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## The role of outcrops in the diversity of Patagonian vegetation: Relicts of glacial palaeofloras?

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### ABSTRACT

Outcrops around the world enhance biodiversity as they provide heterogeneous environments and varied habitats for species with different requirements than those living in the surroundings, and in this way they increase alpha and beta diversity. We studied the floristic composition of the vegetation of rock outcrops in northwestern Patagonia, Argentina, and compared them to the surrounding matrix of shrubland and steppe. For this we sampled 50 outcrops and 50 matrix plots close to them, identified all the species present, and analyzed their floristic composition with Detrended Correspondence Analysis (DCA). We also analyzed the floras of the north and south faces of the outcrops. The resulting ordinations were related to geographic gradients of the region. The proportions of alien to native species, different life forms, and phylogenetic groups of the outcrop floras were compared to the matrix with G-tests. Our results showed similar dominant families, life form proportions and percentage of alien species in the outcrops and the surrounding matrix. However, species composition of the outcrops was markedly different. North Patagonian outcrops present several taxa not found in the matrix, especially in their southern, less insolated walls. The previously recorded distribution of most of these exclusive species is found in colder areas further south. Thus, we hypothesize that outcrops could be acting as relicts of cold-adapted glacial paleofloras that were probably more extended during glacial times and retreated south after the last glacial maximum.

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### Introduction

Loss of biodiversity is affecting important characteristics of ecosystems around the world (Naeem et al., 1994; Díaz et al., 2006). For the planning of sound conservation actions to arrest this threat, factors related to the biodiversity of the considered region should be well known. This should include the study of particular environments within major habitats, given that heterogeneity, as for example that provided by rock outcrops, can enhance biodiversity (Barthlott et al., 1993). Outcrops generally provide habitats for species with different requirements than those living in the surrounding. For example, rock outcrops such as inselbergs in tropical regions can be micro-climatologically and edaphically dry environments posing severe constraints for the vegetation (Porembski et al., 1996; Changwe and Balkwill, 2003). This can favour the evolution of dry-adapted specialized or endemic species (Williamson et al., 1997). If outcrops are located in humid forest

environments they can provide habitat resource for savanna elements (e.g., Porembski et al., 1996), if in desert ones they provide more humid and favourable microenvironments (e.g., Burke, 2002). In this way, rock outcrops may increase local biodiversity. Outcrops also act as shelter for differential life-forms respect to the matrix due to differences in fire and grazing pressures (Clarke, 2002; Milchunas and Noy-Meir, 2002).

Due to their distinctive features, outcrops called the attention of botanists for over two centuries (Walters and Wyatt, 1982). Many of these studies were conducted mainly in Africa and North America (e.g., in Africa: Burke, 2003a; Changwe and Balkwill, 2003; Porembski et al., 1996; in North America: Burbank and Platt, 1964; Wyatt and Fowler, 1977). Other studies were carried out within tropical South America in Brazil, Venezuela and French Guiana (e.g., Gröger and Barthlott, 1996; Porembski et al., 1998; Meirelles et al., 1999; Jacobi et al., 2007; Sarthou et al., 2010). Several of the studies focus on the application of island theory (MacArthur and Wilson, 1967; MacArthur, 1972) to outcrop biodiversity (Wyatt and Fowler, 1977), deal with succession and speciation processes (Burbank and Platt, 1964; Houle and Phillips, 1989; Williamson et al., 1997; Sarthou et al., 2009, 2010) or have shown very specific adaptations to these extreme environments (e.g. Porembski and Barthlott, 2000). But most of them focus on studying the

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floristic composition of these particular environments in relation to its relevance to conservation (Wyatt and Fowler, 1977; Phillips, 1982; Walters and Wyatt, 1982; Escudero and Pajarón, 1996; Porembski et al., 1996; Clarke, 2002; Changwe and Balkwill, 2003).

Floristic composition of rock outcrops and its relationship with the surrounding matrix of vegetation varies according to the studied region. Comparisons between outcrop and matrix showed floristic similarities in the Succulent Karoo, South Africa (Desmet and Cowling, 1999). On the other hand, the same comparisons showed floristic differences in the east coast of Australia, in the Ivory Coast, Brazil, and in east South Africa within serpentine environments (Porembski et al., 1996, 1998; Clarke, 2002; Changwe and Balkwill, 2003). In Dunbar Valley, South Africa, serpentine environments are very particular given their high nickel concentrations, and the floristic composition similarity with non-serpentine environments is very low (Changwe and Balkwill, 2003). Outcrops of New England, Australia, also showed floristic dissimilarities respect to the forest matrix they are embedded in (Clarke, 2002). Inselberg composition in the Ivory Coast differed completely from the surrounding forest in relation to the species found on them (Porembski et al., 1996), and similar results were found for saxicolous vegetation mats on inselbergs in Brazil Atlantic rainforest (Porembski et al., 1996). Whether the composition of the outcrops is particular and different from the surrounding matrix is relevant for the development of any sound conservation strategy aiming to maximize its effectiveness and protection.

In many regions of the world, the diversity of microhabitats within outcrops, with differences both in temperature and moisture to the surrounding matrix, has enabled the persistence of species beyond their main range in the face of climatic fluctuations (Hopper et al., 1997). Outcrops of deserts have been reported to function as refugia for plants that have survived in the area from periods when the continuous extensions of moister climate enabled their penetration (e.g., Danin, 1999). Outcrops of temperate regions have been suggested to house relicts of a cold-adapted flora that is retreating polewards due to climate warming (e.g., Hampe & Petit, 2005). In general, the presence of these presumably relict floras has been related to climatic oscillations during Pleistocene and Holocene times (Danin, 1999). Topographic buffers such as rock outcrops are thus important in the view of expected changes in climatic conditions, regardless of the nature of the change (Burke, 2003b). Therefore, outcrops can be very important in relation to conservation of species, populations and communities that may be affected by global climate change.

One of the main threats of the current globalized world is the invasion of alien species, and the distinctive outcrop floras can be seriously affected by them. Despite some outcrops free from invaders can be found (Meirelles et al., 1999), many studies show the presence of alien species on different types of rocky environments (e.g., Porembski et al., 1996; Wisser et al., 1996; Biedinger and Fleischmann, 2000). The lack of exotic species in some Brazilian outcrops is explained by the drought periods and harshness of outcrops, natives being the only ones adapted to such conditions (Meirelles et al., 1999). But it has been observed that plant community composition of the matrix surrounding outcrops can influence their alien flora (Wisser and Buxton, 2008). Therefore, nearby settlements, disturbance and roads can introduce aliens and affect outcrop floras. The presence of exotic species in southern Appalachian or in the Ivory Coast outcrops reflects the presence of species pre-adapted to colonize open spaces in the surroundings (Porembski et al., 1996; Wisser et al., 1996).

Even though there are many studies of the flora of tropical inselbergs and of outcrops of temperate areas of the Northern Hemisphere, fewer studies have been performed in temperate regions of the southern hemisphere. In temperate South America the floras of outcrops have not been much considered by

botanists. A few studies from Argentina describe plant diversity of outcrops (Frangi, 1975; Cabido et al., 1990; Funes and Cabido, 1995; Anchorena and Cingolani, 2002; Méndez, 2010). In the present study we aimed to analyze the role of outcrops in the maintenance or enhancement of biodiversity by studying the floristic composition of north Patagonian outcrops, and comparing them with the matrix vegetation. We also considered differences among north and south faces given that the drier, more insolated slopes or the more humid and cold ones could provide diverse habitats for species with different requirements. With this work we aimed to answer these questions: (1) Do Patagonian outcrops support a distinctive native flora that is different from the matrix vegetation in composition and life-forms? (2) How does this flora vary regionally among outcrops and locally within outcrops? (3) Is the outcrop flora different in number and composition of alien species in relation to the matrix flora? (4) Can these outcrops enable the persistence of species beyond their main range in the face of climatic fluctuations? The answers to these questions are necessary to produce relevant conservation strategies in times of global climate change.

## Methods

### Study area

We selected our study area in northwestern Patagonia, Argentina, between 41°57'21.36"–40°41'56" S and 70°33'56.5"–71°22'36" W (Fig. 1) based on previous studies in the region (Speziale et al., 2010). This area lies east of the Andes in the ecotone between two biogeographic regions: the Patagonian province of the Neotropical Region and the Subantarctic province of the Antarctic region (Cabrera, 1976). It is characterized by changes in precipitation patterns due to the rain shadow produced by the westerly winds from the Pacific on the southern Andes (Ezcurra and Brion, 2005; Speziale et al., 2010). The vegetation matrix surrounding the outcrops varies from west to east (Speziale et al., 2010). The western area includes a forest-shrubland ecotone which changes to a low xeric shrubland and finally to a dry steppe matrix towards the east (Speziale et al., 2010). Most precipitation occurs from April to September ranging from ca. 1000 mm/year to the west, in the woodland – shrubland, to less than 300 mm/year to the east, in the dry Patagonian steppe (Speziale et al., 2010; Speziale and Ezcurra, 2011).

The study area comprises different types of landscapes, mostly erosive relief over volcanites, lava plains, and landforms originated by glacio-fluvial and glacio-lacustrine deposits (Giacosa and Heredia, 2001). These differences determine a heterogeneous environment with a rich flora (Anchorena and Cingolani, 2002). Most of the studied outcrops correspond to the Huitrera formation (Late Paleocene – Medium Eocene). This formation is abundant in porphyry and andesitic lavas and basalts. Outcrops to the southwest belong to the Ñirihua formation (Late Oligocene – Medium Miocene), except for one which belongs to the Ventana formation (Oligocene). The Ñirihua formation is characterized 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 southeast belong to the Pilcaniyeu Pluton (Lower Jurassic). This formation is characterized by a granitic facies formed by biotitic granites. The furthest one to the southeast corresponds to Campana formation characterized by olivine basalts, whereas the one further east belongs to Estratos de Comallo, the oldest formation of the studied outcrops (Triassic – Lower Jurassic), composed by ignimbrites, andesites and basalts (Giacosa and Heredia, 2001). Even though their origins differ, most outcrops are similar in that most of them are of volcanic origin

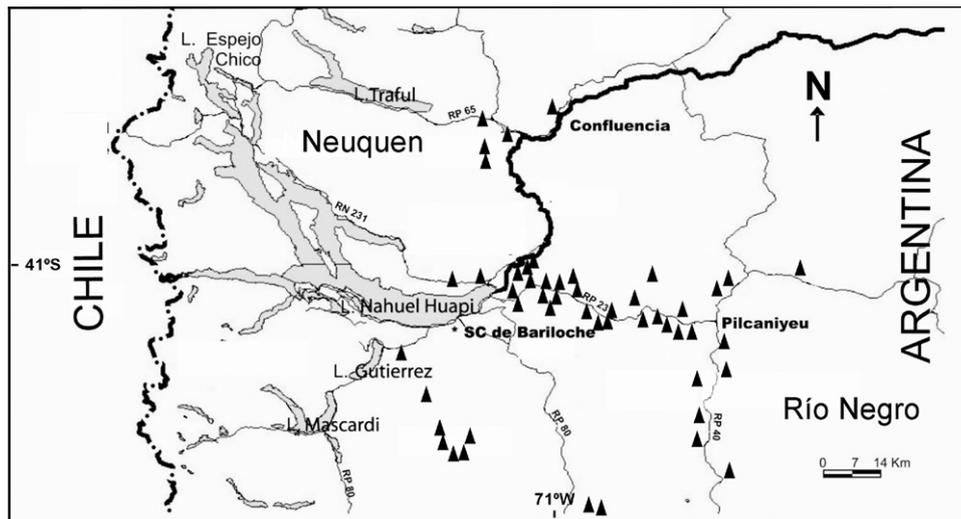


Fig. 1. Study area showing the distribution of the studied sites (▲). Each site corresponds to an outcrop and a matrix plot both located closed to each other.

and predominantly composed of porphyry and andesitic lavas and basalts.

#### Data collection

We studied the floristic composition of 50 outcrops ranging between 10 and 30 m diam. and located between 800 and 1500 m a.s.l., within a shrubland–steppe matrix (Fig. 2). All plants growing on outcrops were identified to species, and voucher herbarium specimens were collected. We used *Flora Patagónica* (Correa, 1969–1988) for identification. Nomenclature follows Zuloaga et al. (2008). Data on taxonomic status (family, genera, and species), geographic distribution (provinces of Argentina), origin (native or alien), and life forms (trees, shrubs, perennial herbs, and annuals or biennials) of all the species were taken from the same sources. Within each outcrop, we also sampled two plots 20 m<sup>2</sup> (10 m × 2 m), on their north and south faces respectively, assuming that due to different degrees of insolation they could be microclimatically different and therefore could present different floristic compositions.

To obtain information on floristic characteristics of the vegetation matrix for comparisons, we established 50 sampling plots 100 m<sup>2</sup> (10 m × 10 m), i.e., one matrix plot for each outcrop. This plot size has been shown as adequate for the determination of species richness and composition in shrubland and herbaceous vegetation (Otýpková and Chytrý, 2006). We placed each plot approximately 200 m away from the nearest rock outcrop and upslope or to the sides to avoid its influence due to runoff. We located plots in places that were representative of the local natural vegetation of shrubland–steppe, separated at least 100 m from roads, and without recent signs of fire, overgrazing, or other anthropogenic disturbances.

#### Data analyses

We recorded species presence–absence data for each outcrop and vegetation matrix plot. To analyze these data we used Detrended Correspondence Analysis (DCA; ter Braak and Smilauer, 1998). This analysis groups the outcrops and matrix plots on a factorial plane according to their floristic similarities. To relate the resulting ordination to geological formations and geographical latitude, longitude and altitude, these latter variables were included in the same analysis as supplementary. We also analyzed species data on the vegetation growing on outcrops and their floristic relations

to matrix plots, and to southern floras and high elevation floras that were obtained from other authors (Moore, 1983; Ferreyra et al., 1998) and treated as supplementary. DCAs were performed on native species given that we are looking at outcrops particularities and alien species that homogenize biotas (McKinney, 2006). Rare species (low frequency in our data set) were downweighted in all the analyses.

To examine differences in floristic composition between outcrops and matrix, each genus was assigned to its family and then sorted into seven phylogenetic groups: (1) pteridophytes, (2) gymnosperms, (3) monocots, (4) basal angiosperms, (5) basal eudicots, (6) rosids, and (7) asterids following the Angiosperm Phylogeny Website tree (Stevens, 2001) that is based on the molecular phylogenies published by APG (2009). The proportions of genera of different phylogenetic groups were compared between outcrops and matrix with G-tests. We also compared proportions of different life-forms, most species-rich families, most frequent species, and proportions of alien and native species with G-tests. We assessed differences in position within the floristic gradient between the studied habitats (rock outcrops and vegetation matrix) and distribution of species (species found on north or south faces) with Mann–Whitney U-test or Kruskal–Wallis nonparametric tests, given that our data did not conform parametric assumptions. We used ANOVAs to compare distributions of outlier species found beyond their main range on particular faces, on both faces, or in the matrix.

## Results

### Floristic characteristics of outcrop vegetation

The vascular flora of outcrops in northwestern arid Patagonia includes 189 species belonging to 117 genera in 51 families. The number of species per outcrop averages 15, and ranges between one and 33 species. Approximately 50% of the species belong to just three families. Best represented families are Poaceae (49 species), Asteraceae (35), and Rosaceae (7), followed by Caryophyllaceae and Onagraceae (5). Many plant families are rare, as 32 families are represented by just one genus and 23 families are represented by just one species. Best represented genera are *Poa* (7), *Senecio* (6), *Festuca* (6), and *Bromus*, *Jarava* and *Trisetum* (5). More than 55% of the species were found only in one sample and more than 65% in just two. Only 15 species can be considered common, being found in 30% of the samples or more. Perennial herbs are the most



**Fig. 2.** Outcrop near national route 40, south of Pilcaniyeu, Rio Negro, Argentina, within a landscape matrix of Patagonian steppe dominated by *Mulinum spinosum* shrubs and *Pappostipa speciosa* tussock grasses.

represented life-form, followed by shrubs, with few annuals or biennials (Table 1). Alien species represent 14.8% of the flora found on the outcrops, annual or biennial herbs being their most common life forms. Families with more alien species were Poaceae, Asteraceae, Caryophyllaceae, and Brassicaceae (Table 2).

**Table 1**  
General description of the outcrops and matrix floras.

	Outcrops	Matrix
<i>Taxonomy</i>		
Total species	182	179
Total genera	117	120
Total families	50	48
<i>Richest families</i>		
Poaceae	49	32
Asteraceae	37	39
Rosaceae	7	7
Fabaceae	4	9
<i>Genera with more species (# of species per genera within brackets)</i>		
	<i>Poa</i> (7)	<i>Poa</i> (8)
	<i>Senecio</i> (6)	<i>Baccharis</i> (5)
	<i>Festuca</i> (6)	<i>Senecio</i> (5)
	<i>Bromus</i> (5)	<i>Adesmia</i> (5)
<i>Life forms</i>		
Perennial herbs	102	92
Shrubs	46	42
Annual/biennial herbs	31	40
Trees	3	4
<i>Origin</i>		
Natives	155	151
Aliens	27	28
<i>Distribution of natives</i>		
Locally exclusive to outcrops (Results of this work)	70	
Endemic to Patagonian steppe (Beeskov et al., 2005)	7	7
Regional endemics (Zuloaga et al., 2008)	122	109
Endemics of Argentina (Zuloaga et al., 2008)	33	42

We found 39 genera with 69 native species exclusively on the studied outcrops when compared with the surrounding matrix (Table 3). Five species of ferns belong to this group. The most frequent of these outcrop species were *Ribes cucullatum*, *Trisetum spicatum*, *Cheilanthes glauca*, *Cystopteris fragilis* and

**Table 2**  
Alien species found only on outcrops (R) or both on outcrops and matrix plots (R–M). Alien species found only in matrix plots are not shown.

Site	Family	Species	Life-form
R	Chenopodiaceae	<i>Chenopodium album</i>	Annual or biennial herb
	Poaceae	<i>Arrhenatherum elatius</i>	Perennial herb
		<i>Holcus lanatus</i>	Annual or biennial herb
R–M	Rubiaceae	<i>Schedonorus pratensis</i>	Perennial herb
		<i>Galium aparine</i>	Annual or biennial herb
		Asteraceae	<i>Hypochaeris radicata</i>
	Asteraceae	<i>Lactuca serriola</i>	Annual or biennial herb
		<i>Taraxacum officinale</i>	Perennial herb
	Asteraceae	<i>Tripleurospermum perforatum</i>	Annual or biennial herb
		<i>Myosotis stricta</i>	Annual or biennial herb
		Brassicaceae	<i>Descurainia sophia</i>
	Caryophyllaceae	<i>Draba verna</i>	Annual or biennial herb
		<i>Cerastium arvense</i>	Perennial herb
		<i>Cerastium glomeratum</i>	Annual or biennial herb
	Geraniaceae	<i>Holosteum umbellatum</i>	Annual or biennial herb
		<i>Erodium cicutarium</i>	Annual or biennial herb
	Onagraceae	<i>Epilobium brachycarpum</i>	Annual or biennial herb
		<i>Plantago lanceolata</i>	Perennial herb
Poaceae		<i>Apera interrupta</i>	Annual or biennial herb
		<i>Bromus tectorum</i>	Annual or biennial herb
<i>Holcus lanatus</i>		Annual or biennial herb	
<i>Hordeum murinum</i>		Annual or biennial herb	
<i>Poa pratensis</i>		Perennial herb	
<i>Vulpia bromoides</i>		Annual or biennial herb	
<i>Vulpia myuros</i>		Annual or biennial herb	
Polygonaceae		<i>Rumex acetosella</i>	Perennial herb
Portulacaceae	<i>Claytonia perfoliata</i>	Annual or biennial herb	
Scrophulariaceae	<i>Verbascum thapsus</i>	Annual or biennial herb	

**Table 3**

Native species only found on outcrops but not in the matrix plots. N–S indicates if the species was only found on north (N) or south (S) faces, or in both north and south faces (N–S), either from the same outcrop or in different ones. Argentina: distribution within Argentinian provinces: Buenos Aires (BSA), Catamarca (CTM), Chubut (CHU), Córdoba (COR), Corrientes (CRT), Formosa (FMS), Entre Ríos (ETR), Jujuy (JJY), La Pampa (LPM), La Rioja (LRJ), Mendoza (MDZ), Neuquén (NQN), Río Negro (RNG), Salta (SLT), Santa Cruz (STC), San Juan (SJM), San Luis (SLS), Tierra del Fuego (TRF), Distrito Federal (DF). Chile: distribution within Chilean regions. Freq: number of outcrops where the species was recorded.

Face	Family	Species	Life form	Argentina	Chile	Freq		
S	Apocynaceae	<i>Diplolepis descolei</i>	Perennial herb	CHU, NQN, RNG		1		
	Asteraceae	<i>Chilotrichum diffusum</i>	Shrub	CHU, MDZ, NQN, RNG, STC, TRF	VIII–XII	1		
		<i>Hieracium glaucifolium</i>	Perennial herb	CHU, NQN, RNG, STC	VII–X	1		
		<i>Leucheria millefolium</i>	Perennial herb	CHU, NQN, RNG, STC	VII–XII	1		
		<i>Nassauvia juniperina</i>	Perennial herb	CHU, STC <sup>a</sup>		1		
		<i>Perezia fonkii</i>	Perennial herb	NQN, RNG	IX–X	1		
		<i>Senecio gnidioides</i>	Shrub	NQN, RNG	VIII–XII	1		
		<i>Senecio pachyphyllos</i>	Shrub	MDZ, NQN, RNG	VI–IX	2		
		Boraginaceae	<i>Phacelia nana</i>	Annual herb	CHU, JJY, LRJ, MDZ, SLT, TCM	I–II	1	
			Brassicaceae	<i>Noccaea magellanica</i>	Perennial herb	CHU, MDZ, NQN, RNG, STC, SJN, TRF	V–XII	1
		Caryophyllaceae		<i>Colobanthus lycopodioides</i>	SubShrub	CHU, MDZ, NQN, RNG, STC, SJN, TRF	XII	2
				<i>Spergula depauperata</i>	Perennial herb	MDZ, NQN, RNG, SJN	V–X	2
		Loasaceae	<i>Blumenbachia silvestris</i>	Perennial herb	CHU, MDZ, NQN, RNG	V–IX	1	
		Onagraceae	<i>Epilobium nivale</i>	Perennial herb	CHU, MDZ, NQN, RNG, STC	IV–XII	1	
	Poaceae	<i>Bromus pellitus</i>	Perennial herb	STC, TRF <sup>a</sup>	XII	1		
		<i>Bromus tunicatus</i>	Perennial herb	CHU, MDZ, NQN, RNG, STC	IV–XII	1		
		<i>Festuca magellanica</i>	Perennial herb	CTM, CHU, COR, LRJ, MDZ, NQN, RNG, STC, TRF	IV–XII	1		
			<i>Festuca thermanum</i>	Perennial herb	CHU, NQN, TRF <sup>a</sup>	VII–XII	1	
			<i>Jarava sorianoii</i>	Perennial herb	CHU, STC <sup>a</sup>		1	
			<i>Poa secunda</i>	Perennial herb	CHU, NQN, RNG, STC	V–VI, XII	1	
			<i>Poa spiciformis</i>	Perennial herb	CHU, STC, TRF <sup>a</sup>	XII	1	
			<i>Rytidosperma lechleri</i>	Perennial herb	CHU, MDZ, NQN, RNG	IV–XII	1	
			<i>Trisetum flavescens</i>	Perennial herb	NQN, RNG	XII	1	
		Pteridaceae		<i>Adiantum chilense</i>	Perennial herb	BSA, CTM, CHU, COR, LPM, LRJ, MDZ, NQN, RNG, STC, SJN, SNL	I–XII	2
			Saxifragaceae	<i>Saxifraga magellanica</i>	Perennial herb	CHU, COR, JJY, NQN, RNG, STC, SNL, TRF	VII–XII	2
		Verbenaceae	<i>Junellia seriphioides</i>	Shrub	CTM, CHU, JJY, LPM, LRJ, MDZ, NQN, RNG, SLT, SJN, SNL	II	1	
		N	Asteraceae	<i>Baccharis patagonica</i>	Shrub	CHU, NQN, RNG, STC, TRF	VII–XII	1
	<i>Conyza aff. magnimontana</i>			Perennial herb	RNG		1	
	<i>Gamochaeta neuquensis</i>			Perennial herb	NQN, RNG	XII	3	
	<i>Gamochaeta nivalis</i>			Perennial herb	CHU, MDZ, NQN, RNG, TRF	VII–X	1	
	Escalloniaceae		<i>Escallonia rosea</i>	Shrub	CHU <sup>a</sup>	VII–XII	1	
			<i>Escallonia rubra</i>	Shrub	CHU, NQN, RNG, STC	VI–X	1	
	Euphorbiaceae		<i>Stillingia patagonica</i>	Shrub	CHU, MDZ, NQN, RNG, STC		1	
Fabaceae	<i>Astragalus cruckshanksii</i>		Perennial herb	CHU, MDZ, NQN, RNG, STC, SJN	III–VII	1		
Onagraceae	<i>Clarkia tenella</i>		Annual herb	CHU, NQN, RNG	IV–X	1		
	<i>Oenothera odorata</i>		Annual herb	BSA, CHU, COR, LPM, MDZ, NQN, RNG, STC, SJN	XI–XII	1		
Poaceae	<i>Agrostis vidalii</i>		Perennial herb	CHU, NQN, RNG	X–XI	2		
	<i>Chascolytrum subaristatum</i>		Perennial herb	BSA, CTM, CHC, CHU, COR, CRT, ETR, JJY, LPM, MSN, NQN, RNG	IV–X	2		
			<i>Festuca scabriuscula</i>	Perennial herb	NQN, RNG	VIII–X	1	
			<i>Poa subenervis</i>	Perennial herb	MDZ, STC, SJN	XII	1	
			<i>Podagrostis sesquiflora</i>	Perennial herb	MDZ, RNG	VII–X	1	
			<i>Trisetum barbinodes</i>	Perennial herb	MDZ, NQN, RNG	VII–IX	1	
			<i>Vulpia antucensis</i>	Annual herb	BSA, CHU, LPM, MDZ, NQN, RNG, STC	II–XII	2	
	Rhamnaceae		<i>Discaria chacaye</i>	Shrub	CHU, NQN, RNG, STC, TRF	V, IX–XII	1	
Rosaceae	<i>Potentilla chiloensis</i>		Perennial herb	NQN	VI–XI	1		
Solanaceae	<i>Pantachanta ameghinoi</i>		Shrub	CHU, MDZ, NQN, RNG		1		
N–S	Asteraceae		<i>Conyza larrainiana</i>	Shrub	CHU, MDZ, NQN, RNG, SCR	X–XII	3	
			<i>Gamochaeta polybotrya</i>	Perennial herb	CHU, MDZ, NQN, RNG, SCR, TRF	VIII	2	
			<i>Perezia calophylla</i>	Perennial herb	NQN, RNG	X	2	
		<i>Senecio tricuspoidatus</i>	Shrub	CHU, SCR, TRF <sup>a</sup>	XI–XII	1		
		Buddlejaceae	<i>Buddleja araucana</i>	Shrub	MDZ, NQN, RNG	III–VIII	2	
	Cactaceae	<i>Austrocactus patagonicus</i>	Shrub	LPM, MDZ, NQN, RNG, SCR	IX–XI	3		
	Dryopteridaceae	<i>Cystopteris fragilis</i>	Perennial herb	CTM, CHU, COR, JJY, MDZ, NQN, RNG, SLT, SCR, SJN, SNL, TRF	VII, XII	8		
			<i>Polystichum chilense</i>	Perennial herb	CHU, NQN, RNG, SCR, TRF	X–XII	3	
			<i>Polystichum plicatum</i>	Perennial herb	BSA, CHU, COR, MDZ, NQN, RNG, SCR, TRF	IV–XII	1	
	Ericaceae	<i>Gaultheria mucronata</i>	Shrub	CHU, NQN, RNG, SCR, TRF	IV, VI, VIII–XII	1		
	Grossulariaceae	<i>Ribes cucullatum</i>	Shrub	CHU, MDZ, NQN, RNG, SCR, TRF	V–XII	5		
	Nothofagaceae	<i>Nothofagus pumilio</i>	Tree	CHU, NQN, RNG, SCR, TRF	VII–XII	2		
	Plumbaginaceae	<i>Armeria maritima</i>	Perennial herb	CHU, COR, MDZ, NQN, RNG, SCR, TRF	IV–XII	3		
	Poaceae	<i>Agrostis inconspicua</i>	Perennial herb	CTM, CHU, JJY, LRJ, NQN, RNG, SCR, TRF, TCM	V–XII	11		

Table 3 (Continued)

Face	Family	Species	Life form	Argentina	Chile	Freq
		<i>Jarava neaei</i>	Perennial herb	BSA, CTM, CHU, LPM, MDZ, NQN, RNG, SCR, SJN	IV–VII, XI	3
		<i>Nassella filiculmis</i>	Perennial herb	BSA, CHU, COR, CRT, ETR, LPM, MDZ, MSN, NQN, RNG, STF, SNL	VIII–X	2
		<i>Jarava ibarii</i>	Perennial herb	CHU, MDZ, NQN, SCR	XII	2
		<i>Rytidosperma virescens</i>	Perennial herb	CHU, MDZ, NQN, RNG, SCR, TRF	IV–XII	2
		<i>Trisetum preslei</i>	Perennial herb	CHU, MDZ, NQN, RNG, SJN	IV–XII	3
		<i>Trisetum spicatum</i>	Perennial herb	CHU, COR, NQN, RNG, SCR, TRF	V–XII	5
	Pteridaceae	<i>Cheilanthes glauca</i>	Perennial herb	CHU, MDZ, NQN, RNG, SCR	IV–XI	6
	Valerianaceae	<i>Valeriana carnosa</i>	Perennial herb	CHU, MDZ, NQN, RNG, SCR, TRF	VI–XII	2

<sup>a</sup> Current distribution record is further south of the study area.

*Agrostis inconspicua* (Table 3). Twenty were only found on north faces and 26 were only found on south faces. Of the species found only in southern walls, 64% reach cold southern regions such as Tierra del Fuego (Moore, 1983; Zuloaga et al., 2008), whereas only 35% of the species found only in northern faces extend to these cold situations as well.

**Floristic relationships among outcrops**

Results of DCA showed that the ordination of outcrops according to the floristic composition of their native plants followed mostly altitudinal, latitudinal and longitudinal gradients (Fig. 3). In the study area, these geographic gradients are related to temperature and precipitation, with the wetter western sites in the upper right and the coldest southern and higher elevation sites

in the lower right of the diagram, but also to geology, according to distance to the Andes. The different geological formations are related to floristic composition, especially the occurrences at the Ñirihuau and Ventana formations are located to the right of the diagram (Fig. 1). Therefore the flora of the outcrops shows important changes following these gradients that are related to both climate and substrate. Species that contribute mostly to axis 1 are (number of occurrence in brackets) *Chilotrimum diffusum* (1), *Nothofagus pumilio* (2), *Bromus pellitus* (1), *Oxalis adenophylla* (2), towards the positive end, and *Blechnum microphylla* (1), *Polemonium micranthum* (2) and *Blumenbachia silvestris* (1) to the negative one. Axis 2 is contributed mostly by *Diplolepis descolei* (1), *Epilobium nivale* (1), *Festuca magellanica* (1), *Imperata condensata* (1) towards the positive end, and *Perezia calophylla* (2), *Rytidosperma virescens* (2), and *Montiopsis polycarpoides* (1) to the negative one. Even though rare species with one or two only occurrences may be considered as having too much influence in ordinations, we must bear in mind that they were downweighted during the analysis, and that they are important because they represent outcrop singularities.

**Floristic relationships between outcrops and matrix vegetation**

When studying the flora of the outcrops in relation to the vegetation of the matrix plots (Table 1) we found no significant differences in numbers of species, genera and families ( $G\ test = 0.05, p = 0.97, df: 2$ ), or percentage of alien species ( $G\ test = 0.02, p = 0.86, df: 1$ ). Alien species represent 15.64% of the matrix flora, being mainly annual or biennial herbs. The overall comparison of life-forms growing in each environment was not different ( $G\ test = 2.55, p = 0.47, df: 3$ ), nor the proportions of genera belonging to different phylogenetic groups ( $G\ test = 10.6, p = 0.06, df: 5$ ).

DCA ordination showed that the flora of every rock outcrop was separated from that of its corresponding matrix plot (Fig. 4). Two groups were formed, the rock outcrops to the lower left and the matrix plots to the upper right of the diagram. Outcrops with negative values of Axis 2 were farther away from their matrix relatives than those with positive values. The outcrops showing a higher similarity to their corresponding matrix plots are those of Ventana and Ñirihuau formations that are found to the west of the study area. The coordinates of the outcrops on Axis 1 of the floristic ordination were significantly different from the coordinates of the matrix plots (Mann–Whitney U test =  $-7.05; p \leq 0.001$ ). The supplementary inclusion in this analysis of a “High Andean site” (with species that reach high elevations, i.e. above 1700 m, Ferreyra et al., 1998) and a “Tierra del Fuego site” (with species that reach southernmost latitudes, i.e. higher than 50°S, Moore, 1983) results in that outcrops fall near these plots because they have several cold-adapted species that are also present in High Andean sites and in Tierra del Fuego.

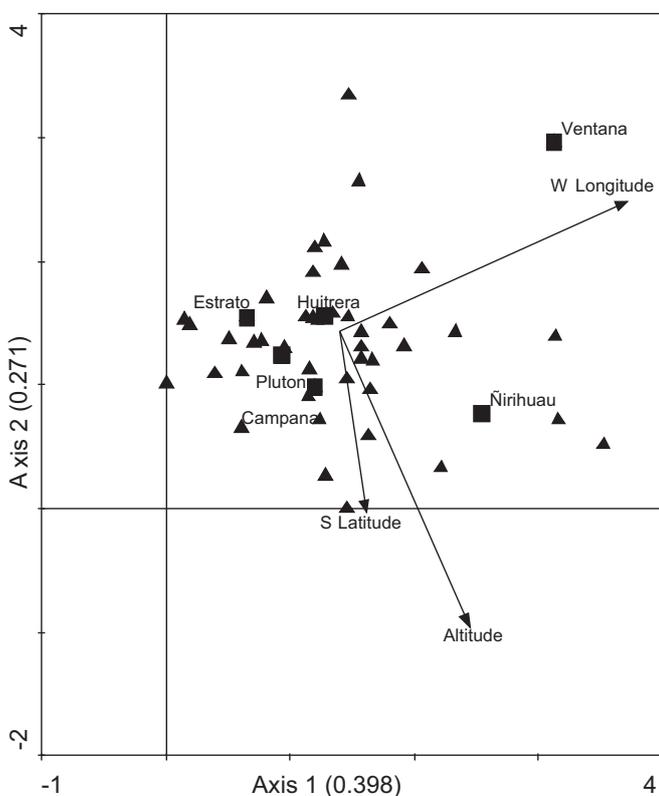
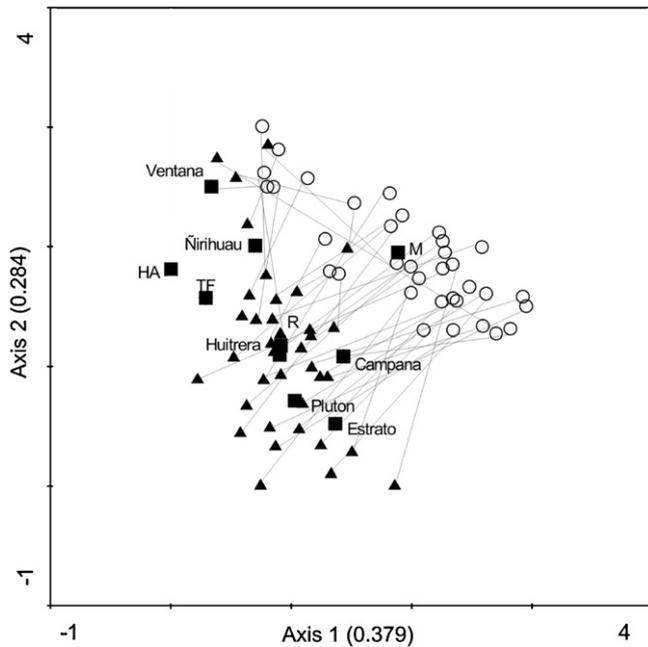


Fig. 3. DCA ordination of outcrops according to their native floristic composition. Geographical variables latitude, longitude and altitude as well as geological formation of the outcrops are treated as supplementary and projected as black squares on to the ordination. Total inertia = 4.84. Cumulative percentage variance of species data = 13.9% for the first two axes. Axes eigenvalues are given within brackets.



**Fig. 4.** DCA ordination of outcrops and matrix plots according to their native floristic composition. Nominal variables Tierra del Fuego (TF), high-Andean (HA), rock outcrop (R) or matrix (M) are treated as supplementary and projected on to the ordination. Total inertia = 5.087. Cumulative percentage variance of species data = 12.5% for the first two axes. Axes eigenvalues are given within brackets.

### Species beyond their main range

There is a high proportion of taxa which are outliers respective to their main range of distribution in the region (Table 3). Twenty six species found on outcrops were found beyond their recorded distribution according to Zuloaga et al. (2008), seven of which are aliens and twelve of the natives ones live exclusively on outcrops. Some species are widely distributed within Argentina, whereas others can be found in several provinces either to the north or south of the country. Considering the distribution of these main-range outlier species, we found that those found only on outcrops are less widely distributed than species that we found both on the outcrops and in the matrix plots (ANOVA  $F_{(1,19)}: 19.02$ ;  $p \leq 0.001$ ). In general, outlier species found only on outcrops correspond to southern taxa and are mainly found on south faces (Table 3).

### Discussion

Results of this work show that the flora of the north Patagonian outcrops is rich and diverse, and that floristic composition variation follows mostly altitudinal, latitudinal and longitudinal gradients. In this area, these geographic gradients are related to steep regional gradients in temperature and precipitation that are important determinants of vegetation structure and composition of other plant communities (e.g., Ferreyra et al., 1998; Speziale et al., 2010). Nevertheless, rock-types determined by geological formations also appear to contribute to differences among outcrop floras. Outcrops that act as reservoirs of rare or specialist species have been reported on special substrates such as limestone outcrops of South Africa, and on granite-gneiss and ironstone inselbergs in Brazil (Meirelles et al., 1999; Changwe and Balkwill, 2003; Jacobi et al., 2007).

Life form spectra reflect the environmental conditions in which the species grow (Raunkjær, 1934). Despite therophytes and short-lived perennials were proposed as indicators of the harsh edaphic and climatic factors in outcrops of Africa (Porembski et al., 1996) and North America (Phillips, 1982), we found long-lived perennials as dominants in Patagonian outcrops. This is also the case of granite-gneiss outcrops in Brazil, where perennial monocots were preponderant (Meirelles et al., 1999). In our study, Poaceae was the family with more species followed by Asteraceae elements. Both families arose or increased in Patagonia during the late Miocene–early Pliocene when aridization and cooling established and dominated since the late glacial period; thus, they are representatives of harsh environments (Whitlock et al., 2006; Barreda and Palazzesi, 2007).

Patagonian outcrops show an important presence of exotic species (14.8%), and most of them also occur in the matrix. The drought and harshness of outcrops was proposed as determining the absence of alien species in the outcrop flora (Meirelles et al., 1999). Nevertheless, exotic species are found on outcrops and the percentage of non-natives varies widely from 3% in Southern Appalachian outcrops, through 29% in small-sized inselbergs of West Africa, to 46% in granitic outcrops of the Seychelles (Wiser, 1994; Porembski et al., 1996; Biedinger and Fleischmann, 2000). Weeds are especially pre-adapted for colonizing the sometimes, due to environmental fluctuations, short-term available favourable habitats on rocks (Porembski et al., 1996; Sarthou et al., 2009). Our results indicate a similar proportion of few short-lived and of abundant perennial species in the matrix and on the outcrops for native species, but the opposite proportion of these life-forms for aliens. On the outcrops we found very few perennial aliens, among which are *Rumex acetosella* and *Taraxacum officinale* that were already found on outcrops of the Southern Appalachian mountains (Wiser et al., 1996). The low proportion of annuals in native vegetation has already been shown for other southern floras as the result of “empty” niches (e.g. New Zealand: Wardle, 1991; Chile: Arroyo et al., 2000; Argentina: Speziale and Ezcurra, 2011). The influence of open niches on the invasion process on outcrops remains to be studied. Invasions could especially affect many outcrop species, that are very important to conserve for reasons of being at the limit of their distributions (Hampe and Petit, 2005). In northern Patagonia introduced exotic species have much modified natural environments, especially in species-rich areas near human settlements (Speziale and Ezcurra, 2011). Previous results support the prediction that, as the surrounding matrix becomes more modified, invasion by exotics will make outcrop vegetation less distinct from its matrix (Wiser and Buxton, 2008). Testing these ideas is vital for understanding the importance of outcrops in relation to regional biodiversity and to ensure that their integrity is maintained (Wiser and Buxton, 2009).

Our data revealed that although the floras of outcrops from northern Patagonia share similar dominant families and proportions of different phylogenetic groups with the adjacent matrix, they host a particular assemblage of native species with a large portion (36.5%) absent from the matrix. Despite this distinctiveness, we found that in the native flora strict endemic species of outcrops were low. The proportion of endemic species on outcrops varies greatly around the world. It is high for outcrops in unglaciated USA (Baskin and Baskin, 1988). It is low on inselbergs in Atlantic Central Africa, limestone outcrops of South Africa (2%), or completely absent in inselbergs of the Ivory Coast in West Africa and of South Africa (Porembski et al., 1996; Burke et al., 1998; Changwe and Balkwill, 2003; Mignaut et al., 2010). Explanations for the low levels of endemism of some outcrop floras focus on the extinction of local endemics or on the impossibility to evolve new endemic species. High extinction rates are favoured by the harsh environment of outcrops, or by a combination of reduced area and high

isolation (Porembski et al., 1996; Burke et al., 1998). Low isolation or lack of time to evolve, and a climate dominated by strong winds transporting propagules or pollen can prevent as well the evolution of endemics (Porembski et al., 1996; Burke et al., 1998). The low proportion of endemics (3.9%) we found in our study, in an area of strong winds which was in part glaciated until 14,000 years ago (Markgraf, 1991) could indicate a lack of evolution of endemic species related to the climatic harshness and the recent availability of the outcrop environment.

Despite the low number of endemic elements, the singularity of the outcrop flora is given in part by exclusive species that are outliers from their main, generally more southern distribution. Part of these new records could reflect lack of botanical collections in some areas, or could also be a bias of floristic studies towards particular taxonomic groups; yet Patagonia is one of the floristically best collected and known regions of southern South America (Correa, 1969–1988). Hence, the new records could also imply expansions or reductions of distributions due to climate changes. The dynamics of distributions subject to external fluctuations produced by past climate change can impact on the vegetation patterns observed today. Therefore, although present vegetation of Patagonia is greatly associated with current environmental conditions, variations may be better viewed as the resultant of interactions between modern climate and historical events (Ferreyra et al., 1998).

It is very likely that these outlier species relative to the main distribution range, which are present in southern faces of the outcrops, were dominant during former periods with different climatic conditions. Paleoenvironmental information from the southern Andes for full glacial times (approx. 14,000 years B.P.) suggest temperatures 4 °C cooler than present and lowering the vegetation belts of more than 600 m, higher effective moisture, and greater windiness (Markgraf, 1991). These conditions probably greatly expanded the area available for species that are now representatives of communities of cold humid sites. During postglacial times climatic change produced warmer and more xeric conditions, especially after 8000 years B.P. (Markgraf, 1991), which resulted in an increase of the area available for species of warm and dry communities. These Holocene changes could have reduced the availability of habitats for cold-adapted species (Ferreyra et al., 1998), even though during the last 5000 years BP some intervals of relative low temperature and higher precipitation have also been reported (Rabassa and Clapperton, 1990).

The main recorded distribution of many of the outlier species we found on outcrops is more to the southern and cooler areas of the continent. It is possible that with the warmer and drier climate trend that started after the end of the last glacial period, most cold-adapted (microthermic) species present in northern Patagonia retreated upwards to High Andean mountain tops or southwards to higher latitudes from their northern periglacial or glacial distributions. But some may have been able to survive in abiotic refuge sites, such as the cold southern walls of rock outcrops. This could explain the presence in extra-Andean Patagonia of several more southern species that we found isolated from their main distribution range. The species assemblages of southern walls of Patagonian outcrops may therefore represent relicts of a paleo-flora, as has been suggested similarly for outcrop floras of other regions of the world (e.g. Danin, 1999; Porembski and Barthlott, 2000; Anthelme et al., 2008; Catling, 2009).

In summary, outcrops of Patagonia house a locally diverse and regionally varied flora that is distinct from the vegetation matrix due to a series of exclusive species. Several of these species are important in that they are representatives of a cold-adapted flora that is especially prone to extinction due to climate warming. Exotic species related to disturbed surroundings are a considerable threat to these outcrop floras, and their presence and abundance should be further monitored.

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## References

- Anchorena, J., Cingolani, A.M., 2002. Identifying habitat types in a disturbed area of the forest-steppe ecotone of Patagonia. *Plant Ecol.* 158, 97–112.
- Anthelme, F., Waziri Mato, M., Maley, J., 2008. Elevation and local refuges ensure persistence of mountain specific vegetation in the Nigerien Sahara. *J. Arid Environ.* 72, 2232–2242.
- Angiosperm Phylogeny Group III, 2009. An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161, 105–121.
- Arroyo, M.T.K., Marticorena, C., Matthei, O., Cavieres, L., 2000. Plant invasions in Chile: present patterns and future predictions. In: Mooney, H.A., Hobbs, R. (Eds.), *Invasive Species in a Changing World*. Island Press, Washington, DC, pp. 385–421.
- Barreda, V., Palazzesi, L., 2007. Patagonian vegetation turnover during the Paleogene-early Neogene: origin of arid-adapted floras. *Bot. Rev.* 73, 31–50.
- Barthlott, W., Gröger, A., Porembski, S., 1993. Some remarks in the vegetation of tropical inselbergs: diversity and ecological differentiation. *Biogeographica* 69, 105–124.
- Baskin, J.M., Baskin, C.C., 1988. Endemism in rock outcrop plant communities of unglaciated eastern United States: an evaluation of the roles of the edaphic, genetic and light factors. *J. Biogeogr.* 15, 829–840.
- Beeskow, A.M., Monsalve, M.A., Duro, A., 2005. Identification of sites with higher levels of diversity in endemic vascular flora from Argentinean Patagonia. *Anales Inst. Patagonia (Chile)* 30, 5–20.
- Biedinger, N., Fleischmann, K., 2000. Seychelles. In: Porembski, S., Barthlott, W. (Eds.), *Inselbergs: Biotic Diversity of Isolated Rock Outcrops in Tropical and Temperate Regions*. *Ecol. Stud.*, 146. Springer, Berlin, pp. 277–290.
- Burbank, M.P., Platt, R.B., 1964. Granite outcrop communities of the piedmont plateau in Georgia. *Ecology* 45, 292–306.
- Burke, A., 2002. Island-matrix relationships in Nama Karoo inselberg landscapes. I. Do inselbergs provide a refuge for matrix species? *Plant Ecol.* 160, 79–90.
- Burke, A., 2003a. How special are Etendeka mesas? Flora and elevation gradients in an arid landscape in north-west Namibia. *J. Arid Environ.* 55, 747–764.
- Burke, A., 2003b. Inselbergs in a changing world – global trends. *Divers. Distrib.* 9, 375–383.
- Burke, A., Jürgens, N., Seel, M.K., 1998. Floristic affinities of an inselberg archipelago in the southern namib desert – relict of the past, centre of endemism or nothing special? *J. Biogeogr.* 25, 311–317.
- Cabido, M., Acosta, A., Diaz, S., 1990. The vascular flora and vegetation of granitic outcrops in the upper Córdoba mountains Argentina. *Phytocoenologia* 19, 267–281.
- Cabrera, A.L., 1976. *Regiones Fitogeográficas Argentinas*. ACME, Buenos Aires, Argentina.
- Catling, P.M., 2009. Composition, phytogeography, and relict status of the vascular flora of alvars and cliff tops southwest of Great Slave Lake, Northwest Territories, Canada. *Rhodora* 111, 189–208.
- Clarke, P.J., 2002. Habitat islands in fire-prone vegetation: do landscape features influence community composition? *J. Biogeogr.* 29, 677–684.
- Correa, M.N., 1969–1988. *Flora Patagonica*. INTA, Buenos Aires, Argentina.
- Changwe, K., Balkwill, K., 2003. Floristics of the Dunbar Valley serpentine site, Songimvelo Game Reserve, South Africa. *Bot. J. Linn. Soc.* 143, 271–285.
- Danin, A., 1999. Desert rocks as plant refugia in the Near East. *Bot. Rev.* 65, 93–170.
- Díaz, S., Fargione, J., Chapin III, F.S., Tilman, D., 2006. Biodiversity loss threatens human well-being. *PLoS Biol.* 4 (8), e277.
- Desmet, P.G., Cowling, R.M., 1999. Biodiversity, habitat and range-size aspects of a flora from a winter-rainfall desert in north-western Namaqualand, South Africa. *Plant Ecol.* 142, 23–33.
- Escudero, A., Pajarón, S., 1996. La vegetación rupícola del Moncayo silíceo, una aproximación basada en un Análisis Canónico de Correspondencias. *Lazararo* 16, 105–132.
- Ezcurra, C., Brion, C., 2005. *Plantas del Nahuel Huapi, catálogo de la flora vascular del Parque Nacional Nahuel Huapi*. Argentina. Universidad Nacional del Comahue y Red Latinoamericana de Botánica, San Carlos de Bariloche, Argentina.
- Ferreyra, M., Cingolani, A.M., Ezcurra, C., Brand, D., 1998. High-Andean vegetation and environmental gradients in northwestern Patagonia, Argentina. *J. Veget. Sci.* 9, 307–316.

- Frangi, J., 1975. Sinopsis de las comunidades vegetales y el medio de las Sierras de Tandil (Provincia de Buenos Aires). *Bol. Sociedad Argentina Botán.* 16, 293–319.
- Funes, G., Cabido, M., 1995. Variabilidad local y regional de la vegetación rupícola de las Sierras Grandes de Córdoba, Argentina. *Kurtziana* 24, 173–188.
- Giacosa, R., Heredia, N., 2001. Hoja geológica 4172-IV San Carlos de Bariloche. Instituto de Geología y Recursos Minerales. Servicio Geológico Minero, Buenos Aires.
- Gröger, A., Barthlott, W., 1996. Biogeography and diversity of the inselberg (Laja) vegetation of southern Venezuela. *Biodive. Lett.* 3, 165–179.
- Hampe, A., Petit, R.J., 2005. Conserving biodiversity under climate change: the rear edge matters. *Ecol. Lett.* 8, 461–467.
- Hopper, S.D., Brown, A.P., Marchant, N.G., 1997. Plants of Western Australian granite outcrops. *Journal of the Royal Society of Western Australia* 80, 141–158.
- Houle, G., Phillips, D.L., 1989. Seed availability and biotic interactions in granite outcrop plant communities. *Ecology* 70, 1307–1316.
- Jacobi, C.M., do Carmo, F.F., Vincent, R.C., Stehmann, J.R., 2007. Plant communities on ironstone outcrops: a diverse and endangered Brazilian ecosystem. *Biodiv. Conserv.* 16, 2185–2200.
- MacArthur, R.H., 1972. *Geographical Ecology*. Princeton University Press, Princeton, New Jersey.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- Markgraf, V., 1991. Late Pleistocene environmental and climatic evolution in southern South America. *Bamberger Geogr. Schr.* 11, 271–281.
- McKinney, M.L., 2006. Urbanization as a major cause of biotic homogenizations. *Biol. Conserv.* 127, 247–260.
- Meirelles, S.T., Pivello, V.R., Joly, C.A., 1999. The vegetation of granite rock outcrops in Rio de Janeiro, Brazil, and the need for its protection. *Environ. Conserv.* 26, 10–20.
- Méndez, E., 2010. La vegetación saxícola y de taludes del flanco oriental del Cordón del Plata (Luján de Cuyo, Mendoza, Argentina). *Bol. Sociedad Argentina Botán.* 45, 119–147.
- Mignaut, T., Senterre, B., Müller, J.V., Lejoly, J., Parmentier, I., 2010. Shrubby and forest fringe communities of the inselberg-rainforest ecotone in Atlantic Central Africa. *Plant Ecol. Evol.* 143, 128–137.
- Milchunas, D.G., Noy-Meir, I., 2002. Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos* 99, 113–130.
- Moore, D.M., 1983. *Flora of Tierra del Fuego*. Anthony Nelson, London, UK, and Missouri Botanical Garden Press, Saint Louis, Missouri.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H., Woodfin, R.M., 1994. Declining biodiversity can affect the functioning of ecosystems. *Nature* 368, 734–737.
- Otápková, Z., Chytrý, M., 2006. Effects of plot size on the ordination of vegetation samples. *J. Veget. Sci.* 17, 465–472.
- Phillips, D.L., 1982. Life-forms of granite outcrop plants. *Amer. Midland Natural* 107, 206–208.
- Porembski, S., Barthlott, W., 2000. Granitic and gneissic outcrops (inselbergs) as centers of diversity for desiccation-tolerant vascular plants. *Plant Ecol.* 151, 19–28.
- Porembski, S., Szarzynski, J.-P.M., Barthlott, W., 1996. Biodiversity and vegetation of small-sized inselbergs in a West African rain forest (Taï, Ivory Coast). *J. Biogeogr.* 23, 47–55.
- Porembski, S., Martinelli, G., Ohlemüller, R., Barthlott, W., 1998. Diversity and ecology of saxicolous vegetation mats on inselbergs in the Brazilian Atlantic rainforest. *Divers. Distrib.* 4, 107–119.
- Rabassa, J., Clapperton, C.M., 1990. Quaternary glaciations of the southern Andes. *Quatern. Sci. Rev.* 9, 153–174.
- Raunkiaer, C.C., 1934. *The Life Forms of Plants and Statistical Plant Geography*. Oxford University Press, Oxford, UK.
- Sarthou, C., Kounda-Kiki, C., Vaçulik, A., Mora, P., Ponge, J.-F., 2009. Successional patterns on tropical inselbergs: a case study on the Nouragues inselberg (French Guiana). *Flora* 204, 396–407.
- Sarthou, C., Larpin, D., Fonty, É., Pavoin, S., Ponge, J.-F., 2010. Stability of plant communities along a tropical inselberg ecotone in French Guiana (South America). *Flora* 205, 682–694.
- Speziale, K.L., Ezcurra, C., 2011. Patterns of alien plant invasions in northwestern Patagonia, Argentina. *J. Arid Environ.* 75, 890–897.
- Speziale, K.L., Ruggiero, A., Ezcurra, C., 2010. Plant species richness–environment relationships across the Subantarctic–Patagonian transition zone. *J. Biogeogr.* 37, 449–464.
- Stevens, P.F., 2001 onwards. *Angiosperm Phylogeny Website*. Version 9, June 2008 (and more or less continuously updated since).
- ter Braak, C.J.F., Smilauer, P., 1998. *CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination*. Microcomputer Power, New York.
- Walters, T.W., Wyatt, R., 1982. The vascular flora of granite outcrops in the Central mineral Region of Texas. *Bull. Torrey Bot. Club* 109, 344–364.
- Wardle, P., 1991. *Vegetation of New Zealand*. Cambridge University Press, Cambridge, UK.
- Whitlock, C., Bianchi, M.M., Bartlein, P.J., Markgraf, V., Marlon, J., Walsh, M., McCoy, N., 2006. Postglacial vegetation, climate, and fire history along the east side of the Andes (lat 41–42.5), Argentina. *Quatern. Res.* 66, 187–201.
- Williamson, S.D., Robinson, E.R., Balkwill, K., 1997. Evolution of two endemic serpentine taxa in Mpumalanga. *African J. Bot.* 63, 507–513.
- Wiser, S.K., 1994. High-elevation cliffs and outcrops of the Southern Appalachians: vascular plants and biogeography. *Castanea* 59, 85–116.
- Wiser, S.K., Buxton, R.P., 2008. Context matters: matrix vegetation influences native and exotic species composition on habitat islands. *Ecology* 89, 380–391.
- Wiser, S.K., Buxton, R.P., 2009. Montane outcrop vegetation of Banks Peninsula, South Island, New Zealand. *NZ. J. Ecol.* 33, 164–176.
- Wiser, S.K., Peet, R.K., White, P.S., 1996. High-elevation rock outcrop vegetation of the Southern Appalachian Mountains. *J. Veget. Sci.* 7, 703–722.
- Wyatt, R., Fowler, N., 1977. The vascular flora and vegetation of the north Carolina granite outcrops. *Bull. Torrey Bot. Club* 104, 245–253.
- Zuloaga, F.O., Morrone, O., Belgrano, M.J. (Eds.), 2008. *Catálogo de plantas vasculares del Cono Sur (Argentina, Sur de Brasil, Chile, Paraguay y Uruguay)*. Missouri Botanical Garden Press, Saint Louis, Missouri.