

# Colonization of mid- and late-Holocene moraines by lichens and trees in the Magellanic sub-Antarctic province

Irene A. Garibotti<sup>1,2</sup> · Ricardo Villalba<sup>1</sup>

Received: 14 May 2016 / Revised: 8 August 2016 / Accepted: 8 February 2017  
© Springer-Verlag Berlin Heidelberg 2017

**Abstract** Understanding the process of primary succession is a relevant topic in restoration and global change ecology, and provides the basis for classic dating methods in geomorphology, such as lichenometry and dendrochronology. The aim of this study is to investigate the colonization by lichens and vascular plants of two pro-glacial chronosequences encompassing the late- and mid-Holocene periods in the sub-Antarctic sub-region of South America. We use this information to address questions related to the pattern of Magellanic forests recovery after disturbance and the applicability of lichenometry for developing glacier retreat chronologies. Progression of succession to a state with high vascular plant cover was slow, and some moraines remained unforested for about 2000 years. Our results contrast with previous reports indicating a quick development of mature forest states on disturbed terrains, suggesting large regional variability on the course of succession. Environmental conditions seem propitious for lichens that colonize immediately after moraine formation. Lichens grow at relatively high rates in comparison to other world areas, but half as fast as in Antarctica and sub-Antarctic islands. Growth rates for the *Rhizocarpon* Ram. em. Th. Fr. sub-gen. *Rhizocarpon* group increase with lichen sizes up to ca. 50 mm and decrease in larger thalli, leading to a sigmoidal lichenometric growth curve that extends the applicable range of lichenometry to the last 5700 years

in dry sites in the Magellanic province of the sub-Antarctic sub-region. Our results suggest that lichenometry is an effective technique in multi-proxy approaches for reconstructing glacier fluctuations, and agree with early studies in Antarctica suggesting that lichen annual growth rate is a sensitive attribute for the biomonitoring of climate changes.

**Keywords** Glacier retreat · Primary succession · *Nothofagus* temperate forests · Pioneer species · *Rhizocarpon* · Lichenometry

## Introduction

Increasing levels of human disturbance and concerns on the ecological effect of climate changes pose particular interest on vegetation succession (Walker and Del Moral 2003). The understanding of community assembly and successional regimes can provide insights for prediction of short- and long-term effects of climatic change and other disturbances on terrestrial ecosystems, and contribute to the implementation of valid practices for ecological restoration (Prach and Walker 2011). Primary succession has also been of interest in geological research. Based on the assumption of rapid colonization by lichens and trees on the disturbed terrains, lichenometry and dendrochronology have been used as a proxy for dating surfaces of unknown exposure age, such as glacier moraines, lava flows, rockslides and fault earthquakes (Innes 1985; Solomina 2002).

The sub-Antarctic sub-region in South America includes a large forested landscape with areas lightly affected by anthropogenic disturbances. Thus, it provides the unique opportunity for studying the effect of climate changes on physical and biological systems with reduced influences of confounding human activities. In addition, the presence

✉ Irene A. Garibotti  
ireneg@comahue-conicet.gob.ar

<sup>1</sup> Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, CCT-CONICET Mendoza, C.C. 330, 5500 Mendoza, Argentina

<sup>2</sup> Present Address: Instituto de Investigaciones en Biodiversidad y Medioambiente, CCT-CONICET Patagonia Norte, Quintral 1250, 8400 Bariloche, Argentina

in the Patagonian Andes of steep gradients in temperature and rainfall determine a large heterogeneity in habitats over relative short distances (Veblen et al. 1996; Villalba et al. 2003). Different ecological processes along these gradients are related to changes in climate conditions. The characterization of such ecological differences will help predict the impacts of climate changes on ecosystems.

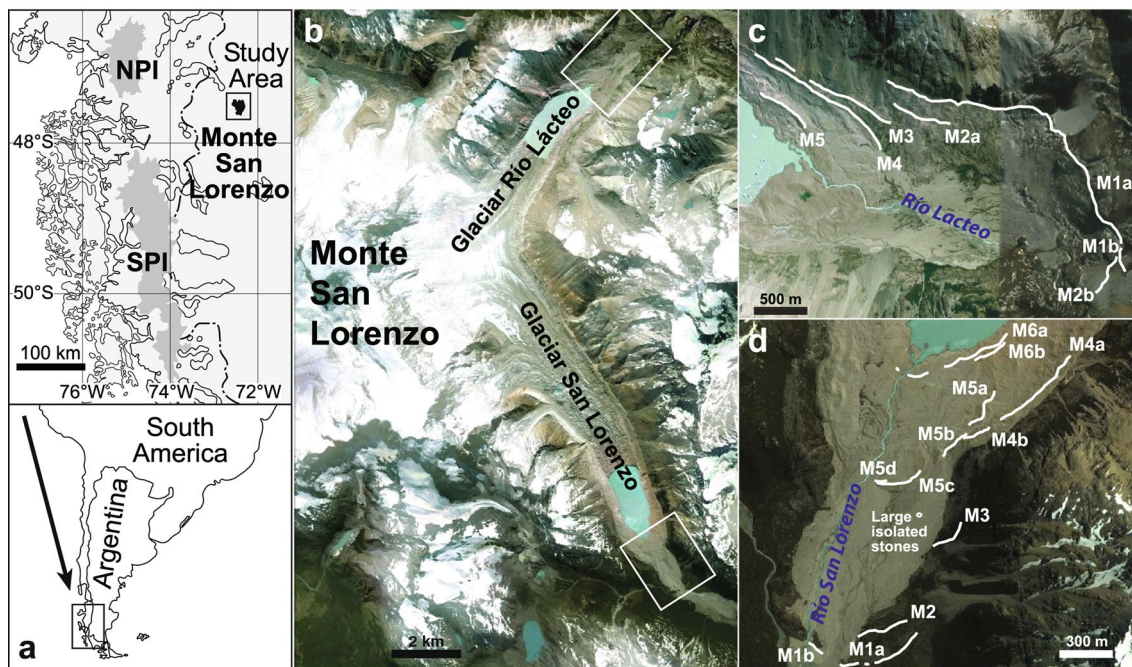
Glacier retreat is a remarkable sign of climate changes in the sub-Antarctic sub-region in South America, and primary succession a conspicuous component on this landscape (Armesto et al. 1992; Villalba et al. 2005; Perez et al. 2016). Studies of primary succession in this sub-region are rare. Previous studies indicate that lichens are swift colonizers in bare surfaces exposed by glacier retreat or other disturbances (Veblen and Ashton 1979; Garibotti et al. 2011c). Pioneer lichen species are replaced by a more diverse lichen- and moss-dominated community, and by vascular plants as succession proceeds (Garibotti et al. 2011b). The colonization time lag for *Nothofagus* trees can vary from a few years to several decades (Lawrence and Lawrence 1959; Villalba et al. 1990; Armesto et al. 1992; Winchester and Harrison 2000), and the rate of progression to a *Nothofagus*-dominated community is also highly variable, ranging from 30 to 250 years (Garibotti et al. 2011b, c; Sancho et al. 2011; Arróniz-Crespo et al. 2014). Local scale conditions and climatic factors associated with latitudinal and elevation gradients may play an important role in determining these differences in successional rates. Old-growth forests are generally monospecific, with the species *Nothofagus pumilio* dominating the sub-alpine forests in the southern Andes from about 35°S to 55°S at the southernmost point of the continent in Tierra del Fuego. These forests are usually not found in compositional equilibrium or climax condition due to recurrent disturbances such as mass movements, volcanic ash deposition, fire, wind-blown down and flooding (Veblen et al. 2016).

The relatively little knowledge on ecological primary succession in the sub-Antarctic sub-region in South America introduces some limitations on the use of lichenometry and dendrochronology methods for dating Holocene landforms and processes. For example, ecological data on succession are necessary to support assumptions concerning lichen and tree population dynamics, such as colonization and mortality rates. This information determines the possibility of accurately estimating lichen and tree ecesis and identifying the first-generation individuals on the disturbed surfaces (Loso and Doak 2005; Koch 2009). Recently, Osborn et al. (2015) summarized well-established limitations of the lichenometric technique and discourage the continuity of its use for absolute dating due to the reduced knowledge on lichen biology. In spite of these criticisms, a large body of information on paleoenvironmental reconstruction, hazard assessment and geomorphological

processes around the world is based on lichenometry, and most studies have shown a good level of agreement between ages estimated using lichenometry and other dating techniques (e.g. Konrad and Clark 1998; Savoskul 1999; Benson et al. 2007; Barclay et al. 2009; Licciardi et al. 2009; Young et al. 2009; Wiles et al. 2010; Badding et al. 2013). The use of this technique for over 80 years has resulted in a considerable amount of data on lichen growth rates, with several studies showing that lichen colonization and growth rates are strongly related to variability in climate conditions (Porter 1981; Evans et al. 1999; Matthews 2005; Garibotti and Villalba 2009; Trenbith and Matthews 2010; Garibotti et al. 2011a; Roof and Werner 2011). Accordingly, lichen growth rate has been proposed as a suitable parameter for monitoring the impact of global climate change in Antarctic and sub-Antarctic areas (Sancho and Pintado 2004; Sancho et al. 2011).

In this study, we analyzed the colonization of lichens and trees along two long-term chronosequences of glacier retreat spanning the last 5500 years in the Magellanic province of the sub-Antarctic sub-region. We simultaneously consider lichens and vascular plants since they are organisms with contrasting ecological requirements, contributing to a better understanding of the responses and processes of individual organism groups. In the context of ongoing global changes, it is relevant to determine the different responses of lichens and vascular species to climate changes in polar and sub-polar areas (Cornelissen et al. 2001; Bokhorst et al. 2007). In addition, a better understanding of the pattern of lichen and tree colonization provides an ecological perspective to address questions about the use of lichenometry and dendrochronology methods. Therefore, we seek to address ecological and methodological issues that derive from the analysis of the primary succession process. The specific aims of the study are to (1) use a retrospective approach to evaluate lichen and vascular plant establishment in the primary terrains, (2) estimate changes in lichen growth rates with thallus size and calibrate a lichenometric dating curve, (3) critically examine the usefulness of lichenometry and dendrochronology to date mid- and late-Holocene glacial events in this sub-polar area, and (4) use a multiproxy dating approach based on a combination of historical documents, lichenometry, dendrochronology and radiocarbon ages to reconstruct past fluctuations of Río Lácteo and Río San Lorenzo glaciers at Monte San Lorenzo in southern Patagonia (Fig. 1).

To retrospectively evaluate lichen and vascular plant colonization, we applied lichenometry and dendrochronology methods in conjunction with vegetation mapping through remotely sensed images. We used the lichens within the genus *Rhizocarpon* Ram. em. Th. Fr. sub-gen. *Rhizocarpon* group and the tree *Nothofagus pumilio* (Poepp. et. Endl.) Krasser (lenga) as our focal species of study. Three



**Fig. 1** **a** Location map of Monte San Lorenzo in the southern Andes and **b–d** moraine (M) sequences at Glaciar Río Lácteo and Glaciar San Lorenzo. *NPI* North Patagonia Icefield, *SPI* South Patagonian Icefield

attributes make these species of special relevance for study in the Magellanic rainforests: (1) they contribute to key stages of primary succession in Magellanic forests, with lichens within the *R.* sub-gen. *Rhizocarpon* dominating early rock-surface colonization and being replaced by a tree stratum dominated by *N. pumilio* in the later stages of succession (Garibotti et al. 2011b); (2) they are long-living organisms, with *R.* sub-gen. *Rhizocarpon* apparently having maximum lifespans around 9000 years (Benedict 2009; Armstrong and Bradwell 2010), and *N. pumilio* a longevity of approximately 400–500 years; (3) the *R.* sub-gen. *Rhizocarpon* has been widely studied in the region, Antarctica and other areas, allowing to put our results in regional and global contexts.

## Methods

### Study area

The Southern Andes represents the largest ice-covered region in the Southern Hemisphere outside Antarctica, including the North and South Patagonian Icefields and many other areas with smaller ice masses. Monte San Lorenzo, located in the border between Argentina and Chile (47°35'S, 72°18'W), constitutes a relatively large ice-capped mountain independent from the two Patagonian Icefields (Fig. 1a). It is the highest mountain in the

Argentinean Patagonian Andes (3706 m) and the largest easternmost glacierized area in southern South America. It is covered by a glacier surface area of ca. 140 km<sup>2</sup> with four large valley glaciers, three in the Argentinean sector (Falaschi et al. 2013). We studied Río Lácteo and Río San Lorenzo valleys at Monte San Lorenzo that exhibit sequences of five and six distinct and well-preserved moraine ridges (M), respectively (Fig. 1).

The climate in the southern Patagonian Andes is temperate and windy, dominated by the persistent westerly flow that determines abundant precipitations evenly distributed throughout the year. The Andes is a major orographic range representing a massive barrier to the Westerlies. In southern Patagonia, the Andes generates a steep west–east precipitation gradient from ca. 8000 mm/year in the highest peaks to less than 300 mm/year within 100 km east of the main divide (Villalba et al. 2003; Lenaerts et al. 2014). Regional climate models estimate that Monte San Lorenzo area receives more than 2000 mm of annual precipitation (Lenaerts et al. 2014). However, precipitation amounts strongly depend on local topography, so that annual precipitation may be much lower in the eastern Argentinean side of Monte San Lorenzo due to the marked rain shadow effect. In Río San Lorenzo valley, 9 years (2002–2009 and 2012–2014) of temperature and relative humidity records indicate a mean annual temperature of 4.2°C, ranging from 0°C in July to 8°C in January, and air relative humidity of 64%. Air relative humidity is uniformly distributed

throughout the year, indicating that precipitation occurs all year round. The study area is characterized by sub-Antarctic deciduous forests largely dominated by *N. pumilio* with small patches of *N. antarctica* that typically grow in transitional areas characterized by precipitation of ca. 800 to 1000 mm per year (Veblen et al. 1996).

### Vegetation colonization and coverage

Vascular plant colonization on glacier forelands was assessed through remotely sensed images. Percent cover of tree and non-tree vegetation was quantified using digital image classification based on 500-point random samples within the polygon that defines the moraine and intermoraine areas (i-Tree Canopy, i-Tree Software Suite v6.1., USDA Forest Service). The analysis was based on the high-spatial resolution imagery available through Google Maps. Several studies have demonstrated the accuracy of Google Earth imagery for spatial location, proportion and distances (Fisher et al. 2013 and references therein).

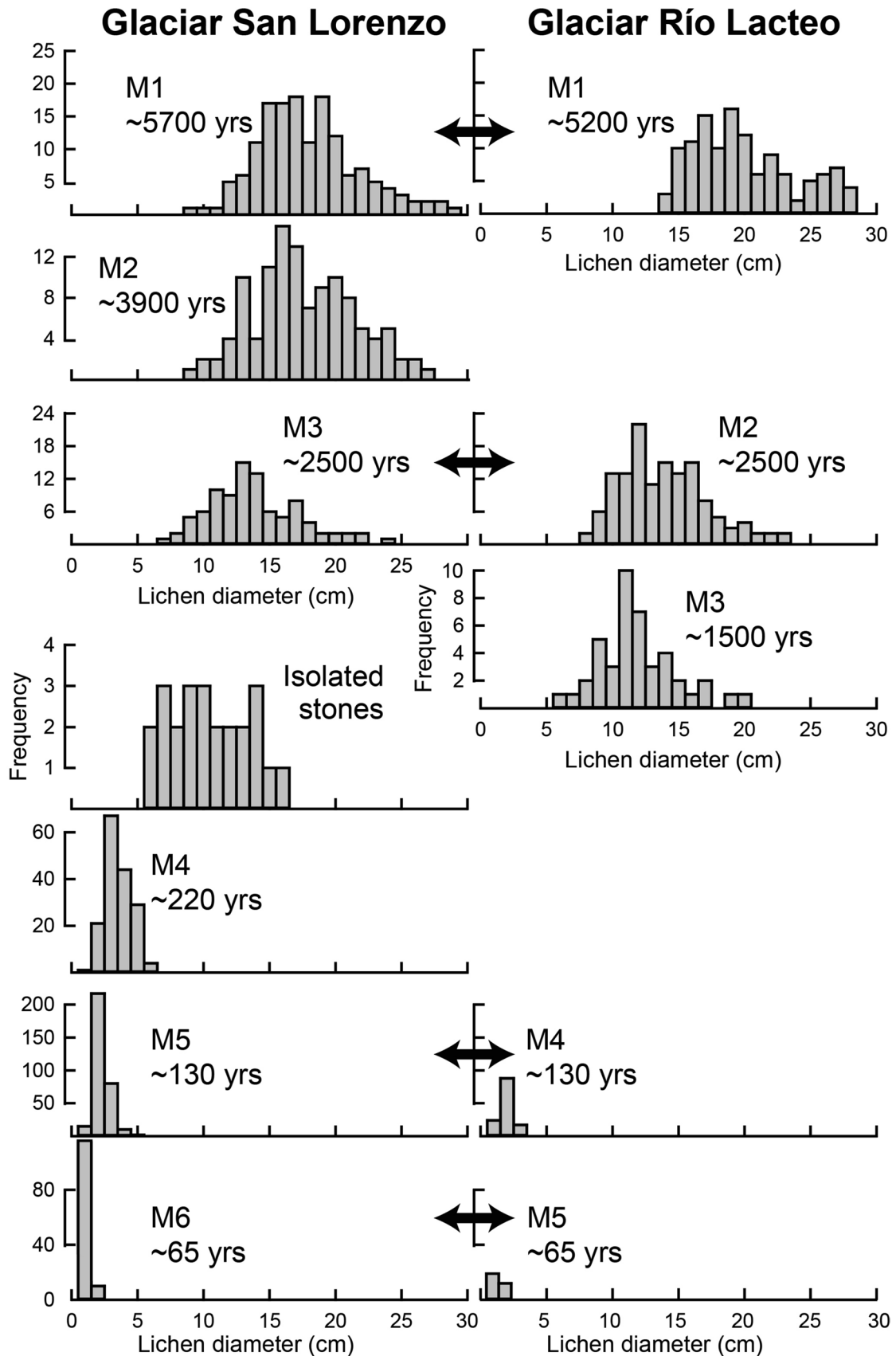
Dendrochronological methods were used to estimate the ages of the oldest trees growing on the moraines. Since trees are rare or absent on most internal moraines, most trees were sampled in the distal moraines. In addition, many trees showing a krumholz form limit the use of dendrochronological sampling for age determination. *N. pumilio* trees growing on lateral and terminal moraines were sampled using 5-mm increment borers. Cores were taken as close to the root collar as possible to minimize potential errors associated with increasing sampling heights. Most trees were cored between 30 and 100 cm from the trunk base. For *N. pumilio* trees, errors in age estimation from cores sampled up to 1 m above the root collar do not exceed 15 years (Winchester and Harrison 2000; Masiokas et al. 2010). Cores were mounted using standard dendrochronological procedures (Stokes and Smiley 1996), and tree ages were derived from ring counts under a stereomicroscope.

### Lichen colonization and growth rates

To reduce the uncertainties of the lichenometric method (Osborn et al. 2015), we were particularly careful regarding moraine search strategies, lichen identification, lichen measurements and post-field data processing. To eliminate uncertainties associated with different methods, we applied the same methodology for estimating the lichenometric dating curve and for dating surfaces of unknown age. Criteria for selecting the most adequate methods are given in Garibotti and Villalba (2009). We measured the sizes of *R.* sub-gen. *Rhizocarpon* specimens on the moraines following the classical lichenometric procedures recommended by Innes (1985) and McCarroll (1995). Measurements were conducted on the moraine crests and proximal slopes, and

the entire length of individual moraines was searched for the largest thalli. The longest axis of the largest specimen of the *R.* sub-gen. *Rhizocarpon* on individual boulders was measured using a flexible steel ruler. Our data include 2867 thallus measurements. Healthy lichens without evidences of thalli coalescence, such as a break in the areolae pattern or a strip of prothallus between the areolae, were measured. Thalli showing irregular borders or degradation were not included. Consistent size–frequency histograms of the largest lichens on each moraine were produced (Fig. 2) to properly assess whether the recorded lichens belong to a single homogeneous population (McCarroll 1995). In addition, the size of the largest thallus and the mean of the five largest thalli shows a consistent relationship ( $r^2=0.99$ ), suggesting that the largest lichen is not anomalous and belongs to the sampled population. We based our results on the analysis of the largest lichen thallus in each population since lichen growth rates estimated using this method provide a simple relationship between lichen size and surface age. This parameter can be compared to previous results obtained in Antarctic, sub-Antarctic and other world areas to infer lichen colonization and growth rate variability across environments. Although different statistical methods have been proposed for modeling changes in population structure over time and estimating uncertainties in lichenometry, their reliability is still under discussion due to insufficient knowledge on lichen biology (Innes 1983a; McCarthy 1999; Loso et al. 2014).

We refer our results to the *R.* sub-gen. *Rhizocarpon* group since morphology-based species circumscriptions in the field are misleading, and the precise identification of the species requires microscopic examination and chemical spot testing. Lichen specimens were collected from different moraines and identified in the laboratory following the microscopic examination of the reproductive structures and using chemical spot tests. We used the taxonomic keys proposed by Poelt et al. (1988), although we acknowledge that the taxonomy of the genus is under review (Roca Valiente et al. 2016). No *Rhizocarpon* taxonomy is presently available for the Southern Andes. The species identified were: *R. geographicum* (L.) DC., *R. riparium* Rasanen and *R. ridescens* (Nyl.) Zahlbr., belonging to the section *Rhizocarpon*, and the species *R. superficiale* (Schaerer) Vainio that pertains to the section *Superficiale*. Due to the dominance of *R. geographicum* in the collected samples (35 out of 40 samples), we assumed that most lichenometric measurements were made on this species, reducing the uncertainties of measuring species with different growth rates. No samples from the section *Alpicola* were identified, which colonize later but grow faster than those of the section *Rhizocarpon* (John 1989). Previous studies in the region did not report a successional replacement of the section *Rhizocarpon* by *Alpicola* (Garibotti et al. 2011b), as it has



**Fig. 2** Size–frequency distributions of the largest lichens on the studied moraines at Glaciar Río Lácteo and Glaciar San Lorenzo

been reported in the northern Hemisphere (Innes 1983b; Matthews and Trenbith 2011).

To constrain lichen colonization and growth rates, we measured the size of lichens growing on control points from which precise dating control is available based on historical photos and published radiocarbon dating (Table 1). The references for control point dating are: (1) Historical aerial photos taken in 1958 by the Military Geographic Institute of Argentina, which show the fronts of Glaciar Río Lácteo and Glaciar San Lorenzo in contact with M5 and M6, respectively (Fig. 3a, b). The aerial photographs provide a minimum age for M5 and M6 formation of 54 years at the time of field sampling. (2) A historical photo taken in 1937 by de Agostini (1945), which shows the front of Glaciar Río Lácteo laying behind M4 (Fig. 3c, d), and suggests a minimum age of 75 years for M4 formation. (3) Mercer (1968) indicated that the outermost terminal moraine (M1) at the Río Lácteo valley closed the drainage of a small nearby valley creating a lagoon in the distal side of the moraine. A piece of wood buried in this lagoon by approximately 1 m of clay and 1 m below the present level of the lake was radiocarbon dated to  $5223 \pm 353$  cal years

BP by Mercer (1968). The author indicated that this wood remnant correspond to the drowned forest that was killed as a consequence of lagoon formation by M1.

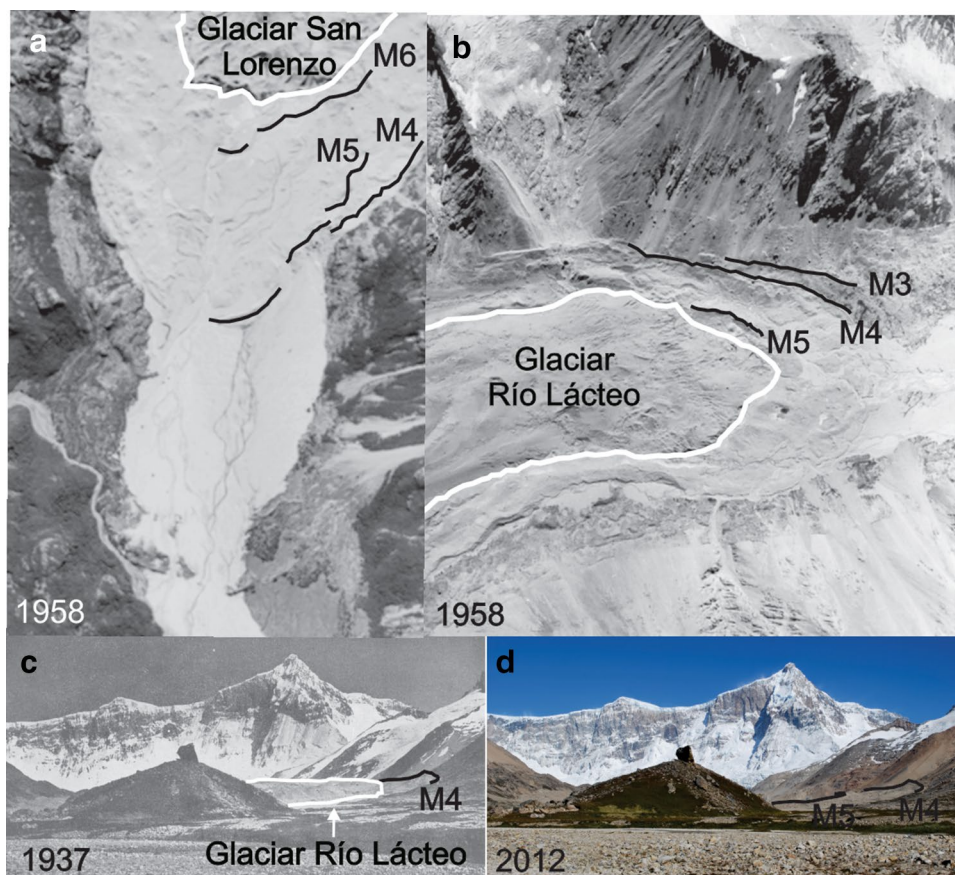
Lichen mean annual growth rates were indirectly determined for thalli of different sizes based on moraine ages and the largest lichens growing on a particular moraine. Since indirect determined growth rates integrate the effect of changing climate conditions on lichen growth, this metric should be used to represent lichen growth over long periods (Trenbith and Matthews 2010; Roof and Werner 2011). Alternative models of lichen growth rate (surface age vs. lichen growth rates) have been proposed for the *R.* sub-gen. *Rhizocarpon* group, each leading to a characteristic lichenometric growth curve (surface age vs. thallus size). In this study, the lichen growth rate models proposed by Trenbith and Matthews (2010) for Norway, which leads to linear, concave-upward, convex-upward and sigmoidal growth curves, were considered to recalibrate the lichenometric growth curve from *R.* sub-gen. *Rhizocarpon* developed by Garibotti and Villalba (2009) for relatively dry sites in the Patagonian Andes. We also considered a logarithmic and linear composite growth curve model that

**Table 1** Lichenometric and reference dates for the moraine sequences of Glaciar Río Lácteo and Glaciar San Lorenzo at Monte San Lorenzo, in the Magellanic province of the the sub-Antarctic sub-region

Glacier	Largest lichen size (cm)	Estimated age (years)	Reference age (years BP)	Source of reference date
<b>Glaciar Río Lácteo</b>				
Moraine 1a	27.9	$5250 \pm 360$	$5220 \pm 353$	Radiocarbon dating by Mercer (1968)
Moraine 1b	27.9	$5250 \pm 360$		
Moraine 2a	21.8	$1930 \pm 40$		
Moraine 2b	22.7	$2180 \pm 50$		
Moraine 3	19.8	$1490 \pm 20$		
Moraine 4	2.7	90	>75	Terrestrial photo by de Agostini (1945)
Moraine 5	1.9	65	>54	Aerial photo by the Military Geographic Institute of Argentina
<b>Glaciar San Lorenzo</b>				
Moraine 1a	27.2	$4520 \pm 260$		
Moraine 1b	28.3	$5750 \pm 430$		
Moraine 2	26.4	$3880 \pm 180$		
Moraine 3	23.6	$2470 \pm 70$		
Large isolated stones	15.7	$910 \pm 5$		
Moraine 4a	5.7	220		
Moraine 4b	4.8	180		
Moraine 5a	3.4	120		
Moraine 5b	3.1	110		
Moraine 5c	3.0	100		
Moraine 5d	3.6	130		
Moraine 6a	1.9	65	>54	Aerial photo by the Military Geographic Institute of Argentina
Moraine 6b	1.8	60		

Lower-case letters correspond to different sectors of the moraines as shown in Fig. 1. Reference dates are available for four of the studied moraines. Ages of moraines were estimated using a sigmoid lichenometric growth model, with error in the older surfaces corresponding to the uncertainty over the radiometric dating of M1 in Glaciar Río Lácteo

**Fig. 3** **a, b** Aerial photographs showing the position of Río Lácteo and San Lorenzo glacier front in 1958, and **c, d** paired photograph showing changes in Glaciar Río Lácteo extension between 1937 (de Agostini 1945) and 2012 (photo by R. Villalba). Numbers for the moraines as given in Fig. 1



has been shown to best fit data from Alaska (Wiles et al. 2010). The best-fit model for our data was determined by visual inspection of scatter graphs and regression analyses between lichen sizes and annual growth rates. An analysis of variance (ANOVA) for the regression indicates whether under the fitted model the independent variable significantly contribute to the prediction of the dependent variable. We selected the model that explains the largest proportion of the total variance in the data, with significant coefficients for all the non-linear terms. Dating of glacier deposits of unknown age was based on the new lichenometric growth curve.

## Results

### Tree colonization and forest development

Not all moraines in the Río Lácteo and Río San Lorenzo valleys are vegetated. As inferred from remote images, the conspicuous colonization of moraine fields by vascular plants started ~65 to 130 years after moraine formation. Coverage of vascular vegetation increases gradually after ecesis (Table 2). We observed in the field that the youngest moraines are not yet colonized by trees. The most internal

moraines with *N. pumilio* trees are estimated to be 2100 and 2350 years old for Río Lácteo and Río San Lorenzo valleys, respectively. On the outermost moraines studied for Glaciar Río Lácteo and Glaciar Río San Lorenzo, forest canopy cover remains sparse, with approximately 50% of the vegetation cover corresponding to trees. The oldest *N. pumilio* trees sampled on these moraines were 310 and 350 years old, respectively (Table 2).

### Lichen colonization and growth rates derived from control points

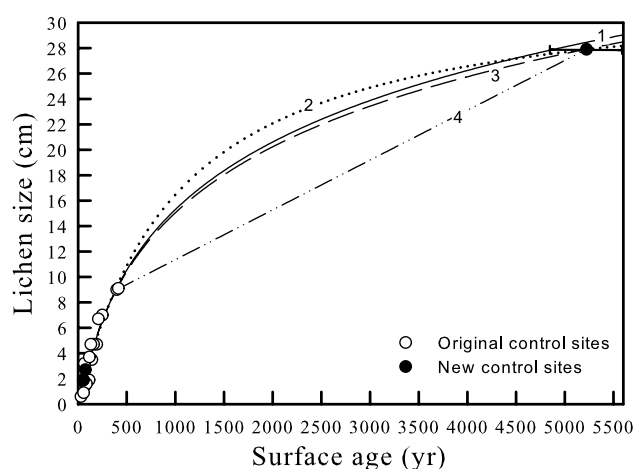
The largest lichens of *R.* sub-gen. *Rhizocarpon* measured in M5 at Glaciar Río Lácteo and M6 at Glaciar San Lorenzo are 1.9 cm in diameter (Table 1), estimated to be 64 years old using the lichenometric curve for relatively dry areas in Patagonia (Fig. 4). According to this age and the minimum precise control date of moraines formation derived from the historical photos of the glaciers (Fig. 3a, b), lichens appeared to have colonized immediately after moraine formation, showing a mean rate of growth of approximately  $0.30$  to  $0.35$  mm year<sup>-1</sup>.

M4 at the Glaciar Río Lácteo has a maximum lichen diameter of 2.7 cm and an estimated age of 93 years (Table 1). Lichens are ~18 years older than the minimum

**Table 2** Percent cover of vegetation (tree and non-tree) and age of the oldest *Nothofagus pumilio* (lenga) tree sampled on the inter-moraine surface areas in the forelands of Glaciar Río Lácteo and Glaciar San Lorenzo at Monte San Lorenzo

Estimated date of the surface	Tree cover (%)	Vegetation non-tree cover (%)	Bare soil (%)	Tree age (years)
<b>Glaciar Río Lácteo</b>				
>5250 years	52.0±3.2	47.2±3.2	0.8±0.6	310
2200–1500 years	62.7±3.1	34.1±3.0	3.2±1.1	–
1500–90 years	0	33.2±3.0	66.8±3.0	–
90–65 years	0	6.0±2.4	94.0±3.4	–
<65 years	0	0	100	–
<b>Glaciar San Lorenzo</b>				
>5750 years	41.8±3.1	49.8±3.1	8.4±1.8	350
5750–3900 years	53.2±3.2	46.8±3.2	0	246
3900–2500 years	76.4±2.7	25.6±2.8	0	196
2500–220 years	20.8±2.6	41.2±3.1	38.0±3.1	–
220–130 years	0	1.1±1.1	98.9±1.1	–
<130 years	0	0	100	–

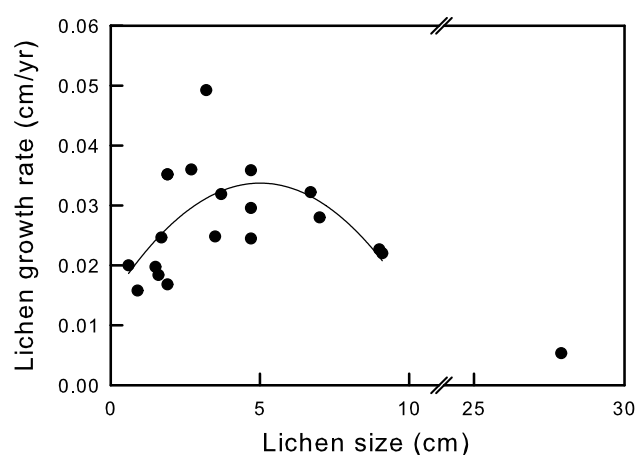
The age of the studied surfaces is constrained by the moraines that form their boundaries



**Fig. 4** Alternative models for fitting the lichenometric dating curve for *Rhizocarpon* Ram. Em Th. Fr. sub-gen. *Rhizocarpon* group in dry sites in the Magellanic province of the sub-Antarctic sub-region: (1) extrapolated original logarithmic, (2) new sigmoid, (3) new logarithmic and (4) new composite curve models. White dots indicate the control points used in the previous established lichenometric curve (Garibotti and Villalba 2009) and black dots indicate the new control points used in this study for recalibrating the original curve. An error bar (2 sigma) is shown for the earlier control point due to uncertainty over the radiometric dating

date of moraine formation estimated from the historical photo taken in 1937 by de Agostini (1945, Fig. 3c, d). Based on this lichenometric age, the lichen mean growth rate is approximately  $0.30 \text{ mm year}^{-1}$ .

At the Río Lácteo valley, M1 is formed by very large boulders colonized by specimens of lichens of the *R.* sub-gen. *Rhizocarpon* with a maximum size of 27.9 cm in diameter (Table 1). The diameters of the lichens growing on M1 are consistent with the  $^{14}\text{C}$  age, providing a minimum



**Fig. 5** Parabolic growth rate model for thalli of *Rhizocarpon* Ram. Em Th. Fr. sub-gen. *Rhizocarpon* growing in dry sites in the Magellanic province of the sub-Antarctic sub-region

moraine age of 4900 years based on the extrapolation of the original lichenometric curve for dry sites. Radiocarbon dating yields a range of ages from 4867 to 5573 cal years BP for M1, implying that the mean growth rate of the larger lichens growing in this moraine is estimated to be between  $0.05$  and  $0.06 \text{ mm year}^{-1}$ .

A scatter graph combining the lichen size–age data from the control points and those previously published for other relatively dry areas in the region shows that annual mean growth rates varied from  $0.16$  to  $0.50 \text{ mm year}^{-1}$  for lichens sizes below 10 cm in diameter (Fig. 5). A linear growth rate model poorly fits the data ( $R=0.10$ ,  $p=0.69$ ) indicating that growth rates are not likely constant as lichen size increases. Similarly, logarithmic and exponential models indicating either a decrease or an increase in growth



rates with lichen size poorly fit the data ( $R=0.29$ ,  $p=0.22$ ;  $R=0.09$ ,  $p=0.71$ , respectively). A quadratic polynomial model describes the data substantially better ( $R=0.58$ ,  $p<0.05$ ), suggesting a rise in growth rates with size for lichens smaller than 5 cm and a decline in growth rates for larger lichens. The very slow growth rates estimated for the largest lichens also provide evidence for declining growth rates in larger lichens. In consequence, the best-fit model for growth rate leads to a sigmoidal lichenometric curve that can be used for dating surfaces of unknown ages (Fig. 4). Figure 4 also shows the piecewise logarithmic and linear composite model, which is an alternative model of lichenometric growth curve used in Alaska. It is important to note that the lack of control points in the range from 450 to 5200 years hampers the statistical validation of the composite model fit to our data. Following a parsimonious criterion, we consider that the sigmoidal growth curve is the best model for our data because it requires estimating three regression coefficients, whereas the alternative composite model is based on five regression coefficients.

### Moraine chronology

Lichen sizes on the moraines deposited by Glaciar Río Lácteo and Glaciar San Lorenzo dated four pre-Little Ice Age (LIA) glacier events (Table 1). An earlier event of glacier advance with a minimum date of 5750–5250 years BP was recorded at both glaciers, glacial deposits at Glaciar San Lorenzo were associated with a second event ca. 3880 years BP, a minimum date of 2470–2180 years is assigned to a third glacier advance in both glaciers, and M3 at Río Lácteo valley supports a fourth pre-LIA glacier event ca. 1490 years BP. Minimum date estimates from the innermost moraines of Glaciar Río Lácteo and Glaciar San Lorenzo suggest the occurrence of three glacier advances during the LIA period. M4 at Glaciar San Lorenzo indicates a glacier event ca. 220 years ago, and at both glaciers, two minor events occurred at 130–90 and 65 years ago.

## Discussion

### Vegetation primary succession

The long-term development of vegetation on the San Lorenzo glacier forefields suggests contrasting patterns of colonization by the lichens *R.* sub-gen. *Rhizocarpon* and the tree *N. pumilio*. Following Glaciar Río Lácteo and Glaciar San Lorenzo retreats, lichens establish on the newly exposed surfaces whereas vascular plants colonize at least a century after moraine formation. The development of the sparse tree coverage on newly exposed surfaces has taken around 2000 years (Tables 1, 2). These results contrast

with those reported for many sites in the sub-Antarctic sub-region of South America, where post-glacial and volcanic areas showed a fast succession progress from bare ground to mature stages dominated by trees. For example, after glacier retreat development of a tree-dominated community takes 30 to 80 years in the Southerly Islands of the Sub-Antarctic sub-region (ca. 54°S, Sancho et al. 2011; Arróniz-Crespo et al. 2014), 40–50 years in Torres del Paine (ca. 51°S, Armesto et al. 1992), 150 to 250 years in Glaciar Seco (ca. 50°S, Garibotti et al. 2011b), and around 75 years in Glaciar San Rafael (ca. 46°S, Heusser 1964). In northern-located areas in the Patagonian Andes, trees began to establish within a year or two following disturbances (Lawrence and Lawrence 1959; Veblen and Ashton 1979). As far as we know, our study along millennial chronosequences on glacier forelands is the first to report that advanced stages of succession can be significantly retarded in a sub-Antarctic environment.

In the southern temperate forests, the possibility of multiple ecosystem responses to disturbance has not been thoroughly investigated. It has been usually considered that the life history traits of *Nothofagus* species, including effective seed dispersal, abundant seedling establishment and fast tree growth rates, favor the rapid recovery of southern temperate forests (Veblen et al. 2016). Our results suggest that this understanding may not apply to all successional situations. Similar patterns of slow vegetation primary succession have been identified in polar, sub-polar and alpine areas of the Northern Hemisphere, where the transition from pioneer to mature stages might exceed 3000 years (Tishkov 1986; Svoboda and Henry 1987; Jones and Henry 2003; Asselin et al. 2006; Robbins and Matthews 2010). The persistence of a reduced vegetation cover in areas which are climatically conducive for the development of a well-vegetated or forested state has been related to the occurrence of alternative successional pathways. Alternative successional pathways can be consequence of among-site spatial and temporal variability in environmental conditions (Robbins and Matthews 2010), differences in landscape context affecting initial plant colonization (Fastie 1995), or the effect of historical events such as episodic adverse climate conditions (Lévesque and Svoboda 1999) and recurrent severe disturbances (Asselin et al. 2006). Our retrospective approach is not adequate for testing specific mechanistic hypothesis, but it provides a useful framework for further studies analyzing the factors that determine alternative successional pathways over broad, geographical scales. This knowledge will substantially contribute to understand regional patterns of *N. pumilio* forest recovery. Given that the sub-Antarctic sub-region in South America is subjected to increasing frequency and severity of disturbance events related to variations in temperature and precipitation due to global climate changes (Villalba

et al. 2005; Veblen et al. 2011), a good understanding of alternative successional patterns is helpful in predicting the ecological impact of disturbances and climate change. In addition, given that successional pathways can have long-lasting effects on ecosystem functioning, consideration of local-scale peculiarities on ecosystem recovery and the causes of *N. pumilio* regeneration failure has the potential to contribute to the implementation of restoration and conservation practices. Unfortunately, forest management conservation practices in the sub-region have mostly relied on spontaneous succession and restoration practices have been only locally applied.

### Methodological considerations of dating methods

The dendrochronological dating of exposed surfaces deals with the difficulty of accurately estimating the time between exposure and tree establishment. In the Patagonian Andes, numerous dendrochronological studies have recorded a large variability in the ecesis of *Nothofagus* species ranging from 1 to 90 years. With a mean lifespan in the order of 400 years, *Nothofagus* species have frequently been used for dating glacier fluctuations related to the LIA events (Villalba et al. 1990; Winchester and Harrison 2000; Strelin et al. 2008; Masiokas et al. 2010). Current forest trimlines in glacier forelands have been interpreted as the limit of maximum glacial extent during the LIA, and innermost, sparsely vegetated moraines are assigned to post-LIA advances (e.g. Villalba et al. 1990; Aravena 2007; Strelin et al. 2008, 2014; Menounos et al. 2013; Winchester et al. 2014). However, the appreciation of forested and unforested moraines as corresponding to pre- and post-LIA landforms is quite subjective, as it is based on the classical concept of succession towards a mature community state (Clements 1916). A growing body of evidences suggests that diverging successional processes may lead to alternative vegetation states (Fukami and Nakajima 2011). In climate-stressed sub-Arctic areas, tree regeneration failure produces the persistence of unforested landscapes over thousands of years (Payette et al. 2001; Asselin et al. 2006). This seems to be the case in Monte San Lorenzo, where tree ecesis on a millennial scale limits the differentiation of post- and pre-LIA moraines based on vegetation development. Indeed, M1 in Glaciar Río Lácteo corresponds to a mid-Holocene advance according to radiocarbon dating (Table 1, Mercer 1968), but was preliminarily attributed to the LIA maximum expansion based on tree ring analyses (Table 2, García-Zamora et al. 2004). Similarly, in the northwestern side of Monte San Lorenzo at Río Tranquilo valley, Aravena (2007) attributed LIA ages to moraines within the forest trimline based on dendrochronological dating. More recently, Aravena (2014) rectified

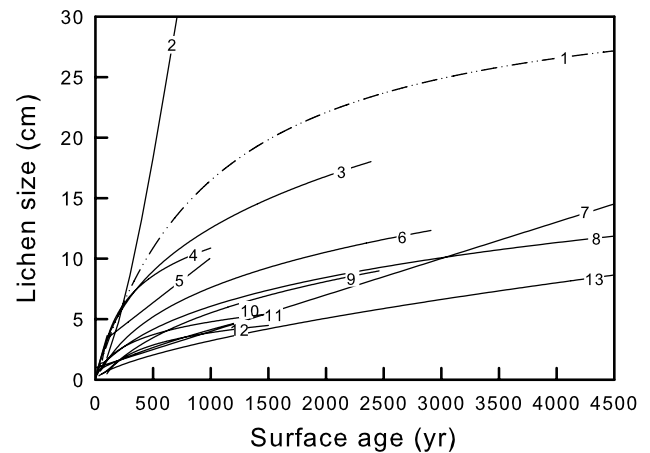
these dates to the mid-Holocene period based on cosmogenic surface exposure dating. Therefore, errors in tree ring age estimations could be in the order of thousands of years if the capability of vascular plants to colonize exposed terrains is not taken into account.

Lichenometry is a dating technique that relies on the accurate estimation of lichen ecesis and growth rates in the area of study. This information is used to construct the lichenometric dating curves. Lichen lifespan constrains the age range of lichenometry applicability. In the Monte San Lorenzo forelands, age estimations of the largest specimens of *R.* sub-gen. *Rhizocarpon* growing on the control points provide dates close to the known surface ages (Table 1), suggesting that these lichens colonized shortly after moraine formation. Our results agree with studies in Antarctica and sub-Antarctic sub-region reporting lichen ecesis in the range of 3 to 13 years and propitious conditions to early lichen colonization (Winchester and Harrison 2000; Sancho and Pintado 2004; Sancho et al. 2011). On the other hand, based on radiocarbon dating, Mercer (1968) estimated that M1 in the Río Lácteo valley was deposited 4867–5573 year BP (Table 1). Lichens growing on M1 are the largest ever reported in the sub-Antarctic sub-region (Table 1), and coincide with lichens of large size (i.e. larger than 10 cm) estimated to be millenary in age in the sub-Arctic region (Miller and Andrews 1972; Denton and Karlén 1973; Andrews and Barnett 1979; Sancho et al. 2007; Benedict 2009; Armstrong and Bradwell 2010; Matthews and Trenbirth 2011). We inferred that the best-fit lichenometric growth model for *R.* sub-gen. *Rhizocarpon* group is a sigmoidal curve, which is common to this group in some sub-polar areas (Bradwell and Armstrong 2007). However, major uncertainties remain for ages between 450 and 5200 years BP given the absence of control points within this age range (Fig. 4). Therefore, the new lichenometric sigmoidal curve can be consistently applied for accurately dating surfaces formed during the last five centuries in dry sites in the Patagonian Andes, as this is covered by numerous control points relying on historical records, dendrochronologic dating of in-situ stumps or trees on moraines and radiocarbon dating of organic material (Fig. 4, Garibotti and Villalba 2009). We suggest that the applicability of the lichenometric curve can be extended to the mid-Holocene period provided that new control points for ages between 450 and 5200 years BP are included. Dating progressively older surfaces has the largest prediction errors due to uncertainty in determining whether the lichens growing on the moraine correspond to the first generation (Loso and Doak 2005; Rosenwinkel et al. 2015). Mortality rates of early colonizers are unknown and should be analyzed in further studies for improving the applicability of lichenometry in the sub-Antarctic sub-region of South America. This information will contribute to model lichenometry uncertainties.

Lichen growth rates are also modulated by climate. Therefore, lichenometric growth curves should be used in areas with relatively homogeneous environmental conditions (similar elevation, precipitation regimen, slope exposition; Rosenwinkel et al. 2015). In Monte San Lorenzo area, the growth rate of *R. sub-gen. Rhizocarpon* during the mature phase (ca. 0.3 mm per year) is about half as fast as farther south in sub-Antarctic islands and some Antarctic regions (0.5–0.6 mm per year; Sancho and Pintado 2004; Sancho et al. 2011). The lichen species *Placopsis perrugosa* (Nyl.) Nyl. exhibited a similar difference in growth rate between continental and insular areas in the sub-Antarctic sub-region of South America (Winchester and Harrison 2000; Sancho et al. 2011). Previous studies have attributed regional variations in lichen growth rates in Antarctic and sub-Antarctic areas to the prevailing regional precipitation gradient (Sancho et al. 2007, 2011; Garibotti and Villalba 2009; Garibotti et al. 2011a). Regional variations in lichen growth rates have also been reported for areas in the Northern Hemisphere, with growth rates for the *R. sub-gen. Rhizocarpon* ranging from 0.01 to 1.0 mm per year in relatively dry continental and cold oceanic climates, respectively (e.g. Porter 1981; Evans et al. 1999; Matthews 2005; Bradwell and Armstrong 2007; Armstrong and Bradwell 2010; Trenbith and Matthews 2010). In spite of the low growth rates of *R. sub-gen. Rhizocarpon* in Monte San Lorenzo in a regional context, they are fairly high in comparison to other world areas (Fig. 6). Our lichenometric curve is close to those calibrated over time scales of millennia for temperate areas such as New Zealand, Sweden and Norway (Denton and Karlén 1973; Gellatly 1982; Matthews and Trenbith 2011), but lichen growth rates are faster than under extreme climate conditions in Canada, Alaska, Russia and the high-altitude mountains in Peru and Kenya (Benedict 1967; Miller and Andrews 1972; Andrews and Barnett 1979; Calkin and Ellis 1984; Mahaney and Spence 1989; Robdell 1992; Savoskul 1999; Solomina et al. 2007). Therefore, it seems that the sub-Antarctic sub-region is conducive for rapid lichen colonization and growth, attributes that lead Sancho and Pintado (2004) and Sancho et al. (2007, 2011) to propose the usefulness of lichens for monitoring the ecological impact of climate change. In this context, our results provide new data on the indirectly derived growth rates for *R. sub-gen. Rhizocarpon* in the sub-Antarctic sub-region of South America.

### Holocene neoglaciations at Monte San Lorenzo

The precise timing of the first neoglaciation in the southern Patagonian Andes has been largely debated (reviewed in Glasser et al. 2004; Aniya 2013). Several studies on different valley glaciers estimated deposition dates for outer terminal moraines to 8500–7500 years BP, suggesting that



**Fig. 6** Comparison of the *Rhizocarpon* Ram. Em Th. Fr. sub-gen. *Rhizocarpon* lichenometric growth curves developed for dry sites in the Magellanic province of the sub-Antarctic sub-region with those from other world areas: 1 New sigmoid curve model for dry sites in southern Patagonian Andes; 2 Southern Norway (Matthews and Trenbith 2011); 3 Swedish Lapland, Sweden (Denton and Karlén 1973); 4 Mount Cook, New Zealand (Gellatly 1982); 5 Mount Kenya, Africa (Mahaney and Spence 1989); 6 Southern Alaska (Denton and Karlén 1973); 7 Barnes Ice Cap, Canada (Andrews and Barnett 1979); 8 Cordillera Blanca, Perú (Robdell 1992); 9 Colorado Front Range, USA (Benedict 1967); 10 Cordillera Blanca, Perú (Solomina et al. 2007); 11 Brooks Range, Alaska (Calkin and Ellis 1984); 12 Baffin Island, Canada (Miller and Andrews 1972); 13 Kamchatka, Russia (Savoskul 1999)

the onset of neoglaciation in southern Patagonia occurred in the early-Holocene (Douglass et al. 2005 and references therein). More frequently, minimum limiting ages estimated by radiocarbon dating indicate that glaciers reached their maximum extent 4500–4000 years BP (Mercer 1968, 1970), probably corresponding to a glacier advance culminating between 6000–5000 years ago, as has recently been estimated using cosmogenic nuclide surface exposure dating (Menounos et al. 2013; Strelin et al. 2014). In the eastern slope of Monte San Lorenzo, geomorphological evidences for an early-Holocene neoglaciation advance has not been reported (Mercer 1968, 1970). Our lichenometric dating and the radiocarbon dating by Mercer (1968) of the outermost neoglaciation moraines indicate that both Glaciar Río Lácteo and Glaciar San Lorenzo reached their maximum extensions around 5750–5250 years ago (Table 1). These dates are in agreement with the neoglaciation chronology proposed at a regional scale for the Southern Patagonian Andes by Aniya (2013).

Our data suggest that the studied glaciers underwent at least three other events of extensive advance during the mid-Holocene. However, dating of these events is preliminary since is based on the interpolation of the lichenometric curve over the period without control points (Fig. 4; Table 1). At Río San Lorenzo valley, M2 corresponds to

an event that culminated ca. 3900 years ago. Geomorphic evidences for this event were not found at the Río Lácteo valley, and we assumed that they have been overridden or superposed by more recent advances (Fig. 1; Table 1). Aniya (2013) proposed an extended period of neoglaciation from 4500 to 3300 years BP or the occurrence of a second neoglacial event between 3600–3300 years BP. The presence at Río San Lorenzo valley of separate glacier deposits with lichenometric ages of 5750 and 3900 years (M1 and M2, respectively) supports two independent pulses of glacier advance corresponding to Neoglaciations I and II.

Lichenometric ages of M2 at Río Lácteo valley and M3 at Río San Lorenzo valley constrain another glacier advance at the eastern flank of Monte San Lorenzo to the period between 2500–2200 years (Fig. 1; Table 1). These dates are consistent within the most widely accepted ages for Neoglaciation III in southern South America estimated between 2700 and 2000 years BP (Lawrence and Lawrence 1959; Mercer 1982; Glasser et al. 2004; Aniya 2013). In addition, a glacier advance at Río Lácteo valley culminating around 1500 years ago (M3, Fig. 1; Table 1) is consistent with Neoglacial IV, bracketed by Aniya (2013) between 1600 and 900 years BP. After the Neoglacial IV, both glaciers underwent considerable retreat and their extensions were much smaller during the LIA (Fig. 1). Our results for Monte San Lorenzo are consistent with those identified in the South and North Patagonian Icefields indicating relatively minor expansion of Patagonian glaciers during the LIA than during earlier neoglacial events (Glasser et al. 2005; Strelin et al. 2014). The LIA advances (Neoglacial V) at the studied valleys are bracketed by ages of 220 and 60 years (Table 1). These dates are largely synchronous to advances recorded in outlet glaciers from the northern Patagonian Icefield that reached their LIA maximum extent sometime during the early nineteenth century. In contrast, available records for the southern Patagonian Icefield region suggest that glaciers reached their LIA maxima two centuries earlier (Masiokas et al. 2009).

## Conclusions

This study provides new insights on primary succession after glacier retreat in the sub-Antarctic sub-region of South America. On the eastern slope of Monte San Lorenzo, deglaciated areas have remained open with a sparse cover of vascular plants over long periods, indicating that primary succession following glacier retreat may take more than 2000 years to complete. Comparison with previous studies reporting rapid vegetation changes suggests considerable variations in primary succession

process at a regional scale. Consequently, a comprehensive view on the dynamics of regeneration and recruitment of *N. pumilio* forests over broad biogeographical scales is needed. Additional studies across the Patagonian Andes will allow distinguishing whether the successional pattern recorded at our study area is a particular case and test the mechanistic hypothesis on the effect of environmental factors on *N. pumilio* regeneration at different spatial scales. This information will contribute to the ecology of the region, and the generation of valid tools for restoration and global change ecology.

Although environmental conditions are not conducive to rapid vascular plant colonization, lichens colonize and achieve relatively high growth rates at the Río Lácteo and Río San Lorenzo valleys. In consequence, lichens represent an interesting tool for the ecological and geochronological research in the sub-Antarctic sub-region of South America. Our results add new data to the analysis of regional variability in lichen growth rates, contributing to previous studies that point up the relevance of lichens as a tool for monitoring climate changes (Sancho et al. 2011). We demonstrate that variations in lichen size facilitate the grouping of moraines corresponding to pre- and post-LIA events, and provide minimum dates for moraine deposition consistent with the regional pattern of glaciers fluctuations over the southern Patagonian Andes. Lichenometry also provided a good approximation of the successional progression, thus being useful for estimating tree ecesis and whether trees on a landform are the first-forest generation. By comparing lichen sizes on selected boulders with those recorded across the moraine, lichenometry may also help reducing uncertainties in cosmogenic dating due to boulder surface erosion, exhumation, shielding or inheritance. Considering that precise dating can only be guaranteed by using multiproxy dating approaches, and that lichenometric,  $^{10}\text{Be}$  and  $^{14}\text{C}$  dating are consistent for reconstructing glacier fluctuations during the mid- and late-Holocene (Konrad and Clark 1998; Savoskul 1999; Benson et al. 2007; Barclay et al. 2009; Licciardi et al. 2009; Young et al. 2009; Wiles et al. 2010; Badding et al. 2013), we reinforce the potential use of lichens as a tool for reconstructing glacier variations during the mid- and late-Holocene and we urge for further research to improve age calibration curves in the sub-Antarctic sub-region.

**Acknowledgements** We thank the personnel of the Parque Nacional Perito Moreno for their assistance during fieldwork. This study was partially funded by CONICET (PIP 112-2011010-0809), the Inter-American Institute for Global Change Research (IAI) through CRN2047, and the Australian Research Council (ARC DP120104320).

## References

- Andrews JT, Barnett M (1979) Holocene (Neoglacial) moraine and proglacial lake chronology, Barnes Ice Cap, Canada. *Boreas* 8:341–358
- Aniya M (2013) Holocene glaciations of Hielo Patagónico (Patagonia Icefield), South America: a brief review. *Geochem J* 47:97–105
- Aravena JC (2007) Reconstructing climate variability using tree rings and glacier fluctuations in the southern Chilean Andes. Dissertation, The University of Western Ontario
- Aravena JC (2014) Reconstructing glacier fluctuations in Southernmost Chilean Andes: advances and future challenges. In: Luckman BH (ed) IAI CRN-CRA2047, documenting, understating and projecting changes in the hydrological cycle in the American Cordillera, San Rafael, Argentina, p 6
- Armesto JJ, Casassa I, Dollenz O (1992) Age structure and dynamics of Patagonian beech forests in Torres del Paine National Park, Chile. *Vegetatio* 98:13–22
- Armstrong RA, Bradwell T (2010) Growth of crustose lichens: a review. *Geogr Ann* 92A:3–17
- Arróniz-Crespo M, Pérez-Ortega S, De los Ríos A, Green TGA, Ochoa-Hueso R, Casemiro MA, de la Cruz MT, Pintado A, Palacios D, Rozzi R, Tyskland N, Sancho LG (2014) Bryophyte-cyanobacteria associations during primary succession in recently deglaciated areas of Tierra del Fuego (Chile). *PLoS One* 9:e96081
- Asselin H, Belleau A, Bergeron Y (2006) Factors responsible for the co-occurrence of forested and unforested rock outcrops in the boreal forest. *Landsc Ecol* 21:271–280
- Badding ME, Briner JP, Kaufman DS (2013)  $^{10}\text{Be}$  ages of late Pleistocene deglaciation and Neoglaciation in the north-central Brooks Range, Arctic Alaska. *J Quat Sci* 28:95–102
- Barclay DJ, Wiles G, Calkin PE (2009) Holocene glacier fluctuations in Alaska. *Quat Sci Rev* 28:2034–2048
- Benedict JB (1967) Recent glacial history of an alpine area in the Colorado Front Range, U.S.A. 1. Establishing a lichen-growth curve. *J Glaciol* 6:817–832
- Benedict JB (2009) A review of lichenometric dating and its applications to archeology. *Am Antiquity* 74:143–172
- Benson L, Madole R, Kubik PW, McDonald RI (2007) Surface-exposure ages of Front Range moraines that may have formed during the Younger Dryas, 8.2 cal ka, and Little Ice Age events. USGS Staff—Published Research Paper 759
- Bokhorst SF, Huiskes A, Convey P, Aerts R (2007) The effect of environmental change on vascular plant and cryptogam communities from the Falkland Islands and the Maritime Antarctic. *BMC Ecol* 7:15. doi:10.1186/1472-6785-7-15
- Bradwell T, Armstrong RA (2007) Growth rates of *Rhizocarpon geographicum* lichens: a review with new data from Iceland. *J Quat Sci* 22:311–320
- Calkin PE, Ellis JM (1984) Development and application of lichenometric dating curve, Brooks Range, Alaska. In: Mahaney WC (ed) Quaternary dating methods. 1st edn. Elsevier Science Publishers, Amsterdam, pp 227–246
- Clements FE (1916) Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington, Washington
- Cornelissen JHC, Callaghan TV, Alatalo JM, Michelsen A, Graglia E, Hartley AE, Hik DS, Hobbie SE, Press MC, Robinson CH, Henry GHR, Shaver GR, Phoenix GK, Jones DG, Jonasson S, Chapin FS III, Molau U, Neill C, Lee JA, Melillo JM, Sveinbjörnsson B, Aerts R (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *J Ecol* 89:984–994
- de Agostini AM (1945) Andes Patagónicos: Viajes de exploración a la cordillera patagónica austral. 1st edn. Talleres Gráficos de Guillermo Kraft, Buenos Aires
- Denton GH, Karlén W (1973) Lichenometry: Its application to Holocene moraine studies in southern Alaska and Swedish Lapland. *Arct Alp Res* 5:347–372
- Douglass DC, Singer BS, Kaplan MR, Ackert RP, Mickelson DM, Caffee MW (2005) Evidence of early Holocene glacial advances in southern South America from cosmogenic surface-exposure dating. *Geology* 33:237–240
- Evans DJA, Archer S, Wilson DJH (1999) A comparison of the lichenometric and Schmidt hammer dating techniques based on data from the proglacial areas of some Icelandic glaciers. *Quat Sci Rev* 18:13–41
- Falaschi D, Bravo C, Masiokas M, Villalba R, Rivera A (2013) First glacier inventory and recent changes in glacier area in the Monte San Lorenzo Region (47°S), Southern Patagonian Andes, South America. *Arct Antarct Alp Res* 45:19–28
- Fastie CL (1995) Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology* 76:1899–1916
- Fisher GB, Bookhagen B, Amos CB (2013) Channel planform geometry and slopes from freely available high-spatial resolution imagery and DEM fusion: implications for channel width scalings, erosion proxies, and fluvial signatures in tectonically active landscapes. *Geomorphology* 194:46–56
- Fukami T, Nakajima M (2011) Community assembly: alternative stable states or alternative transient states? *Ecol Lett* 14:973–984
- García-Zamora G, Villalba R, Delgado S, Trombetta D, Masiokas M, Cali S, Ripalta A, Hernandez J (2004) Glacier fluctuations during the past centuries in the Argentinean sector of Cerro San Lorenzo (47°40'S), southern Patagonia. In: Second Symposium on Mass Balance of Andean Glaciers, Glacier Shrinkage in the Andes Consequences for Water Resources, Huaraz, Perú, 2004. p 34
- Garibotti IA, Villalba R (2009) Lichenometric dating using *Rhizocarpon* subgenus *Rhizocarpon* in the Patagonian Andes, Argentina. *Quat Res* 71:271–283
- Garibotti IA, Borrero K, Borrero LA (2011a) Aplicación de técnicas liquenométricas en la arqueología en Patagonia utilizando *Rhizocarpon* subgénero *Rhizocarpon*. In: Borrero LA, Borrero K (eds) Bosques, montañas y cazadores: investigaciones arqueológicas en Patagonia Meridional. 1st edn. Dunken, Buenos Aires, pp 85–103
- Garibotti IA, Pissolito CI, Villalba R (2011b) Spatiotemporal pattern of primary succession in relation to mesotopographic gradients on recently deglaciated terrains in the Patagonian Andes. *Arct Antarct Alp Res* 43:555–567
- Garibotti IA, Pissolito CI, Villalba R (2011c) Vegetation development on deglaciated rock outcrops from Glaciario Frías, Argentina. *Arct Antarct Alp Res* 43:35–45
- Gellatly AF (1982) Lichenometry as a relative-age dating method in Mount Cook National Park, New Zealand. *N Z J Bot* 20:343–353
- Glasser NF, Harrison S, Winchester V, Aniya M (2004) Late Pleistocene and Holocene palaeoclimate and glacier fluctuations in Patagonia. *Global Planet Chang* 43:79–101
- Glasser N, Jansson KN, Harrison S, Rivera A (2005) Geomorphological evidence for variations of the North Patagonian Icefield during the Holocene. *Geomorphology* 71:263–277
- Heusser CJ (1964) Some pollen profiles from the Laguna San Rafael area, Chile. In: Cranwell LM (ed) Ancient Pacific floras. 1st edn. Bishop Press, Honolulu, pp 95–114
- Innes JL (1983a) Size frequency distributions as a lichenometric technique: an assessment. *Arct Alp Res* 15:285–294
- Innes JL (1983b) Use of an aggregated *Rhizocarpon* 'species' in lichenometry: an evaluation. *Boreas* 12:183–190

- Innes JL (1985) Lichenometry. *Prog Phys Geog* 9:187–254
- John EA (1989) Note on the sizes of largest thalli of three species of *Rhizocarpon* (subgenus *Rhizocarpon*) at a rockslide in the Canadian Rocky Mountains. *Arct Alp Res* 21:185–187
- Jones GA, Henry GHR (2003) Primary plant succession on recently deglaciated terrain in the Canadian High Arctic. *J Biogeogr* 30:277–296
- Koch J (2009) Improving age estimates for late Holocene glacial landforms using dendrochronology—some examples from Garibaldi Provincial Park, British Columbia. *Quat Geochronol* 4:130–139
- Konrad SK, Clark DH (1998) Evidence for an early neoglacial glacier advance from rock glaciers and lake sediments in the Sierra Nevada, California, U.S.A. *Arct Alp Res* 30:272–284
- Lawrence DB, Lawrence EG (1959) Recent glacier variations in southern South America. 1st edn. American Geographical Society, New York
- Lenaerts JTM, van den Broeke MR, van Wessem JM, van de Berg WJ, Van Meijgaard E, van Ulft LH, Schaefer M (2014) Extreme precipitation and climate gradients in Patagonia revealed by high-resolution regional atmospheric climate modeling. *J Climate* 27:4607–4621
- Lévesque E, Svoboda J (1999) Vegetation re-establishment in polar “lichen-kill” landscapes: a case study of the Little Ice Age impact. *Polar Res* 18:221–228
- Licciardi JM, Schaefer JM, Taggart JR, Lund DC (2009) Holocene glacier fluctuations in the Peruvian Andes indicate northern climate linkages. *Science* 325:1677–1679
- Loso MG, Doak DF (2005) The biology behind lichenometric dating curves. *Oecologia* 147:223–229
- Loso MG, Doak DF, Anderson RS (2014) Lichenometric dating of Little Ice Age glacier moraines using explicit demographic models of lichen colonization, growth, and survival. *Geogr Ann* 96:21–41
- Mahaney WC, Spence JR (1989) Lichenometry of neoglacial moraines in Lewis and Tyndall cirques on Mount Kenya, East Africa. *Band* 25:175–186
- Masiokas M, Rivera A, Espizua LE, Villalba R, Delgado S, Aravena JC (2009) Glacier fluctuations in extratropical South America during the past 1000 years. *Palaeogeogr Palaeoclimatol Palaeoecol* 281:242–268
- Masiokas M, Luckman BH, Villalba R, Ripalta A, Rabassa J (2010) Little Ice Age fluctuations of Glaciario Río Manso in the north Patagonian Andes of Argentina. *Quat Res* 73:96–106
- Matthews JA (2005) “Little Ice Age” glacier variations in Jotunheimen, southern Norway: a study in regionally controlled lichenometric dating of recessional moraines with implications for climate and lichen growth rates. *Holocene* 15:1–19
- Matthews JA, Trenbith HE (2011) Growth rate of a very large crustose lichen (*Rhizocarpon* subgenus) and its implications for lichenometry. *Geogr Ann* 93:27–39
- McCarroll D (1995) Lichens: lichenometric dating of diachronous surfaces. *Earth Surf Proc Land* 20:829–831
- McCarthy DP (1999) A biological basis for lichenometry? *J Biogeogr* 26:379–386
- Menounos B, Clague JJ, Osborn G, Thompson DP, Ponce F, Goehring B, Maurer M, Rabassa J, Coronato A, Marr R (2013) Latest Pleistocene and Holocene glacier fluctuations in southernmost Tierra del Fuego, Argentina. *Quat Sci Rev* 77:70–79
- Mercer JH (1968) Variations of some Patagonian glaciers since the Late-glacial. *Am J Sci* 266:91–109
- Mercer JH (1970) Variation of some Patagonian glaciers since the Late-Glacial: II. *Am J Sci* 269:1–25
- Mercer JH (1982) Holocene glacier variation in southern South America. In: Karlén W (ed) *Holocene Glaciers*, vol 18. 1st edn. Striae, Uppsala, pp 35–40
- Miller GH, Andrews JT (1972) Quaternary history of northern Cumberland peninsula, east Baffin Island, North West Territory, Canada. VI. Preliminary lichen growth curve. *Geol Soc Am Bull* 83:1133–1138
- Osborn G, McCarthy DP, LaBrie A, Burke R (2015) Lichenometric dating: science or pseudo-science? *Quat Res* 83:1–12
- Payette S, Fortin M-J, Gamache I (2001) The subarctic forest-tundra: the structure of a biome in a changing climate. *Bioscience* 51:709–718
- Perez CA, Aravena JC, McCulloch RD, Armesto JJ, Parfitt R (2016) Patterns of ecosystem development in glacial foreland chronosequences: a comparative analysis of Chile and New Zealand. *N Z J Bot* 54:156–174
- Poelt J, Cernohorsky Z, Schaefer J (1988) *Rhizocarpon* Ram. em. Th. Fr. subgen. *Rhizocarpon* in Europe. *Arct Alp Res* 20:292–298
- Porter SC (1981) Lichenometric studies in the Cascade Range of Washington: Establishment of *Rhizocarpon geographicum* growth curves at Mount Rainier. *Arct Alp Res* 13:11–23
- Prach K, Walker LR (2011) Four opportunities for studies of ecological succession. *Trends Ecol Evol* 26:119–123
- Robbins JA, Matthews JA (2010) Regional variation in successional trajectories and rates of vegetation change on glacier forelands in South-Central Norway. *Arct Antarct Alp Res* 42:351–361
- Robbelle DT (1992) Lichenometric and radiocarbon dating of Holocene glaciation, Cordillera Blanca, Perú. *Holocene* 2:19–29
- Roca Valiente B, Hawksworth DL, Perez Ortega S, Sancho LG, Crespo A (2016) Type studies in the *Rhizocarpon geographicum* group (Rhizocarpaceae, lichenized Ascomycota). *Lichenologist* 48:97–110
- Roof S, Werner A (2011) Indirect growth curves remain the best choice for lichenometry: evidence from directly measured growth rates from Svalbard. *Arct Antarct Alp Res* 43:621–631
- Rosenwinkel S, Korup O, Landgraf A, Dzhumabaeva A (2015) Limits to lichenometry. *Quat Sci Rev* 129:229–238
- Sancho LG, Pintado A (2004) Evidence of high annual growth rate for lichens in the maritime Antarctica. *Polar Biol* 27:312–319
- Sancho LG, Green TGA, Pintado A (2007) Slowest to fastest: Extreme range in lichen growth rates supports their use as an indicator of climate change in Antarctica. *Flora* 202:667–673
- Sancho LG, Palacios D, Green TGA, Vivas M, Pintado A (2011) Extreme high lichen growth rates detected in recently deglaciated areas in Tierra del Fuego. *Polar Biol* 34:813–822
- Savoskul OS (1999) Holocene glacier advances in the eadwaters of Sredniaya Avacha, Kamchatka, Russia. *Quat Res* 54:14–26
- Solomina O (2002) Dendrogeomorphology: research requirements. *Dendrochronologia* 20:233–245
- Solomina O, Jomelli V, Kaser G, Ames A, Berger B, Pouyaud B (2007) Lichenometry in the Cordillera Blanca, Perú: “Little Ice Age” moraine chronology. *Global Planet Change* 59:225–235
- Stokes MA, Smiley T (1996) An introduction to tree-ring dating. 1st edn. University of Arizona Press, Tucson (**Arizona**)
- Strelin J, Casassa G, Rosqvist G, Holmlund P (2008) Holocene glaciations in the Ema Glacier valley, Monte Sarmiento Massif, Tierra del Fuego. *Palaeogeogr Palaeoclimatol Palaeoecol* 260:299–314
- Strelin J, Kaplan MR, Vandergoes MJ, Denton GH, Schaefer JM (2014) Holocene glacier history of the Lago Argentino basin, Southern Patagonian Icefield. *Quat Sci Rev* 101:124–145
- Svoboda J, Henry GHR (1987) Succession in marginal Arctic environments. *Arct Alp Res* 19:373–384
- Tishkov RJ (1986) Primary succession in Arctic tundra on the west coast of Spitsbergen (Svalbard). *Polar Geogr Geol* 10:148–156
- Trenbith HE, Matthews JA (2010) Lichen growth rates on glacier forelands in southern Norway: preliminary results from a 25-year monitoring programme. *Geogr Ann* 92A:19–39
- Veblen AT, Ashton DH (1979) Successional pattern above timberline in south-central Chile. *Vegetatio* 40:39–47

- Veblen TT, Hill RS, Read J (1996) The ecology and biogeography of *Nothofagus* forests. 1st edn. Yale University Press, New Haven
- Veblen TT, Holz A, Paritsis J, Raffaele E, Kitzberger T, Blackhall M (2011) Adapting to global environmental change in Patagonia: what role for disturbance ecology? *Austral Ecol* 36:891–603
- Veblen AT, Gonzalez ME, Stewart GH, Kitzberger T, Brunet J (2016) Tectonic ecology of the temperate forests of South America and New Zealand. *N Z J Bot* 54:223–246
- Villalba R, Leiva JC, Rubulis S, Suarez J, Lenzano L (1990) Climate, tree-ring, and glacial fluctuations in the Río Frías Valley, Río Negro, Argentina. *Arct Antarct Alp Res* 22:215–232
- Villalba R, Lara A, Boninsegna JA, Masiokas M, Delgado S, Aravena JC, Roig FA, Schmelter A, Wolodarsky A, Ripalta A (2003) Large-scale temperature changes across the southern Andes: 20th-century variations in the context of the past 400 years. *Clim Change* 59:177–232
- Villalba R, Masiokas M, Kitzberger T, Boninsegna JA (2005) Biogeographical consequences of recent climate changes in the Southern Andes of Argentina. In: Huber UM, Bugmann HKM, Reasoner MA (eds) *Global change and mountain regions, an overview of current knowledge*. 1st edn. Springer, Dordrecht, pp 157–168
- Walker LR, Del Moral R (2003) *Primary succession and ecosystem rehabilitation*. 1st edn. Cambridge University Press, Cambridge
- Wiles GC, Barclay DJ, Young NE (2010) A review of lichenometric dating of glacial moraines in Alaska. *Geogr Ann* 92A:101–109
- Winchester V, Harrison S (2000) Dendrochronology and lichenometry: colonization, growth rates and dating of geomorphological events on the east side of the North Patagonian Icefield, Chile. *Geomorphology* 34:181–194
- Winchester V, Sessions M, Valdivia Cerda J, Wünderlich O, Clemmens S, Glasser N, Nash M (2014) Post-1850 changes in Glacier Benito, North Patagonian Icefield, Chile. *Geogr Ann* 96:43–59
- Young NE, Briner JP, Kaufman DS (2009) Late Pleistocene and Holocene glaciation of the Fish Lake valley, northeastern Alaska Range, Alaska. *J Quat Sci* 24:677–689