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RESEARCH ARTICLE

Patterns of ecosystem development in glacial foreland chronosequences: a comparative analysis of Chile and New Zealand

CA Pérez[a], JC Aravena[b], WA Silva[a], R McCulloch[c], JJ Armesto[a,d] and R Parfitt[e]

[a]Instituto de Ecología y Biodiversidad, Santiago, Chile; [b]Instituto de la Patagonia, Universidad de Magallanes, Punta Arenas, Chile; [c]Biological and Environmental Sciences, University of Stirling, Stirling, UK; [d]Departamento de Ecología, Pontificia Universidad Católica de Chile, Santiago, Chile; [e]Research Division of Soils and Landscapes, Landcare Research, Christchurch, New Zealand

ABSTRACT
After catastrophic disturbances, depleted substrates are readily colonised by organisms that capture nitrogen from the atmosphere and extract phosphorus from minerals. Our main objective was to compare the pattern of ecosystem development following deglaciation in Chile and New Zealand. Results show a similar pattern of C and N accumulation and decline in soil chronosequences, similar decline in biological nitrogen fixation (BNF) and similar δ^{15}N-enriched signal at later stages, providing evidence for the existence of progressive, maximal and retrogressive phases of ecosystem development. However, contrasting patterns between Chilean and New Zealand sites are evident during the progressive phase, when higher C/N, C/P and N/P ratios are found in soils and leaves in Chile than in New Zealand, suggesting a higher nutrient limitation and nutrient use efficiency in the former. Highest rates of BNF were found at the early stages of both the Chilean and New Zealand chronosequences. Contrasting patterns across regions were the lack of a decline in soil total P, and the depleted values in soils of ^{15}N during the progressive phase in the Chilean chronosequences, but enriched values, suggesting an open nitrogen cycle, during retrogression in both the Chilean and the New Zealand chronosequences. Overall, these results provide evidence for the existence of retrogression with ecosystem development in the sub-Antarctic region of the world, even when comparing contrasting biomes, climatic regions and geological substrates.

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Biological nitrogen fixation; Franz Josef; retrogression; soil/leaves stoichiometry; sub-Antarctic forests

Introduction

One of the most striking features shaping the fiord landscape in the Strait of Magellan, southern Chile is the rapid glacial retreat since c. 14,600–18,000 yr BP (McCulloch et al. 2005; Kaplan et al. 2008), continuing until the present (Boyd et al. 2008; Fernandez et al. 2011; Hall et al. 2013). In New Zealand, glaciers also experienced a rapid retreat starting c. 18,000 yr BP and continuing until today, following a warming trend in the southern

CONTACT CA Pérez ✉ cperez@bio.puc.cl

hemisphere (Hall et al. 2013). Glacial retreat produces a denuded substrate, completely depleted of soil organic matter and N, although P may become highly available in P-rich minerals (Richardson et al. 2004; Parfitt et al. 2005). However, soil may still be depleted of available P in P-poor primary minerals such as granite (Pérez et al. 2014a, 2014b). In recently exposed substrate, organisms that can capture N from the atmosphere and are able to mine essential elements from denuded substrates are likely to begin ecosystem development (Chapin et al. 1994; Hobbie et al. 1998). Biological nitrogen fixation (BNF) is a key process in primary succession by providing access to new N. Accordingly, in the glacial foreland of Magellan Strait, rates of BNF are high in the early stages of post-glacial succession when soil N availability is minimal (Arróniz et al. 2014; Pérez et al. 2014a). Once N-fixing organisms are established they start to accumulate C, N and P, giving way to the progressive phase of ecosystem development, where primary productivity and soil processes increase soil nutrient availability. Accumulation reaches a maximum at intermediate stages of succession in a few centuries (c. 500 yr) or millennia. If no disturbance occurs, then increasing leaching losses of critical elements such as P produce a decline in ecosystem productivity, giving way to the retrogressive phase of succession, generally taking place at tens of thousands of years of ecosystem development. However, the onset of retrogression varies widely across biomes depending on regional climate, geological substrates and the type of disturbance originating ecosystem development (Peltzer et al. 2010).

In spite of relatively rapid rates of C, N and P accumulation during ecosystem development, in short-term chronosequences (<500 yr) in glacial forelands, the concomitant increase in both soil and plant C/N and C/P ratios along the chronosequence suggests that limitation by both N and P tends to increase over time (Hobbie et al. 1998; Pérez et al. 2014a). Longer-term chronosequences (>500 yr), such as Franz Josef glacier in New Zealand and the volcanic island of Hawaii, show strong declines in P availability due to leaching—documenting a retrogressive phase of ecosystem development. According to classic succession theory, P limitation should be higher in late succession, whereas N limitation should be higher in young successional stages, under low N availability over denuded substrates (Walker & Syers 1976; Crews et al. 1995; Vitousek & Farrington 1997; Richardson et al. 2004; Wardle et al. 2004; Parfitt et al. 2005; Peltzer et al. 2010). In addition, several chronosequences document a decline in tree species diversity correlated with greater nutrient limitation during retrogression as suggested by higher soil C/N and C/P ratios (Wardle et al. 2008). An exception was the Franz Josef chronosequence, where there was a positive correlation between tree species diversity and increasing soil C/P and N/P ratios (Wardle et al. 2008). Similarly, southern temperate *Nothofagus* forests in Chile exhibit an increase in tree species diversity during the retrogressive phase over P-poor soils (Pérez et al. 2014b). Further, in the Franz Josef chronosequence, Mason et al. (2012) report a slight decline of basal areas and a convergence of traits of dominant resource-retentive species as P declines with soil age. More recently, Laliberté et al. (2013) postulate a general conceptual model explaining how the high diversity in the chemical forms of limiting elements, the soil spatial heterogeneity, the role of aboveground and belowground heterotrophs along with soil development are directly affecting total plant diversity.

A vast number of studies on paedogenesis and ecosystem development in glacial forelands are developed in short-term chronosequences (<500 yr BP), however only Franz

Josef belongs to a well-studied long-term chronosequence, including the later phase of retrogression. The present work seeks to test the generality of the retrogression along with ecosystem development in two additional long-term chronosequences, in glacier forelands of the sub-Antarctic region of Chile. In particular, the decline of limiting elements such as N and P, the role of biological processes such as BNF, the chemical traits of leaves and the tightness/openness of the N cycle expressed as the natural abundance of $\delta^{15}N$ in soils. For this purpose we compared: (i) C, N and P concentrations in soils and plants, (ii) plant-available P and N in soils, (iii) soil and plant C, N, P stoichiometry, as indices of nutrient limitation and nutrient-use efficiency, respectively, (iv) the natural abundance of $\delta^{15}N$ in soils, (v) the rates of BNF in the ecosystem, and (vi) the relationship between these changes in plant and soil and nutrients and tree species richness and basal area over successional time.

Our main hypothesis is that long-term chronosequences in glacial forelands of the southern hemisphere show similar patterns of ecosystem development that follow the model proposed by Peltzer et al. (2010). However, geology and the climate of the sub-Antarctic region and its biogeography (floristic assemblages) could modify the coincidence or direction of these predictions, as species have evolved different nutrient acquisition and conservation strategies.

Study sites and methods

Chronosequences in Chile and New Zealand

We studied two long-term chronosequences in the sub-Antarctic region of Chile.

One site was in the glacial foreland of Santa Inés Island (Figure 1, number 2) and the second one was reconstructed (see below) from study sites in glacier forelands of the Reina II Glacier in Cordillera de Darwin and a moraine system in Río Discordia, Tierra del Fuego (Figure 1, numbers 1 and 3). The vegetation in the study region is associated with the strong effect of the westerlies; it is dominated by moorlands on the west exposure of the coastal mountain range in the Magellan Strait, towards a mixed evergreen deciduous forest and the Patagonia steppe in the easternmost region (Figure 1). During the last four centuries gradual glacial retreat in Santa Inés Island (Figure 1) left behind a landscape shaped by moraines of different ages, where a chronosequence was established based on tree-ring studies (Aravena 2007; Pérez et al. 2014a). The youngest moraine studied had an age of c. 40 yr whereas the oldest forest site, according to lacustrine sediment studies, has been free of ice since 16,700 yr BP (Fontana & Bennet 2012). In this glacier foreland we reconstructed a chronosequence (SII) with a total of 10 sites and a substrate age that ranges from 33 to 16,700 yr BP (Table 1). Predominant vegetation was sub-Antarctic rainforest, where the younger sites near the ice front are dominated by the N-fixing summer green herb *Gunnera magellanica* Lam. and deciduous tree species *Nothofagus antarctica* (G. Forst.), which also dominates the progressive phase of ecosystem development. As succession proceeds and the canopy closes, a diverse flora of cryptogams, such as *Schistochila lamellata* (Hook.) Dumort. and the hornwort *Notoceros endiviaefolius* (Mont.) J. Haseg. form a continuous carpet in the forest understorey. The hornworts present a symbiotic association with N-fixing bacteria (Troncoso et al. 2013) contributing to enhance soil N. In older sites, in the maximal phase, the tree stratum becomes

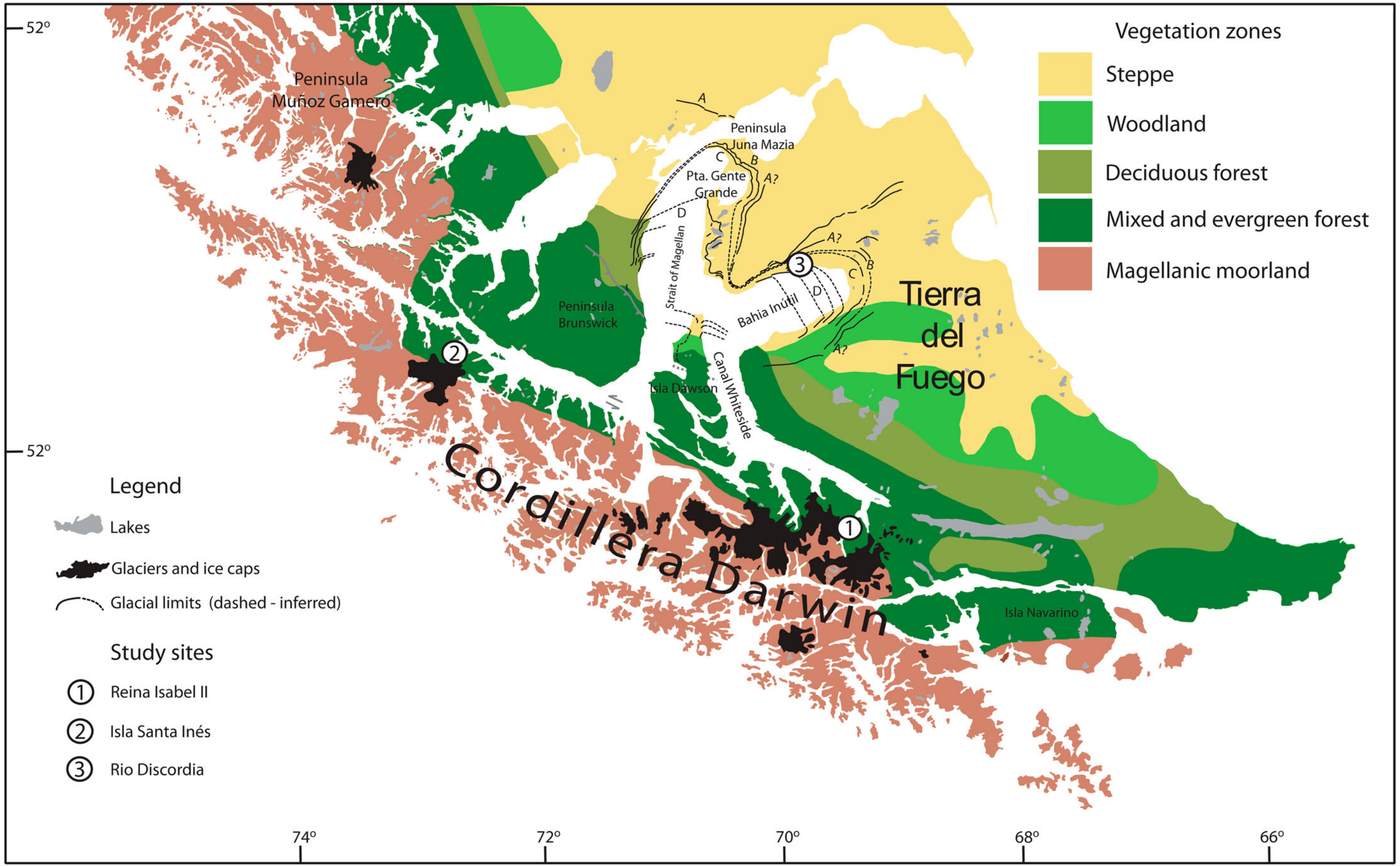

Figure 1 Study sites showing the location of the two Chilean chronosequences in glacial forelands of Reina Isabel II in Cordillera de Darwin (1), in Santa Inés Island (2, SII), and Río Discordia (3), showing the position of the moraine system A, B, C and D in Tierra del Fuego. Study sites 1 and 3 are part of the Cordillera de Darwin (CD) chronosequence and study site 2 forms the Santa Inés Island chronosequence (SII). Main vegetation types in the study region are also indicated.

Table 1 State factors in the two Chilean chronosequences, Santa Inés Island (SII) and Cordillera de Darwin (CD), southern Chile, and the chronosequence from Franz Josef glacier (FJ), New Zealand.

	Franz Josef (FJ)	Santa Ines Island (SII)	Cordillera de Darwin (CD)
Latitude	43°25′S	53°45′S	54°41′S
Annual Precipitation	3652–6520 mm	2800 mm	350–500 mm
Annual Temperature	10.8°C	6.9°C	5.9–6.3°C
Geological Substrate	Schists, gneiss	Diorite	granitoide
Elevation	200–240 m	24–58 m	0–200 m
Soil texture	gravelly sand–sandy silt	silt loam–silt	silt loam–silt
P-apatite	0.08%	0.04%	n.a.
Chronosequence span (yr BP)	5–120,000	33–16,700	5–40,000
Forest type	southern temperate rainforest	sub-Antarctic rainforest	sub-Antarctic forest–Patagonic steppe
Early successional species	*Coriaria arborea*	*Gunnera magellanica*	*Gunnera magellanica*
Progressive phase Mid successional species	*Myrsine divaricata* *Griselina litoralis* *Schefflera digitata*	*Nothofagus antarctica*	*Nothofagus antarctica*
Maximum phase successional species	*Metrosideros umbellata-Weinmannia racemosa*	*Nothofagus betuloides-Drimys winteri*	*Nothofagus betuloides-Drimys winteri*
Retrogressive phase Late successional species	*Weinmannia racemosa-Dacrydium cupressinum*	*Pilgerodendron uviferum-Nothofagus betuloides*	*Chiliotrichum diffusum-Festuca magellanica*

dominated by the evergreen *Nothofagus betuloides* (Mirb.) Blume and *Drimys winteri* J.R. Forst & G. Forst. As the canopy opens up in the retrogressive phase, the conifer *Pilgerodendron uviferum* (D. Don) Florin finds a place in the overstorey. A diverse cryptogamic flora covers the forest floor and the bark of standing trees. A more detailed description of the vegetation changes for this chronosequence is presented by Pérez et al. (2014a).

During the Last Glacial Maximum, the Darwin Glacier in Cordillera de Darwin extended more than 150 km eastward from its present position reaching Bahia Inútil in the island of Tierra del Fuego (Figure 1). A moraine system has been described from east to west in Río Discordia, Tierra del Fuego recording different glacial cycles: series A (>40,000 yr BP), B (c. 25,000 yr BP), C (c. 20,000 yr BP) and D (with a minimum age of c. 17,000 yr BP) (Figure 1) (McCulloch et al. 2005, Darvill et al. 2015). The Reina Isabel II Glacier in Cordillera Darwin is a relict portion of a glacial field that completely covered Tierra del Fuego during the Last Glacial Maximum and is now restricted to the top of Cordillera de Darwin (Figure 1). In the glacial foreland of Glacier Reina Isabel II we defined three successional stages. The youngest site, dated c. 5 yr of age, is located on the slopes of a hill in front of the proglacial lake (Arroniz et al. 2014). Based on tree-ring counts, we also dated two other sites of 57 and 150 yr of post-glacial development. Based on these records we reconstructed a long-term chronosequences for the Cordillera de Darwin (CD, Table 1). The total number of sites at CD was eight with substrate ages that span from 5 to c. 40,000 yr BP. The vegetation growing on the series of moraines in the Patagonian steppe of Tierra del Fuego (Figure 1) is characterised as species-rich scrubland with c. 55 vascular species but no tree strata (Pérez et al., unpublished data).

The Franz Josef (FZ) glacier chronosequence is located in the temperate region of New Zealand, and has a slightly warmer and wetter climate (Richardson et al. 2004) than any of the Chilean chronosequences, developing on schist substrates richer in P-apatite than the Chilean chronosequences (Table 1). The three chronosequences studied (two in Chile and one in New Zealand) have well-drained soils, as indicated by the soil texture. However highly organic soils in the Chilean chronosequence may confer a higher water retention capacity for the Chilean soils. Vascular plants with symbiotic N fixers (non-legume) dominate the early stage of succession in the three chronosequences. The data for the FJ chronosequence used in this study belong exclusively to published data (Richardson et al. 2004; Parfitt et al. 2005; Turner et al. 2007; Menge & Hedin 2009; Menge et al. 2011). The sites included in the comparisons are: Glacier terminal (5 yr BP), Young terrace (60 yr BP), Peter's Pool (130 yr BP), Wahio Footbridge 1 (280 yr BP), Wahio Footbridge 2 (500 yr BP), Upper Wombat (5000 yr BP), Mapourika 12,000 yr BP) Ōkārito Forest (60,000 yr BP) and Deep Creek Ridge (120,000 yr BP).

Chemical analysis of soils and plants

Following the contour line of each moraine and after completely removing the O1 horizon, and the profuse living cryptogamic carpet, six samples of surface soil (10 cm depth) (which belong to a humic top soil where organic material is undistinguishable from the mineral soil fraction) were randomly taken at each site and separated by c. 10 m from each other. They were sieved (2 mm) for chemical analysis. Fresh leaves at each site were collected from hand-reachable leaves in three individuals per dominant (1–5 species, n per site = 3–15) woody species in the forested sites and per dominant vascular species in the non-forested sites. Because of the high frequency of cloudy days and the short summer season in the forested sites of the study area, we assumed that there were no significant differences in nutrient concentration between 'sun' and 'shade' leaves. Plant-available soil nitrogen ($N_a = NH_4^+ - N + NO_3^- - N$) was extracted in a 0.021 mol/L $KAl(SO_4)_2$ solution (1:4) and ammonium and nitrate were determined by means of fractionated steam distillation (Pérez et al. 1998). Plant available P (P_a) was extracted from soil by the CAL (Calcium–Acetate–Lactate) method and its concentration was determined by the colorimetric molybdenum blue method (Steubing & Fangmeier 1992). Total content of carbon (Ct) and nitrogen (Nt) in soils and plants were determined from dry and ground samples by flash combustion in a Carlo Erba NA 2500. The natural abundances of ^{15}N isotope, expressed as $\delta^{15}N$ (‰), were determined from three or four surface soil samples in each site. Determinations were made in a Thermo Delta V Advantage Isotope Ratio mass spectrometer, at the Universität Trier, Germany. Total phosphorus (Pt) from ground soil and plant material was extracted with a concentrated sulphuric acid and water peroxide solution in a Hach Digesdahl digestor and determined by colorimetry with the molybdenum blue method (Steubing & Fangmeier 1992).

Biological nitrogen fixation

The rates of BNF were determined using the acetylene reduction assay (Myrold et al. 1999), using samples taken from the following N-fixer community types: (i) soil carpets of *Gunnera magellanica* during early succession, (ii) cryptogamic soil carpets, (iii) cryptogamic epiphytes and (iv) litter layer (O1 horizon) of successional forests. Samples were kept as cold as possible during the field trip, stored in the refrigerator after the arrival to the laboratory and analysed usually not later than 4 days for *Gunnera* and cryptogamic flora and not later than 7 days for the litter layer. In the laboratory, six samples per N-fixer community type were incubated for up to 2 days, inside hermetically closed glass jars, maintained at c. 23 °C filled with a mixture of air and acetylene at 10% volume/volume.

An additional sample for each substrate N-fixer community type and study site was incubated without acetylene as a control. Three gas samples per jar were taken periodically and analysed for ethylene production in a Schimadzu gas chromatograph equipped with a Porapack column and FID detector. Ethylene concentration was determined from a calibration curve of 100 ppm ethylene balance in nitrogen of Scotty™ analysed gases. Acetylene reduction activity was estimated from the slope of the lineal fit of the ethylene production during up to 2 days of incubation referred to dry weight. Annual rates of non-symbiotic N fixation per N-fixer community type (*Gunnera*, O1, soil carpets and epiphytes) were estimated assuming a stoichiometric and theoretical conversion factor of 1/3 of the acetylene reduction activity, multiplied by their respective biomass. Estimated BNF per site was obtained by adding the rates for each N-fixer community type. For a detailed description of vegetation and biomass sampling, see Pérez et al. (2014a, 2014b). No estimations of tree basal area are available for the CD chronosequences.

All analyses, except for ^{15}N, were performed at the Biogeochemistry Laboratory, Pontificia Universidad Católica de Chile, Santiago.

Tree sampling

In each moraine, an area was selected at the top of the slope facing the glacier, where one circular 15-m radius plot (0.053 ha) was established. All trees > 5 cm trunk diameter at breast height (dbh, at 1.3 m from the ground) found within the plot were identified to species and their dbh was measured. Basal areas per tree species were calculated from dbh data.

Statistical analysis

A mean value of chemical parameters of surface soils and total BNF was obtained per substrate age. A mean value of nutrient content in leaves for the sampled species per substrate age was obtained without correcting for species abundances. In the case of Franz Josef, reported values in the figures belong to means and when the standard error was also given in the published tables, values are included in the graphs. To detect trends in some variables along the chronosequences, a LOWESS (locally weighted scatterplot) smoothing with a span of 0.6 was applied using the program R (2014). To evaluate the relationship between tree richness and basal area with soil and leaf stoichiometry, Pearson correlation analyses were performed with the program Statistica 7.0. Statistical significance was considered at $P < 0.05$.

Results

Changes in soils C, N and P

At a substrate age < 500 yr BP both Ct and Nt content in soils increased more rapidly in both Chilean chronosequences than in the FJ chronosequence (Figure 2A,B). The Ct content of the SII soils reached up to c. 500 g/kg, which did not decrease along the chronosequence. Although Ct content presented similar low values at substrate age > 17,000 yr BP in both CD and FJ, Nt content was higher in the Chilean than in the FJ

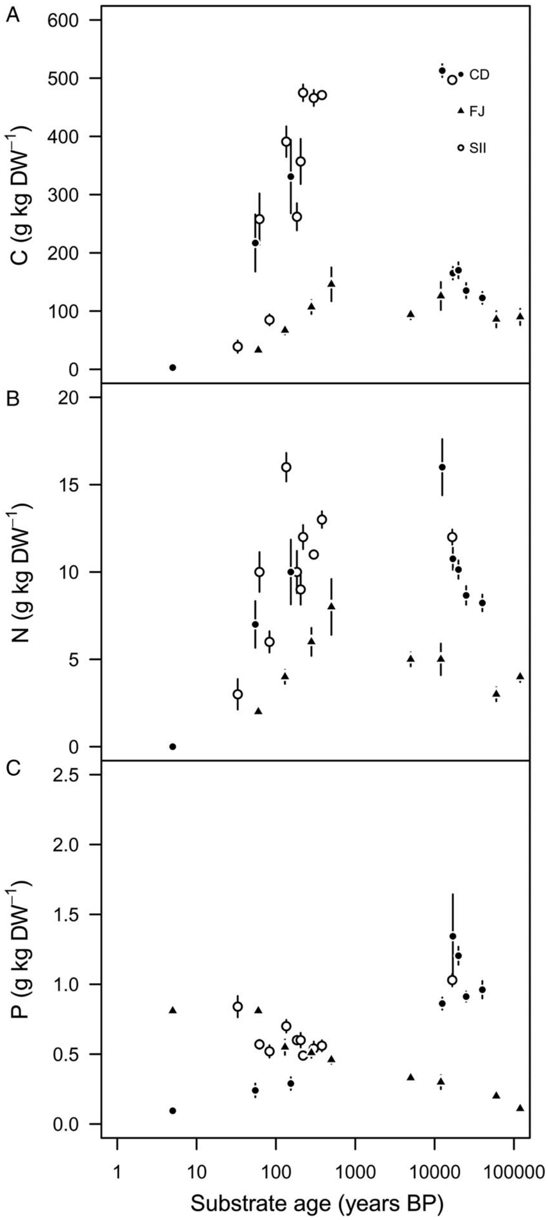

Figure 2 **A,** Total carbon, **B,** Total nitrogen and **C,** Total phosphorus concentrations in surface soils from two Chilean chronosequences, Santa Inés Island (SII) and Cordillera de Darwin (CD), southern Chile, and the chronosequence from Franz Josef (FJ) glacier, New Zealand. In the Chilean chronosequence, $n = 6$ (means ± one SE are shown).

chronosequences (Figure 2B). In the CD site, soil Pt showed an increasing trend along the chronosequence, which contrasted with the standing decreasing trend recorded in the FJ chronosequence (Figure 2C). At substrate age < 500 yr BP, soil Pt showed a decreasing trend in the SII chronosequence, resembling the declining trend in FJ, but at substrate age of 16,700 yr BP this trend reversed.

In the Chilean chronosequences the soil C/N ratios (Figure 3A) increased steeply, but in FJ there was a declining trend at substrate age < 500 yr BP. Although at substrate age > 12,500 yr BP, the C/N ratio tended to decrease in the CD chronosequence, FJ showed the reversed trend. The soil C/P ratios (Figure 3B) showed an overall increasing trend

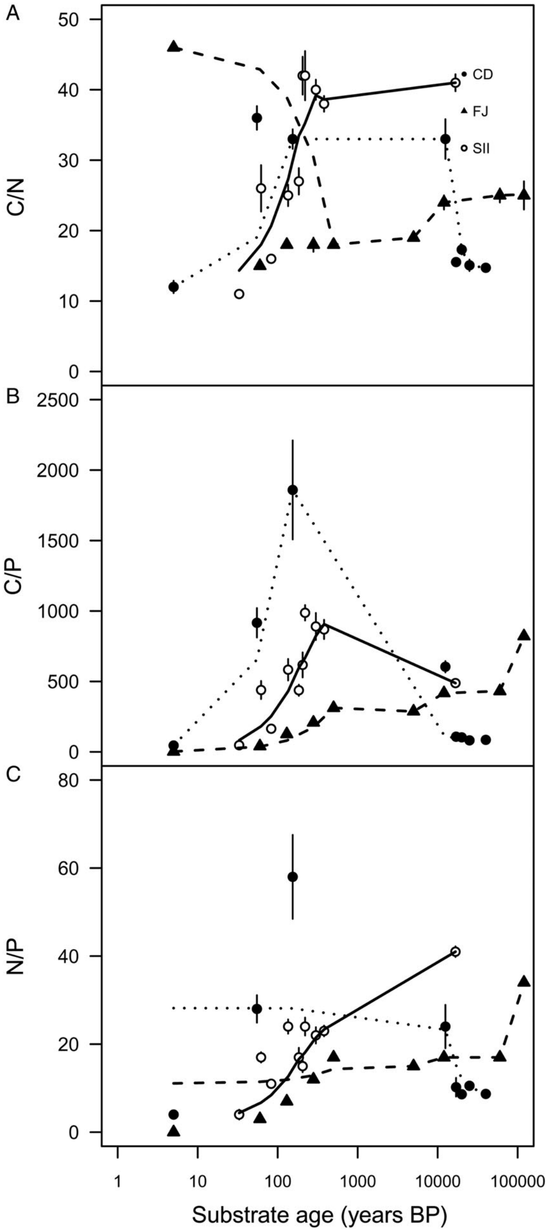

Figure 3 Element stoichiometry for **A,** C/N, **B,** C/P and **C,** N/P ratios in surface soils from two Chilean chronosequences, Santa Inés Island (SII) and Cordillera de Darwin (CD), southern Chile, and the chronosequence from Franz Josef glacier (FJ), New Zealand. In the Chilean chronosequences, *n* = 6 (means ± one SE are shown).

along the three chronosequences at substrate age < 500 yr BP, but then it reversed in the Chilean chronosequences. Whereas soil N/P ratios (Figure 3B) in CD and FJ did not show changes at substrate age < 12,500 yr BP, the SII chronosequence showed a standing increasing trend. The CD showed a decreasing trend at substrate age > 12,500 yr BP.

Corresponding with the steep increase in Nt in both Chilean chronosequences and Pt in the CD chronosequence at substrate age < 400 yr , available N and P in soils also showed a steep increase (Figure 4). FJ showed similar low values along the chronosequence. At substrate age > 12,500 yr BP all three chronosequences reached similar contents of N_a (Figure 4A) and at substrate age > 17,000 yr BP for P_a (Figure 4B).

Changes in leaf C, N and P

Leaf Nt varied in parallel along the three chronosequences compared in both Chile and New Zealand, with an overall trend to a decline over the entire chronosequence (Figure 5A).

Although leaf Pt showed a trend to decrease in the SII site at substrate age < 400 yr BP, in the FJ chronosequence leaf Pt values were constantly higher, but decreased at substrate

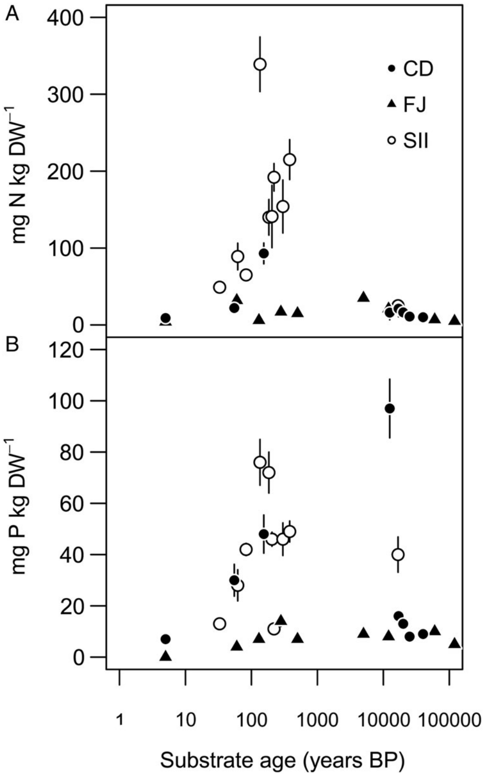

Figure 4 **A,** Available nitrogen (N_a) and **B,** available phosphorus (P_a) in surface soils in two Chilean chronosequences in southern Chile, Santa Inés Island (SII) and Cordillera de Darwin (CD), and in the chronosequence from Franz Josef glacier, New Zealand. In the Chilean chronosequences, $n = 6$ (means ± one SE are shown).

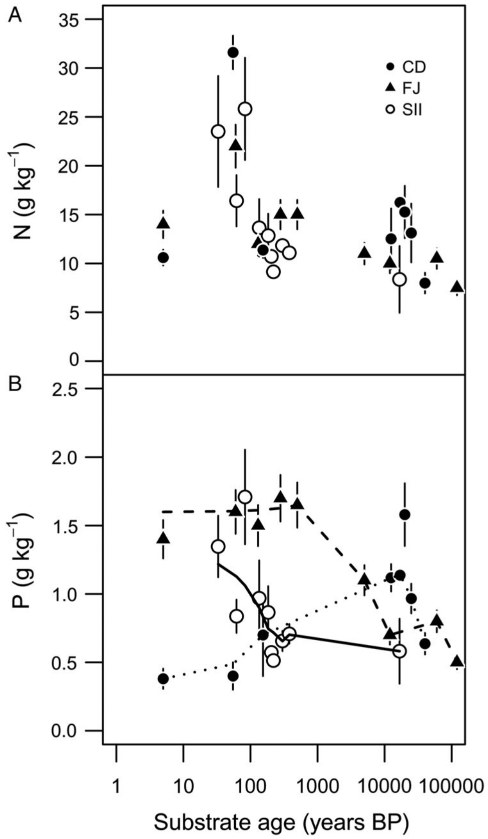

Figure 5 Foliar contents of **A,** total nitrogen (N) and **B,** phosphorus (P) in two Chilean chronosequences, Santa Inés Island (SII) and Cordillera de Darwin (CD), southern Chile and in the chronosequence from Franz Josef glacier (FJ), New Zealand. In the Chilean chronosequences, $n = 3$ to $n = 15$ (means ± one SE are shown).

age > 5000 yr BP (Figure 5B). In the CD site, there was an overall increasing trend in leaf Pt content, but it then declined at substrate age > 17,000 yr BP (Figure 5B).

We found a similar increasing trend in C/N ratio of green leaves along the three chronosequences studied in Chile and New Zealand (Figure 6A). Leaf C/P ratios in the Chilean chronosequences showed an increasing trend at substrate age < 400 yr BP, whereas in FJ chronosequence values were constantly lower than in Chile (Figure 6B). Regarding N/P ratio in fresh leaves, the CD sites presented the highest values (Figure 6C) at substrate age < 150 yr BP. At substrate age > 12,500 yr BP in both Chile and New Zealand, all the chronosequences converged to similar C/P and N/P ratios (Figure 6C).

Biological nitrogen fixation

The annual rates of BNF fixation were higher in the earliest stage of the CD and FJ chronosequences, thereafter BNF rates were lower and similar in the three chronosequences (Figure 7).

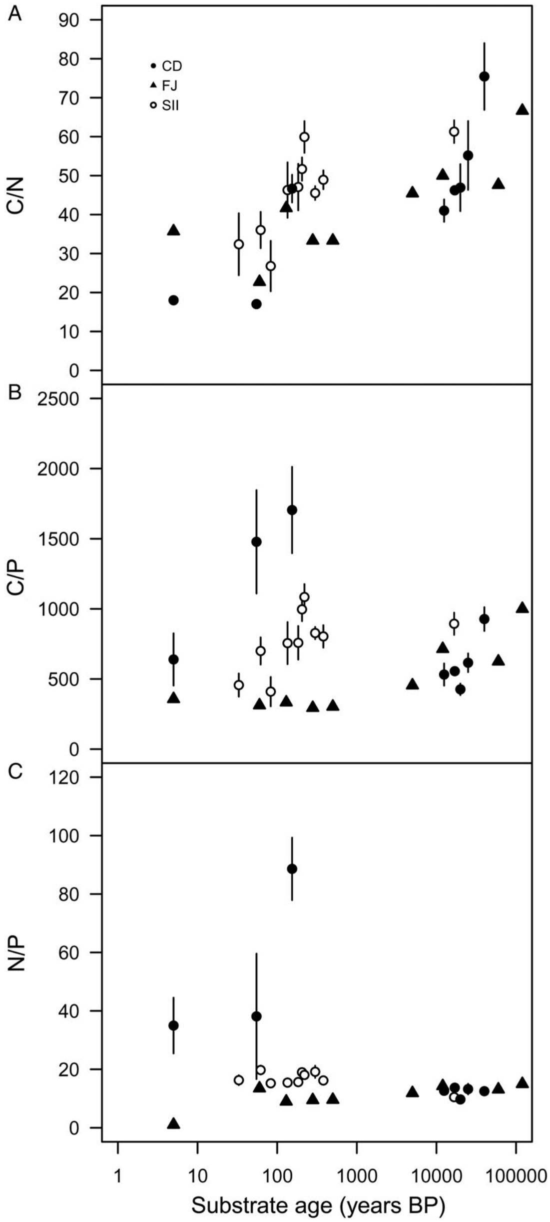

Figure 6 Element stoichiometry **A,** C/N; **B,** C/P; and **C,** N/P ratios in green leaves from two Chilean chronosequences, Santa Inés Island (SII) and Cordillera de Darwin (CD), southern Chile, and the chronosequence from Franz Josef glacier (FJ), New Zealand. In the Chilean chronosequences, $n = 3$ to $n = 15$ (means ± one SE are shown).

Content of $\delta^{15}N$ in soils

The values of $\delta^{15}N$ along both chronosequences in Chilean sites were depleted, as shown by the highly negative values and with a decreasing trend at substrate ages < 12,500 yr BP (Figure 8). An enrichment of $\delta^{15}N$ was obtained in the substrate ages > 17,000 yr BP in the Chilean chronosequences reaching similar values as the FJ chronosequence (Figure 8).

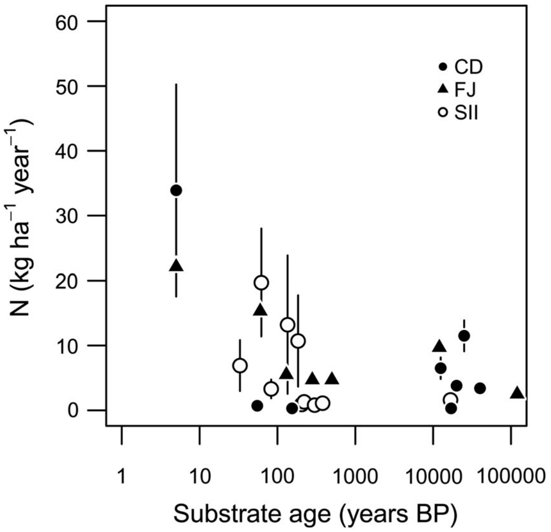

Figure 7 Rates of biological nitrogen fixation measured in four substrates, *Gunnera magellanica*, cryptogamic carpets on the forest floor, litter, and cryptogamic epiphytes, in two Chilean chronosequences, Santa Inés Island (SII) and Cordillera de Darwin (CD), southern Chile, and in the chronosequence from Franz Josef glacier (FJ), New Zealand. In the Chilean chronosequences: $n = 6$ (means ± one SE are shown).

Tree richness, basal areas and stoichiometry

Basal area showed a similar increasing trend at substrate age < 500 yr BP in FJ and SII, which was followed by a strong decrease at substrate age of 120,000 yr BP in the

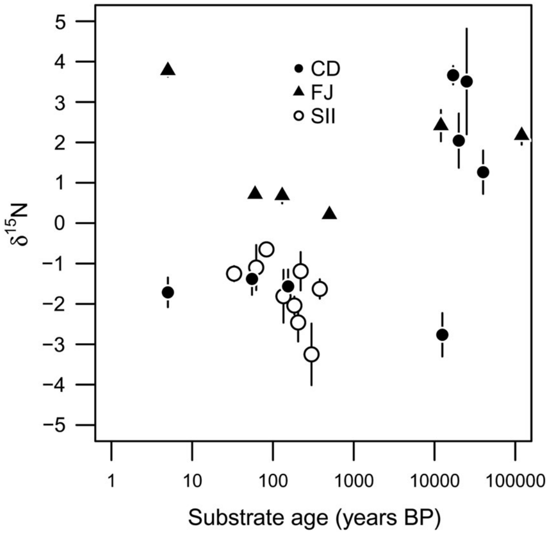

Figure 8 Natural abundances of ^{15}N in surface soils in the two Chilean chronosequences, Santa Inés Island (SII) and Cordillera de Darwin (CD), southern Chile and in the chronosequence from Franz Josef glacier (FJ), New Zealand. In the Chilean chronosequences, $n = 3$ to $n = 6$ (means ± one SE are shown).

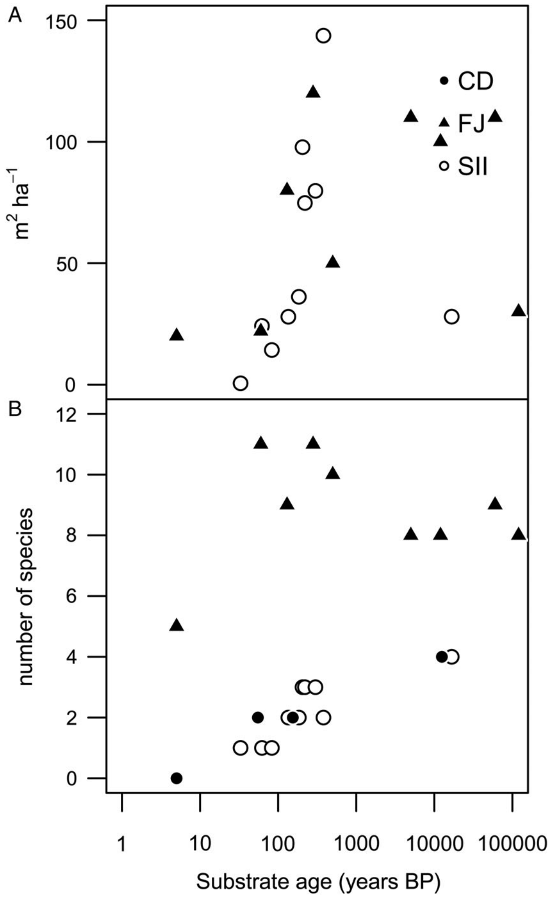

Figure 9 Changes in tree species **A,** richness and **B,** basal areas during postglacial succession in the Chilean chronosequences, Santa Inés Island (SII) and Cordillera de Darwin (CD), southern Chile, and in the chronosequence from Franz Josef glacier (FJ), New Zealand. Basal area was not available for the CD chronosequence.

former and at substrate age of 16,700 yr BP in the latter (Figure 9A). Tree species richness showed an increase along the three chronosequences in both Chile and New Zealand; however, values of tree species richness were much higher for all sites in the FJ glacier chronosequence than for the Chilean sites (Figure 9B).

In the SII chronosequence, tree species richness values correlated significantly, and positively, with soil C/N and N/P ratios ($r = 0.86$ and $r = 0.78$, respectively, $P < 0.05$). A similar positive correlation was observed for leaf C/N and C/P ratios ($r = 0.91$ and $r = 0.81$, respectively, $P < 0.05$). While Bbasal area correlated positively and significantly with soil C/N and C/P ratio ($r = 0.72$ and $r = 0.79$, respectively, $P < 0.05$), but no correlations were found between basal area and leaf stoichiometry.

Discussion

Nutrient accumulation, limitation and efficiency in use of nutrients

The patterns of total soil carbon and nitrogen accumulation and decline are similar among the Chilean chronosequences and the FJ temperate forest chronosequence. These overall patterns provide evidence of progressive, maximal and retrogressive phases of ecosystem development in post-glacial sites. Major differences among the chronosequences are observed for sites assigned to the progressive phase of nutrient and biomass accumulation occurring at substrate ages < 500 yr BP. The evidence for the onset of retrogression in the Chilean chronosequences is at substrate age > 17,000 yr BP. Higher Nt and Ct accumulation during the progressive phase and higher Nt concentrations during the retrogressive phase, as observed in both Chilean chronosequences, may be attributed to the rapid accumulation of recalcitrant carbon products in soils. This process of humification is evidenced by the rapid increase in soil C/N ratio over successional time, which translates into a declining N availability as forests approach the retrogressive phase. This pattern is consistent with the expectation that N limitation increases with the progress in ecosystem development. We postulate that accumulation of carbon in these soils via humification would be enhanced by the cold and strongly oceanic environment of the sub-Antarctic region. Volcanic activity in southern Chile may also exert a strong positive effect on organic matter accumulation in soils (Matus et al. 2014). In a post-volcanic long-term chronosequence in south-central Chile the contents of total C in progressive phases reach up to 300 g/kg, which is also higher than the rates reported for the FJ chronosequence, during this stage of succession (Pérez et al. 2014b).

In contrast to C and N, trends in soil P content show contrasting patterns when comparing Chilean and New Zealand chronosequences. A possible cause for the declining soil P content during the retrogressive phase in the FJ glacier chronosequences is the crystallisation of amorphous minerals during paedogenesis, so that they lose their capacity to retain P, mainly as inositol phosphate (Turner et al. 2007; Peltzer et al. 2010). Based on this hypothesis, we can explain the accumulation of total soil P along the Chilean chronosequences in both the CD and SII sites, by considering the reduced leaching associated with lower precipitation, in addition to the accumulation of more recalcitrant forms of organic P (higher C/P) compared with FJ glacier sites. Accordingly, during the progressive phase of succession, higher soil C/N and C/P ratios in both Chilean chronosequences are associated with higher N and P availability compared with the FJ glacier sites in New Zealand. During the retrogressive phase, soil P availability is reduced in both Chilean and New Zealand chronosequences, probably because of stronger immobilisation of P in soil organic matter, which should lead to higher P-limitation in older stages of both chronosequences.

Increasing trends for soil C/N, C/P ratios in both the SII (Chile) and FJ (New Zealand) chronosequences during the progressive phase are consistent with decreases in the element contents of fresh leaves of trees. However, in the case of sub-Antarctic forests of SII, the higher magnitude of the increases in C/P and N/P ratios in foliage suggests that the decrease in the N and P concentration in leaves of the species forming the sub-Antarctic forest is linked to improved use of elements compared with the species that form the temperate forest chronosequence in FJ, New Zealand. The constant foliar N/P ratio > 12.5 documented along the entire post-glacial chronosequence in Chile, suggests stronger P limitation, not limited to the retrogressive phase, as was the case for the New Zealand chronosequence in FJ (Richardson et al. 2004). Contrasting patterns of P accumulation in leaves during the progressive phase of the chronosequences were observed in the three sites (SII, CD and FJ), which could be explained by marked differences in P use strategies among trees in each region, an interesting possibility that should be explored in future studies.

Regarding the standing increase in basal and tree richness documented by the SII chronosequence for the sites included in the progressive phase of succession, this is linked to increasing C/N, C/P and N/P ratios in soils. Likewise, tree species richness is associated with an increase in foliar C/N and C/P ratios. Consequently, shifting tree assemblages across the Chilean successional series drive changes in nutrient use efficiency, from less efficient N users such as the deciduous tree *Nothofagus antarctica,* which is dominant in early succession, to more efficient N users, such as the evergreen *Nothofagus betuloides*, *Drimys winteri* and the conifer *Pilgerodendron uviferum*, which occur in the late successional forest stands. Similarly, an increase in nutrient resorption efficiency and a shift from resource-acquiring to nutrient-retaining species has been reported in the New Zealand chronosequence from FJ (Richardson et al. 2005, Mason et al. 2012). More diverse belowground nutrient use strategies have been linked to a decrease in total soil P and an increase in soil N/P ratio in the Australian Jurien Bay dune chronosequence (Zemunik et al. 2015).

Biological nitrogen fixation and ^{15}N in soils

A strikingly similar pattern was documented by our postglacial chronosequences regarding BNF rates. The highest rates of BNF reaching up to c. 20–30 kg/ha/yr were measured during the earliest stage of ecosystem development, due primarily to the symbiotic association of the actinobacteria *Frankia* with the shrub *Coriaria* and the association of the cyanobacteria *Nostoc* with the summer green herb *Gunnera*, in the New Zealand and Chilean chronosequences, respectively. Moreover, during the retrogressive phase in both Chilean and New Zealand postglacial sites BNF rates decay to similar values, when understorey bryophytes, cryptogamic epiphytes and the litter layer acquire a more prominent role in total BNF.

Declines in the natural abundances of $\delta^{15}N$, with striking contrasting values, however, are found in surface soils of both the Chilean and New Zealand chronosequences up to substrate age of 12,500 yr BP. During the progressive phase in both Chilean and New Zealand chronosequences, increasingly depleted values of ^{15}N in soils and a stronger decline in soil ^{15}N with stand age may result from several N transformation processes acting in synchrony. In other words, the accumulation of ^{15}N depleted N from N fixation, a higher accumulation of N from ^{15}N-depleted litter, and lower N losses via leaching and/or denitrification over successional time (Högberg 1997) led to higher retention capacity of ^{15}N-depleted products. In contrast, the strong enrichment in $\delta^{15}N$ values at substrate age > 17,000 yr BP in the Chilean chronosequences and > 12,000 yr BP in the FJ chronosequence is evidence for an increase in the loss of $\delta^{15}N$-depleted products during the retrogressive phase along with ecosystem development.

Conclusions

Postglacial ecosystem development followed strikingly similar patterns in southern South America (SII and CD sites) and in New Zealand (FJ glacier sites) despite different floristic assemblages, climatic regimens and geological substrate. At all sites, we document a progressive, maximum and retrogressive phase of succession marked by similar patterns of accumulation of total C and N in soils. In both Chilean and New Zealand chronosequences N and P limitation (associated with higher soil C/N and C/P ratios) and higher use of nutrients (higher foliar C/N and C/P) showed increasing trends during the progressive phase. These trends are accompanied by concomitant increases in tree species richness in the Chilean chronosequences and greater diversity of belowground functional traits related to nutrient-use strategies in the New Zealand, FJ chronosequences. A strong decrease in basal area occurred at substrate age c. 17,000 yr BP, confirming the onset of retrogression in the Chilean chronosequence.

Major differences between Chilean and New Zealand postglacial chronosequences were observed in the magnitude of soil and plant element contents and soil and foliar (C/N, C/P, N/P) stoichiometry during the progressive phase of ecosystem development. Notably, no significant decline in total soil P over the course of succession and more depleted ^{15}N during the progressive phase were documented in the Chilean chronosequences, suggesting a slower and tighter internal N and P cycle. However, the strong δ^{15}N enrichment at substrate age > 17,000 yr BP suggests an increase in loss of N during retrogression in the Chilean and FJ chronosequences. A similar trend of enrichment in soils attributed to fractionating losses during retrogression is reported for volcanic soils in the south-central region of Chile (Pérez et al. 2014b) and the northern Arizona, USA (Selmants & Hart 2008) long-term chronosequences.

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