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Vegetation Development on Deglaciated Rock Outcrops from Glaciar Frías, Argentina

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Abstract

The retreat of glaciers during past decades has led to the emergence of large rock outcrops in many glaciated areas around the world. Primary succession of vegetation in glacier forelands has been described for many regions, but most studies have been conducted on glacial deposits, whereas deglaciated rock outcrops have received little attention. This study assesses the pattern of primary succession on a chronosequence of five rock outcrops exposed during the past 140 years by the retreat of Glaciar Frías in the Patagonian Andes, Argentina. Data on floristic composition and species cover for algae, lichens, ferns, bryophytes, and vascular plants were recorded on sampling plots. Ordination and classification analyses discriminate three major successional stages, each dominated by a different species assemblage, suggesting directional replacement of species in the succession. The pioneer stage is dominated by the crustose lichen *Placopsis perrugosa*, the mid-successional stage by a lichen-moss mat dominated by the moss *Racomitrium lanuginosum*, and the late-successional stage by a large diversity of vascular plants. The low density of *Nothofagus dombeyi* saplings in the late-successional site indicates that plant succession is still in progress 140 years after deglaciation. Progress in succession appears to be influenced by species life-cycle traits and facilitative interactions among species. The comparison of the successional processes between rock outcrops and unconsolidated glacial deposits suggests that the vegetation sequence is similar, but the rate of succession is slower on rock outcrops. The development of a ground lichen-moss cover, previous to the widespread colonization by vascular plants, accounts for the slower succession progress on rock outcrops. The establishment of *Nothofagus* stands takes at least 100 yrs longer on the rock outcrops than on glacial deposits. Under predicted climate warming, most Patagonian Andes glaciers will continue the retreat along steep bedrock slopes, where similar, long-term vegetation successional patterns to those observed on Glaciar Frías foreland will eventually occur.

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Introduction

Climatic warming in mountain ecosystems influences the dynamics of the vegetation through changes in ecophysiological processes and in disturbance regimes (Körner, 2005). In addition, climatic warming affects glaciated-mountain ecosystems by determining glacier retreat that exposes extended areas of bare terrain to biological colonization (Matthews and Whittaker, 1987; Chapin et al., 1994). Studies of ecosystem development on recently deglaciated terrains in Europe and North America provide comprehensive information on successional vegetation changes and the mechanisms driving succession (Matthews, 1992). The relative importance of vegetation traits, biological interactions, and environmental forces driving the processes of species colonization and replacement are well known (Svoboda and Henry, 1987; Walker and Chapin, 1987; Chapin et al., 1994). In addition, it has been shown that landscape characteristics, stochastic processes, and disturbance events have a large influence on vegetation successional patterns (del Moral et al., 1995; Matthews, 1999).

Large rock outcrops have emerged during past decades from beneath glaciers in many glacierized areas, such as Patagonia, the Alps, and North America (Rivera and Casassa, 2004; Paul et al., 2007; Pelto, 2009). Most studies of primary succession on deglaciated terrains have been performed on unconsolidated glacial sediments, whereas there is little empirical data on vegetation development on bedrock outcrops (Matthews, 1992). Rock outcrops are stressful environments subjected to high thermal contrasts, drought due to low water holding capacity, substrate instability due to intense water runoff, and limiting soil formation (Shure and Ragsdale, 1977; Sarthou et al., 2009). Our knowledge about the primary succession on rock outcrops is mainly based on studies conducted within forested landscapes. In general, the vegetation establishment on outcrops is initiated by the early development of a lichen cover and an organic matter layer, and the succession progress is frequently associated with the deepening of the soil layer (Burbanck and Phillips, 1983; Uno and Collins, 1987; Asselin et al., 2006). The development of a mature forest community on rock outcrops is slow and periods of ca. 1000 years have been reported (Asselin et al., 2006). A similar slow vegetation development occurs on lava flows, where the pioneer cryptogam colonizers are replaced by higher plants ca. 600 years after the lava emplacement (Cutler et al., 2008). Hence,

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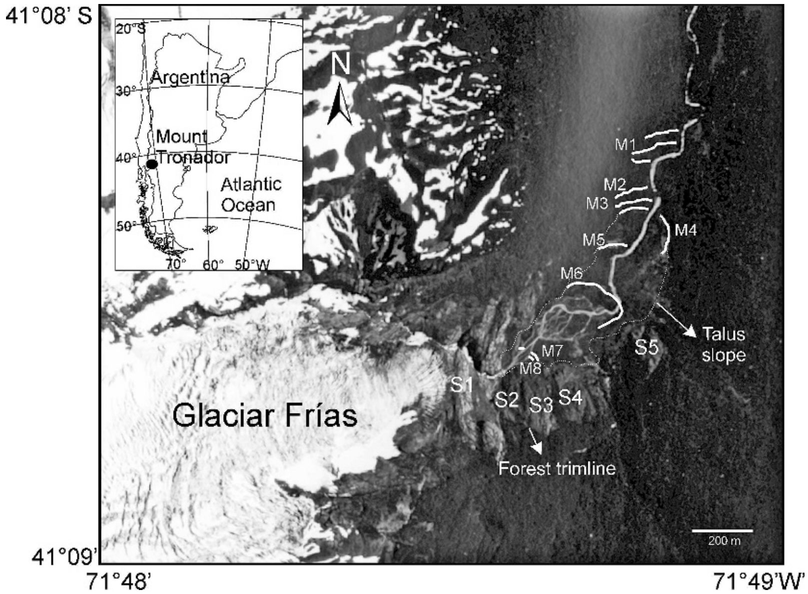

FIGURE 1. Location map of Glaciar Frías foreland in the north Patagonian Andes showing the position of the frontal moraines (M) and the sampling sites (S). Estimated dates of moraines and sampling sites exposition are given in Table 1.

successional processes involving interactions between different vegetation groups are expected to occur on long-term temporal scales on deglaciated rock outcrops. Additional analyses on deglaciated rock outcrops are required to properly understand the landscape changes related to glacier retreat along mountain bedrock slopes, and to predict short- and long-term effects of changing climate on glaciated-mountain ecosystems.

The retreat of glaciers is a conspicuous sign of climate changes during the last century in the Patagonian Andes (Luckman and Villalba, 2001; Masiokas et al., 2010), yet investigations of primary succession on recently deglaciated terrains have been relatively rare in this area. Some studies have analyzed the vegetation on glacier moraines (Lawrence and Lawrence, 1959; Heusser, 1960, 1964; Pisano, 1978; Rabassa et al., 1981; Veblen et al., 1989; Dollenz, 1991; Armesto et al., 1992) and the influence of some specific biological interactions on plant colonization (Henríquez, 2004; Henríquez and Lusk, 2005). These studies have mostly focused on *Nothofagus* establishment and have rarely considered other components of the vegetation, such as algae, lichens, and bryophytes. Moreover, the study of the primary succession in general has received little attention within *Nothofagus* forests in the southern hemisphere (Orwin, 1972; Archer et al., 1973; Ashton and Moore, 1978; Wardle, 1980; Sommerville et al., 1982).

The aim of this study is to document and assist understanding of the primary succession process on rock outcrops following glacier retreat. Glaciar Frías, in the north Patagonian Andes, offers an excellent opportunity for the study of vegetation succession on rocky environments. Five rock outcrops have been exposed by glacier recession from its Neoglacial maximum and provide a chronosequence of sites covering the last 140 years (Fig. 1). In this paper we describe the pattern of primary succession of vegetation on the Glaciar Frías outcrops and infer the possible mechanisms driving vegetation development in these stressful environments. The study integrates all vegetation groups (algae, lichens, ferns, mosses, and vascular plants) allowing a thorough analysis of the community changes over time. In addition, successional pattern on rock outcrops at Glaciar Frías were compared with vegetation establishment on unconsolidated glacial deposits reported in the literature for the Patagonian Andes. By conducting this analysis we explore possible future vegetation landscape changes in mountain regions as glaciers continue retreating along bedrock slopes.

Methods

STUDY AREA

Glaciar Frías is the northernmost ice body of Mount Tronador (41°10′S, 71°50′W), one of the highest mountains (3554 m) in the northern Patagonian Andes (Fig. 1). The climate of the zone is temperate and wet. Available climatic data from the Mascardi weather station, 20 km east from Glaciar Frías, indicate a mean annual temperature of 7.6 °C (January mean 12.9 °C, July mean 2.4 °C). Total annual precipitation in the Frías valley is ca. 4300 mm (Barros et al., 1983; Villalba et al., 1990). The vegetation in the Frías valley corresponds to the Valdivian temperate rain forest, which is a multistratified forest dominated by the evergreen *Nothofagus dombeyi* and the conifer *Fitzroya cupressoides* (Ezcurra and Brion, 2005).

The chronology of Glaciar Frías recession is well known from the study of historical drawings, written records, terrestrial and aerial photographs, direct measurements of ice front, and the dendrochronological dating of moraines. The maximum Neoglacial advance of Glaciar Frías was reached ca. AD 1660 (Rabassa et al., 1978; Villalba et al., 1990), and the glacier has subsequently retreated more than 1500 m along the Frías valley (Fig. 1). A sharp forest trim-line defines the boundary between the glacier foreland and the mature forest not affected by the last major Neoglacial advance. A well-preserved sequence of frontal moraines remains in the bottom of the valley as evidence of seven minor readvances of Glaciar Frías since the last Neoglacial maximum (Villalba et al., 1990; Masiokas, 2008). The most recent readvance occurred during the years 1976–1977 (Rabassa et al., 1979).

At the Glaciar Frías foreland the bottom and slopes of the valley show contrasting environments. Along the bottom of the Frías valley wet meadows cover the glaciofluvial deposits and vascular plants grow on the frontal moraines. In contrast, along the valley slopes, bedrock outcrops without glacial sediments on top are mostly covered by lichens and bryophytes with sparsely distributed vascular plants. Inclination of the valley slopes is around 30°.

The study sites are located on the southern valley side, where five granodiorite rock outcrops have been successively exposed by the retreat of Glaciar Frías (Fig. 1). Exposure dates for the rock outcrops were estimated from the dates of the moraines (Villalba

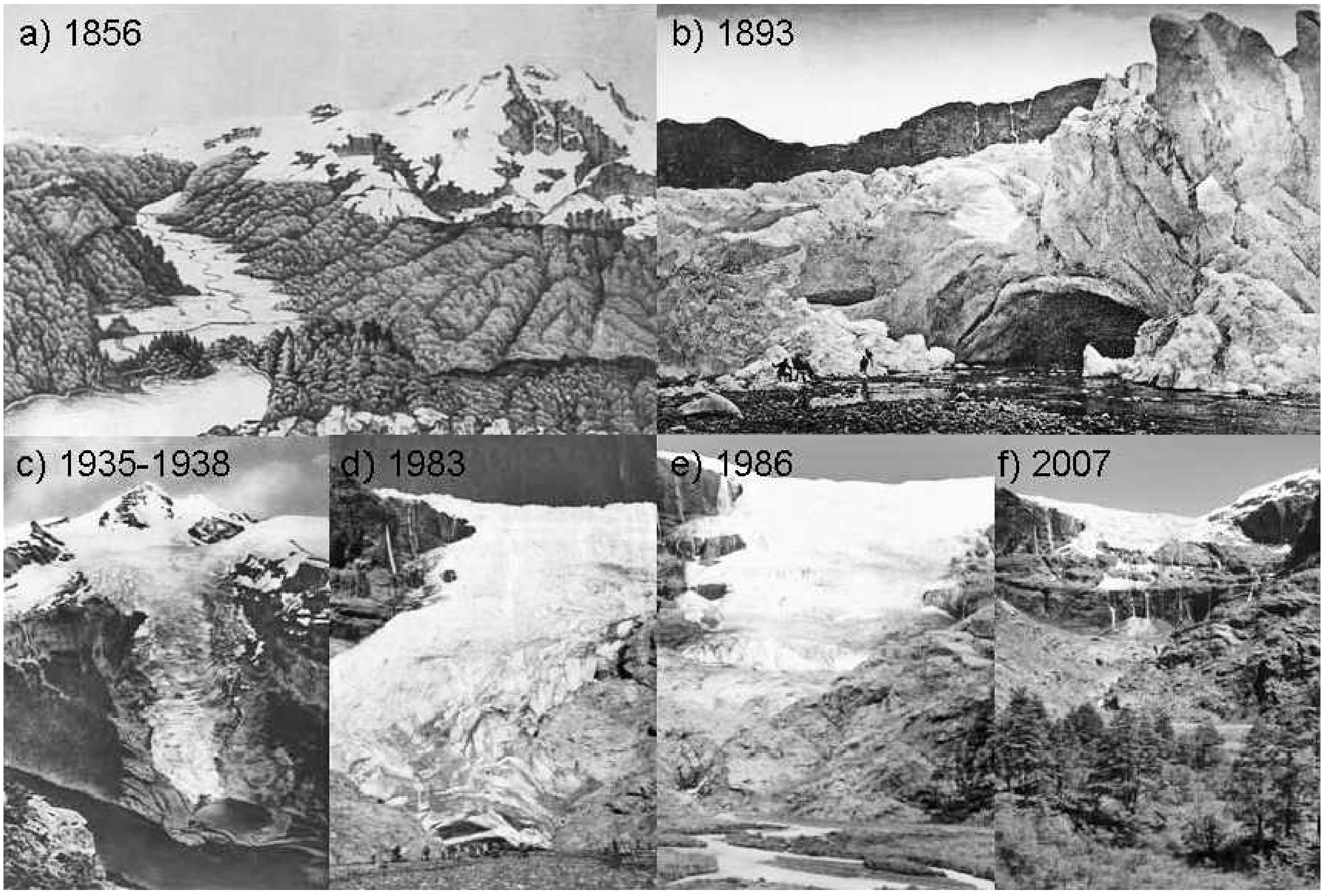

FIGURE 2. Selected historical photographs and drawings of Glaciar Frías used to constrain the exposure dates of the rock outcrops in the study sites. Historical sources: (a) Fonck (1896), (b) Steffen (1909), (c) De Agostini (1945), (d) anonymous (IANIGLA archive), (e and f) R. Villalba.

et al., 1990; Masiokas, 2008), direct measurements of ice front positions (Rabassa et al., 1978), and the analysis of old terrestrial and aerial photographs (Fig. 2). Study sites were located between points of known exposure times, so the mean of these dates was used as an estimation of the sampling site age. The five rock outcrops studied are a chronosequence covering the past 140 years (Table 1). As the glacier forefield represents a spatial chronosequence, the analysis of the vegetation growing on sites exposed at different ages was used to infer the process of primary succession (Pickett, 1989; Foster and Tilman, 2000; Walker et al., 2010).

SAMPLING DESIGN

Rock outcrops are characterized by high compositional heterogeneity in vegetation due to the presence of a large variety of microhabitats modulated by topography (Wiser et al., 1996; Matthes-Sears and Larson, 2006; Opazo Medina et al., 2006). The rock outcrops exhibit meso- and micro-scale topographic variability due to the presence of drainage channels between outcrops and small cracks on the rock surface, respectively. Inspection of the area evidences striking differences in vegetation between rock surfaces and drainage channels. However, drainage channels constitute a minor fraction of the Glaciar Frías rock outcrop landscape. In consequence, our study focused in the analysis of the vegetation growing on the rock surfaces, the major landscape features on the deglaciated valley slopes.

We randomly located 10 sampling plots in each study site. Plots of 5 × 10 m were used for analyzing ferns and vascular plants, and subplots of 1 × 1 m for analyzing the cryptogamic flora (algae, lichens, ferns, and bryophytes). Within each plot and subplot the species were recorded and their coverage visually estimated. Cover estimates for lichens and bryophytes were recorded to the species level whenever possible or by genera or morphological groups when field identification was not feasible. In addition, a floristic inspection throughout the study area was conducted to detect the presence of species not occurring in the plots. Lichens and mosses not identified in the field were collected for later taxonomical determination in the laboratory. Voucher specimens are deposited at the Argentinean Institute of Snow, Ice and Environmental Sciences (IANIGLA). Nomenclature for vascular plants follows Zuloaga and Morrone (1999a, 1999b), and for lichens and bryophytes Brummitt and Powell (1992).

Altitude, aspect, slope, surface topography, canopy coverage, percentage of the substrate covered by pebbles, and percentage of bare rock outcrop and bare soil were recorded at each plot. Surface topography was categorized as elevated, depressed, and flat with respect to the surrounding area. Inclination of the sampling plots depends on microtopography, and the slope at each sampling plot was estimated using clinometers. Percent canopy coverage was estimated using a spherical densitometer.

DATA ANALYSES

Patterns of variation in plant diversity along the successional sequence were assessed using indices of species diversity and plots of the species-abundance distribution (Lambshead et al., 1983;

TABLE 1

Exposure dates for sampling sites estimated from historical information and dendrochronological dating of frontal moraines. Historical information includes: TP (terrestrial photographs), AP (aerial photographs), D (drawings), and FP (direct measurement of glacier front positions). The historical drawing by Hess in 1856 and the terrestrial photos are shown in Figure 2. Dates of moraines from Villalba et al. (1990).

Sampling site	Estimate date of site deglaciation	Estimated site age (years)	Dates of moraines limiting site date	Evidences of site exposition dates from historical information
S1	1984	24	none	The AP from 1981 and the TP from 1983 (Anonymous) show Glaciar Frías covering S1 at these dates. The TP from 1986 (IANIGLA) shows S1 uncovered by ice.
S2	1960	48	AD 1942 (M7) to 1977 (M8)	The TP taken between 1935 and 1938 by De Agostini (1945) and the AP from 1944 show S2 covered by ice. The FP by Rabassa et al. (1978) shows that S2 was uncovered by ice in 1977.
S3	1924	84	AD 1914 (M6) to 1942 (M7)	The TP taken between 1935 and 1938 by De Agostini (1945) shows S3 uncovered by ice.
S4	1903	109	AD 1881 (M5) to 1914 (M6)	The TP from 1893 (Steffen, 1909) shows a >50-m-tall ice front. This photograph relocation suggests that S4 was covered by ice in 1893.
S5	1868	140	AD 1839 (M4) to 1881 (M5)	The etching (D) by Hess (Fonck, 1896) shows the whole study area covered by Glaciar Frías in 1856.

Magurran, 1988). Three diversity indices which provide complementary information on community structure were selected: the Shannon index (H′) combines species richness and evenness; the reciprocal of Simpson's index (1/D) measures species dominance depending on the proportional abundance of all species; and the Berger-Parker index gives a value of dominance of the most abundant species, dividing the coverage of the dominant species by the total coverage of the species.

The vegetation data were analyzed by Detrended Correspondence Analysis (DCA), which ordinates sampling plots according to their floristic composition and species coverage, allowing assessment of overall patterns in vegetation changes (Jongman et al., 1995). The ordination matrix contained 71 species in 50 sampling plots. Detrending was performed by segments, and rare species were not down-weighted. Vegetation data were also analyzed using a Two-Way Indicator Species Analysis (TWINSPAN) in order to determine vegetation groups (VG) characteristic of the different successional stages (Leps and Šmilauer, 1999). This analysis works with qualitative data, so quantitative data of species coverage was transformed to qualitative variables called pseudospecies, which are defined by cut-levels of species coverage (Jongman et al., 1995). In our analysis pseudospecies cut levels were set at 0, 2, 5, 20 and 50%, representing the whole range of species coverage. The minimum group size for division was 7, and a maximum of 4 levels of division was used.

The influence of different variables on vegetation changes were indirectly assessed correlating the DCA ordination axes with the dates of site exposure and environmental variables. In addition, a Canonical Correspondence Analysis (CCA) was applied to directly assess the main patterns of variation in the vegetation community accounted for by the explanatory variables (Jongman et al., 1995). The variables included were site exposure date, slope, surface topography, canopy coverage, and percentage of bare rock outcrop, bare soil, and pebbles. A Monte Carlo permutation test was used to test the significance of the first ordination axis (Leps and Šmilauer, 1999). In addition, the statistical significance of the partial effect of each explanatory variable (variability explained by a given variable after accounting for the effects of the other variables under analysis) was estimated by a Monte Carlo permutation test as the respective variable was step-wise added to the model.

Results

GENERAL PATTERNS IN SPECIES RICHNESS, COVER, AND DIVERSITY

A total of 97 species were identified in the floristic surveys performed on the rock outcrops studied at Glaciar Frías foreland. These include species from 10 different life forms, trees; shrubs; herbs; graminoid herbs; ferns; mosses; foliose, fruticose, and crustose lichens; and algae (the full list of species is available from the corresponding author upon request). Fourteen additional species (9 graminoid herbs, 2 mosses, and 3 crustose lichens) were not identified due to the absence of reproductive structures at the time of sampling.

A general pattern of increasing species numbers and total plant cover occurred along the spatial chronosequence (Table 2). From the youngest to the oldest site (sites 1 to 5) the number of species increased from 31 to 44 and total plant cover increased from 44 to 154%, respectively. In the earliest exposed sites, total plant cover exceeded 100% due to the development of a multistratified community. Crustose lichens dominate the recently exposed sites (sites 1 to 3), but decline in the oldest sites 4 and 5. Cover of vascular plants, mosses, and foliose and fruticose lichens gradually increase with age. Ferns and algae are poorly represented at the study outcrops.

The species-abundance distributions at each study site are shown in Figure 3. The curves for all five sample sites indicate the presence of one or two dominant species (>10% cover), a variable number of species with intermediate abundance (between 1 and 10% cover), and a large number of rare species (<1% cover). Dominance increases over time, as indicated by the steep initial portions of the species rank-abundance curves, but there is also a general trend of increasing diversity through the successional sequence, with higher species richness and more even distribution of abundance among the species of intermediate abundance (Fig. 3). Interpretation of the species diversity indices is problematic because the rank-abundance curves from sites 2, 3, and 4 intersect each other, indicating that these communities are not comparable in terms of intrinsic diversity (Lambshead et al., 1983). Comparison of the species diversity indices for the oldest site 5 and the earlier site 1 (their rank-abundance curves do not intersect; Fig. 3) agree with the interpretation of the rank-

TABLE 2

Community structure in the five study sites along the Glaciar Frías forefield: mean ± standard deviation cover of each vegetation group and diversity indices. Estimated exposure dates of sites are given in Table 1; site 1 is the youngest and site 5 the oldest.

	Site 1	Site 2	Site 3	Site 4	Site 5
Species number	31	33	37	33	44
Total vegetation cover (%)	44.6 ± 21.0	81.1 ± 34.7	116.8 ± 33.9	82.0 ± 33.2	153.9 ± 46.9
Vascular plant cover (%)	8.7 ± 4.9	15.7 ± 9.6	17.5 ± 16.1	10.4 ± 8.2	47.2 ± 46.7
Fern cover (%)	0.1 ± 0.3	0.1 ± 0.3	0.5 ± 1.6	0.1 ± 0.3	0
Moss cover (%)	11.8 ± 8.0	23.5 ± 18.3	41.3 ± 24.0	45.4 ± 29.0	72.7 ± 22.5
Crustose lichen cover (%)	17.1 ± 22.8	27.4 ± 14.0	34.0 ± 19.1	12.6 ± 8.9	5.3 ± 4.9
Foliose and fruticose lichen cover (%)	6.7 ± 8.8	14.4 ± 10.0	23.5 ± 16.2	13.5 ± 9.1	28.4 ± 15.5
Algae cover (%)	0.2 ± 0.4	0	0	0	0.3 ± 0.9
Shannon index (H′)	2.34	2.48	2.45	2.21	2.45
Simpson index (1/D)	1.18	1.14	1.15	1.23	1.23
Berger-Parker index (d)	0.33	0.24	0.28	0.39	0.41

abundance curves suggesting a trend of increasing species diversity in the vegetation community and of dominance of the most abundant species as succession progresses (Table 2).

VEGETATION ASSEMBLAGES

The species classification by TWINSPAN differentiated six major vegetation assemblages. Based on the time of entering in the successional sequence and the period in which a species achieves the maximum coverage, the vegetation assemblages were differentiated as corresponding to the pioneer, mid-, or late-successional stage (Table 3). The pioneer species are those that colonized the recently exposed sites but disappeared in older sites, the mid-successional species prevailed in the middle-aged sites, whereas the late-successional species appear late in the succession.

The pioneer species dominate the community for about 50 years (sites 1 and 2) and decrease in coverage later in the succession (Table 3). The dominant species in the pioneer-successional stage are the crustose lichen *Placopsis perrugosa*, forming a dense cover on the rock outcrops, and the moss *Andreaea* sp., growing in small cracks on the rock surfaces. Besides these, the lichens *Stereocaulon speciosum* and *Placopsis stenophylla*, the moss *Racomitrium lanuginosum*, and the small shrubs *Senecio argyreus*, *Baccharis racemosa*, and *Gaultheria pumila* are also present with relatively high coverage in the early stage (Table 3). A large diversity of vascular plants (classified in the VG1) colonizes early the fine material accumulated between rock outcrops (Table 3). Most of these vascular species are only sporadically present in the younger and not in the older sites, thus we assumed that they are present by chance and not actually part of the successional sequence on the rock outcrops. Indeed, ordination analysis of the composition and coverage data shows that these species are clearly separated in the right side of the ordination graph, outside the center of the diagram where the sample sites lie (Fig. 4), indicating a minor influence of VG1 plants on the sites ordination.

The mid-successional stage is dominated by the moss *R. lanuginosum.* This species became prominent about 80 years after site exposure (site 3), and in combination with the fruticose lichens *Stereocaulon* spp., *Cladonia lepidophora*, and *C. subchordalis* forms a dense lichen-moss carpet on the rock surfaces (Table 3). After about 140 years the lichen-moss mat covered more than 90% of the rock surface on site 5. Other characteristic species of the mid-successional stage were the shrubby vascular plants *Gaultheria pumila* and *G. caespitosa.* In addition, species typical of the pioneer and late-successional stages, such as *Senecio argyreus* and *Escallonia alpina*, respectively, were present with relatively high coverage in middle-aged sites (Table 3).

The late-successional stage is characterized by the invasion of a large diversity of vascular plant species, which on average contribute 47.2% of the total vegetation cover (Tables 2 and 3). Local variability in vegetation development is high, as indicated by the large standard deviation of the mean cover values for the vegetation groups (Table 2). The most relevant vascular plants, in order of their coverage are *Empetrum rubrum*, *Berberis buxifolia*, *Quinchamalium chilense*, *Discaria nana*, *Escallonia alpina*, *Baccharis racemosa*, and some graminoid herbs.

VEGETATION PATTERNS AND EXPLANATORY VARIABLES

Patterns in vegetation composition and species coverage along the spatial chronosequence were explored with DCA and CCA. Both analyses showed the same general pattern, thus only CCA ordination diagrams are shown (Fig. 4). Samples from each study site form groups relatively distinct in the ordination space, although the high within-site variability determines zones of overlap between groups (Fig. 4a). Sites and vegetation assemblages arranged successively along the first ordination axis (Fig. 4), indicating a trend of progressive vegetation change along the chronosequence.

The eigenvalues for the DCA (0.482 and 0.152 for DCA 1 and DCA 2, respectively) were similar to those recorded for the CCA (0.364 and 0.162 for CCA 1 and CCA 2, respectively), suggesting

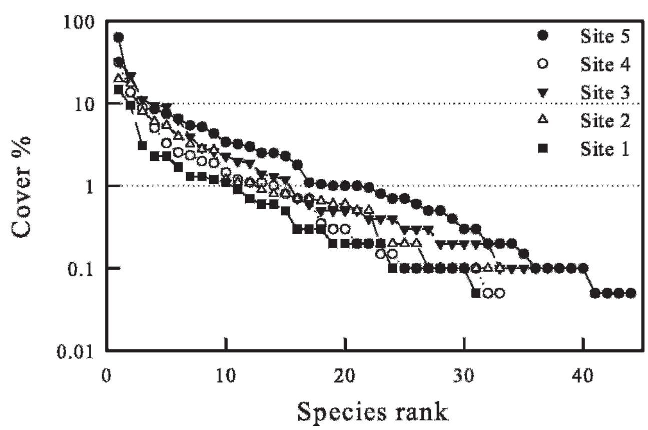

FIGURE 3. Species-abundance distribution plots for each study site. Site 1 is the youngest and site 5 the oldest.

TABLE 3

Mean percent cover (%) of the species in the five study sites at Glaciar Frías foreland. Cover values higher than 1.5% are indicated in bold. Vegetation groups (VG) as defined by TWINSPAN. Estimated exposure date of sites is given in Table 1.

VG	Species	Abbreviated name	Species life form	Site 1	Site 2	Site 3	Site 4	Site 5
			Pioneer species					
1	*Cerastium arvense*	Carve	Herb	0.1				
	Draba gilliesii	Dgill	Herb	0.2				
	Fuchsia magellanica	Fmage	Shrub		0.1			
	Gamochaeta nivalis	Gniva	Herb	0.1				
	Luzula racemosa	Lrace	Herb	0.1				
	Leucheria papillosa	Lpapi	Herb	0.3				
	Rhytidosperma picta	Rpict	Graminae	0.9	0.9	**1.9**	0.3	
	Ribes magellanicum	Rmage	Shrub		0.5			
	Senecio fistulosus	Sfist	Herb	0.3				
	Graminoid herb 2	Gram	Graminae	0.3				
	Placopsis cribellans	Pcrib	Lichen		0.5			
2	*Baccharis racemosa*	Brace	Shrub	1.2	1.2	0.1		**1.8**
	Graminoid herb 1	Gram	Graminae	0.7	0.6	0.4	0.1	0.1
	Placopsis stenophylla	Psten	Lichen	**1.7**	**2.7**		**2.4**	0.1
	Stereocaulon speciosum	Sspec	Lichen	**3.1**	0.7		0.1	0.1
3	*Gunnera tinctoria*	Gtinc	Herb	0.6				
	Senecio argyreus	Sargy	Herb	1.1	**3.2**	**3.9**	**1.5**	
	Graminoid herb 3	Gram	Graminae	0.5	0.2	0.2	0.2	0.3
	Andreaea sp.	Andre	Moss	**9.5**	**17.5**	**9.1**	**13.7**	**8.5**
	Placopsis perrugosa	Pperru	Lichen	**14.8**	**19.8**	**22.0**	**5.1**	**2.5**
	Pseudophebe pubescens	Poube	Lichen		0.2			0.1
	Trentepohlia sp.	Trent	Lichen	0.2				0.3
			Mid-successional species					
4	*Placopsis bicolor*	Pbico	Lichen		**2.8**	**6.4**	1.0	
	Rhizocarpon geminatum	Rgemi	Lichen		0.6	**2.3**		0.4
	Calceolaria biflora	Cbifl	Herb	0.1		0.1		
	Rhizocarpon superficiale	Rsupe	Lichen	0.2				
	Acaena pinnatifida	Apinn	Herb		0.8	0.5		
	Lathyrus magellanicus	Lmage	Herb			0.2		
	Graminoid herb 4	Gram	Graminae		0.1		0.1	
	Acarospora sinoptica	Asino	Lichen			0.4		
	Peltigera rufescens	Prufe	Lichen		0.1			
	Xanthoparmelia cordillerana	Xcord	Lichen			0.5	0.1	
5	*Gaultheria pumila*	Gpumi	Shrub	1.3	**4.0**	**2.9**	0.2	**6.5**
	Rumohra adiantiformis	Radia	Fern	0.1	0.1	0.5	0.1	
	Graminoid herb 5	Gram	Graminae	0.2	0.1	0.4	0.2	0.6
	Graminoid herb 6	Gram	Graminae	0.6	1.1	1.4	0.7	**2.3**
	Unidentified crustose lichen	Lich	Lichen	0.1	0.1	0.3	0.1	0.1
	Cladonia lepidophora	Clepi	Lichen		**5.4**	**9.5**	**2.6**	**8.7**
	Rhizocarpon geographicum	Rgeog	Lichen		0.7	**2.6**	0.8	1.0
	Stereocaulon spp.	Ster	Lichen	**2.3**	**8.0**	**11.2**	**8.9**	**13.5**
	Sterocaulon botryosum	Sbotr	Lichen	1.3		**2.0**	1.1	
	Racomitrium lanuginosum	Rlanu	Moss	**2.3**	**6.0**	**32.2**	**31.7**	**63.2**
	Gaultheria caespitosa	Gcaes	Shrub		1.1	1.2	**1.9**	**3.4**
	Muhlenbergia sp.	Muhl	Graminae				0.4	
	Silene chilensis	Schil	Herb			0.3		0.7
	Lecidea auriculata	Lauri	Lichen	0.2				0.2
	Rinodina sp.	Rino	Lichen	0.1	0.2		**3.3**	1.1
			Late-successional species					
6	*Berberis buxifolia*	Bbuxi	Shrub		0.8	1.3	0.1	**5.4**
	Chloraea alpina	Calpi	Herb		0.2	0.1	0.1	0.8
	Fragaria chiloensis	Fchil	Herb			0.6	0.3	0.2
	Graminoid herb 7	Gram	Graminae	0.1		0.1	0.2	1.1
	Cladonia subchordalis	Csubc	Lichen			0.3	0.7	**5.2**
	Neofuscelia plana	Nplan	Lichen				0.1	0.1
	Quinchamalium chilense	Qchil	Herb		0.7	0.7	1.1	**4.3**
	Escallonia alpina	Ealpi	Shrub		0.1	0.2	**2.0**	**3.0**
	Nothofagus dombeyi	Ndomb	Tree			0.5		1.0
	Pseudopanax laetevirens	Plaet	Shrub					1.0
	Buellia sp.	Buel	Lichen					0.1

TABLE 3

Continued.

VG	Species	Abbreviated name	Species life form	Site 1	Site 2	Site 3	Site 4	Site 5
	Baccharis nivalis	Bniva	Herb					0.5
	Discaria nana	Dnana	Shrub				1.2	**3.2**
	Empetrum rubrum	Erubr	Shrub			0.2		**7.5**
	Sisyrinchium arenarium	Saren	Herb					0.2
	Graminoid herb 8	Gram	Graminae					0.2
	Graminoid herb 9	Gram	Graminae					0.5
	Trisetum sp.	Tris	Graminae			0.2		**2.5**
	Unidentified moss	Moss	Moss					1.0
	Cladonia pocillum	Cpoci	Lichen					0.1
	Pseudocyphellaria encoensis	Penco	Lichen					0.7
	Carex sp.	Carex	Graminae			0.1		0.1

that the explanatory variables included in the canonical analysis are adequate for explaining the variation in species composition and cover. In addition, the species-environmental correlations were relatively high for both analyses (Table 4), revealing a strong relationship between changes in the vegetation and the explanatory variables available. The first DCA and CCA axes are significantly and strongly correlated to site exposure dates (Fig. 4a, Table 4), indicating that the dominant pattern in community structure is the successional change associated with increasing time since site deglaciation. The second ordination axes are significantly correlated to surface topography, showing positive values for depressed surfaces and negative values for elevated surfaces (Fig. 4a, Table 4). Thus, microtopographic heterogeneity, such as elevated, depressed, and flat surface topography, can partially explain the within-site variability in vegetation structure. The canonical axes are also significantly correlated with percentage of bare rock surface, percentage of bare soil, and canopy coverage, reflecting the progressive occupation of the bare terrain by the vegetation as succession progresses.

Discussion

Primary succession on the bedrock outcrops of Glaciar Frías foreland follows a model of directional replacement of species (*sensu* Svoboda and Henry, 1987). An initial stage dominated by a crustose lichen is followed by a mid-successional stage characterized by a lichen-moss mat, whereas vascular plants diversified and increased in coverage during the late-successional stage (Fig. 4, Table 3).

The pioneer crustose lichen *Placopsis perrugosa* is a successful colonizer, with high growth rate and dispersal ability, and is frequently found dominating recently deglaciated terrains in Chile, New Zealand, and Antarctica (Orwin, 1970; Lindsay, 1978; Galloway, 1992). This lichen formed pure stands on the study rock outcrops during the first 50 years after deglaciation (Table 3). With increasing terrain age, *P. perrugosa* centers disintegrate probably due to limitations in nutrient transport from the periphery to the center of the thallus (Nash, 1996). The declining of *P. perrugosa* on the older study surfaces seems to be exclusively related to the species life-cycle, as no different lichens or mosses overgrow or develop in close contact to *P. perrugosa* competing for space.

Lichens are considered to be initiators of succession on rock surfaces because they significantly enhance rock weathering, derive inorganic nutrients from the rocks, and provide organic materials (Adamo and Violante, 2000). In addition, the presence of external cephalodia with cyanobacteria capable of fixing nitrogen in *P. perrugosa* significantly increases the nitrogen stock in the new substrates, where nitrogen is a limiting nutrient for plant colonization (Vitousek, 1994). However, we noted that rock surfaces exposed by *P. perrugosa* as the lichen centers degraded show little evidence of disaggregation and fragmentation, suggesting that the colonization of this lichen does not contributed much to rock weathering. In addition, *P. perrugosa* disappears from the rock surfaces before the widespread colonization by mid-successional species, indicating that there is not a direct interaction between this lichen and later colonizers. Therefore, the early colonization by *P. perrugosa* seems to contribute little to the establishment of later colonizers on rock outcrops in the study area. Our observations are consistent with studies questioning the role of pioneer crustose lichens in the primary succession process. For example, Longton (1992) and Kurina and Vitousek (2001) considered that crustose lichens are able to colonize bare surfaces early because of their ruderal life-cycle traits, but do not have relevant positive effects on later colonizers.

The development of a lichen-moss mat between 50 and 80 years after deglaciation marks the transition from the pioneer to the mid-successional stage. The species that dominated the mat (*Racomitrium lanuginosum*, *Cladonia* spp., and *Stereocaulon* spp.) are common pioneer colonizers during primary succession on glacier forelands, lava flows, and high mountain environments (Veblen and Ashton, 1979; Veblen et al., 1989; Vetaas, 1994; Hodkinson et al., 2003; Cutler et al., 2008). They are highly tolerant to stressful environmental conditions and have the ability to rapidly spread over intact rock surfaces as their rhizoids are able to penetrate into the superficial layers of rocks (Longton, 1992; Adamo and Violante, 2000). After about 110 years the lichen-moss mat forms an almost continuous, thick layer (ca. 15 cm) of organic material on rock surfaces at Glaciar Frías.

The expansion of the lichen-moss mat is followed by the high recruitment and increase in coverage of vascular plants (Tables 2 and 3). It is well known that cryptogamic mats contribute to soil formation by entrapping particulate material and retaining remnants of dead vegetation (Longton, 1992). The formation of a soil layer is highly relevant in rocky environments where growth of large-sized vascular plants is controlled by the presence of sites with adequate soil volume for root deployment (Burbanck and Phillips, 1983; Matthes-Sears and Larson, 1999). Cryptogams can also benefit vascular plants by ameliorating the physical and chemical environment, contributing nitrogen to the environment and entrapping plant seeds (Belnap et al., 2001; Breen and Lévesque, 2006). Therefore, the colonization of vascular plants observed during mid- and late-succession in the study area (Tables 2 and 3) likely has been facilitated by the earlier

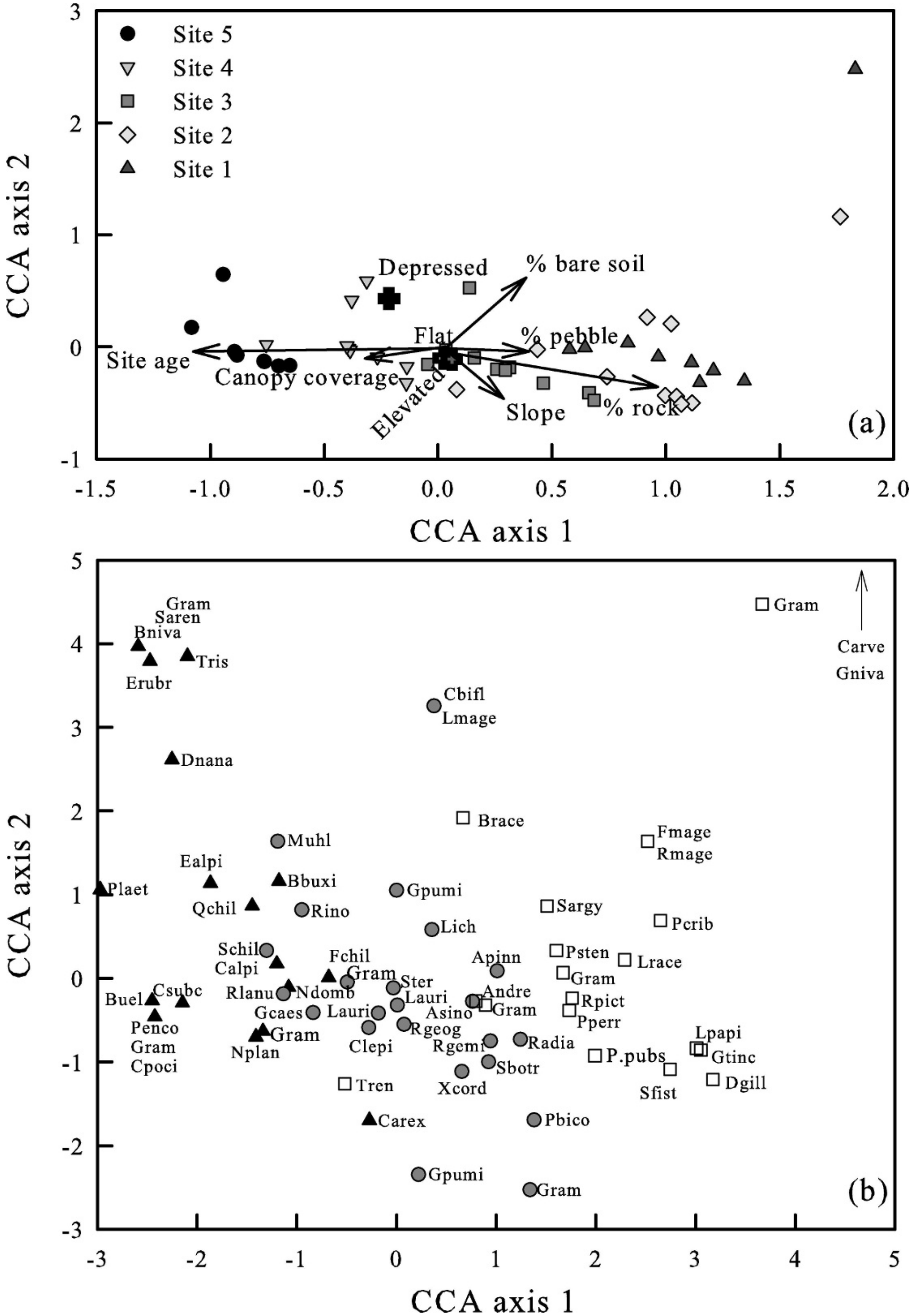

FIGURE 4. Results of the canonical correspondence analysis (CCA) of species and samples. (top) Ordination of sampling plots and explanatory environmental variables. The quantitative environmental variables are shown by vectors and the variable topography as centroids of each category. (bottom) Ordination of species. Species are differentiated as: □ Pioneer, ● Mid-successional and ▲ Late-successional, according to their classification in the TWINSPAN analysis. Species abbreviations are given in Table 3. Eigenvalues for the first and second axes are 0.364 and 0.163, respectively.

development of a cryptogamic carpet of mosses and fruticose lichens on the rock surfaces.

The colonization of vascular plants follows a physiognomic succession. Small, trailing shrubs and compact cushions (e.g. *Senecio argyreus*, *Gaultheria pumila*, *G. caespitosa*, *Baccharis racemosa*, *Empetrum rubrum*, *Discaria nana*, and *Escallonia alpina*) form a woody carpet by covering large portions of the rock surfaces by horizontal spreading and vegetative reproduction. As succession

TABLE 4

Correlation values (*r*) between vegetation ordination axes and explanatory variables. DCA (Detrended Correspondence Analysis); CCA (Canonical Correspondence Analysis). Species-environment correlations on DCA 1 and DCA2: $r = 0.86$ and $r = 0.37$, respectively; and on CCA 1 and CCA 2: $r = 0.89$ and $r = 0.83$, respectively. The statistical significance level of each explanatory variable was estimated in base of their partial effects (variability explained by the variable after accounting for the effects of other variables) as each variable is added to the model. All three categories of Topography were tested in conjunction for significance of their effect. Significance levels: **$P < 0.01$, *$P < 0.05$.

Variables	DCA correlations		CCA intra-set correlations		
	DCA 1	DCA 2	CCA 1	CCA 2	Partial *F*-value
Site age	−0.80	−0.05	−0.94	0.02	6.16**
Slope	0.24	0.08	0.26	−0.29	1.06
% bare rock outcrop	0.71	−0.04	0.81	−0.36	1.66*
% bare soil	0.26	0.15	0.33	0.75	2.89*
% pebble	0.30	−0.01	0.34	0.01	1.25
Canopy coverage	−0.19	−0.03	−0.21	−0.01	1.97*
Topography depressed	−0.16	0.02	−0.14	0.49	
Topography flat	0.02	0.22	0.01	−0.09	2.61**
Topography elevated	0.12	−0.17	0.12	−0.37	

progresses, herbs, erect shrubs, and small *Nothofagus dombeyi* trees (up to 2 m high) colonize the rock outcrops, forming a community with many overlapping strata (Table 3). On deglaciated terrains and alpine treelines in the southern Patagonian Andes, the emergence, growth, and survival of *N. antarctica* and *N. pumilio* seedlings increase under the canopy of shrubs (e.g. *Empetrum rubrum*) or adult trees (Cuevas, 2000; Henríquez and Lusk, 2005). Veblen and Ashton (1979) also reported that the establishment of *Nothofagus* spp. on volcanic ashes needs the protection from strong winds given by prostrate shrubs. Although individuals of *Nothofagus* are sometimes initial colonizers on recently deglaciated surfaces (Lawrence and Lawrence, 1959; Villalba et al., 1990; Masiokas, 2008), in general they are isolated trees associated with safe sites, such as cracks protected from wind (Veblen et al., 1989). For example, Villalba et al. (1990) reported a solitary 29-year-old *N. pumilio* growing on moraine 7 at Glaciar Frías, indicating that no other specimen succeeded in establishing on this moraine during the subsequent three decades. Therefore, the protection provided by other plants can be of outmost importance for the regeneration of a *Nothofagus* stand under the severe environmental conditions prevailing in the Patagonian Andes.

Our study provides a detailed example of vegetation development on bedrock slopes following deglaciation, which can be compared to successional trajectories reported in the literature for unconsolidated glacial deposits in the Patagonian Andes. Unfortunately, few studies on unconsolidated deposits have included cryptogams, making difficult the comparison of the earlier stages of vegetation development on the different surfaces. Lichenological studies nearby Glaciar San Rafael, a wet-maritime area in the Patagonian Andes, showed that *Placopsis* spp. not only dominate boulders and rock surfaces but also consolidated gravel (Galloway, 1992). The dominance of *Placopsis* spp. has also been reported in other Patagonian glaciers (Winchester and Harrison, 2000). At Glaciar Casa Pangue, approximately 4 km to the west of Glaciar Frías (Fig. 1), cryptogams account for 57% of the total coverage on moraines 40 years after deglaciation (Veblen et al., 1989). The lichen *Stereocaulon* and the moss *Racomitrium* are common constituents of the community in the earlier stages of vegetation development in Glaciar Casa Pangue (Veblen et al., 1989). Therefore, there is a striking similarity in the vegetation communities developing on rock faces and glacial deposits during the pioneer and mid-stages of the primary succession.

The woody carpet of prostrate shrubs observed on Glaciar Frías outcrops is a common stage of vegetation succession on areas exposed by glacier retreat or affected by volcanism in the Patagonian Andes (Heusser, 1964; Veblen and Ashton, 1979; Veblen et al., 1989; and personal observations). On unconsolidated glacial deposits, the shrubby vegetation is usually replaced by *Nothofagus*-dominated forests within 75 years since glacier retreat (Heusser, 1964; Villalba et al., 1990). In contrast, we recorded a sparse coverage of *N. dombeyi* saplings in the rock outcrops exposed for more than 140 years (Table 3). This indicates that vegetation development is greatly delayed on rock outcrops compared to unconsolidated deposits. It is known that the slower community establishment on bare rock outcrops is related to the long time required for the formation of a ground vegetation cover and an organic matter layer (Asselin et al., 2006). These observations are consistent with our results indicating that once the lichen-moss mat develops, a large diversity of vascular plants rapidly colonized the rock surfaces. Indeed, the coverage of the vascular plants increased almost fivefold between sites 4 to 5, i.e. in a period of approximately 35 years (Fig. 3, Table 2). In summary, vegetation development requires at least 100 years longer on bedrock outcrops than on unconsolidated glacial deposits and is closely related to the time required for the formation of a cryptogamic carpet.

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