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Small shifts in microsite occupation could mitigate climate change consequences for mountain top endemics: a test analyzing saxicolous lichen distribution patterns

Juan Manuel Rodriguez[1] · **Daniel Renison**[1] · **Edith Filippini**[1] · **Cecilia Estrabou**[1]

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Abstract The extent to which small shifts among local topographic microsites could mitigate the effects of larger-scale climate change in arctic–alpine systems including mountain top organisms is largely unknown. This study is among the first to evaluate the relative contribution of microsite and altitude as a proxy for climate change on saxicolous lichen communities. We registered 107 lichen species in 54 boulders ranging from 900 to 2700 m.a.s.l. and in a large array of microsites in central Argentina. Communities ordinated along NMS multivariate analysis axes 1, 2 and 3 presented a cumulative R^2 of 80%. The three axes were explained by altitude with axis 1 only being explained by altitude. Axis 2 was also explained by slope and aspect whereas axis 3 was explained by the interaction of altitude with aspect indicating that aspect was important only at lower altitudes but not at the mountain top. Lichen cover and richness were similar throughout the altitudinal gradient. We interpret that under a climate warming scenario, lower altitude species occupying pole ward facing slopes will have to migrate upwards while at the mountain top—for most communities—there still is scope for microsite segregation to compensate climate change.

Keywords Argentina · Lichen communities · Species richness · Lichen cover · Rock outcrops · Succession

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✉ Juan Manuel Rodriguez
juan.rodriguez@unc.edu.ar

[1] IIByT (CONICET - Universidad Nacional de Córdoba)/CERNAR FCEFyN - Universidad Nacional de Córdoba), Av. Velez Sarsfield 1611, X5016GCA Córdoba, Argentina

Introduction

Mountain top endemic species in low mountain ranges will not be able to migrate upwards to remain within their climate envelope, and it is thus presumed that climate change is a serious threat to these species (i.e. Thomas 2011). However, mountains are topographically very heterogeneous and recently developed techniques like thermal imaging and miniature data loggers have shown that microclimatic conditions at mountain sites vary greatly from site to site even at short distances (Scherrer and Körner 2010, 2011). The heterogeneous microclimatic conditions may buffer the effects of climate warming so the species climate envelope may move short distances into cooler sites rather than greater uphill distances to find similar climate conditions. If mountain top organisms are not segregated by microsites but segregated at lower altitudes—for example, situated at the pole facing cooler slopes—it would be expected that mountain top climate specialists will be able to survive by using cooler microsites as postulated by Scherrer and Körner (2011). Instead, if mountain top species are already segregated and restricted to the coolest sites at the mountain top, there is little margin for migration under a climate warming scenario. Thus, it is important to know the distribution of mountain species according to their elevation and segregation by microsites to determine whether the heterogeneous topography of mountain tops could buffer future climate warming.

Many studies that have attempted to determine the influence of climate change on species distribution have the drawback that climate change is often aligned with other changes such as land abandonment and reduction in livestock densities which confounds what are the ultimate reasons for upward migration (i.e. for tree lines: Cairns and Moen 2004; Speed et al. 2011). In mountainous regions, rock outcrops are particularly important habitats from the point of view of biodiversity conservation as they harbor a diverse biota usually under well protected situations inaccessible to human disturbances such as agriculture, fires and livestock trampling (i.e. for birds: García et al. 2008; for plants: Sylvester et al. 2014). In particular, lichens growing on rock outcrops could make a particularly good study system more isolated than other taxa from confounding human disturbances. Lichens are highly significant in terms of species richness, biomass and nutrient cycling (Lange et al. 1998; Matveyeva and Chernov 2000). Furthermore, lichens conform a good study system to understand the spatial structuring of organisms in relation to altitude and microsite selection (i.e. Bruun et al. 2006). The influence of climate change on the distribution of saxicolous lichen communities would be mainly caused by an increase in temperature and changes in precipitation patterns whereas the main influence of microsite characteristics on temperature would be due to boulder surface slope inclination and aspect which affects sun incidence and capture of precipitations. Saxicolous lichen communities are also influenced by geochemical composition of rocks and the surface area of the substrate among others (Armesto and Contreras 1981; Armstrong and Welch 2007; Kuntz and Larson 2006; Rajakaruna et al. 2012). These variables must be kept fixed or considered as co-variables to study main effects.

Here we study saxicolous lichen community variation along an altitudinal gradient in central Argentina to determine how lichen communities are structured in an altitudinal gradient and in relation to microsite with differing sun and precipitation incidence. We thus pretend to help determine what margin exists for climate change in our study area and propose the use of this methodology for other similar regions where climate history is not known in detail as occurs in vast regions of the Southern Hemisphere (Fraser et al. 2012). In our study region 30% of the mountain surface consists of natural rocks outcrops (Cingolani et al. 2008) mainly covered by lichens. Notwithstanding saxicolous lichen abundance in our study region, to date no studies have been published on their diversity, community structure and ecosystem importance, and only a few taxonomic studies have been performed (Estrabou and Adler 1999; Estrabou et al. 2006; Rodriguez et al. 2011).

We attempt to answer the question of how does the saxicolous lichen community structure change with altitudinal and microtopographical variation in the Mountains of central Argentina. We use this information to discuss what may happen to lichen and other communities under a climate warming scenario. Given that there are no studies reporting glaciers in our studied mountains, we assume they have been covered by vegetation and lichens throughout the past glaciations and we consider the mountain top endemics—inhabiting these and other similar mountains—to be vulnerable to climate warming (i.e. for a tree species, Marcora et al. 2008). Thus, our hypothesis was that lichen communities should be structured according to elevation and microsite even at the mountain top, with several mountain top species already situated at the cooler microsites and vulnerable under a scenario of climate warming.

Materials and methods

Study site

The Córdoba mountain range in central Argentina has a North–South orientation and heights up to 2884 m.a.s.l. The landscape is composed of a mosaic of tall tussock grasslands, pasture lands, natural granite outcrops, exposed rock surfaces created by soil erosion, and woodland fragments dominated almost exclusively by *Polylepis australis* (Cingolani et al. 2004, 2008). Rock outcrops occupy near 30% of the mountain area in central Argentina with most of the outcrops on the steeper slopes and lesser in the relatively flatter altiplano (Cingolani et al. 2008). These rock outcrops are covered by lichens and in much less proportion by mosses, ferns and vascular plants, and in the case of the well-studied taxa they harbor a diverse biota including several endemic plant and animal species (Funes and Cabido 1995; García et al. 2008).

The climate of the area is typically continental with low winter temperatures, large temperature variations, rains concentrated in the warmer season, frequent frosts during most of the year and occasional snowfalls (Colladon and Pazos 2014). The temperature shows well-defined annual fluctuations, which determines a thermal winter and a short cool summer. The studied altitudinal gradient ranged from 900 to 2700 m.a.s.l. and was situated in the eastern slopes of the Cordoba mountain range. Given the importance of the chemistry of the rock on lichen communities (Rajakaruna et al. 2012), in order to avoid the effect of the type of rock, we chose rock outcrops composed entirely of gneiss which was the most abundant rock type in the study transect. We avoided sampling in the few granite intrusions existing in the area-including those areas above 2700 m.a.s.l. which were composed almost exclusively of granite.

In our study area there is a good fit between altitude, temperature and moisture with temperature decreasing with altitude (Marcora et al. 2008) and moisture increasing with altitude (more rainfall, Colladon and Pazos 2014). Mean annual temperatures range from 15.7 °C at 900 m.a.s.l. to 7.4 °C at 2700 m.a.s.l. and precipitations span from 752 mm at 1000 m.a.s.l. to 1007 mm at 2384 m.a.s.l. (Colladon and Pazos 2014; Marcora et al. 2008). For a map of the studied gradient see Marcora et al. (2008).

Sampling

We performed a transect design where the selected sample points—rock outcrops—were situated along an altitudinal gradient that ranged from 900 to 2700 m.a.s.l. The 54 sample points were rock outcrops wider than 3 m and separated by at least 50 m from each other. In each outcrop, we measured frequency and cover of lichen species in three grids of 40 × 40 cm each (162 grids in total), with each grid divided in one hundred 4 × 4 cm quadrates to help estimate cover percentages. The grids were positioned equidistant in the middle part of the boulder surface. A dataset of quantitative environmental variables were also measured at each sampled rock outcrop: altitude (m.a.s.l.), area of rock outcrop (m^2), slope inclination (degrees) and aspect (degrees from the north). Slope and aspect were also measured in the 50-m area surrounding each sample point. The altitudes between 1000 and 1200 m.a.s.l. were not sampled because, at these altitudes, implanted pine forestation covered rock outcrops and notably changed lichen composition (personal observations).

Identification of species

In general, we analyzed morphological, anatomical, reproductive and chemical characteristics following routine-techniques including macroscopic and microscopic observations of sections of thallus and identification of secondary metabolites by TLC (Thin Layer Chromatography; Orange et al. 2001). The principal keys used in the samples identification were Estrabou et al. (2006), Nash et al. (2002), Sipman (2005), and Rodriguez et al. (2011). A specimen of each identified species is deposited in CORD herbaria. The taxonomy of crustose lichens has been poorly examined in the region. Therefore we identified crustose lichens at species level, genus or morphological groups (Ponzetti and McCune 2001).

Data analysis

To determine which measured abiotic factors influenced lichen distribution patterns we used Generalized Linear Models (Guisan et al. 2002), with significance estimated by means of deviance tests. Predictors were excluded from the model when the level of significance was higher than 0.05. We fitted each model using all applicable link functions and selected the one minimizing deviance of the model. Model selection was conducted using nonlinear fittings in R project software version 2.6.2 and INFOSTAT (Di Rienzo et al. 2014).

We calculated the response variables using the abundance data of the three measured grids per boulder surface, which were averaged and represented a sampling unit or rock outcrop. We used, as response variable, the values of the first three axes of a multivariate analysis which summarized community composition -see below. Also, we used total lichen cover and species richness. We considered using Shannon diversity index as a response variable but, we have always obtained the same pattern of results as with species richness-with which it was highly correlated (Pearson rank correlation; 0.89, $P < 0.001$). Then, to simplify, we did not report the results on diversity.

The values of the first three axes of variation used as response variables were obtained using Non Metric Multidimensional Scaling (NMS, McCune and Grace 2002) for lichen frequency and cover—separately. In order 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 five or less sample points (10% of frequency; McCune and Grace 2002).

Settings for NMS method in PCORD was as follows: the relative Sørensen index of dissimilarity was used. The analysis was run with 500 iterations per run and 999 runs in total using 0.005 as stability criterion and 20 iterations to evaluate stability. Pearson's correlation coefficients were calculated to compare environmental variables and multivariated axes. The number of axes was set to three (McCune and Grace 2002; McCune and Mefford 2011). The multivariated analysis showed similar patterns for frequency and cover data. We report the NMS plot for frequency of species because it was the analysis that obtained less stress. We also calculated the coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space (McCune and Grace 2002).

As predictor variables, we used altitude (m.a.s.l.), area of rock (m^2), slope (degrees), northness and eastness at the sample points in the rock outcrop and at a larger scale 50 m around the sampling points. Northness and eastness were calculated through cosine and sine transformations of slope aspect, respectively.

We classified the species according to altitudinal specialization (MT: mountain top species, IA: Intermediate altitude species, LM: Lowermost species, AG: Altitudinal generalist), according to the altitudinal range of where the species was registered (see Table 2).

Results

We identified 107 lichen species (Table 1). Forty-five species were crustose (including squamulose), 47 foliose and 15 fruticose. Forty-five species were registered in four or less sample points (less than 10% of frequency) and excluded from the multivariate matrix (Table 1). The most diverse genera in the gradient were *Xanthoparmelia* (13 species), *Punctelia* (9), *Usnea* (8) and *Acarospora* (7).

The NMS determination coefficients for lichen species frequency presented a cumulative R^2 of 80% in the first three axes. Altitude presented high correlation with all three axes of the NMS analysis, additionally, slope presented correlation with the second axis, and the aspect presented correlation with the third axis (Fig. 1). At one extreme of the altitude correlation line we found 18 species with high frequency at higher altitudes including several species registered only between 2000 and 2700 m.a.s.l. such as *Buellia dispersa*, *Ochrolechia parella*, *Placomaronea candelaroides*, *Psiloparmelia distincta*, *Rhizocarpon geographicum*, *Teloschistes nodulifer*, *Usnea durietzii*, *U. lutii*, *U. saxidilata* (Fig. 1; Table 2). At the other extreme of the altitude correlation we find ten species registered with higher frequency at the lower altitudes such as *Cladonia fimbriata*, *Flavoparmelia haysomii*, *Lecanora* sp. 1, *Lepraria* sp., *Normandina pulchella*, *Parmotrema reticulatum Punctelia perreticulata, P. punctilla, Usnea amblyoclada and Xanthoparmelia farinosa*. Between these groups, there was a host of species insensitive to altitude or located at intermediate elevations (Table 2). Axis 2 was strongly correlated to slope and slightly to altitude (Fig. 1). Typical species registered at vertical slopes were *Hypotrachyna revoluta*, *Ramalina pilulifera*, *Usnea cornuta*, while *Placomaronea candelaroides*, *Rhizocarpon geographicum* (species at the upper and lower end of axis 2, Fig. 1) were registered at flatter slopes.

The best model for NMS axis 1 included altitude ($P < 0.0001$) as the main predictor variable which explained the 41.51% of the variability (Fig. 2). The best model for NMS axis 2 was an additive model including altitude ($P = 0.0001$), slope ($P = 0.0009$) and aspect of boulder side ($P = 0.0184$) which together explained 44.17% of the variability (25.60, 12.34 and 6.22% respectively) with no significant interaction term (Fig. 3).

Table 1 Identified lichen species in studied altitudinal gradient, growth form (*C* crustose, *F* foliose, *Fr* fruticose)

Lichen species	Growth form
Acarospora chrysops	C
Acarospora altoandina	C
Acarospora boliviana	C
Acarospora lorentzii	C
Acarospora mahuiana	C
***Acarospora* sp. 1**	C
***Acarospora* sp. 2**	C
Bryophytes	–
Buellia aethalea	C
Buellia aff. *dispersa*	C
Buellia dispersa	C
Buellia halonia	C
Buellia venusta	C
***Caloplaca* “amarilla”**	C
Caloplaca “roja”	C
Caloplaca littorea	C
Caloplaca cinnabarina	C
Caloplaca saxicola	C
***Caloplaca* sp.**	C
Candelariella vitellina	C
Catinaria sp.	C
Cladonia fimbriata	Fr
Dictyonema pavonia	F
Dimelaena oxygena	C
Diploschistes bisporus	C
Diploschistes scruposus	C
Flavoparmelia caperata	F
Flavoparmelia haysomii	F
Flavoparmelia papillosa	F
Heterodermia japonica	F
Heterodermia leucomela	F
Heterodermia sp.	F
Heterodermia squamulosa	F
Hypotrachyna leiophylla	F
Hypotrachyna revoluta	F
***Lecanora* “negra”**	C
Lecanora dispersa	C
Lecanora farinacea	C
Lecanora rupicola	C
Lecanora polytropa	C
***Lecanora* sp. 1**	C
Lecidea sp. 1	C
Lecidea sp. 2	C
Lepraria sp.	C

Table 1 continued

Lichen species	Growth form
Leptogium cyanescens	F
Macrospora verrucosa	C
Neofuscelia imitatrix	F
Normandina pulchella	F
Ochrolechia parella	C
Pannaria varesii	C
Paraparmelia rupicola	F
Parmotrema chinense	F
Parmotrema crinitum	F
Parmotrema pilosum	F
Parmotrema reticulatum	F
Parmotrema tandilensis	F
***Pertusaria* sp. 1**	C
***Pertusaria* sp. 2**	C
Phaeophyscia cloantha	F
Physcia tribacia	F
Placomaronea candelaroides	F
Protoparmelia badia	C
Psiloparmelia distincta	F
Punctelia colombiana	F
Punctelia hypoleucites	F
Punctelia microsticta	F
Punctelia perreticulata	F
Punctelia punctilla	F
Punctelia semansiana	F
Punctelia sp.	F
Punctelia stictica	F
Punctelia subpraesignis	F
Ramalina decipiens	Fr
Ramalina pilulifera	Fr
Rhizocarpon cumulatum	C
Rhizocarpon inorense	C
Rhizocarpon geographicum	C
***Rhizocarpon* sp.**	C
Rinodina oxydata	C
Sarcogyne regularis	C
Stereocaulon ramulosum	Fr
Teloschites nodulifer	Fr
Umbilicaria africana	F
Umbilicaria polyrrhiza	F
Usnea amblyoclada	Fr
Usnea columbiana	Fr
Usnea cornuta	Fr

Table 1 continued

Lichen species	Growth form
Usnea durietzii	Fr
Usnea hieronymii	Fr
Usnea krogiana	Fr
Usnea lutii	Fr
Usnea saxidilatata	Fr
Vascular plants	–
***Verrucaria* sp.**	C
Xanthoparmelia cordillerana	F
Xanthoparmelia cotopaxiensis	F
Xanthoparmelia farinosa	F
Xanthoparmelia hypopsila	F
Xanthoparmelia microspora	F
Xanthoparmelia mougeotti	F
Xanthoparmelia plitii	F
Xanthoparmelia punctulata	F
***Xanthoparmelia* sp.**	F
Xanthoparmelia submougeotti	F
Xanthoparmelia subtinctina	F
Xanthoparmelia taractica	F
Xanthoparmelia wrightiana	F

In bold species presents in more than 10% of sample points and incorporated in the multivariate analysis. Vascular plants and bryophytes are included in the list as a group

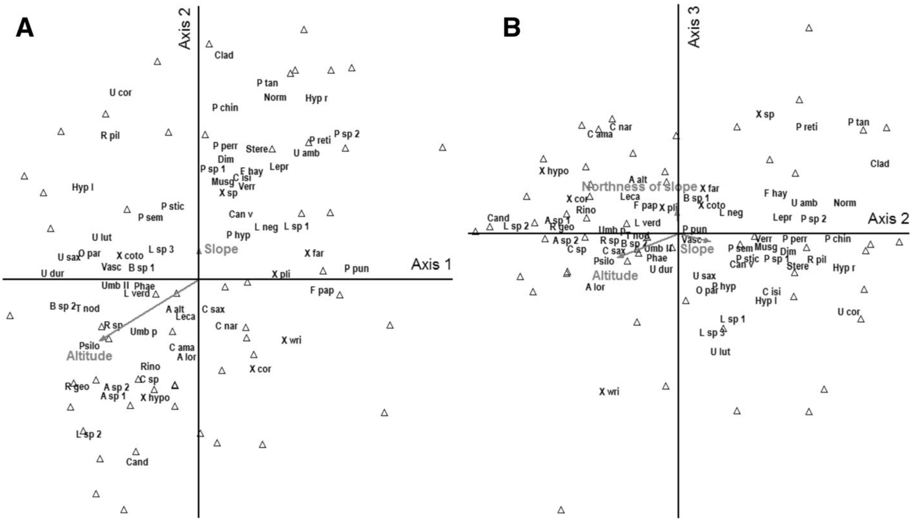

Fig. 1 Non metric Multidimensional Scaling (NMS) plot of sample points (*open triangle*) and species applied to frequency of lichen species. See Table 1 for names of species. *Gray lines* show correlations of environmental variables with the axes. **a** Axis 1 versus Axis 2. **b** Axis 2 versus Axis 3

The best model for the NMS axis 3 also included altitude (P = 0.0079) and aspect (P = 0.0278) however in this case, the interaction of altitude and aspect was significant

Table 2 Lichen species presents in more than 10% of sample points, *Acron.* acronym used in multivariate bi-plots, altitudinal specialization (*MT* mountain top species, *IA* Intermediate altitude species, *LM* Lowermost species, *AG* Altitudinal generalist), and altitudinal range of where the species was registered

Lichen species	Acron.	Altitudinal specialization	Altitude m.a.s.l. (Min–mean–max)
Acarospora altoandina	A alt	AG	938–1843–2595
Acarospora lorentzii	A lor	AG	922–1969–2595
Acarospora sp. 1	A sp 1	AG	922–2070–2679
Acarospora sp. 2	A sp 2	AG	934–2049–2679
Bryophytes	Musg	AG	922–1855–2679
Buellia dispersa	B sp 1	AG	922–1874–2653
Buellia halonia	B sp 2	MT	1920–2306–2679
Caloplaca "amarilla"	C ama	IA	1376–1814–2595
Caloplaca cinnabarina	C nar	AG	922–1664–2595
Caloplaca littorea	C isi	AG	934–2004–2679
Caloplaca saxicola	C sax	IA	1473–2033–2679
Caloplaca sp.	C sp	IA	1366–2016–2538
Candelariella vitellina	Can v	IA	1366–2047–2679
Cladonia fimbriata	Clad	IA	922–1467–2170
Dimelaena oxygena	Dim	IA	1554–1591–1640
Flavoparmelia haysomii	F hay	LM	938–1479–1920
Flavoparmelia papillosa	F pap	IA	1369–1932–2353
Hypotrachyna leiophylla	Hyp l	IA	1620–2144–2492
Hypotrachyna revoluta	Hyp r	IA	1366–1906–2653
Lecanora "negra"	L neg	IA	1552–2158–2679
Lecanora dispersa	L sp 2	IA	1367–2284–2679
Lecanora farinacea	L verd	AG	938–2107–2653
Lecanora rupicola	L sp 3	IA	1538–1584–2492
Lecanora sp. 1	L sp 1	LM	1366–1547–1899
Lepraria sp.	Lepr	LM	922–1532–2353
Normandina pulchella	Norm	LM	922–1362–1944
Ochrolechia parella	O par	MT	1995–2342–2653
Parmotrema chinense	P chin	IA	934–1791–2595
Parmotrema reticulatum	P reti	LM	922–1477–1998
Parmotrema tandilensis	P tan	IA	934–1580–2492
Pertusaria sp. 1	P sp 1	AG	922–1841–2595
Pertusaria sp. 2	P sp 2	IA	934–1614–2595
Phaeophyscia cloantha	Phae	IA	1584–2101–2448
Placomaronea candelaroides	Cand	MT	2259–2435–2679
Protoparmelia badia	Leca	IA	1548–1834–2492
Psiloparmelia distincta	Psilo	MT	1548–2235–2679
Punctelia hypoleucites	P hyp	IA	1369–2039–2595
Punctelia perreticulata	P perr	LM	934–1588–2086
Punctelia punctilla	P pun	LM	922–1357–1920
Punctelia semansiana	P sem	IA	1376–1769–2595
Punctelia stictica	P stic	AG	934–1973–2653
Ramalina pilulifera	R pil	AG	938–2037–2653

Table 2 continued

Lichen species	Acron.	Altitudinal specialization	Altitude m.a.s.l. (Min–mean–max)
Rhizocarpon geographicum	R geo	MT	2221–2507–2679
Rhizocarpon sp.	R sp	MT	1944–2372–2653
Rinodina oxydata	Rino	AG	922–1949–2679
Stereocaulon ramulosum	Stere	IA	1620–2134–2595
Teloschites nodulifer	T nod	MT	2239–2515–2653
Umbilicaria africana	Umb II	IA	1376–1830–2332
Umbilicaria polyrrhyza	Umb p	IA	1366–2019–2679
Usnea amblyoclada	U amb	LM	922–1576–2221
Usnea cornuta	U cor	IA	1944–2266–2595
Usnea durietzii	U dur	MT	2221–2431–2595
Usnea lutii	U lut	MT	2086–2408–2679
Usnea saxidilatata	U sax	MT	1376–2307–2653
Vascular plants	Vasc	AG	922–1787–2448
Verrucaria sp.	Verr	LM	1548–1566–1620
Xanthoparmelia cordillerana	X cor	IA	1376–1775–2353
Xanthoparmelia cotopaxiensis	X coto	IM	1548–1566–1620
Xanthoparmelia farinosa	X far	LM	922–1439–2120
Xanthoparmelia hypopsila	X hypo	IA	1552–2114–2555
Xanthoparmelia plitii	X pli	AG	922–1581–2259
Xanthoparmelia sp.	X sp	AG	922–1587–2595
Xanthoparmelia wrightiana	X wri	IA	1473–1783–2353

($P = 0.002$). This model explained the 30% of the variability (9.87, 6.81 and 13.32% respectively) and the interaction suggests a decreasing effect of aspect with altitude (Fig. 4).

Number of species per sampled rock outcrop was similar throughout the altitudinal gradient ($P = 0.64$) and 16.31 ± 5.65 species per rock outcrop on average. The highest species richness was found at vertical outcrop sides and at south aspects, while the lowest richness was on flat boulder tops and north aspects (all P values < 0.05, see Fig. 5; Table 3). Also at steeper slopes, the north aspects showed higher richness.

Sampled boulders were similarly covered by lichen species in all situations, with an average cover of 49.90 ± 17.76%. The total lichen cover did not relate with any of the measured environmental variables (Table 3).

Discussion

Our study showed that lichen communities were structured mainly according to elevation and secondarily with slope throughout the whole elevational gradient and aspect at the lower altitudes. Thus the results did not support the hypothesis that mountain top species were situated at the cooler southern aspects and they imply that there is scope for microsite segregation of mountain top species in case of future climate warming.

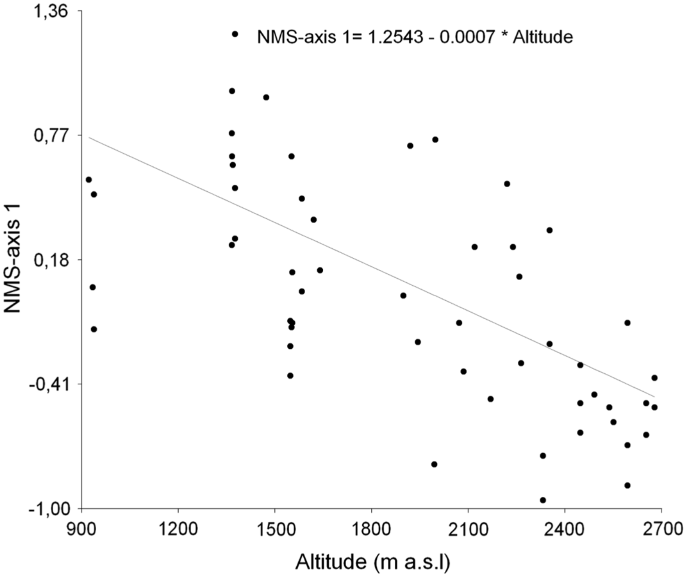

Fig. 2 Relation between the Non Metric Multidimentional Scaling first axis for frequency of lichen species and altitude

This finding is in line with a recent report for our study system were reductions of temperature and increases of precipitation during the last 1500 years are inferred through reconstruction of past vegetation, albeit using an un-replicated soil core (Giorgis et al. 2015). Thus, mountain top endemics could have been expanding downwards in the last 1500 years, and presumably with future climate warming there still is margin for upward contraction of their range, and eventually their retraction to cooler microsites. In addition to the hypothesis about the future of mountain top endemics, our data set provides a host of natural history and ecological information on lichen communities.

In comparison to previous studies on corticolous lichens from warmer and dryer areas of the Chaco region reporting 21–53 species (Estrabou et al. 2006, 2014; Filippini et al. 2014; Rodriguez et al. 2009), we found 107 species in our study area, including crustose ones. It is important to consider that crustose species may have been underestimated in our study due to the lack of previous studies on taxonomy of this group of species. However the foliose and fruticose species could be identified using previous taxonomic work (Estrabou and Adler 1999; Rodriguez et al. 2011). We also report species with high frequency or exclusive to the higher altitudes (Table 2) sharing an Andean or Patagonic distribution (Estrabou 2000) as occurs with other taxa in our study area (i.e. for plants: Cabido et al. 1998, for birds: Nores 1995). The fact that we registered 45 rare species with less than 10% in frequency is in accordance to other studies of lichen communities in areas of high diversity which also report a high frequency of rare species (Cáceres et al. 2007; Kuntz and Larson 2006; Pinokiyo et al. 2008). This suggests a high specialization in niches due to the several variables that could influence lichen growth, such us humidity, light or exposition to UV radiation (Rubio et al. 2002). This result also suggests that rock outcrops support a reservoir of lichen biodiversity (Matthes et al. 2000).

The community composition revealed an expected relation with altitude and secondarily with others environmental variables -mainly slope throughout the whole gradient and

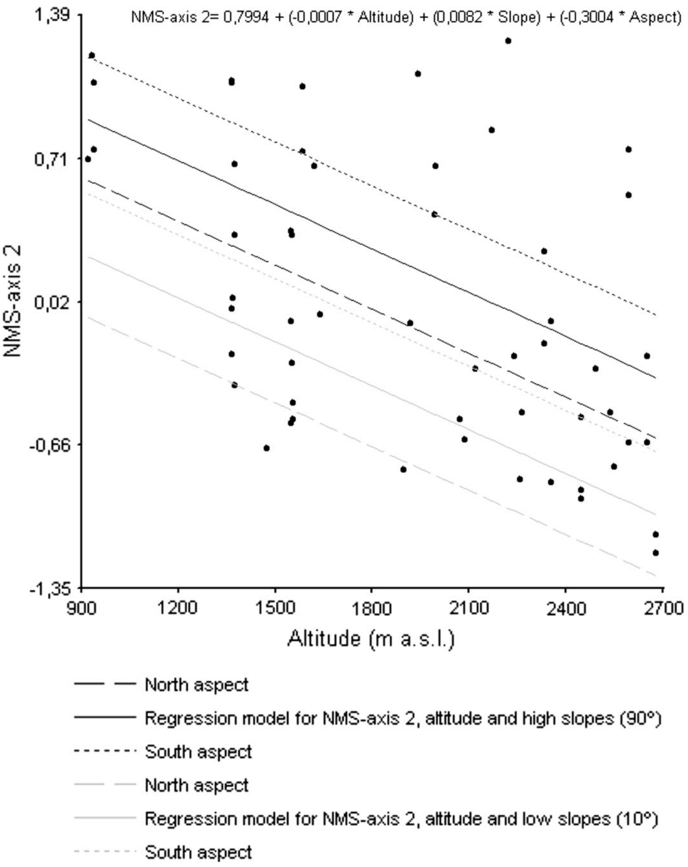

Fig. 3 Relation between the Non Metric Multidimentional Scaling second axis for frequency of lichen species, altitude and northness of boulder side. Regression model for the minimun slope (in *black*) and the maximun slope (in *gray*)

aspect at the lower altitudes. Presumably, some species that have a wide tolerance to environmental conditions cannot grow in microhabitat with better conditions due to competitive exclusion (Armstrong and Welch 2007). Although our study did not evaluate competition we can provide indirect evidence. For example: frequency of crustose growth forms such as *Acarospora*, *Caloplaca* or *Rinodina* is inversely related to the slope (Fig. 1). Crustose species disappear at high slopes in conjunction with an increase of foliose or fruticose species such as *Parmotrema* or *Usnea*, presumably because foliose and fruticose species overgrow the crustose species at higher slopes (Armstrong 1975, 2015). Moreover the high altitude community that was differentiated by slope did not seem to respond to aspect. Lichens on rocks of low slope have a more mesic environment due to poor drainage, but can also receive sunshine all day long and thus tend to receive more radiation than vertical rock surfaces (John and Dale 1990).

The absence of a relation between diversity and altitude in our studied gradient has been reported in previous studies on lichen communities (Bässler et al. 2015; Nascimbene and Marini 2015), whereas other studies showed maximum diversity at middle altitudes due to the overlapping of species ranges (Baniya et al. 2010; Pinokiyo et al. 2008; Wolf 1993). To

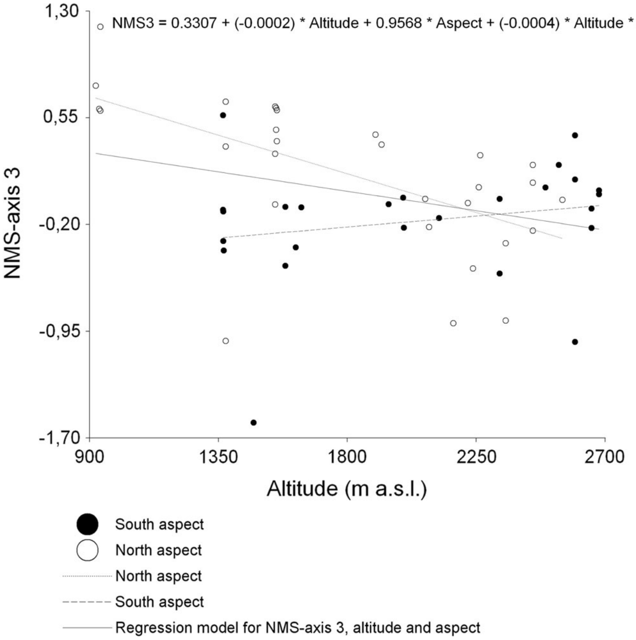

Fig. 4 Relation between the Non Metric Multidimentional Scaling third axis for frequency of lichen species, altitude and aspect

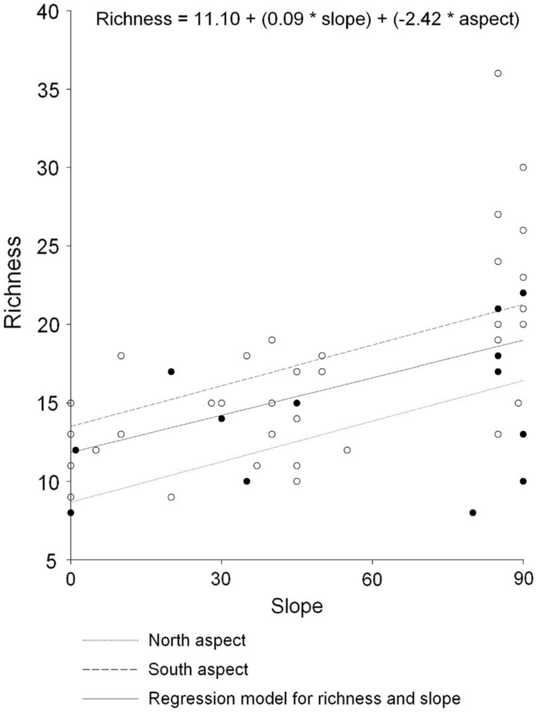

Fig. 5 Species richness variation relative to slope and aspect to the boulder side. The *empty circles* indicate the sites from south aspect, while the *full circles* indicates the sites from north aspect

Table 3 Generalized Linear Models on richness and cover of lichens

Community traits	Variables	Coeff.	SE	Z value	P value
Richness	Altitude (m.a.s.l.)	0.0001	0.0001	0.4700	0.6384
	Northness of slope	−0.0649	0.0505	−1.2837	0.1992
	Eastness of slope	0.0667	0.0776	0.8586	0.3905
	Slope of boulder side	0.0065	0.0011	5.8100	**<0.0001**
	Area of rock	0.0010	0.0010	1.0577	0.2902
	Northness of boulder side	−0.1418	0.0644	−2.2013	**0.0277**
	Eastness of boulder side	0.0131	0.0461	0.2848	0.7758
Cover	Altitude (m.a.s.l.)	<0.0001	<0.0001	−0.0955	0.9243
	Northness of slope	0.1562	0.2390	0.6538	0.5165
	Eastness of slope	0.4353	0.3561	1.2225	0.2277
	Slope of boulder side	0.0004	0.0050	0.0798	0.9367
	Area of rock	−0.0040	0.0047	−0.8573	0.3957
	Northness of boulder side	−0.5154	0.2868	−1.7972	0.0789
	Eastness of boulder side	−0.2672	0.2195	−1.2174	0.2297

In bold environmental variables with a P value < 0.05

the best of our knowledge there is no synthesis explaining under what conditions patterns of lichen diversity in relation to altitude could present declining, increasing or unimodal relationships. Austrheim (2002) found an increment on cryptogamic diversity with altitude unlike vascular plant diversity that decreases with altitude. Instead, we showed a richness change with slope and aspect of rock outcrop, both small-scale variables (Fig. 5). In the absence of shadow due to others factors such as trees, the aspect and slope of a rock surface determines the amount of direct and diffuse solar radiation falling upon it (Pentecost 1979). Consequently there are factors that influence the survival of lichen thalli such as water relation, fog capture, degree of insolation and wind exposure (Gilbert 2003; Kuntz and Larson 2006).

Lichen cover did not show variation under any of the variables considered in this study, probably due to their conspicuous presence on all rock surfaces covering around the 50% of the outcrops. The high lichen cover of the rock outcrops highlights that in the mountains of central Argentina lichen communities may have an important contribution to ecosystem function, especially taking into account that the 30% of land cover on the study site are rocks outcrops (Will-Wolf et al. 2002; Cingolani et al. 2008; Seaward 2008; Wolfgang et al. 2012).

In conclusion, our study identified one of the richest saxicolous lichen communities in the region. While altitude strongly influences the species composition, the other variables of microhabitat—especially slope and aspect—have less influence. The aspect influences the frequency and cover of species at low altitudes. In warmer climate, the species may respond differentially according to the habitat now occupied. Lower altitude species occupying south facing slopes will have to migrate upwards, but at the mountain top, for most species there still is the possibility for microsite segregation to compensate climate change under a scenario of warming. Our findings may hold true for other taxa such as plants, fungi and animals.

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