporaceae	1	1	0	С
Acarospora sp. 2	Acarosporaceae	0	1	0	С
Acarospora sp. 3	Acarosporaceae	1	0	0	С
Acarospora sp. 4	Acarosporaceae	0	0	1	С
Acarospora strigata (Nyl.) Jatta	Acarosporaceae	0	1	0	С
Amandinea coniops (Wahlenb.) M. Choisy	Caliciaceae	0	1	0	С
Amandinea sp. 1	Caliciaceae	0	1	0	С
Buellia dispersa A. Massal.	Caliciaceae	1	1	1	С
Buellia sp. 1	Caliciaceae	0	1	0	С
Buellia sp. 2	Caliciaceae	0	0	1	С
Buellia stellulata (Taylor) Mudd	Caliciaceae	1	1	0	С
Buellia sulphurea Malme	Caliciaceae	0	1	1	С
Caloplaca americana (Malme) Zahlbr.	Teloschistaceae	0	1	1	С
Caloplaca ochraceofulva (Müll. Arg.) Jatta	Teloschistaceae	1	1	0	С
Candelariella vitellina (Ehrh.) Müll. Arg.	Candelariaceae	1	1	1	S
Endocarpon adscendens (Anzi) Müll. Arg.	Verrucariaceae	1	1	0	S
Flavoparmelia caperata (L.) Hale.	Parmeliaceae	1	0	0	F
Lecanora polytropa (Hoffm.) Rabenh.	Lecanoraceae	0	1	1	С

Species	Family	GEM	MDO	ARC	GF
Lecidea sp. 1	Lecideaceae	0	1	0	 C
Lecidea sp. 2	Lecideaceae	1	0	0	C
Lecidella sp.	Lecanoraceae	0	1	0	С
Lichen sp. 1	Unknown	1	1	0	С
Lichen sp. 2	Unknown	0	1	0	С
Paraparmelia sp.	Parmeliaceae	1	0	1	F
Pertusaria sp.	Pertusariaceae	1	1	0	С
Phaeophyscia sp.	Physciaceae	0	1	0	F
Physcia tribacia (Ach.) Nyl.	Physciaceae	1	1	0	F
Placomaronea candelarioides Räsänen	Candelariaceae	1	1	1	F
Polycauliona bolacina (Tuck.) Arup	Teloschistaceae	1	1	1	С
Protoparmelia badia (Hoffm.) Hafellner	Parmeliaceae	1	0	0	С
Psiloparmelia distincta (Nyl.) Hale	Parmeliaceae	0	1	0	F
Psora sp.	Psoraceae	1	0	0	S
Punctelia stictica (Delise ex Duby) Krog	Parmeliaceae	1	1	0	F
Ramalina polymorpha (Lilj.) Ach.	Ramalinaceae	1	1	0	Fr
Rhizocarpon disporum (Nägeli ex Hepp) Müll. Arg.	Rhizocarpaceae	0	1	0	С
Rhizocarpon geographicum (L.) DC.	Rhizocarpaceae	0	0	1	С
Rhizocarpon sp. 1	Rhizocarpaceae	0	0	1	С
Rhizoplaca aspidophora (Vain.) Redón	Lecanoraceae	1	1	0	S
Rhizoplaca melanophthalma (DC.) Leuckert	Lecanoraceae	0	0	1	S
Rinodina confragosula (Nyl.) Müll. Arg.	Physciaceae	0	1	0	С
Rinodina longisperma Matzer & H. Mayrhofer	Physciaceae	0	1	0	С
Rinodina oxydata (A. Massal.) A. Massal.	Physciaceae	1	0	0	С
Teloschistes hosseusianus Gyeln.	Teloschistaceae	0	1	0	Fr
Umbilicaria decussata (Vill.) Zahlbr.	Umbilicariaceae	0	0	1	F
<i>Umbilicaria haplocarpa</i> Nyl.	Umbilicariaceae	0	1	0	F
Xanthoparmelia cordillerana (Gyeln.) Hale	Parmeliaceae	1	1	0	F
Xanthoparmelia farinosa (Vain.) T.H. Nash, Elix & J. Johnst.	Parmeliaceae	1	1	0	F
Xanthoparmelia ferraroiana T.H. Nash, Elix & J. Johnst.	Parmeliaceae	0	1	0	F
Xanthoparmelia plittii (Gyeln.) Hale	Parmeliaceae	1	1	0	F
Xanthoparmelia punctulata (Gyeln.) Hale	Parmeliaceae	1	0	0	F
Xanthoparmelia santessonii T.H. Nash & Elix	Parmeliaceae	0	1	0	F

6 de 11

Species	Family	GEM	MDO	ARC	GF
Xanthoparmelia sp. 1	Parmeliaceae	0	1	0	F
Xanthoparmelia sp. 2	Parmeliaceae	1	0	0	F
Xanthoparmelia ulcerosa (Zahlbr.) Hale	Parmeliaceae	0	1	0	F
Xanthoparmelia wrightiana T.H. Nash, Elix & J. Johnst.	Parmeliaceae	1	0	0	F



Figure 2 – a. Average total lichen richness; b. average total lichen cover, in Famatina Mountains (Argentina). GEM = Gemelos 2,581 m.a.s.l.; MDO = Mirador del Ocre 2,897 m.a.s.l.; ARC = Arcoíris 4,500 m.a.s.l. Thin bars correspond to standard error.

The highest richness was found in the intermediate elevation (MDO) with 41 species, followed by GEM with 29 species. Finally, ARC had the least richness, with 10 species. The richness was significantly different for altitude (p value < 0.0001) but not for aspects (p value = 0.330) (Fig. 2a) or for their interaction either. Similar patterns were found for the relative lichen cover and altitude: in the middle altitude (MDO) the cover was higher (35.55%) than GEM (19.64%) and ARC (8.34%) with p value = 0.0003 (Fig. 2b). On the other hand, significant differences were observed for lichen cover between South aspect (29.76%) and North aspect (12.59%), p value = 0.0011. Also, the interaction between both factors was significant with a p value = 0.0036, having a stronger effect at lower and middle altitudes (Fig. 2b). After the exclusion of the rare species from the matrix, the CCA analysis was applied using 27 species (Fig. 3). The first canonical axis indicates that altitude was the most important factor in the ordination, with a canonical correlation coefficient of 0.828 between first axis and altitude. According to the CCA different species composition of lichen communities were found along the three summits studied here. On the other hand, the axis two and aspect had a canonical correlation coefficient of 0.626. It should be noted that the units that belong to ARC do not show a tendency of separation with axis two, indicating a less significant effect of aspect at this altitude.

In accordance with these results, 12 species were confirmed by the ISA as indicator species for altitude, aspect or a specific combination between both variables (Tab. 2). Among them, *Buellia sulphurea, Placomaronea candelarioides, Umbilicaria haplocarpa* are indicators of North MDO and *Endocarpon adcendens* of South GEM. Also this species can be observed in CCA plot (Fig. 3). Furthermore, *Umbilicaria decussta, Rhizoplaca melanophthalma* and *Candelariella vitelina* have great indicator value for ARC. Changes in diversity through an elevation gradient are the results of evolutionary and ecology processes (Rahbek 2005). Thus, lineal relationship, hump-shaped relationship and even no relationship can be observed (Lomolino 2001; Vittoz *et al.* 2010) and different explanations have been suggested. In Famatina mountains we found a humped-shaped pattern with a peak of richness in the intermediate altitude. This is in agreement with



Figure 3 – Canonical correlation analysis (CCA). Black arrows show the correlation between each axis with Altitude and Aspect N-S. \blacktriangle = Gemelos (2,581 m.a.s.l); \bullet = Mirador del Ocre (2,897 m.a.s.l.); \blacksquare = Arcoiris (4,500 m.a.s.l.); black symbols = south aspect; grey symbols = north aspect. Species: B sulph = *Buellia sulphurea*; C amer = *Caloplaca americana*; Psi dis = *Psiloparmelia distincta*; Rhi asp = *Rhizoplaca aspidophora*; Ama sp1 = *Amandinea* sp. 1; P can = *Placomaronea candelarioides*; X ferra = *Xanthoparmelia ferraroiana*; Ac sp1 = *Acarospora* sp1; Pert = *Pertusaria* sp; Ac altan = *Acarospora altoandina*; Phy = *Physcia tribacia*; Um hap = *Umbilicaria haplocarpa*; X cor = *Xanthoparmelia cordillerana*; Rin lg = *Rinodina longisperma*; R oxy = *Rinodina oxydata*; P stic = *Punctelia stictica*; Am con = *Amandinea coniops*; B stel = *Buellia stellulata*; X far = *Xanthoparmelia farinosa*; Xplit = *Xanthoparmelia plitii*; Cal och = *Caloplaca ochraceofulva*; P bol = *Policauliona bolacina*; En ads = *Endocarpon adscendens*; Can vit = *Candelariella vitellina*; A bol = *Acarospora boliviana*; Um dec = *Umbilicara decussata*; Rhiz mel = *Rhizoplaca melanophthalma*.

Table 2 – Indicator Species Analyzes (ISA) p < 0.05, according to areas (summits, aspects and summits and aspects).GEM = Gemelos 2,581 m.a.s.l; MDO = Mirador del Ocre 2,897 m.a.s.l.; ARC = Arcoíris 4,500 m.a.s.l.; GF = growthform; F = foliose; Fr = fruticulose; S = squamulouse; C = crustose; IV = Indicator Value.

Species	GF	Area	IV	р*
Amandinea sp. 1	С	MDO	25	0.0232
Buellia sulphurea		MDO	20	0.0334
	C	MDO-North	80	0.0004
Candelariella vitellina	C	ARC-South	69.8	0.0038
	C	South	31.7	0.0274
Endocarpon adscendens		GEM	19.7	0.0334
	S	GEM-South	79	0.0004
		South	26.3	0.0186
Placomaronea candelarioides		MDO	74.2	0.0002
	С	MDO-North	29.1	0.0234
		North	42.7	0.008
Psiloparmelia distincta	F	MDO	20	0.033
Punctelia stictica	F	MDO	20	0.0364
Rhizoplaca melanophthalma	S	ARC	100	0.0002
	5	ARC-South	64.6	0.0002
Rinodina longisperma	С	MDO	40	0.0004
Umbilicaria decussata	F	ARC	33.3	0.0004
Umbilicaria haplocarpa	F	MDO	50	0.0002
	F	MDO-North	39.1	0.0082

other previous studies (Wolf 1993; Pinokiyo *et al.* 2008; Baniya *et al.* 2010). However our findings are distinct from recent works (Nascimbene & Marini 2015; Bässler *et al.* 2016; Rodríguez *et al.* 2017). Rahbek (2005) argued that shortening the extent of the altitudinal gradient can result in an incomplete pattern. Here we studied a large gradient with more than 2,000 m of elevation between the lowest and the highest site.

Also, the total lichen cover presented the same pattern. This variable is not commonly studied along altitudinal gradients probably because there is not too much change previously observed (Rodríguez *et al.* 2017). Richness and total lichen cover indicate that the intermediate altitude could present optimal conditions for lichens. Many components of climate and local environment

vary in a non-random way along most elevation gradients, so richness varies with these changes in climatic conditions and peaks at elevations characterized by a combination of conditions documented to be optimal for focal species (Lomolino 2001). Also, spatial heterogeneity and habitat diversity are important determinants of species richness at local scale (Lundholm 2009).

The aspect explains variation only for total cover of lichens and its interaction with altitude. As the conditions on south-facing surfaces are favorable, competitive species can survive, while on north aspects only resistant species to unfavorable conditions are present (Armstrong & Welch 2007). Total cover along the elevation gradient and between north and south aspects show significant differences, whereas intermediate top

(MDO) and south aspects had more richness. This affects, in turn, the radiation, exposure and humidity. As a consequence, north-facing surfaces present unfavorable conditions, warmer and less humid than south-facing surfaces (Körner 2007). High surface temperature may have two effects on lichens. First, the thalli may dry out, resulting in the partial loss of cellular water from both symbiotic partners (Honegger 1991). Second, since the thalli will dry out more rapidly after rain, they will lose carbohydrates. resulting in lower growth rates (Armstrong & Smith 1976). At intermediate altitude (MDO), temperatures are moderate, which would explain the high lichen cover at this summit. Also, south aspects did not show any difference with north aspects at Arcoíris top, probably due to overly low temperatures on south aspects at this elevation.

The structure of Famatina saxicolous lichens communities is not uniform, and depends on altitude and aspect, with the latter important only at low and middle altitudes. Temperature, humidity and solar radiation vary across different altitudes (Körner 2007), and thus those species which have high tolerance to extreme climatic conditions may not grow in elevations where conditions are better because of the interspecific competition, while in elevations where conditions are unfavorable, competition goes down, allowing the growth of tolerant species in these conditions (Armstrong & Welch 2007). A similar explanation is relevant to aspect as was mentioned previously. In this way, different altitudes and aspects have different lichens communities, a result observed in other studies (Pinokiyo et al. 2008; Ruas et al. 2015; González et al. 2017; Rodríguez et al. 2017).

Similar to our results, several works where they studied lichen communities showed a high frequency of rare species (Kuntz & Larson 2006; Cáceres *et al.* 2007; Pinokiyo *et al.* 2008; Rodríguez *et al.* 2017). We found that 75 percent of identified species had a frequency lower than 10 per cent, and 65 percent of them were only present in one summit. This suggests niche specialization as a consequence of influencing factors such as solar radiation, temperature and humidity (Rubio *et al.* 2002), factors determined by altitude and aspect (Pentecost 1979; Körner 2003, 2007). On the other hand, this result supports the idea that rock outcrops are reservoirs of lichen biodiversity (Matthes *et al.* 2000).

From analyzing the composition of Famatina saxicolous lichen communities, it can be observed that MDO had the biggest foliose lichen richness, with a similar result reported by Pinokiyo *et al.* (2008) where they found a peak of foliose lichen at middle

altitude. Moreover MDO had four foliose lichens as indicators, ratifying the importance of foliose lichen to this summit. Crustose lichens were dominant along the entire gradient, but this dominance is emphasized in Arcoíris, as a consequence of the reduction of richness of foliose lichens at higher altitudes (Wolf 1993). On the other hand, we noticed the presence of Rhizoplaca melanophthalma as an indicator of Arcoíris. Its distribution is Andean and Patagonic (Leavitt et al. 2013), which is consistent with altitude and conditions of this mountain top. In the same way, we found the existence of species associated with particular tops and aspects characterized by high radiation such as Candelariella vitellina in ARC and Placomaronea candelarioides and Buellia sulphurea for north MDO; they are all species with orange and yellow colors which have chemical substances like rizocarpic acid, that could protect the algae against excessive radiation in these summits (Elix & Stocker-Worgotter 2008).

In this work, we showed a hump-shaped pattern for richness and cover of saxicolous lichens in an elevation gradient. In addition, the microsites, represented by aspects, modified this pattern and interacted with altitude, which was evident at lower altitudes. Finally we found compositional differences among saxicolous lichen communities in the summits studied.

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