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Spatiotemporal Pattern of Primary Succession in Relation to Meso-topographic Gradients on Recently Deglaciated Terrains in the Patagonian Andes

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Abstract

Vegetation in primary succession is influenced by multiple stochastic and environmental factors at different spatial and temporal scales. In this study we analyze the effect of meso-topographic heterogeneity on vegetation development following the retreat of Glaciar Seco in the southern Patagonian Andes. Composition and cover of algae, lichens, mosses, and vascular plants were recorded in 580 plots located in different topographic positions within a chronosequence of eight consecutive moraines. Sample plots were characterized by topographical and surface features. Spatiotemporal patterns in vegetation composition and their relationships to environmental factors were assessed by classification and ordination. We recognized eight communities that correspond to four major successional stages. The successional sequence is characterized by a physiognomic development from pioneer saxicolous lichens (first stage) to secondary colonizer lichens (second stage), followed by shrub colonization (third stage) and the development of *Nothofagus* spp. forests (fourth stage). Alternative successional trajectories on different topographic positions vary in the sequence of these four major successional stages, with the trajectories on the moraine ridge-top and base not going through some of the stages. A variance partition procedure shows that time since deglaciation and topographic position on the moraines account for comparable amounts of vegetation variance, emphasizing the importance of spatiotemporal analysis of vegetation development on heterogeneous landscapes. Broad trends in vegetation development follow environmental gradients. However, emergence and persistence of vegetation patterns can also be attributed to dynamic geomorphic processes such as moraine slope degradation affecting boulder distribution along the moraine foreslope. At the landscape scale, successional trajectories converge to a *Nothofagus*-dominated state, but significant variability remains in the understory due to the differential distribution of cryptogams along the moraine topographic gradient. Convergence is mostly related to the expansion of communities from more favorable sites towards the harsher moraine crest, but it is not a process of gradual deterministic changes along the different successional pathways.

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Introduction

Primary succession has been intensively studied by plant ecologists during the last century to understand several ecological processes such as species interactions, species responses to environmental change, and changes in vegetation community structure over time. An understanding of the ecological processes occurring during the earlier stages of vegetation development is vital for developing ecological restoration programs in disturbed or degraded areas (Walker and Del Moral, 2009). In addition, understanding primary succession can provide insights for prediction of short- and long-term effects of climatic change on disturbed terrestrial ecosystems (Hodkinson et al., 2003; Cannone et al., 2008; Dolezal et al., 2008).

Most studies of primary succession are based on the chronosequence approach that substitutes space for time. Although this approach has been criticized (Johnson and Miyanishi, 2008), its consistency and reproducibility has been demonstrated

(Foster and Tilman, 2000; Walker et al., 2010). The chronosequence approach is based on the assumptions that environments are spatially homogeneous and that communities of different ages have been influenced by similar environmental conditions during succession. However, environmental heterogeneity and stochastic factors affect the course of primary succession, frequently resulting in a mosaic of communities following alternative successional trajectories (e.g. Wiegleb and Felinks, 2001; Raffl et al., 2006; del Moral, 2009).

The analysis of different successional trajectories occurring within a chronosequence provides insight into specific patterns and mechanisms of vegetation development. For example, correlations between environmental and successional gradients allow assessment of the relative contribution of different environmental factors to vegetation development (Vetaas, 1997; Raffl et al., 2006; Dolezal et al., 2008). In addition, spatial variations in succession reflect stochastic processes related to species dispersal and timing of establishment (del Moral, 1999;

Lanta and Lepš, 2009). Whether communities following different successional trajectories eventually converge or diverge is still a matter of controversy in ecology since both successional patterns have been reported. Differentiating the factors that influence the convergence/divergence of vegetation communities also contributes to understanding of the patterns and mechanisms of vegetation assembly (Lepš and Rejmanek, 1991; Fukami et al., 2005; del Moral et al., 2010).

Topography, which influences microclimate and soil properties, is a primary environmental factor determining species distribution (Whittaker, 1989; Franklin et al., 2000; Meentemeyer et al., 2001; Choler, 2005; Bruun et al., 2006; Cutler et al., 2008a; Kharuk et al., 2010). By sampling vegetation in sites with similar aspect and topography, many studies have attempted to control the effects of topographical variations on primary succession. However, the analysis of local-scale processes occurring within study sites, such as those determined by spatial topographic heterogeneity, is important for understanding vegetation development patterns at the landscape scale (Pickett and Cadenasso, 1995). Analyses of small-scale topographical variations have shown that irregularities in the surface constitute “safe sites” (Harper et al., 1965) for plant colonization (Jumpponen et al., 1999; Cutler et al., 2008b). In addition, meso-scale topographic heterogeneity determines spatial patterns in vegetation development within glacial forelands and lava flows (Berhardt, 1986; Matthews and Whittaker, 1987; Whittaker, 1989; Vetaas, 1994; Cutler, 2010). Although variations in meso-topography (intermediate-scale geographic features characterized by the presence of upper, middle, and lower slopes) do not affect early stages of vegetation development (Cutler et al., 2008b), they determine different successional pathways as succession proceeds (Raffl et al., 2006; Dolezal et al., 2008; Cutler, 2010; del Moral et al., 2010). Therefore, at local scales, topography is a major environmental factor shaping the spatial development of vegetation. However, our knowledge of alternative successional trajectories along topographic gradients and the relative importance of time and space variation in determining vegetation development at the landscape scale are still limited.

Glacier forelands offer an excellent opportunity to study primary succession, since most glacier chronosequences are relatively long and well-dated, allowing temporal constraint of the processes in the primary succession (Matthews, 1992). The retreat of glaciers is a conspicuous sign of climate change during the last century in the Patagonian Andes (Masiokas et al., 2009), yet there have been only a few attempts to investigate the processes of primary succession on these sites. Some studies have analyzed the pattern of *Nothofagus* establishment 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; Henríquez and Lusk, 2005). However, these studies have mostly focused on later stages of primary succession and rarely considered other components of the vegetation such as algae, lichens, bryophytes, and small vascular plants. A recent study has analyzed the patterns of vegetation establishment on deglaciated rock outcrops in the Patagonian Andes (Garibotti et al., 2011).

In this study we explicitly examine the influence of topography on the patterns of vegetation development in a chronosequence of moraines exposed by the retreat of Glaciar Seco in the south Patagonian Andes. We explore the relationship between successional trajectories occurring under different topographical conditions, aiming to: (1) characterize the pattern of primary succession on unconsolidated glacial deposits; (2) evaluate differences in successional development caused by environmental heterogeneity associated with topographic

gradients; (3) estimate the relative importance of temporal and spatial factors in the development of vegetation; (4) determine whether convergence/divergence occurs in successional trajectories under different environmental conditions; and (5) assess the implications of multiple pathways for landscape development. Our research was intended to answer the following questions: (1) Which vegetation assemblages characterize the primary successional process on *Nothofagus*-dominated forests? (2) What is the relationship between vegetation succession and topographic variability in glacier forelands? (3) Which are the main factors determining the spatio-temporal development of the vegetation? and (4) How do alternative successional trajectories affect spatial patterns of late-succession vegetation?

Study Area and Chronologies

Glaciar Seco is located in the south Patagonian Andes of Argentina (50.17°S, 73.29°W; Fig. 1). The lack of meteorological stations close to Glaciar Seco does not allow a precise climate characterization of the area. Villalba et al. (2003) summarized the meteorological data available for the southern Patagonian Andes and described the climate in the region as temperate and wet, with precipitation uniformly distributed over the entire year. Mean annual temperature has been estimated at 6 °C, with mean temperature for the coldest (July) month ranging from 0 to 4 °C. The mean temperature for the warmest month (January) ranges between 10 and 16 °C (Villalba et al., 2003). The annual precipitation is ca. 8000 mm over the Southern Patagonian Icefield (Escobar et al., 1992), but abruptly decreases east of the main Andes. The vegetation in the area corresponds to the Magellanic temperate rain forest, a multistratified forest dominated by the evergreen *Nothofagus betuloides* at lower elevations and the deciduous *N. pumilio* from mid-elevations to the upper treeline (Veblen et al., 1996).

Glaciar Seco occupies a U-shaped valley, with steep lateral slopes (Fig. 1). The terminus of the glacier was at an elevation of approximately 445 m above sea level in the year 2009. A sharp forest trim-line defines the boundary between the glacier foreland and the mature forest not affected by the last Neoglacial advance. In the bottom of the valley (ca. 330 m above sea level) a well-preserved sequence of frontal and lateral moraines remains as evidence of eight minor readvances of Glaciar Seco since the last Neoglacial event. The sequence of moraines (M) has a north-to-south orientation across the valley in a narrow altitudinal band (altitudinal difference between M1 and M8 is less than 20 m). Moraines are mostly composed of granite and quartzite boulders.

In this study we applied lichenometric techniques to estimate exposure dates of the eight moraines at Glaciar Seco, following the methods described in Garibotti and Villalba (2009). It is estimated that the Moraine 8 was formed around A.D. 1699 (Table 1), concurrent with a cold period globally identified as the Little Ice Age (Grove, 2004). The most recent readvance occurred in A.D. ~1965 (Moraine 1), and since then Glaciar Seco has been retreating along the steep bedrock slope. Although M1 and M2 were estimated to have similar ages according to lichen sizes, we assigned them to different glacial pulses until more detailed glaciological studies are performed. Moraine 2 is small (Fig. 1) and probably its age has been underestimated from lichen sizes. The available historical information for Glaciar Seco shows a photograph taken in 1953 by Bertone (1960). Repeat photography (Fig. 2) indicates that the glacier front has retreated by about 800 m over the last 56 years (estimated horizontal distance between glacier terminus positions in the historical photograph and present).

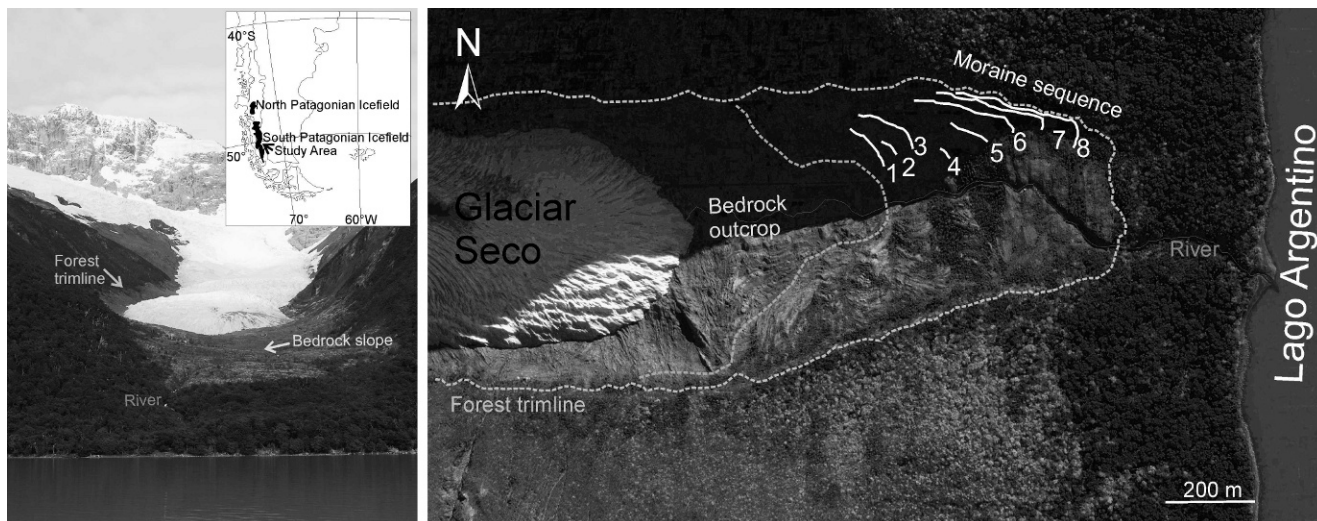


FIGURE 1. Location map and view of the Glaciar Seco foreland in the south Patagonian Andes. Schematic map of the studied moraine sequence. Estimated dates for moraine exposures are given in Table 1.

Methods

SAMPLING DESIGN

Vegetation data were recorded in the sequence of eight moraines during the summer 2009. The sampling strategy was designed to account for the spatial variation in vegetation associated with the topographical gradient between the moraine crest, the mid-slope, and the base. The base position includes the foot- and toe-slope of the moraine. We randomly located 1 m² sampling plots in each moraine position. Depending on moraine size, the number of sampling plots varies between 20 and 30 on each topographic position. At each plot, species of terrestrial green algae, lichens, mosses, and vascular plants growing on rocks and the substrate surface were recorded. Percentage cover of the species was visually estimated. Cover estimates for lichens and bryophytes were recorded to the species level whenever possible or to genera or morphological groups when field identification was not feasible. In addition, a floristic survey 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 were deposited at the Argentinean Institute of

Snow, Ice and Environmental Sciences (IANIGLA). Nomenclature follows Zuloaga and Morrone (1999a, 1999b) for vascular plants, and Brummitt and Powell (1992) for lichens and bryophytes.

At each sampling plot the following environmental parameters were recorded: meso-topographic position on the moraine

TABLE 1

Lichenometric data for the sequence of moraines on the foreland of Glaciar Seco. Minimum dates of moraines exposure are estimated from the largest lichen on the moraine applying a lichenometric dating curve for wet sites in the Patagonian Andes (Garibotti and Villalba, 2009). Thallus that is 10% larger than the second largest thallus was considered anomalous and excluded from the analyses.

Moraine	Largest lichen size (cm)	Number of anomalous thalli	Date (A.D.)	Years since deglaciation
1	1.8	1	1965	44
2	1.8	1	1965	44
3	2.7	0	1941	68
4	3.1	0	1931	78
5	5.1	2	1871	138
6	8.5	0	1749	260
7	8.7	0	1741	268
8	9.7	1	1699	310



FIGURE 2. Paired photographs showing changes in Glaciar Seco extension between 1953 (Bertone, 1960) and 2009 (photo by R. Villalba).

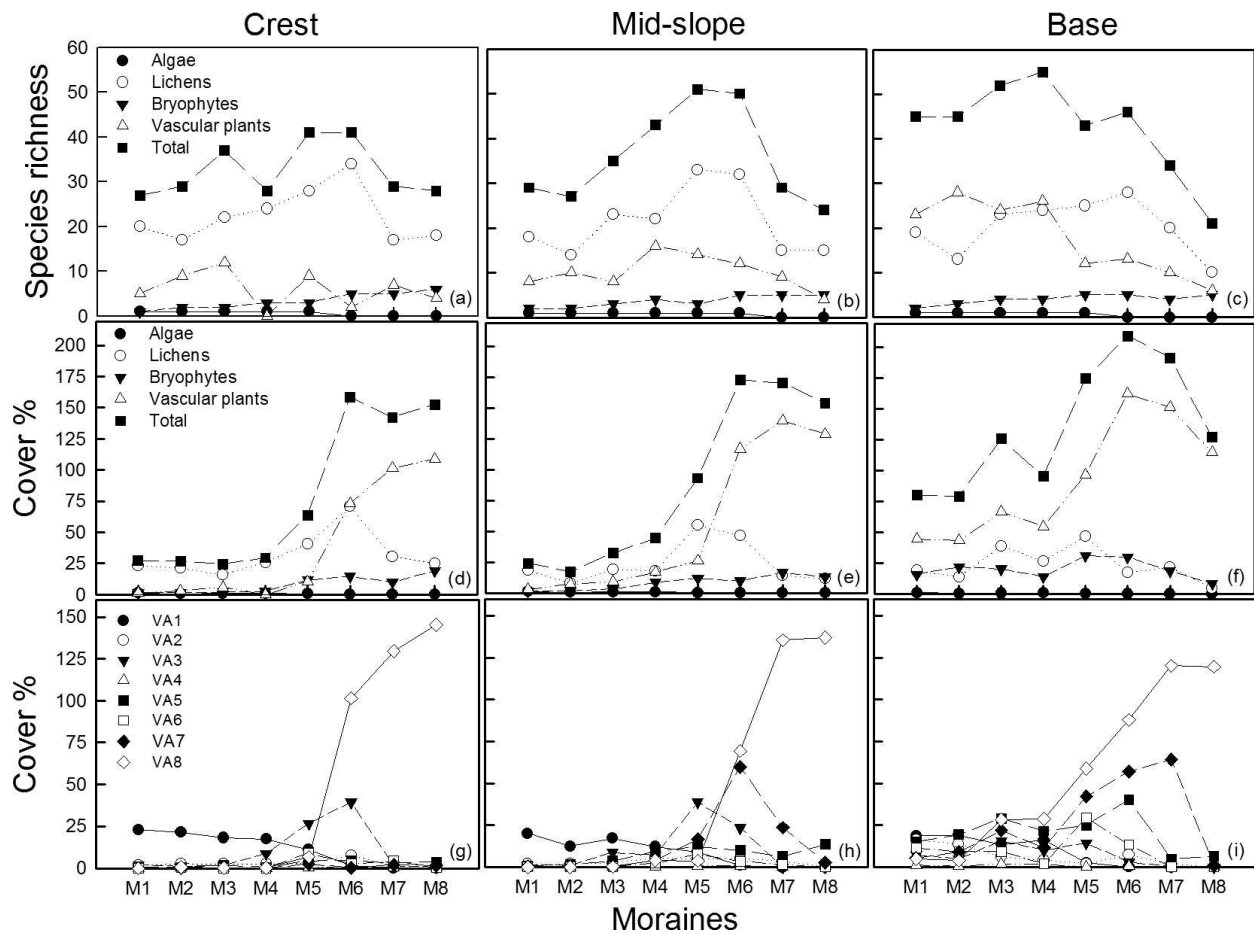


FIGURE 3. Vegetation development along the Glaciar Seco chronosequence. (a–c) Species richness, (d–f) percentage cover of vegetation, (g–i) percentage cover of vegetation assemblages (VA) as defined by a TWINSpan classification analysis.

(crest, mid-slope, or base), aspect, slope, altitudinal distance from moraine ridge, surface micro-topography (elevated, depressed, or flat in relation to the surrounding area), percentage of the bare substrate covered by sand (<0.2 cm), gravel (0.2–5 cm), cobbles (5–30 cm), and boulders (>30 cm), percentage of bare soil, and percentage of the surface covered by litter. The slope at each sampling plot was estimated using a clinometer.

DATA ANALYSES

Vegetation variation along the chronosequence was assessed by calculating mean values for plant cover, species richness, evenness, diversity and heterogeneity at the three topographic positions on each moraine. The Shannon diversity index was used to calculate both sample diversity ($H' = -\sum p_i \ln p_i$) and evenness ($E = H'/\ln S$), where p_i is the proportion of cover represented by the i th species, and S is the total number of species (Magurran, 1988). Heterogeneity of the vegetation within sampling sites was estimated from the results of a Detrended Correspondence Analysis (see below), as the average of the root mean squared deviations for samples across the first four ordination axes (ter Braak and Šmilauer, 1998).

Two-Way Indicator Species Analysis (TWINSpan) was applied to classify species into vegetation assemblages (VA) that co-occur in certain sampling stations (Lepš and Šmilauer, 1999). This analysis can only be applied to qualitative data, so species coverage values were transformed to qualitative variables (pseudospecies) defined by cut-off 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 3 levels of division was used.

The patterns in vegetation composition and coverage were examined using unconstrained and constrained ordination analyses. Both methods are complementary (Jongman et al., 1995). A Detrended Correspondence Analysis (DCA) was calculated to choose the ordination method (linear versus unimodal models) that best represents the species responses to the underlying environmental gradients at Glaciar Seco. Detrending was performed by segments, and rare species were not down-weighted. The length of the first DCA axis was over 4 SD units, indicating that the data are fairly heterogeneous. In consequence, an ordination method based on unimodal rather than linear models is more appropriate for the analysis of our data (Jongman et al., 1995). Therefore, a DCA was used to assess the overall variability in the vegetation data, and a Canonical Correspondence Analysis (CCA) to directly assess the main patterns of variation in the vegetation community accounted for by the measured explanatory variables. The CCA uses a multiple regression analysis to directly relate the vegetation community to the environmental variations. Therefore, the method is based in a linear relationship between the species ordination (species scores) and the measured explanatory variables (Ter Braak, 1986; Austin, 2002). We checked for linearity between the environmental variables and the DCA axes before calculating the constrained ordination. In our data various explanatory variables were correlated, but all were significant

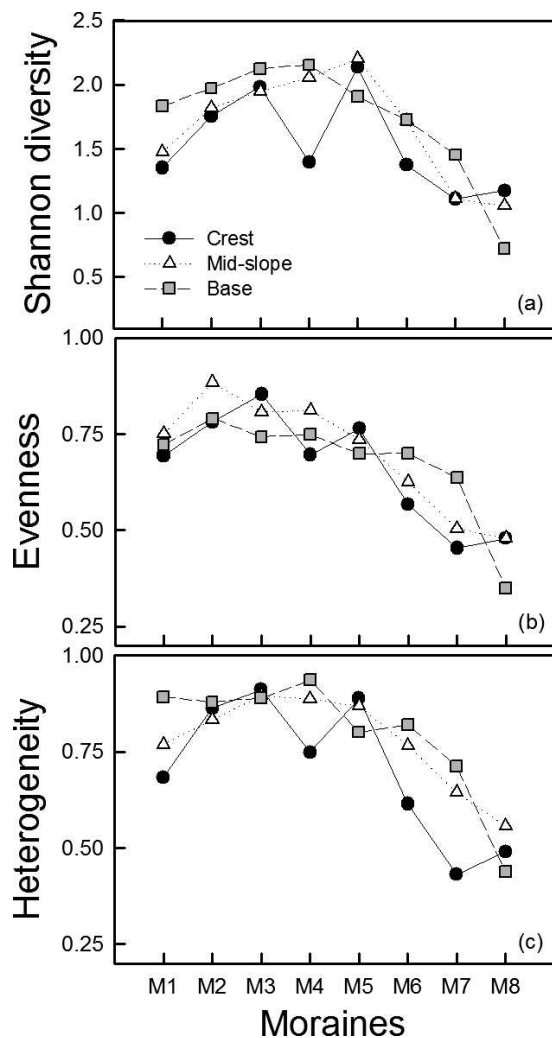


FIGURE 4. Progression of vegetation diversity, evenness, and heterogeneity along the successional chronosequence in three topographic positions of the moraines (crest, mid-slope, and base).

when a regression forward selection was applied. Since multicollinearity does not affect CCA results (Jongman et al., 1995), all the explanatory variables available were included in the analysis to estimate their relative importance in determining the vegetation changes. A Monte Carlo permutation test (499 permutations) was used to test the significance of the first ordination axis (Lepš and Šmilauer, 1999).

A direct gradient analysis with variance partitioning procedure was performed to estimate the proportion of the community variance attributed to variations over time and space. Age since deglaciation and meso-topographic positions were considered as explanatory variables, and an interaction term among these variables was included in the analysis to reflect differences in successional trends between topographic positions. In addition, a variance partitioning procedure was used to estimate the marginal and partial effects of each explanatory variable, i.e. the percentage of the total variability in species data explained by a particular variable including co-variation and after removing co-variation with other variables, respectively. Each variable was tested independently, thus Monte Carlo permutation tests (499 permutations) were calculated for the first axes (canonical axes) to determine whether the relationships between variations in the vegetation and the explanatory variables were significant (Lepš and Šmilauer, 1999).

The relationship between successional trajectories on different meso-topographic positions was examined by computing linear regressions between the sample scores on the first DCA axis and sample ages. A multiple regression model between sample scores and age was constructed to test whether the intercepts and slopes of the regression lines for each topographic position are significantly different. In addition, we used one-way analyses of variance (ANOVA) followed by a Bonferroni correction (Zar, 1996) to test for significant differences among the sample scores for each topographic position on each moraine.

The convergence (divergence) of the communities following different successional trajectories was evaluated by determining whether compositional similarity between plots on different topographical positions increased (decreased) over time. We estimated the similarity between pairs of sites on different topographic positions by calculating the percentage similarity (PS) index. The PS is a similarity index based on the species coverage:

$$PS = 200 \sum_{i=1}^n \min(x_i, y_i) / \sum_{i=1}^n (x_i + y_i), \quad (1)$$

where x_i and y_i are the cover for species i in the two sites, $\min(x_i, y_i)$ is the lower of the two cover values and n is the number of species (Lepš and Šmilauer, 1999). In addition, the degree of convergence/divergence in vegetation development was assessed by calculating separate CCA for sampling plots of the same age with meso-topographic position being the only explanatory variable. These analyses estimate the percentage of total species variability explained by meso-topography at each moraine. A decrease in the determination of species composition by topographic positions during succession is an indication of increasing similarity in vegetation assemblages on different topographic positions. This suggests convergence of successional trajectories. On the contrary, we assumed that successional trajectories diverged when the determination of species composition by meso-topography increases during succession.

Changes in vegetation composition and cover along the successional sequence were estimated by calculating the PS between all pairs of sites along successive moraines. Trends in similarity were computed for each topographic position.

Results

PATTERNS IN VEGETATION COMPOSITION AND COVER

A total of 112 species were recorded in the chronosequence of Glaciar Seco. Figure 3 shows the trends of successional changes in vegetation composition and cover in different topographic positions. Lichens and vascular plants are the most important components of the vegetation community. In general, species richness and cover increase in the younger and middle-age moraines, and then decrease in the older moraines. However, different trends were recorded in the three topographic positions (crest, mid-slope, and base). For all moraine ages, but for M8, the number of species and total cover is higher on the base than in the crest and mid-slope, indicating that a larger number of species is able to colonize this topographic position. In terms of species richness, the moraine base is initially dominated by vascular plants and later by lichen species. In the crest and the mid-slope, lichens dominate species richness all along the succession. In terms of species cover, vascular plants prevail throughout the successional sequence in the base, whereas the crest and mid-slope of the moraines are initially covered by lichens and later by vascular plants.

Trends in vegetation diversity and equitability are similar for all three topographic positions studied in the moraines (Fig. 4, a

TABLE 2

Characteristics of the vegetation assemblages (VA) recorded on Glaciar Seco foreland. VA were assigned to four major successional stages, and the sequence of stages at different topographic positions on the moraines is schematically represented (successional trajectories).

Vegetation assemblages	Successional stages	Assemblage characteristics	Successional trajectories
VA1	First stage	Vegetation assemblage dominated by the lichens <i>Placopsis perrugosa</i> and <i>Stereocaulon</i> spp. (<i>S. vesuvianum</i> , <i>S. alpinum</i> , and <i>S. paschale</i>), and co-dominated by the terrestrial algae <i>Trentepohlia</i> sp., the lichens <i>Xanthoparmelia adpicta</i> and <i>Lecanora atrata</i> , and the herb <i>Baccharis nivalis</i> . Some graminoids are present with low coverage and sparse distribution.	
VA2	High cover throughout	Vegetation assemblage dominated exclusively by the moss <i>Andreaea</i> sp.	
VA3	Second stage	Vegetation assemblage dominated by the lichens <i>Rhizocarpon eupetraeum</i> and <i>R. geographicum</i> , and co-dominated by the lichen <i>Placopsis cribellans</i> and the trailing shrub <i>Berberis empetrifolia</i> .	
VA4	Low cover throughout	Vegetation assemblage dominated by the small, trailing shrub <i>Baccharis magellanica</i> and the perennial herb <i>Schoenus andinus</i> .	
VA5	Third stage	Vegetation assemblage dominated by the shrub <i>Gaultheria mucronata</i> and an unidentified moss. Species of the lichen genera <i>Sticta</i> (<i>S. gaudichaldia</i> , <i>S. weigeli</i> , and <i>S. fuliginosa</i>) and <i>Cladonia</i> (<i>C. pyxidata</i> , <i>C. fimbriata</i> , <i>C. imbricaria</i> , <i>C. sarmentosa</i> , <i>C. squamosa</i> , and <i>C. subchordalis</i>) are also abundant on the crest and mid-slope of the older moraines.	
VA6	Third stage	Vegetation assemblage dominated by the moss <i>Racomitrium lanuginosum</i> . The perennial herb <i>Gunnera magellanica</i> is present with high coverage in the base of the moraines.	
VA7	Third stage	Vegetation assemblage dominated by the shrubs <i>Empetrum rubrum</i> , <i>Escallonia rubra</i> , and <i>Embothrium coccineum</i> , and the lichens <i>Pseudocyphellaria</i> spp. (<i>P. granulata</i> , <i>P. freycinetii</i> , <i>P. malmeana</i> , <i>P. faveolata</i> , and <i>P. coriifolia</i>). The shrub <i>Berberis microphylla</i> is present with high coverage in the base of certain moraines.	
VA8	Fourth stage	Vegetation assemblage dominated by the tree <i>Nothofagus betuloides</i> , and co-dominated by <i>N. pumilio</i> , the moss <i>Racomitrium</i> sp., an unidentified moss, and various lichen species, such as <i>Xanthoparmelia mougeotii</i> , <i>Nephroma australe</i> , <i>Parmelia saxatilis</i> , <i>P. protosulcata</i> , <i>Pseudocyphellaria crocata</i> , <i>Peltigera rufescens</i> , and <i>P. ponjensis</i> .	

and b). Vegetation diversity and equitability increase early in succession, reach a maximum in the middle age moraines, and show a steady decline in older moraines. The vegetation composition within sites is heterogeneous throughout most of the successional sequence, becoming less variable in the earlier exposed moraines (Fig. 4, c). Diversity, equitability, and heterogeneity are relatively low at the crest of moraine 4, where no vascular plants were registered.

The classification of vegetation according to composition and cover data allows delimiting eight vegetation assemblages which represent species with similar distributions among the sampling plots. Table 2 describes the characteristics of each vegetation assemblage, and Figure 3, parts g–i, shows their relative contributions to total vegetation cover along the chronosequence. On the moraine mid-slope the successional trajectory occurs in four stages (Fig. 3, h; Table 2). During the first stage (<80 years, M1–M4), the VA1 species are the pioneer colonizers forming a one-layer community with algae and crustose lichens growing on boulders, and fruticose lichens, graminoids and herbs sparsely distributed on the unconsolidated material between boulders. About 80–140 years since glacier retreat (second stage, M4–M5), the pioneer saxicolous community is replaced by a community dominated by crustose lichens of the genus *Rhizocarpon* (VA3). As succession progresses, shrubby vascular plants (VA7) form a woody carpet covering the ground surface (third stage, ~140–

260 years, M5–M6). Simultaneously, the *Nothofagus* spp. colonization starts and progressively expands to develop a *Nothofagus*-dominated forest (fourth stage, >260 years, M6–M8). Both the shrub- and *Nothofagus*-dominated stages have a rich ground flora of lichens and mosses (Table 2).

The successional trajectories on the base and crest of the moraines do not apparently follow all the successional stages recorded on the moraine mid-slope (Fig. 3, g and i; Table 2). The shorter successional trajectory occurs on the moraine base, where several vegetation assemblages dominated by shrubs, with a rich ground cover of lichens (VA5, VA6, and VA7), are able to colonize the bare terrains from the very beginning. Succession proceeds to a *Nothofagus*-dominated community (VA8) within 80 years following terrain deglaciation (Fig. 3, i; Table 2). The successional trajectory on the moraine crest is similar to that on the moraine mid-slope, but there is a direct replacement of the lichen-dominated communities (second stage) by a *Nothofagus*-dominated community (fourth stage, Fig. 3, g; Table 2). The intermediate shrubland stage (third stage) apparently does not develop on the moraine crest.

A DCA ordination of sampling plots according to the vegetation composition accounted for 14.2% of species variability in the first two axes (Table 3, analysis 1). The ordination diagram mostly separates moraines along the first axis and topographic positions along the second axis (Fig. 5). Vegetation changes from

TABLE 3

Results of the ordination analyses of vegetation composition and coverage. Eigenvalues (λ) and species-environment correlations for the first and second axis (r), Percentage of species variability explained by the first, second and all canonical axes (%-explained), F -ratio of all canonical axes. Probability level of the Monte Carlo permutation test for all canonical axes $P = 0.002$ for all analyses. Variables associated with the time gradient along the first CCA axis are: Age, Litter, and Percentage of the surface covered by sand, gravel and cobble. Variables associated with the spatial gradient along second CCA axis are: Meso-topographic positions, Slope, Microtopography, Distance from ridge and Percentage of the surface covered by boulders. Yr is the age since terrain deglaciation, Topography refer to topographic positions in the moraine (crest, mid-slope and base), and Yr*Topography indicates their interaction terms.

Analysis	Explanatory variables	Covariables	λ_1	λ_2	r first axis	r second axis	%explained		%explained all canonical axes	F -ratio
							first axis	second axis		
1	DCA	All	0.690	0.413	0.902	0.786	8.9	5.3		
2	CCA	All	0.570	0.294	0.919	0.875	7.3	3.8	18.26	11.542
3	CCA	Variables associated to time	0.523	0.158	0.897	0.669	6.7	2.0	10.70	13.759
4	CCA	Variables associated to space	0.312	0.221	0.766	0.736	4.0	2.8	9.63	10.173
5	CCA	Yr, Topography, Yr*Topography	0.568	0.233	0.914	0.779	7.3	3.0	12.98	17.120
6	CCA	Yr	0.511	0.478	0.888	-	6.6	6.1	6.56	40.543
7	CCA	Topography	0.219	0.065	0.756	0.480	2.8	0.8	3.64	10.917
8	CCA	Yr*Topography	0.185	0.048	0.730	0.411	2.5	0.7	3.20	9.528
9	CCA	Yr, Yr*Topography	0.511	0.184	0.887	0.734	6.6	2.3	9.55	20.265

a lichen-dominated community on the left to a *Nothofagus*-dominated forest on the right (Fig. 5, b). Differences in the course of succession due to topographic positions are evident from the trajectories formed by the centroids for each position and moraine (Fig. 5, b). Ordination of species around the site centroids reflects the composition of the vegetation assemblages that follow different successional trajectories, as previously described from the classification analysis.

SPECIES-ENVIRONMENT RELATIONSHIPS

The CCA ordination including all explanatory variables showed a similar pattern to the unconstrained ordination analysis (Fig. 6), suggesting that the selected explanatory variables are those responsible for species composition variation. High species-environment correlations on the first two ordination axes reveal a close relationship between vegetation changes and explanatory variables (Table 3, analysis 2). Although a small part of the community variability can be ascribed to the explanatory variables, values are close to the proportion of species variance explained by the two first DCA axes (14.2%) which represent the best possible hypothetical environmental gradient.

The first canonical axis was mostly associated with age since deglaciation ($r = -0.93$ between CCA1 and age), consistent with a temporal (successional) gradient in species composition. The first ordination axis was also negatively related to percentage of substrate covered by gravel, cobbles, and sand, and positively to litter, an indication of the progressive replacement of bare terrain by vegetation as succession progresses. The second axis was mostly related to the topographic positions in the moraines, with positive values for the crest ($r = 0.76$), close to zero for the mid-slope ($r = 0.02$), and negative for the base ($r = -0.68$), consistent with the spatial gradient in species composition with meso-topography. The percentage of substrate covered by boulders was related to CCA2, reflecting the larger concentration of boulders at the moraine crests. The second ordination axis was also related to moraine slope and distance from ridge, two variables intercorrelated with meso-topography. Elevated and flat surface microtopographies (no sampling plot was classified as depressed) were correlated to the second axis, with flat sampling plots occurring most often in the moraine mid-slope and base.

Temporal and spatial gradients are almost orthogonal (Fig. 6), consistent with relatively independent influences of

successional dynamics and spatial heterogeneity on community structure. The relative contribution of both gradients is similar, as they explained comparable proportions of vegetation variance (Table 3, analyses 3 and 4). Age since deglaciation and meso-topographic positions are the most important variables related to the vegetation gradients, accounting for 71% of the total variance explainable by all the considered variables (Table 3, analysis 5). Both variables are highly significant, a measure of their influences on the recorded vegetation changes (analyses 6 and 7). The interaction term year \times topography is also significant (analysis 8), suggesting that changes in vegetation composition over time vary significantly with meso-topography. Overall, about 52% of the total explainable variance can be ascribed to the successional trend (year plus the interaction term, analysis 9).

All variables used in our analyses explained a relatively small, but significant, proportion of the vegetation compositional variability (Table 4). The percentage of surface covered by litter also contributes to explain the successional gradient, whereas the percentage of surface covered by boulders and the moraine slope contributes to the spatial gradient.

CONVERGENCE/DIVERGENCE

The ordination diagram of the DCA analysis shows that successional trajectories on different topographic positions tend to converge in the early exposed moraines (Fig. 5, b). Linear regressions between site age and sample scores on the first DCA axis (Fig. 7, a) show significant floristic differences between successional trajectories on the base and the other two meso-topographic positions ($p < 0.001$). Non-significant differences were recorded between the successional trajectories on the moraine mid-slope and the crest ($p = 0.335$). However, differences between mean sample scores on each topographic position were significant from moraines 1 to 5 ($p < 0.001$), but non-significant from moraines 6 to 8 ($p > 0.01$). The lack of significant differences in vegetation assemblages on the different topographic positions at the earlier exposed moraines is a clear indication of convergence in successional trajectories. Consistent with these results, paired comparisons of vegetation composition in different topographic positions show an increase in similarity as succession progresses, converging towards comparable levels of similarity in the earliest exposed moraines (Fig. 7, b). Convergence also occurs within sites, decreasing in heterogeneity with terrain age (Fig. 4, c).

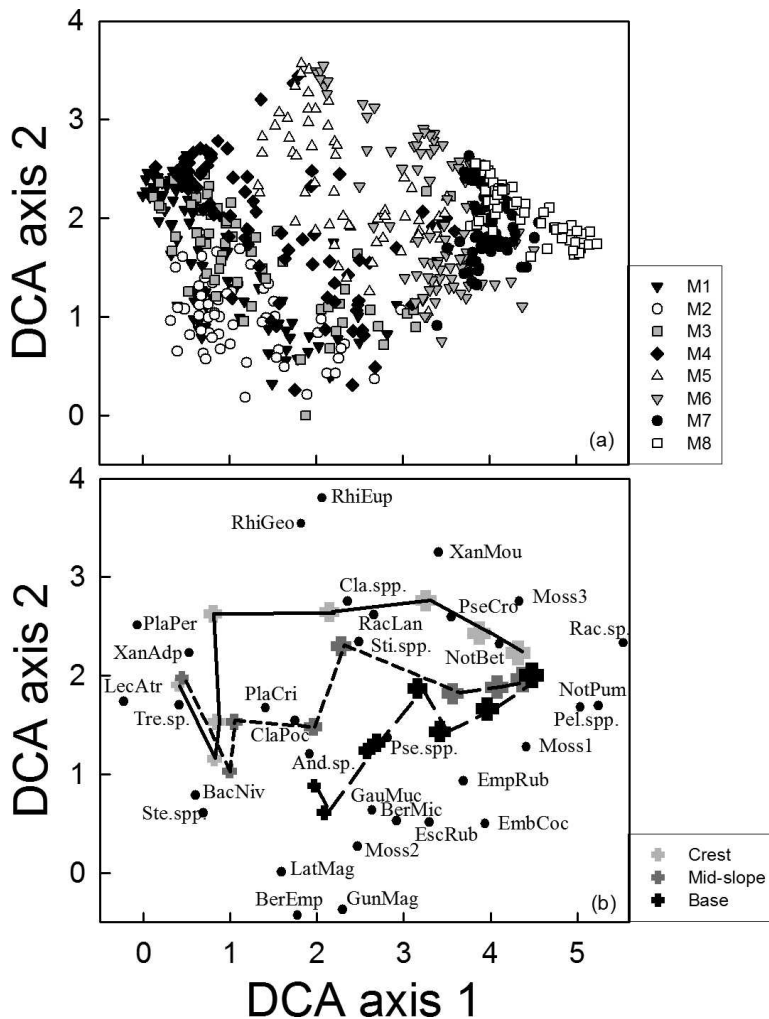


FIGURE 5. Ordination diagrams of the detrended correspondence analysis of vegetation composition and cover for (a) sampling plots and (b) species. In (b) successional trends are displayed as lines connecting the centroids of the successive moraines at the same topographic position. Increasing size of symbols corresponds to increasing age of moraine exposure. Only species with weight >1% are included in the plot. Species abbreviations are: And.sp.: *Andreaea* sp.; BacNiv: *Baccharis nivalis*; BerEmp: *Berberis empetrifolia*; BerMic: *Berberis microphylla*; Cla.spp.: *Cladonia pyxidata*, *C. fimbriata*, *C. imbricaria*, *C. sarmentosa*, *C. squamosa*, and *C. subchordalis*; ClaPoc: *Cladonia pocillum*; EmbCoc: *Embothrium coccineum*; EmpRub: *Empetrum rubrum*; EscRub: *Escallonia rubra*; GauMuc: *Gaultheria mucronata*; GunMag: *Gunnera magellanica*; LatMag: *Lathyrus magellanicus*; LecAtr: *Lecanora atra*; Moss1: Unidentified moss; Moss2: Unidentified moss; Moss3: Unidentified moss; NotBet: *Nothofagus betuloides*; NotPum: *Nothofagus pumilio*; Pel.spp.: *Peltigera rufescens* and *P. ponojensis*; PlaCri: *Placopsis cribellans*; PlaPer: *Placopsis perrugosa*; Pse.spp.: *Pseudocyphellaria granulata*, *P. freycinetii*, *P. malmeana*, *P. faveolata*, and *P. coriifolia*; PseCro: *Pseudocyphellaria crocata*; Rac.sp.: *Racomitrium* sp.; RacLan: *Racomitrium lanuginosum*; RhiEup: *Rhizocarpon eupetraeum*; RhiGeo: *Rhizocarpon geographicum*; Ste.spp.: *Stereocaulon vesuvianum*, *S. alpinum*, and *S. paschale*; Sti.spp.: *Sticta gaudichaldia*, *S. weigelii*, and *S. fuliginosa*; Tre.sp.: *Trentepohlia* sp.; Xan.spp.: *Xanthoparmelia adpicta* and *X. atrobarbatica*; XanMou: *Xanthoparmelia mougeotii*.

Separate canonical correspondence analyses for each moraine show that the topographic position explains an increasing quantity of species variance as succession proceeds, except for the earliest exposed moraine (M8) where meso-topography explains a lower proportion of the vegetation variability (Table 5). However, after about 300 years since deglaciation in M8, topographic positions still account for a significant proportion of the variability in vegetation composition. These results suggest that vegetation variability created by the meso-topographic gradient in the moraines persist throughout the successional sequence.

The similarity between vegetation communities along the successive moraines increased with increasing terrain age (Fig. 8). The relatively low similarities between younger moraines suggest rapid changes in vegetation composition in the earlier stages of

succession. In contrast, higher similarities between the early exposed moraines imply a decline in the rate of vegetation changes in the later stages of succession. However, communities are still changing after 300 years of surface exposure.

Discussion

VEGETATION SUCCESSIONAL TRAJECTORIES

The vegetation development on the Glacier Seco foreland displays clear directional changes along the chronosequence (*sensu* Svoboda and Henry, 1987). The successional sequence can be characterized by four stages, as recorded on the moraine mid-slope (Fig. 3, h; Table 2). Lichens, mosses, and herbs are pioneer

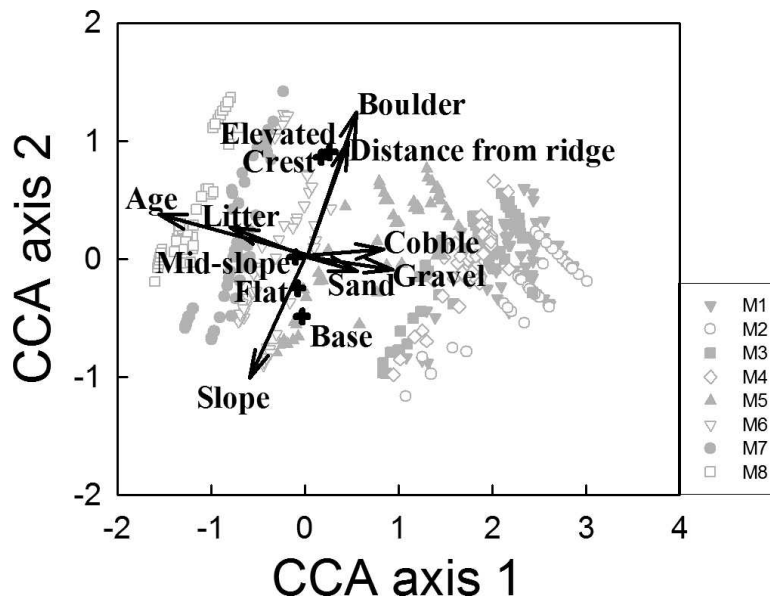


FIGURE 6. Ordination diagram of the canonical correspondence analysis showing the relationship between sampling plots and explanatory variables. Categorical variables are shown as centroids (i.e. meso-topographic positions and microtopography), whereas continuous variables are shown as vectors.

colonizers on deglaciated terrains (first stage, <80 years). During the second stage (~80–140 years), pioneer saxicolous lichens (*Placopsis perrugosa*, *Xanthoparmelia adpicta*, and *Lecanora atrata*) are replaced by secondary colonizer lichens (*Rhizocarpon eupetraeum*, *R. geographicum*, and *Placopsis cribellans*). Colonization seems to be faster on boulders than on fine-grained substrate, as the lichen community dominated by *Rhizocarpon* spp. contributes the largest proportion of total cover during the second stage. About 140 years after glacier retreat, succession becomes dominated by shrubby vascular plants (third stage) and finally by *Nothofagus* forests (fourth stage, >260 years). This pattern of physiognomic development from lichens to trees is consistent with the general trend of successional changes on glacier and volcanic terrains (Matthews, 1992; Cutler et al., 2008a). However, the succession on the Glaciar Seco foreland is peculiar in exhibiting the replacement of saxicolous communities from the first (*Placopsis* dominated) to the second stage (*Rhizocarpon* dominated). These results reveal the existence of succession in lichen communities, a pattern seldom described for primary surfaces (but see Lindsay, 1978; Longton, 1992; Hestmark et al., 2007). Most studies of primary succession are biased to the analysis of phanerogams; however, accounting for the cryptogamic compo-

nents of the vegetation (especially saxicolous species) adds further complexity to the vegetation community assembly on primary surfaces.

Successional trajectories evolving simultaneously in the study area show broad overlap in their compositions, differing mostly in the sequence and timing of the four major successional stages previously described (Fig. 3, g–i; Table 2). Therefore, the successional sequence in Glaciar Seco is deterministic and predictable, although one or more stages may be absent under particular local

TABLE 4

Partial ordination analyses of vegetation composition and coverage. Percentage of species variability explained by each variable including covariation with other factors (marginal effect) and after removing covariation (partial effect). *F*-ratio of all canonical axes estimated using a Monte Carlo permutation test. *P*-value = 0.002 for all analyses, except for sand (*P* = 0.004).

	Marginal %-explained	<i>F</i> -ratio	Partial %-explained	<i>F</i> -ratio
Age	6.6	40.543	4.0	23.45
Meso-topography	3.6	10.917	2.1	6.221
Sand	1.6	9.185	0.5	3.154
Gravel	3.3	19.532	1.1	6.538
Cobbles	2.1	12.691	0.7	4.205
Litter	3.0	17.966	1.6	9.137
Boulders	3.4	20.175	1.7	9.945
Slope	2.8	16.776	1.2	6.879
Micro-topography	2.5	14.972	0.5	3.057
Distance from ridge	2.5	14.962	0.9	5.265

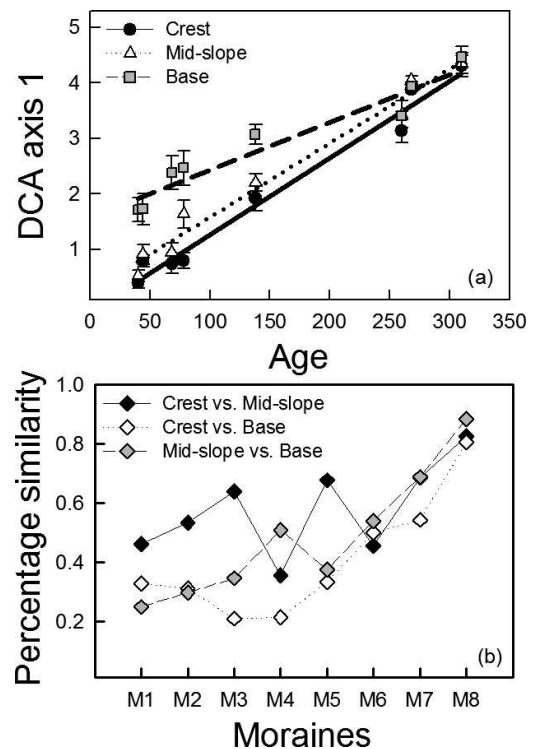


FIGURE 7. Comparison of the successional trajectories for different meso-topographic positions. (a) Linear regressions between the trajectories of the first axis DCA sample scores and time; (b) paired comparison of vegetation composition between meso-topographic positions. Symbols in (a) represents mean sample scores and 95% confidence intervals. All regressions are significant ($p < 0.001$).

TABLE 5

Partial ordination analyses of vegetation composition and coverage for each moraine considering meso-topographic position as explanatory variable. Species-environment correlations for the first and second axis (r), Percentage of species variability explained by all canonical axes (%-explained). F -ratio of all canonical axes estimated using a Monte Carlo permutation test. P -value = 0.002 for all analyses, except for M3 ($P=0.004$).

Moraines	r first axis	r second axis	%-explained all canonical axes	F -ratio
M1	0.890	0.541	10.9	5.333
M2	0.846	0.781	12.7	4.133
M3	0.885	0.653	13.2	4.316
M4	0.918	0.769	15.1	6.83
M5	0.844	0.800	19.4	6.859
M6	0.839	0.788	17.0	8.914
M7	0.926	0.790	21.2	10.394
M8	0.769	0.508	11.1	3.577

conditions. Similar patterns have been recorded on deglaciated terrains elsewhere. Multiple successional trajectories generated by heterogeneous environmental conditions, disturbances, or historical factors show the same dominant species along the succession, even though the number of early and mid-successional stages differs (Fastie, 1995; Raffl et al., 2006). This pattern is due to the particular landscape in which succession on deglaciated terrains occurs. The mature forests on both sides of the valley represent a permanent source of propagules. It is well known that the nearby vegetation has a major influence on the course of succession (Prach and Rehounková, 2006; Lanta and Lepš, 2009). Thus, the proximity to diaspore sources and the potentially small pools of species in deglaciated terrains reduces the stochasticity of colonization, favoring the occurrence of consistent successional sequences in different habitat types. This pattern contrasts with vegetation development on different primary surfaces such as volcanic areas, old fields, and mining sites, where the high diversity of the local flora and the differential availability of propagules generate unpredictable successional trajectories and the development of alternative stable communities (e.g. Wiegleb and Felinks, 2001; del Moral et al., 2010).

CAUSES OF SPATIAL VARIABILITY IN VEGETATION DEVELOPMENT

In concordance to the geocological model of plant succession formulated for glacial areas (Matthews, 1992), our results indicate that meso-topography is an important factor structuring the spatial development of vegetation on the Glaciar Seco forelands (Fig. 5). Vegetation changes occurring in the course of the ~300-year-long successional sequence are comparable to the vegetation variability generated by the spatial gradient in the moraine foreslopes (10.7% and 9.63% of vegetation variance, respectively; Table 3). This implies that the analysis of spatial patterns of vegetation development due to topographic variability allows explanation of twice as much vegetation variability as the classical chronosequence approach does. Indeed, significant interactions between surface age and meso-topography (Table 3) indicate that temporal and spatial factors closely interact to explain vegetation variability. Our results support recent studies emphasizing the importance of analyzing local heterogeneity to understand ecological processes relevant to community assembly in primary succession (e.g. Raffl et al., 2006; del Moral et al., 2009; Cutler, 2010).

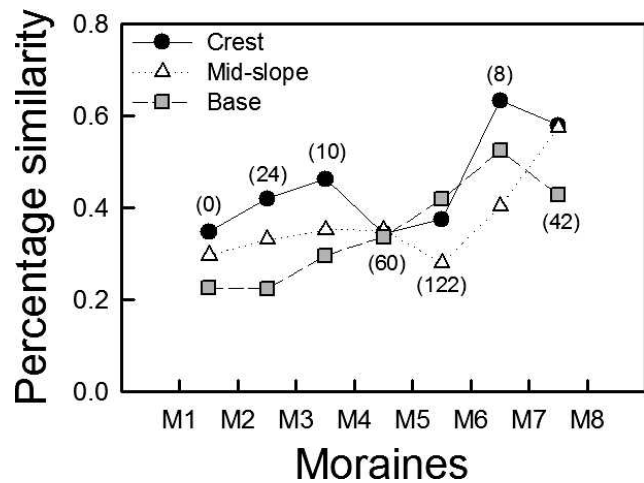


FIGURE 8. Comparison of vegetation composition between successive moraines. Points are located in between the labels for the two moraines compared. Time lapses (in years) between the moraines being compared are indicated in parentheses.

The importance of topography in determining vegetation distribution has been widely discussed in the literature. Topography imposes environmental and resource gradients that influence wind exposure, length of growing season, incident solar radiation, moisture availability, soil development, organic matter and nutrient accumulations (Whittaker, 1989; Franklin et al., 2000; Meentemeyer et al., 2001; Choler, 2005; Bruun et al., 2006; Cutler et al., 2008a; Kharuk et al., 2010). In consequence, variations in environmental conditions across topographic gradients modulate the establishment and growth of plants. The most adverse and favorable conditions for plant growth and establishment generally occur at the ridge-top and the bottom of landforms, respectively (e.g. Vetaas, 1994; Cutler et al., 2008b). Differences in the progression of species richness and cover between topographic positions in Glaciar Seco forelands suggest decreasing rates of vegetation colonization and succession from the base to the crest of moraines (Fig. 3). Therefore, broad trends in vegetation development at Glaciar Seco reflect the controlling effects of topographic-induced environmental gradients.

Vegetation distribution along topographic gradients is also influenced by disturbance processes, such as fire, flood, erosion, mass movement and frost churning (Franklin et al., 2000; Stallins, 2006). Along the primary successional trajectory, disturbances interrupt or reverse the progressive development of vegetation, leading to a mosaic of communities on older terrains (Matthews and Whittaker, 1987; Whittaker, 1989; Hodkinson et al., 2003; Raffl et al., 2006). The influence on vegetation patterns of moraine evolution after deposition has been less studied than other types of disturbance. Following the moraine formation, redistribution of matrix materials is a common process in most unconsolidated glacial deposits. Boulders at the moraine crest gradually become exposed whereas fine-grained materials accumulated at the base (Putkonen and O'Neal, 2006; Schaller et al., 2010). Consistent with these observations, the topographic gradients at the Glaciar Seco moraines are also reflecting differences in the amount of boulders on the surface, with boulders covering most moraine crests (Fig. 6). In addition, our analysis of the floristic and environmental gradients show that the percentage of the surface covered by boulders explains a significant amount of vegetation variability (Table 4), indicating that differences in successional trajectories between topographic positions at Glaciar Seco are partially due to the particle-size distribution along moraine slopes.

Therefore, our results suggest that geodynamic processes of moraine degradation significantly influence the spatiotemporal development of the vegetation in the Glaciar Seco foreland.

The accumulation of boulders on the moraine crest determines the dominance of saxicolous lichen communities for about two centuries after glacier retreat. The lichen assemblages are directly replaced by a tree stratum, without evidence of the transient development of a woody cover of shrubs (Fig. 3, g; Table 2). This abrupt shift in community composition and physiognomy does not seem to follow a sequential process. The growth of *Nothofagus* individuals originally established on the base of older moraines starts to cover the crest of the younger, internal moraines. The effective colonization of *Nothofagus* spp. on the moraine crest at the Glaciar Seco forelands is due to the relatively short distal flanks of the moraines (between 1 and 2 m long), as a result of the partial superimposition of younger moraines upon the earlier moraines. Based on our results we suggest that vegetation succession on the moraine crest is arrested in the lichen-dominated stage until the lateral expansion of mature assemblages determines the progression to a *Nothofagus* forest. Thus, vegetation development on the Glaciar Seco landscape involves interactions between parallel successional trajectories on moraine foreslopes. The late expansion of mature forests partially overrides the early spatial heterogeneity in vegetation development created by meso-topographic gradients.

On the moraine base, the colonization of the shrub and tree strata is apparently not preceded by the development of a ground vegetation cover of cryptogams and herbaceous plants. Although we might have missed the pioneer successional stages at the youngest moraine (44 years at the time of sampling; Table 1), this seems very unlikely given the extremely slow growth rates of lichens. The early colonization by phanerogams is possible due to the favorable microclimatic and edaphic conditions on the moraine base, as previously discussed. In addition, plant establishment in depressed areas is favored by the accumulation of fine-grained substrates and faster soil development (Cutler et al., 2008a). However, the spatial heterogeneity in environmental conditions and the influence of stochastic events on recruitment produce heterogeneous communities in the initial stages of colonization at the moraine base (Fig. 4, c; del Moral, 2009; Robbins and Matthews, 2009). The establishment of phanerogams is usually associated with favorable microsites ("safe sites" *sensu* Harper et al., 1965) that on deglaciated terrains have been characterized as concave surfaces, with relatively coarse-texture substrate and large rocks in their proximities (Jumpponen et al., 1999; Jones and del Moral, 2005). Therefore, multiple environmental factors probably facilitate the pioneer colonization of vascular plants and the fast succession progression on the moraine base.

CONVERGENCE/DIVERGENCE OF THE SUCCESSIONAL TRAJECTORIES

According to the geoecological model of primary succession, vegetation development starts with relatively homogeneous assemblages, which gradually increase in heterogeneity as vegetation development diverges into different successional assemblages modulated by environmental gradients (Cutler et al., 2008a; Dolezal et al., 2008; Robbins and Matthews, 2010). Increasing heterogeneity in the communities is due to a greater sensitivity of late-colonizing species to differences in environmental conditions and to a decreasing impact of disturbances, which in turns allows the establishment of a larger array of species (Robbins and Matthews, 2010). On the other hand, if stochastic dispersal effects and limited

availability of safe sites regulated early assembly of the communities, vegetation variability is higher in the earlier stages of succession (del Moral et al., 2005). Vegetation successional patterns converge later due to the presence of competitive, dominant species, which establish across most of the different environmental conditions (Vetaas, 1994; Baer et al., 2005; Woods, 2007).

The spatiotemporal dynamics for the Glaciar Seco foreland conforms to the second pattern with a strong convergence of the successional trajectories to the development of a *Nothofagus*-dominated forest (Fig. 7). The successional convergence reduces the overall diversity from 56 species in the youngest to 33 species in the earliest exposed moraines, suggesting competitive sorting of the vegetation (Woods, 2007). At the time of our sampling at Glaciar Seco in January 2009, a continuous forest of *Nothofagus* spp. was covering the glacial deposits from the trimline to the base of the M7 and reaching in some sectors the crest of the M6 (Fig. 1). However, significant floristic differences persist among topographic positions after more than 300 years since deglaciation (Table 5). Heterogeneity in late-successional vegetation assemblages is related mostly to differences in accompanying cryptogams, reflecting the remarkably higher richness and coverage of lichens and mosses at the crest than at the base of the earliest exposed moraines (Fig. 3). Floristic differences are also remarkable. The ground cover is mostly characterized by saxicolous lichens at the moraine crest (e.g. *Xanthoparmelia mougeotii*, *Nephroma australe*, *Parmelia saxatilis*, and *P. protosulcata*), whereas terricolous lichens dominated at the moraine mid-slope and base (e.g. *Peltigera rufescens* and *P. ponojensis* at the mid-slope; *Sticta gaudichaldia*, *S. weigeli*, and *S. fuliginosa* at the base). Local differences in vegetation at the ground surface reflect the persistence of large, unburied boulders at the moraine crest, and deeper soil development and litter accumulation on other moraine positions. These patterns suggest that after 300 years since deglaciation, pre-existing spatial heterogeneity in the physical environment is not completely overridden by the forest development. Meso-topographical differences remain influential for understory development on a multi-century time scale. Our results support the observations of del Moral et al. (2010) indicating that even when trees dominate, understory vegetation retains variation initiated during early succession and maintained by topographical differences. On the Glaciar Seco foreland, remaining variations in the lower vegetation strata under the *Nothofagus* dominated canopy is largely the legacy of the redistribution of the matrix material by the slope moraine degradation.

Acknowledgments

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