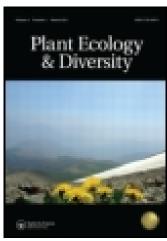
This article was downloaded by: [CSIC Biblioteca], [Dr Karina Speziale]

On: 12 January 2015, At: 07:25 Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer

House, 37-41 Mortimer Street, London W1T 3JH, UK





Plant Ecology & Diversity

Publication details, including instructions for authors and subscription information: http://www.tandfonline.com/loi/tped20

Rock outcrops as potential biodiversity refugia under climate change in North Patagonia

Karina L. Speziale^a & Cecilia Ezcurra^b

- ^a Laboratorio Ecotono, INIBIOMA-CONICET-Universidad Nacional del Comahue, Bariloche, Argentina
- ^b Departamento de Botánica, INIBIOMA-CONICET-Universidad Nacional del Comahue, 8400 Bariloche, Argentina Published online: 26 Nov 2014.

To cite this article: Karina L. Speziale & Cecilia Ezcurra (2014): Rock outcrops as potential biodiversity refugia under climate change in North Patagonia, Plant Ecology & Diversity, DOI: 10.1080/17550874.2014.983200

To link to this article: http://dx.doi.org/10.1080/17550874.2014.983200

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at http://www.tandfonline.com/page/terms-and-conditions



Rock outcrops as potential biodiversity refugia under climate change in North Patagonia

Karina L. Speziale^{a*} and Cecilia Ezcurra^b

^aLaboratorio Ecotono, INIBIOMA-CONICET-Universidad Nacional del Comahue, Bariloche, Argentina; ^bDepartamento de Botánica, INIBIOMA-CONICET-Universidad Nacional del Comahue, 8400 Bariloche, Argentina

(Received 18 March 2013; accepted 29 October 2014)

Background: Under climate-change scenarios, rock outcrops, by providing microclimatically diverse habitats, different from those of surrounding zonal vegetation matrix, may serve as climatic refugia and thereby facilitate the persistence of specialist species.

Aim: We tested whether rock outcrops of southern temperate latitudes could act as local refugia for a cold-adapted flora in the face of global warming.

Methods: We related species composition of 50 outcrops and that of their surrounding vegetation to climatic data at local and regional scales to establish whether species distributions reflected differences that could indicate the existence of climatic refugia.

Results: While at a regional scale, species composition of the outcrops across the study area was related to mean annual precipitation and mean annual maximum temperature, locally, southern faces of outcrops had different species and lower maximum temperatures than insolated north faces and surrounding vegetation plots.

Conclusions: South faces of outcrops by providing cool microhabitats, and currently harbouring species not found in the surrounding zonal vegetation matrix, could serve as local refugia for heat-intolerant plants and other microthermic organism. The degree of 'stability' of these refugia will depend on the degree of future change in climate. Therefore, it is important to plan protected area networks that maximise local environmental heterogeneity, including the protection of rock outcrops both as refugia for cold-adapted species and as potential stepping stones that would allow dispersal of these species between supportive environments through unfavourable ones.

Keywords: climate change; microclimate; refugia; rock outcrops; species composition

Introduction

Rock outcrops form a climatic, hydrological and pedological contrast with surrounding landscapes; therefore, they locally increase habitat diversity, allowing habitat specialisation (Larson et al. 2000) and, through their isolation, may provide protection from certain disturbances, such as fire and grazing (Porembski et al. 1996; Burke 2002; Clarke 2002; Milchunas and Noy-Meir 2002). Rock outcrops provide heterogeneity in part because they present microclimatic differences between their northern and southern faces, due to differences in insolation and wind exposure (Speziale 2012) and the thermic inertia of the exposed bedrock material (Larson et al. 2000). Thus, outcrops represent local variation along large-scale regional gradients of climatic variables, such as temperature and precipitation (Speziale 2012). The importance of rock outcrops for landscape-level ecosystem processes in a changing world has recently been stressed (Burke 2002). Topographic buffers, such as mountains, inselbergs (isolated rocky hills or small mountains rising abruptly from surrounding plane or gentle slope) and outcrops (exposures of bedrock or ancient superficial deposits on the surface of the Earth) provide a greater variety of microclimatic conditions than homogenous landscapes (Anderson et al. 2010), and thus varied habitat niches for a greater number of species. These microclimatic variations can lead to differences in species composition in relation to the surrounding matrix, which, in turn, can change over time in accordance with changing climates. Therefore, outcrops can harbour remnants of a flora that has been more widespread in the past, and act as refugia during climate change as suggested in many parts of the world (Wiser et al. 1996; Burke et al. 1998; Larson et al. 2000; Speziale and Ezcurra 2012).

Outcrop - matrix complexes offer testing hypotheses about contemporaneous local climate refugia by comparing species distributions and climatic variables, similarly to that reported by, for example, Walther et al. (2005) and Scherrer and Körner (2011) for the Alps. It is expected that increases in temperature will greatly affect biota adapted to cold climate, especially in high mountain, or high latitude environments (Birks and Willis 2008; Gottfried et al. 2012; Pauli et al. 2012). The combination of heat and water-stress leads to high leaf temperatures that can be detrimental to some cold-adapted species (Larcher et al. 2010). Also, the performance of species adapted to low temperatures may decline with increasing temperature (Björkman et al. 1980). Therefore, it is important to prioritise the study and protection of sites that could serve as refugia (sensu Keppel et al. 2012) for endangered cold-adapted species under potential future climates change scenarios that predict temperature increases.

We evaluated whether rock outcrops could currently be serving as refugia for a heat-intolerant flora. Following a previous study on North Patagonian outcrops that found the presence of species of generally more southern poleward distributions – probably heat-intolerant and adapted to cold climates – on the southern, cold faces of outcrops (Speziale and Ezcurra 2012), we hypothesised that at the local scale, the southern faces of rock outcrops with cooler microclimatic conditions than the surrounding environment, would favour heat-intolerant species, whereas at a regional scale, mesoclimatic environmental variables would be related to floristic distribution patterns.

Materials and methods

Study area

The study was carried out in north-western Patagonia, Argentina, between 40° 41′-41° 57′ S and 70° 33′-71° 22′ W (Figure 1). This area is characterised by a strong precipitation gradient due to the rain shadow produced by the westerly winds from the Pacific Ocean as they pass over the southern Andes (Paruelo et al. 1998). The study area comprised different landscape types, mostly erosive relief over vulcanites, lava plains, and landforms created by glacio-fluvial and glaciolacustrine deposits (Giacosa and Heredia 2001). These differences resulted in a heterogeneous environment with a rich and diverse flora (Anchorena and Cingolani 2002; Speziale and Ezcurra 2012). All outcrops studied were of volcanic origin and had a predominant composition of porphyry and andesitic lavas and basalts (Speziale and Ezcurra 2012). Most of the studied outcrops belonged to the Huitrera formation (Late Paleocene – Medium Eocene). This formation is abundant in porphyry and andesitic lavas and basalts. Outcrops to the south-west belonged to the Nirihuau formation (Late Oligocene - Medium Miocene), except for one which was of the Ventana formation (Oligocene). The Ñirihuau formation is characterised by conglomerates, tufa, limestone, sandstone and claystone, whereas Ventana formation contains andesitic, rhyolitic and basaltic lavas and pyroclasts, as well as continental and marine claystones, sandstones and conglomerates. A few outcrops to the south-east belonged to the Pilcaniyeu Pluton (Lower Jurassic). This formation is characterised by a granitic facies formed by biotitic granites. The furthest one to the south-east corresponded to the Campana formation, characterised by olivinic basalts, whereas the one further east belonged to Estratos de Comallo, the oldest formation of the studied outcrops (Triassic – Lower Jurassic), composed by ignimbrites, andesites and basalts (Giacosa and Heredia 2001; Speziale and Ezcurra 2012). The elevation of the outcrops ranged from 737 to 1440 m a.s.l.

The vegetation matrix surrounding the outcrops varies along the precipitation gradient from west to east. The western area includes a mesic forest–shrubland ecotone dominated by *Austrocedrus chilensis* trees with an understory of *Schinus patagonica, Lomatia hirsuta, Senecio* sp. and *Baccharis* sp. This changes towards the east to a low xeric shrubland–grassland–steppe dominated by *Mulinum spinosum, Senecio filaginoides* and *S. bracteolatus* shrubs, and *Pappostipa speciosa, Festuca pallescens* and *Poalanuginosa* grasses (Speziale et al. 2010). Most precipitation occurs from April to September, ranging from ca. 1000 mm year⁻¹ in the west to less than 300 mm year⁻¹ in the east, in the dry Patagonian steppe (Paruelo et al. 1998). Prevailing winds in the area blow from the northwest.

Data collection

We selected 50 study sites (Figure 1), ranging from a distance of 1.2 to 22 km between each other, each including a rock outcrop and its surrounding vegetation matrix, separated by at least 100 m from roads and water courses, and without signs of recent fire, overgrazing or other anthropogenic disturbances as assessed by visual examination. The selected rock outcrops ranged between 10 to

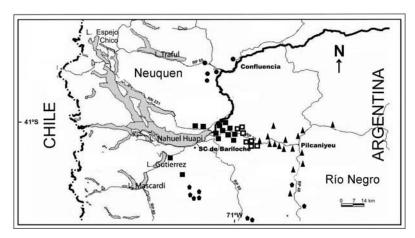


Figure 1. Study area in north-western Patagonia, Argentina, (40° 41′–41° 57′ S and 70° 33′–71° 22′ W), showing the 50 study sites. The different symbols correspond to groups of geographically proximate outcrops with similar floristic composition and climate, as inferred from the results of the CCA ordination presented in Figure 3B.

30 m in diameter within a shrubland-steppe matrix. We established three sampling plots at each study site: two on the outcrops (one on the north face and the other one on the south face), and one in the vegetation matrix. We considered the 'north' face the more insolated and windswept portion of the outcrop extending from north-west, through north, to north-east, and the 'south' face, the more shaded, leeward portion from south-east, through south, to south-west. In the vegetation matrix we established a sampling plot of 100 m² (10 m × 10 m) at random (but not downhill of the outcrops to avoid influence of mineral run-off). In flat terrain we placed the plot at least 100 m from the outcrop in a random direction. We placed each matrix plot in locations that were representative of the regional natural vegetation. Although the study area is partly undulating, the vegetation surrounding the outcrops is mostly homogeneous over an almost flat to 14° sloping surface (Speziale et al. 2010). Assuming that due to different degrees of insolation and windiness the three sampling plots would present different floristic compositions, we identified the species level of all plants.

To obtain microclimatic data we used temperature and humidity sensors (Hobo H8 Dataloggers, Onset Computer Corporation, MA, USA). At 21 of our study locations (Figure 1) we placed a sensor in the middle of the south face (S), another in the middle of the north face (N), and one in the centre of the matrix plot (M; i.e., a total of 63 sensors), in all cases elevated ca. 30 cm from the soil surface to avoid effects of extreme heat or flooding of the surface, and in unshaded places. Each sensor recorded data every 2 h for 1 month in the summer, between January and February, and 1 month in the spring, between October and November 2009. We calculated average minimum, mean and maximum temperatures and relative humidity for each period. In this way, we obtained a value for spring and for summer for each variable for each face and associated matrix plot of an outcrop. We chose these seasons given the regional cold-temperate climate with dry summers, where spring is the season in which the initiation of plant growth can be particularly affected by events, such as late snows and freezing temperatures, and summer is the end of the growth period when drought and high temperatures can occur. Cattle and also presumably human presence destroyed some sensors in both sampling periods. At the end of summer 45 out of the 63 sensors supplied data. The following spring 57 sensors were placed and 42 sensors supplied data.

To assess regional climatic variation we used mean, minimum and maximum annual temperature, intra-annual seasonality in temperature, and mean annual precipitation from the WorldClim database (available at www.world-clim.org). This is a digital database of global climate surfaces developed from data from weather stations for the past 10 years, and interpolated to achieve a spatial resolution of 1 km² (Hijmans et al. 2005). This database is not accurate in highly dissected terrain, such as mountain ranges, but in our undulating study area data are reliable and have been used in previous studies (e.g., Ward 2007; Kumar and Stohlgren 2009; Speziale and

Ezcurra 2012). From the geographic coordinates of each outcrop we extracted values for the climatic variables, using ArcView 3.2. The bioclimatic variables selected have been shown to relate to floristic variation in the study area (Speziale and Ezcurra 2011).

Data analysis

Local scale. We used analysis of variance (ANOVA), blocked by site to analyse the differences or similarities between microclimatic characteristics of the sampling plots in relation to the variables recorded by the sensors. When we found significant differences we carried out Tukey's a posteriori tests to assess which of the studied plots was different from the others.

We carried out canonical correspondence analysis (CCA) to study species composition of the north and south faces and the matrix plots as a function of the temperature and humidity values recorded in situ on each outcrop face and in the matrix plots (Ter Braak and Smilauer 1998). Together with species composition, variables included in this analysis were mean, minimum and maximum summer temperature, relative summer humidity, mean, minimum and maximum spring temperature, and relative spring humidity. A Monte Carlo permutation test was applied to the solution to determine whether the relationship between the environmental variables and species composition was statistically significant. To validate the selected environmental variables in explaining species composition variation, we carried out a correspondence analysis (CA). We then correlated sample scores of both axes 1 and 2 of the CCA and CA analyses by means of the Pearson correlation coefficient (Økland 1996).

Regional scale. We analysed the floristic composition of the outcrops and related it to the regional mean, minimum and maximum annual temperature, intra-annual seasonality in temperature, and mean annual precipitation obtained from WorldClim by means of CCA. We then applied a Monte Carlo permutation test to determine whether the relationship between the environmental variables and composition was statistically significant. We also evaluated the appropriateness of the selected environmental variables by correlating the first and second axes of the CCA with those of a CA. We also compared the between-site species turnover between matrix and outcrop plots throughout the area with detrended correspondence analysis (DCA), by estimating the length of the first axes of matrix and outcrop ordinations. DCA provides a measure of between-site species turnover by scaling the axes in units of average standard deviation of species turnover (Lepš and Šmilauer 2003). We used CANOCO 4.5 for Windows to carry out all multivariate analyses.

Geographical extension of individual species

For the species that we found on the south faces (either only found on south faces or found on both south and north faces),

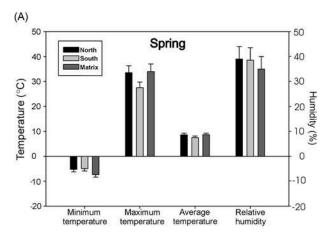
we used available databases and information to determine their recorded distribution in Argentina and Chile and obtain descriptions of their life forms and habitats. We used the most updated database for Argentina, the Instituto de Botánica Darwinion on species (accessed through http://www2.darwin.edu.ar/Herbario/Bases/BuscarIris.asp 6/2012) and regional floristic works (Correa 1969–1998). We used these data to analyse the presence on the outcrops of species whose range was not previously included in the study area.

Results

Local scale

The south faces of the outcrops had lower maximum temperatures than the north faces and the matrix plots both in the spring and in the summer (Figure 2). In contrast, matrix plots recorded lower minimum temperatures than both outcrop faces, as their flat terrain is probably more exposed to cold air and late frosts (Figure 2). The remaining microclimatic variables did not show statistically significant differences (Table 1; Figure 2).

The CCA ordination of species composition indicated that the species of the outcrop faces tended to be



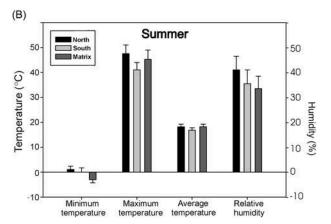


Figure 2. Climatic differences in North Patagonian rock outcrops among the north (North), and south faces (South) and matrix plots (Matrix) in spring (A) and summer (B): minimum spring temperature, maximum spring temperature, mean spring temperature, relative humidity. Error bars = 2 standard errors (A).

Table 1. Differences between north- and south-exposed rock faces and surrounding flat-land matrix plots in relation to microclimatic variables measured with temperature and humidity sensors during the spring and summer as shown by ANOVAs in north-western Patagonia, Argentina.

Season	Variable	DF	F	P
Spring	Maximum temperature	(2,39)	9.54	≤0.001*
	Mean temperature	(2,39)	5.10	0.01*
	Minimum temperature	(2,39)	0.28	0.76
	Relative humidity	(2,39)	0.27	0.76
Summer	Maximum temperature	(2,43)	4.36	0.019*
	Mean temperature	(2,43)	2.8	0.07
	Minimum temperature	(2,43)	11.47	0.001*
	Relative humidity	(2,43)	2.24	0.12

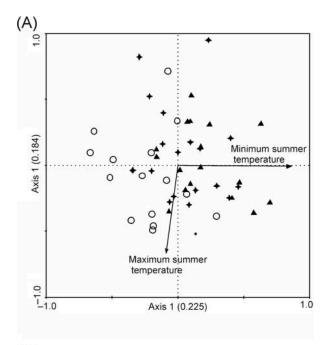
Note: DF, degrees of freedom; F, Fisher's statistic; *P < 0.05.

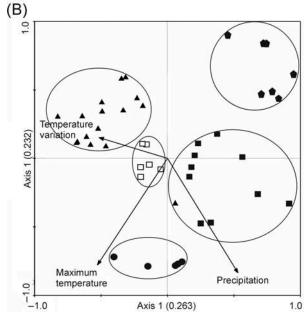
associated with higher minimum summer temperatures, which agreed with the results of the ANOVAs (Figure 3A; Table 2). The total inertia was equal to 5.7 and the cumulative percentage of variance for the relationship of species variables was 42.3. The correlations between the sample scores of the first and second axes of the CCA and CA by means of the Pearson correlation coefficient were 0.61 and 0.71, respectively.

Regional scale

The arrangement of the outcrops resulting from CCA showed that their floristic composition at a regional scale was related to annual precipitation and maximum temperature, the two significant variables in this model (Table 3; Figure 3B). Total inertia was 5.7 and the percentage of variation in the species-environmental variables accumulated by the first two axes was 77.3. Mean and minimum temperatures were removed from the analysis because they were highly correlated (inflation factor >20) and showed a weaker relationship with the axes than maximum temperature. Temperature variation did not contribute significantly to this model. The correlations of the first and second axes of the CCA and CA were 0.94 and 0.85, respectively. Between-site species turnover, estimated as the length of the first axes in DCA, was higher among outcrop sites than among matrix sites, as indicated by their higher axis lengths: 9.5 and 6.4 SD for the first and second axes of outcrops and 3.0 and 2.6 SD for the first and second axes of matrix plots (ordinations not shown).

Five groups of outcrops were formed (Figure 3B). One comprised outcrops that presented intermediate maximum temperatures and lower annual precipitation than the rest (at the negative end of axis 1 and towards the positive end of axis 2). Most of these were in the steppe zone in the easternmost part of the study area. Another group of outcrops showed higher precipitation and maximum temperature (at the positive end of axis 1 and negative end of axis 2). These outcrops were located in a rocky scrubland in the western portion of the study area. A third group was formed exhibiting lower maximum temperatures and intermediate precipitation (at the positive end of both axes).





(A) Relationship between the flora of outcrops and matrix plots and their characteristic microclimate. CCA of the matrix plots (open circles), north faces (triangles) and south faces (stars) as a function of their floristic composition and environmental characteristics recorded with temperature and humidity sensors: relative humidity of spring and summer, spring mean temperature and summer maximum and minimum temperatures. Minimum summer temperature, the only significant variable in the model, and maximum summer temperature, marginally significant, are shown. Total inertia = 5.7; cumulative percentage of variance for the relationship of species variables = 42.3; eigenvalues in brackets. (B) Relationship between the flora of the outcrops and the regional climate. CCA of all the outcrops studied based on their floristic composition and environmental characteristics taken from the database WorldClim: mean annual precipitation, annual maximum temperature and annual variation in temperature. Only significant variables in the model are shown. Total inertia = 5.7; percentage of variation in the speciesenvironmental variables accumulated by the first two axes = 77.3; eigenvalues in brackets. Ellipses around the sampling sites were manually drawn to graphically show those sites that were spatially proximate.

Table 2. Climatic determinants of local variation in species composition of north and south faces of rock outcrops and of matrix plots resulting from Monte Carlo analysis during CCA.

Variable	λA	P	F
Minimum summer temperature Maximum summer temperature Summer relative humidity Minimum spring temperature Mean spring temperature Spring relative humidity Maximum spring temperature	0.20	0.004*	1.70
	0.14	0.056	1.27
	0.15	0.100	1.25
	0.12	0.284	1.10
	0.12	0.366	1.05
	0.12	0.466	1.01
	0.12	0.276	1.06

Notes: Conditional effects (i.e., ability to explain the pattern of species composition considering the effect of other variables) of each variable on species composition of plants that are present in the outcrops. F, Fisher's statistic; *P < 0.05; λA , variance further explained at the time of inclusion in the model.

Table 3. Climatic determinants of regional variation in species composition of the outcrops and matrix plots resulting from CCA.

Variable	λA	P	F
Precipitation Maximum temperature Temperature variability	0.24	0.002*	1.99
	0.23	0.002*	2.00
	0.17	0.088	1.42

Notes: Conditional effects (i.e., ability to explain the pattern of species composition considering the effect of other variables) of each variable on species composition of plants that are present in the outcrops. F, Fisher's statistic; *P < 0.05; λA , additional variance explained at the time of inclusion in the model. Variables included mean annual precipitation (Precipitation); maximum annual temperature (Maximum temperature) and annual temperature variation (Temperature variability).

These outcrops were located to the south. The fourth group, in the centre of Figure 3B, included outcrops generally characterised by average values of precipitation and temperature, which, in turn, were located in the centre of the study area. The last group, at the bottom of Figure 3B, included outcrops located further north-west with the highest annual precipitation and maximum temperatures.

Geographical distribution of species and aspect preference on outcrops

Most of the species (79%) found on the south faces and not in the vegetation matrix showed affinities to cold environments which suggested cold preference, as indicated by their distributions reaching the southernmost province of Argentina (Tierra del Fuego) or southernmost region of Chile (Region XII) (Table S1).

Discussion

Regionally, the compositional turnover of outcrops showed a geographic gradient from west to east that was related to the large differences in annual precipitation and maximum temperature in the region. Across this gradient, the species turnover among the outcrops was higher than the species turnover among vegetation matrix plots, which probably reflects the higher microclimatic and edaphic diversity in the former at a regional scale. In addition, this higher turnover among outcrops may be a result of their greater isolation from each other and dispersal limitations of their species, which can also play an important role in structuring plant communities. At the local scale, maximum temperatures of the southern, more shaded faces of the outcrops are generally lower both in spring and summer, which may determine the presence of coldadapted and/or heat-avoiding species that are not present on the north, sunnier faces or in the open surrounding matrix of the Patagonian steppe. Rock outcrops therefore provide climatic heterogeneity between their north and south faces that brackets that of the matrix and can promote the coexistence of floras of warm and cold regions in a same outcrop and thus increase site biodiversity. Key factors in producing habitat diversity that may result in potential refugia for specialist species have been noted to include decoupling of site climate from regional climate, together with a high diversity of site climatic conditions (Keppel et al. 2012). However, other characteristics of the outcrops, such as topography, hydrology or nutrient availability may also play a role and remain to be tested.

The results of this work therefore support the hypothesis that the outcrops of the study region, in addition to their unique edaphic and geological characteristics, could act as climatic refugia, especially for microthermic (coldadapted and/or heat-intolerant) species (Speziale and Ezcurra 2012). However, if this is the case, repeated sampling in time is required to prove it. The majority of the species found on the south faces are near their northern limits of distribution and extend to the cooler southern tip of South America, which might suggest their heat intolerance. These species were probably distributed more extensively in the area during the last ice age (Speziale and Ezcurra 2012), when temperatures were about 4°C cooler than today (Markgraf 1991). Evidence from modelling studies and marine sediment cores also shows that the regional maximum extension of the Patagonian Ice sheet coincided with a 6 °C lowering in sea surface temperatures in the south-east Pacific off southern Chile (Glasser et al. 2008). It is likely that the distributions of the species now found on the south faces of Patagonian rock outcrops were more extensive during this colder period, and that they have generally withdrawn to a more southward distribution after the last glacial maximum, leaving a few relict populations in the southern shaded, cool faces of outcrops. In this sense, the North Patagonian outcrops could be acting as interglacial climatic refugia (also termed 'holocene cryptic refugia' (Birks and Willis 2008) and 'glacial relicts' (Cox and Moore 2010; Hampe and Jump 2011), allowing the survival of relict populations of cold-adapted (microthermic) species on their southern faces (Speziale and Ezcurra 2012).

Geographic ranges of species contract and expand in accordance with climate change, as was the case during the glacial and interglacial periods of the Quaternary. However, inasmuch as temperate-adapted taxa are generally confined to refugia during cold glacial periods, coldadapted taxa present their maximum range contraction and are confined to refugia during warm interglacial periods (Birks and Willis 2008; Stewart et al. 2010). This is related to the fact that species generally respond to climatic changes independently of each other, due to the idiosyncratic adaptations and special environmental tolerances characteristic of each species (Wiens and Graham 2005; Stewart et al. 2010). Therefore, the term refugium, defined as the geographic region or regions that a species inhabits during the period of a glacial/interglacial cycle that represents the maximum range contraction of a species, and it can include different categories based both on geographic location and whether the refugium is inhabited by a temperate- or a cold-adapted species (Stewart et al. 2010). So rock outcrops could serve as refugium to different species over time as climate changes.

The strong correlations between the sample scores on the constrained (CCA) vs. unconstrained (CA) ordinations showed that the selected climatic and microclimatic variables explained most of the observed compositional variation. Changes in maximum temperature and precipitation were reflected in compositional variation along regionalscale latitudinal and longitudinal gradients. At the local scale, the influence of higher minimum summer temperatures of outcrop faces vs. the surrounding matrix was reflected in their respective compositional differences. However, the compositional variation that was not explained by these climatic and microclimatic variables could be accounted for by other variables that are also known to influence outcrop vegetation, but this was not included in our analysis. Rock outcrops contrast markedly with surrounding habitats in their thin and less continuous soil cover (Crowther 1984; Larson et al. 2000) and consequently low levels of available moisture in these soils, which could affect species presence. Other factors, such as fire regime and grazing intensity, could also partly influence the pattern, but data to test this were not available for the study area.

Climate change can affect different species in different ways. Faced with past climate changes in the region during the last glacial period, certain woody species, such as Nothofagus pumilio (Premoli et al. 2010), or herbaceous steppe species, such as Hypochaeris (Tremetsberger et al. 2009), apparently took refuge in several ice-free environments and began postglaciar recolonisation from there. However, the type of response of each species to cooling or warming climates may be species specific (idiosyncratic), depending on niche conservatism (Wiens and Graham 2005) regarding the thermic affinities of the species. For example, populations of Hypochaeris incana appear to have been widely distributed in Patagonia during the ice ages, becoming more or less restricted in their distribution to isolated populations with subsequent warming and aridification in postglacial times (Tremetsberger et al. 2009). Also, data on

populations of the cold-adapted high-elevation tree *Nothofagus pumilio* provide no evidence for wide-range postglacial colonisation from warmer northern localities as generally predicted for trees, and suggest local survival in southernmost South America during ice ages (Premoli et al. 2010). Cold-adapted species may withstand glacial periods, but may be especially affected during periods of extreme warm conditions of interglacials, or today due to global warming. Topographic variability creates a multitude of fine-scale thermal habitats, which offers a 'safer' place to live under conditions of climate change, either warmer or colder, than flat terrain (Scherrer and Körner 2011). This could be the case of the colder portions of rock outcrops which could be offering refuge to heat intolerant species.

Identifying climatic refugia should be considered in selecting candidate areas for conservation (Rose and Burton 2011; Keppel et al. 2012), particularly to protect cold-adapted and/or microthermic species that could be most affected by increases in temperature. This is most important in a scenario of global warming where the environments available to some species may become fragmented (Opdam and Wascher 2004; Birks and Willis 2008). In the Southern Hemisphere, species of cold areas, such as the Andean ranges, are especially threatened due to limitations of land area extension in higher cold latitudes. The continuity of the numerous North Patagonian outcrops through gradients of precipitation and temperature (Paruelo et al. 1998; Speziale et al. 2010; Speziale and Ezcurra 2012), that additionally are situated in an area intermediate between two biogeoregions, the Patagonian and Subantarctic graphic (Speziale et al. 2010), makes them especially important particularly for the conservation of species subject to distribution changes. In the studied area, outcrops present a flora that is more diverse than the surrounding matrix (Speziale and Ezcurra 2012), and their composition changes markedly from outcrops having high temperature variation and low annual precipitation to those having lower temperature variation and higher precipitation. This regional climatic variation, together with their local microclimatic diversity, increases the possibility of the outcrops becoming, or actually serving as potential refugia. Thus, appropriate protection of outcrops should be encouraged in relation to their role as biodiversity refugia, as has been proposed for other regions (e.g., Burke 2003; Michael et al. 2010; Zimmermann et al. 2010; Keppel and Wardell-Johnson 2012) particularly considering that most of them are on private lands.

Conclusions

Rocky habitats are patches with microclimatic differences that remain undisturbed or less modified in comparison with surrounding vegetation when the latter is affected by fire and/or grazing (Burke 2003; Michael et al. 2010), factors that will likely to further increase owing to anthropogenic change and global warming. Therefore, it is

important to plan protected area networks that maximise geographical gradients and local environmental heterogeneity, thereby allowing migrational movements by assuring the availability of a range of microclimates that facilitate the persistence of meta-populations (Gillson and Willis 2004). Effective conservation strategies in northern Patagonia should include the protection of rock outcrops both as refugia for cold-adapted species and as potential stepping stones and corridors that would allow dispersal of these species between supportive environments through unfavourable ones.

Acknowledgements

We are grateful for the interesting comments made by Stephan Halloy and two anonymous reviewers on previous versions of this manuscript. We thank Administración de Parques Nacionales (APN) of Argentina for allowing us to work in their parks and reserves, and D. Marty, R. Shanahan, and J. Jones for authorisation to work on private land. We also thank A.I. Bugiolochi, M. L. Suarez, F. Barbar, and H., C., and S. Lambertucci for their assistance during fieldwork. Our special appreciation to A. Cingolani, S. Lambertucci, Donald Bran and A. Ruggiero for useful discussion in relation to this project. CE and KS are scientific research members of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) of Argentina.

Funding

This work was partially supported by funding from ANPCYT-FONCYT, Argentina to projects PICT 11826 and 38148 BID 1728 OC/AR.

Supplemental data

Supplemental data for this article can be accessed here.

Notes on contributors

Karina Lilian Speziale is interested in biodiversity conservation, plant ecology and biogeography, with a focus on Patagonian flora and biological invasions.

Cecilia Ezcurra has research interests in plant taxonomy, evolution and biogeography. She is particularly interested in the biogeographic history and origin of the diversity of the extant flora of the Andes.

References

Anchorena J, Cingolani A. 2002. Identifying habitat types in a disturbed area of the forest-steppe ecotone of Patagonia. Plant Ecology. 158:97–112.

Anderson MG, Ferree CE. 2010. Conserving the stage: climate change and the geophysical underpinnings of species diversity. PLoS One. 5:e11554.

Birks HJB, Willis KJ. 2008. Alpines, trees, and refugia in Europe. Plant Ecology & Diversity. 1:147–160.

Björkman O, Badger MR, Armond PA. 1980. Response and adaptation of photosynthesis to high temperatures. In: Turner NC, Kramer PJ, editors. Adaptation of plants to water and high temperatures stress. New York, NY: Wiley.

Burke A. 2002. Island-matrix relationships in Nama Karoo inselberg landscapes. Part I: do inselbergs provide a refuge for matrix species? Plant Ecology. 160:79–90.

- Burke A. 2003. Inselbergs in a changing world global trends. Diversity and Distributions. 9:375–383.
- Burke A, Jürgens N, Seely MK. 1998. Floristic affinities of an inselberg archipelago in the southern Namib desert-relic of the past, centre of endemism or nothing special? Journal of Biogeography. 25:311–317.
- Clarke PJ. 2002. Habitat islands in fire-prone vegetation: do landscape features influence community composition? Journal of Biogeography. 29:677–684.
- Correa MN. 1969–1998. Flora Patagónica. Buenos Aires: INTA; p. 1–7.
- Cox CB, Moore PD. 2010. Biogeography: an ecological and evolutionary approach. Malden, MA: Wiley-Blackwell.
- Crowther J. 1984. Soil carbon dioxide and weathering potentials in tropical karst terrain, peninsular Malaysia: a preliminary model. Earth Surface Processes and Landforms. 9:397–407.
- Giacosa R, Heredia N. 2001. Hoja Geológica 4172-IV, San Carlos de Bariloche, Provincia de Río Negro y Neuquén. Instituto de Geología y Recursos Minerales, Servicio Geológico Minero Argentino.
- Gillson L, Willis KJ. 2004. "As Earth's testimonies tell": wilderness conservation in a changing world. Ecology Letters. 7:990–998.
- Glasser NF, Jansson KN, Harrison S, Kleman J. 2008. The glacial geomorphology and Pleistocene history of South America between 38°S and 56°S. Quaternary Science Reviews. 27:365–390.
- Gottfried M, Pauli H, Futschik A, Akhalkatsi M, Barančok P, Alonso JLB, Coldea G, Dick J, Erschbamer B, Fernández Calzado MR, et al. 2012. Continent-wide response of mountain vegetation to climate change. Nature Climate Change. 2:111–115.
- Hampe A, Jump AS. 2011. Climate relicts: past, present, future. Annual Review of Ecology, Evolution and Systematics. 42:313–333.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology. 25:1965–1978.
- Keppel G, Van Niel KP, Wardell-Johnson GW, Yates CJ, Byrne M, Mucina L, Schut AGT, Hopper SD, Franklin SE. 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. Global Ecology and Biogeography. 21:393–404.
- Keppel G, Wardell-Johnson GW. 2012. Refugia: keys to climate change management. Global Change Biology. 18:2389–2391.
- Kumar S, Stohlgren T. 2009. Maxent modeling for predicting suitable habitat for threatened and endangered tree Canacomyrica monticola in New Caledonia. Journal of Ecology and Natural Environment. 1:94–98.
- Larcher W, Kainmüller C, Wagner J. 2010. Survival types of high mountain plants under extreme temperatures. Flora – Morphology, Distribution, Functional Ecology of Plants. 205:3–18.
- Larson DW, Matthes U, Kelly PE. 2000. Cliff ecology: pattern and process in cliff ecosystems. Cambridge, MA: Cambridge University Press.
- Lepš J, Šmilauer P. 2003. Multivariate analysis of ecological data using Canoco. Cambridge, MA: Cambridge University Press.
- Markgraf V. 1991. Late Pleistocene environmental and climatic evolution in southern South America. Bamberger Geographische Schriften. 11:271–281.
- Michael DR, Lindenmayer DB, Cunningham RB. 2010. Managing rock outcrops to improve biodiversity conservation in Australian agricultural landscapes. Ecological Management and Restoration. 11:43–50.
- Milchunas DG, Noy-Meir I. 2002. Grazing refuges, external avoidance of herbivory and plant diversity. Oikos. 99:113–130.

- Økland RH. 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? Journal of Vegetation Science. 7:289–292.
- Opdam P, Wascher D. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biological Conservation. 117:285–297.
- Parmesan C. 1996. Climate and species' ranges. Nature. 382:765–766.
- Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution and Systematics. 37:637–669.
- Paruelo JM, Jobbágy EG, Sala OE, Lauenroth WK, Burke IC. 1998. Functional and structural convergence of temperate grassland and shrubland ecosystems. Ecological Applications. 8:194–206.
- Pauli H, Gottfried M, Dullinger S, Abdaladze O, Akhalkatsi M, Alonso JLB, Coldea G, Dick J, Erschbamer B, Calzado RF, et al. 2012. Recent plant diversity changes on Europe's mountain summits. Science. 336:353–355.
- Peters RL. 1985. The greenhouse effect and nature reserves. Bioscience. 35:707–717.
- Porembski S, Szarzynski J, Mund J-P, Barthlott W. 1996. Biodiversity and vegetation of small-sized inselbergs in a West African rain forest (Taï, Ivory Coast). Journal of Biogeography. 23:47–55.
- Premoli AC, Mathiasen P, Kitzberger T. 2010. Southern-most Nothofagus trees enduring ice ages: genetic evidence and ecological niche retrodiction reveal high latitude (54°S) glacial refugia. Palaeogeography, Palaeoclimatology, Palaeoecology. 298:247–256.
- Rose NA, Burton PJ. 2011. Persistent climate corridors: the identification of climate refugia in British Columbia's central interior for the selection of candidate areas for conservation. Journal of Ecosystems and Management. 12:101–117.
- Scherrer D, Körner C. 2011. Topographically controlled thermalhabitat differentiation buffers alpine plant diversity against climate warming. Journal of Biogeography. 38:406–416.
- Speziale KL. 2012. Composición y diversidad de la flora de afloramientos rocosos del norte de la patagonia y su relación con factores ambientales a distintas escalas [Ph.D. dissertation]. [Bariloche]: Universidad Nacional del Comahue.
- Speziale KL, Ezcurra C. 2011. Patterns of alien plant invasions in northwestern Patagonia, Argentina. Journal of Arid Environments. 75:890–897.
- Speziale KL, Ezcurra C. 2012. The role of outcrops in the diversity of Patagonian vegetation: relicts of glacial palaeofloras? Flora – Morphology, Distribution. Flora – Morphology, Distribution, Functional Ecology of Plants. 207:141–149.
- Speziale KL, Ruggiero A, Ezcurra C. 2010. Plant species richness–environment relationships across the Subantarctic–Patagonian transition zone. Journal of Biogeography. 37:449–464.
- Stewart JR, Lister AM, Barnes I, Dalen L. 2010. Refugia revisited: individualistic responses of species in space and time. Proceedings of the Royal Society B: Biological Sciences. 277:661–671.
- Ter Braak CJ, Smilauer P. 1998. CANOCO reference manual and user's guide to CANOCO for windows: software for canonical community ordination. New York, NY: Microcomputer Power.
- Tremetsberger K, Urtubey E, Terrab A, Baeza CM, Ortiz MÁ, Talavera M, König C, Temsch EM, Kohl G, Talavera S, et al. 2009. Pleistocene refugia and polytopic replacement of diploids by tetraploids in the Patagonian and Subantarctic plant Hypochaeris incana (Asteraceae, Cichorieae). Molecular Ecology. 18:3668–3682.

- Walther G-R, Beißner S, Burga CA. 2005. Trends in the upward shift of alpine plants. Journal of Vegetation Science. 16:541–548.
- Ward DF. 2007. Modelling the potential geographic distribution of invasive ant species in New Zealand. Biological Invasions. 9:723–735.
- Wiens JJ, Graham CH. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution, and Systematics. 36:519–539.
- Wiser SK, Peet RK, White PS. 1996. High-elevation rock outcrop vegetation of the Southern Appalachian Mountains. Journal of Vegetation Science. 7:703–722.
- Zimmermann M, Vischer-Leopold M, Ellwanger G, Ssymank A, Schröder E. 2010. The EU habitats directive and the German Natura 2000 network of protected areas as tool for implementing the conservation of relict species. In: Relict Species. Berlin: Springer. p. 323–340.