Phosphorus conservation during post-fire regeneration in a Chilean temperate rainforest

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Abstract Nitrogen and phosphorus are the main elements limiting net primary production in terrestrial ecosystems. When growing in nutrient-poor soils, plants develop physiological mechanisms to conserve nutrients, such as reabsorbing elements from senescing foliage (i.e. nutrient retranslocation). We investigated the changes in soil N and P in post-fire succession in temperate rainforests of southern Chile. In this area, forest recovery often leads to spatially scattered, discrete regeneration with patches varying in age, area, species richness and tree cover, representing different degrees of recovery from disturbance. We hypothesized that soil nutrient concentrations should differ among tree regenerating patches depending on the progress of forest regeneration and that nutrient resorption should increase over time as colonizing trees respond to limited soil nutrients. To evaluate these hypotheses, we sampled 40 regeneration patches in an area of 5 ha, spanning a broad range of vegetation complexity, and collected soil, tree foliage and litter samples to determine N and P concentrations. Nutrient concentrations in leaf litter were interpreted as nutrient resorption proficiency. We found that soil P was negatively correlated with all the indicators of successional progress, whereas total soil N was independent of the successional progress. Foliar N and P were unrelated to soil nutrient concentrations; however, litter N was negatively related to soil N, and litter P was positively related with soil P. Finally, foliar N:P ratios ranged from 16 to 25, which suggests that P limitation can hamper post-fire regeneration. We provide evidence that after human-induced fires, succession in temperate forests of Chile can become nutrient limited and that high nutrient retranslocation is a key nutrient conservation strategy for regenerating tree communities.

Key words: arrested succession, nitrogen, N:P ratio, resorption proficiency, retrogression.

INTRODUCTION

Leaf traits such as long leaf lifespan, low element concentrations and high nutrient resorption from senescing foliage are important nutrient conservation mechanisms in low fertility environments (Vitousek 1982; Boerner 1984; Killingbeck 1996; Aerts & Chapin 2000; Parfitt *et al.* 2005; Richardson *et al.* 2005; Reed *et al.* 2012). Nutrient resorption, that is, the withdrawal of nutrients from senescing leaves or before abscission, can make reabsorbed nutrients directly available for plant growth (Chapin 1980; Killingbeck 1986; Aerts 1990). Such internal nutrient recycling mechanism reduces plant dependence on slow soil nutrient release via litter decomposition processes (Aerts 1996). Nutrient resorption plays a key role when plants grow on nutrient-poor soils (Craine

& Mack 1998; Richardson *et al.* 2005, 2008; Reed *et al.* 2012). Nutrient resorption proficiency (NRP) is measured as the nutrient concentration in litter (Killingbeck 1996) and hence high NRP produces low quality litter for decomposers and therefore low return rates of nutrients to the internal ecosystem cycle (Gosz *et al.* 1976; Aerts 1997; Aerts & Chapin 2000; Satti *et al.* 2003). A fertilization experiment by Kozovits *et al.* (2007) in phosphorus-poor tropical soils showed that nitrogen (N) and phosphorus (P) additions had no significant effects on foliar nutrient concentrations but enhanced litter nutrient contents, hence litter quality. Consequently, resorption rates are responsive to soil nutrient availabilities and plants seem to respond to changes in soil fertility by modulating resorption proficiency.

Nutrient limitation characterizes the development of vegetation in highly weathered soils in the absence of rejuvenating disturbances that promote soil nutrient availability (Vitousek & Reiners 1975; Wardle *et al.* 2004). For example, during soil pedogenesis mineral P is gradually occluded and lixiviated, and

such changes in soil P could lead to a decline in forest biomass and productivity (Coomes *et al.* 2005; Gaxiola *et al.* 2010). This 'retrogressive phase' (Vitousek & Farrington 1997; Wardle *et al.* 2004) can result from nutrient depletion or decreased availability, and can only be reversed through major disturbances (i.e. those that are sufficiently severe to rejuvenate soils) (Peltzer *et al.* 2010). In the absence of disturbances, for example, earthquakes or recurrent fires, P limitation will develop over time if no other sources of mineral P are available (Walker & Syers 1976; Wardle *et al.* 2004). However, not all disturbances result in resetting soil P availability; the effects of disturbance on available nutrient stocks depend greatly on ecosystem nutrient status, resilience capability, as well as on the characteristics of the disturbance (Vitousek & Reiners 1975; Boerner 1982).

Wildfires often decrease the availability of N and P in terrestrial ecosystems (Kauffman *et al.* 1995; Caldwell *et al.* 2002). N is primarily lost by volatilization at relatively low temperatures (~200°C), in contrast to mineral P that has volatilization temperatures above 600°C (Boerner 1982; Raison *et al.* 1985). Although N is easily volatilized, N fixation can rapidly build up soil N availability to near pre-fire values within decades (Jorgensen & Wells 1971; Tiedemann *et al.* 1978; Pérez *et al.* 2004). In contrast, P compounds are lost mainly through convection of the ash when the bulk of the biomass is above-ground (Boerner 1982). Consequently, fire disturbance can significantly reduce soil N and P via different mechanisms, while at the same time, recovery processes of these two nutrients follow different pathways and these differences can have important consequences for ecosystem regeneration.

Human-set fires have historically been used to clear forestland in temperate Chile (Armesto *et al.* 2009). As naturally ignited wildfires are extremely rare events in these temperate rain forests, the recurrence of anthropogenic fire has greatly altered the dynamics of secondary forest succession (Kitzberger & Veblen 1999; Díaz & Armesto 2007; Díaz *et al.* 2007; Veblen *et al.* 2011). Arrested ecosystem succession has been reported across extensive burned areas, which results from altered hydrology after loss of the forest canopy (Díaz & Armesto 2007; Díaz *et al.* 2007; Albornoz *et al.* 2013). Furthermore, fires in this region leave behind a vegetation matrix composed of unburned remnant patches of trees, coarse woody residues and low shrubs (Aravena *et al.* 2002; Carmona *et al.* 2002). Albornoz *et al.* (2013) showed that within a post-fire matrix in southern Chile, tree establishment was scattered and patchy over 5 ha. Fifty years after human-set fire, remnant regenerating tree patches have expanded and new patches have appeared, and large patches support higher tree species richness and biomass than

small patches (Albornoz *et al.* 2013). In addition to soil hydrology, fires alter soil chemistry and nutrient availability and change landscape structure and species composition (Certini 2005; Úbeda & Outeiro 2009). However, whether tree regeneration in southern temperate forests is also hampered by reduced nutrient availability has rarely been studied.

In this study, we addressed the role of nutrient limitation as a factor controlling post-fire forest recovery in a Chilean temperate rainforest subjected to human-set fire about 50 years ago (Albornoz *et al.* 2013). Because soil N and P concentrations are reduced after fire, trees in regenerating patches are expected to show strong nutrient conservation mechanisms, particularly nutrient resorption, to cope with low nutrient availability and slow internal ecosystem recycling associated with poor quality litter. Here, we seek to document (i) the changes in soil N and P availabilities during post-fire regeneration in the soils of established tree patches, asking whether soil N and P follow different recovery trends during secondary succession and (ii) the responses of the tree community to changes in soil N and P availabilities during secondary succession. We hypothesize that high N and P resorption from senescent leaves represents an effective nutrient retention mechanism in these patches due the impoverished post-fire soil conditions.

MATERIALS AND METHODS

Study site

The study was conducted within a secondary successional area at Senda Darwin Biological Station (SDBS) in northern Chiloé Island, southern Chile (41°50'S; Fig. 1). The regional climate is wet temperate, with strong oceanic influence (Di Castri & Hajek 1976), with a mean annual precipitation at Senda Darwin of 2110 mm (average of the past 12 years); mean minimum and maximum monthly temperatures are 3°C in July and 17°C in January, respectively (SDBS, meteorological records 1999–2007). Soils in the study area are highly weathered andisols (i.e. ñadis) characterized by an impermeable hardpan layer at about 50–60 cm depth (Veith & Garleff 1996), which results in a shallow water table and waterlogged soils during the austral winter (June–August), especially in disturbed successional areas (Díaz & Armesto 2007; Albornoz *et al.* 2013).

Within an area of 115 ha, SDBS contains a representative sample of rural landscape that characterizes southern Chile (Carmona *et al.* 2010) providing the opportunity to investigate and understand the dynamics of temperate ecosystems within the context of land use in southern South America (Armesto *et al.* 1998). Current vegetation within SDBS contains deforested areas dominated by pastures and scrublands as well as patches of old-growth and secondary North Patagonian evergreen broad-leaved temperate forests. The canopy of these forests is dominated by *Podocarpus*
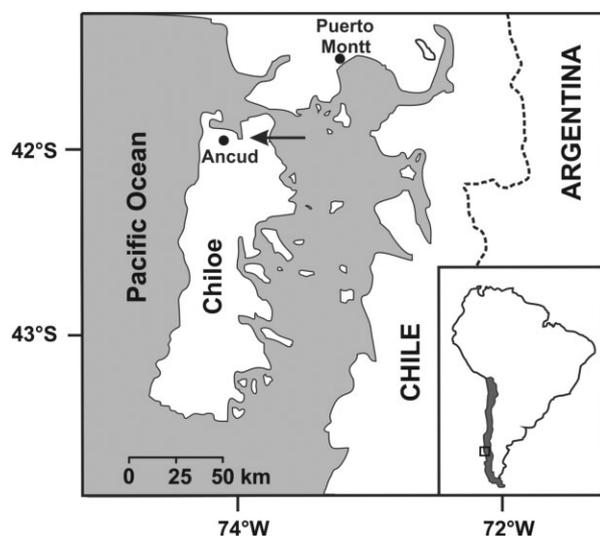
Fig. 1. Location of study area in Chiloé Island, southern Chile. The arrow indicates the location of Senda Darwin Biological Station.
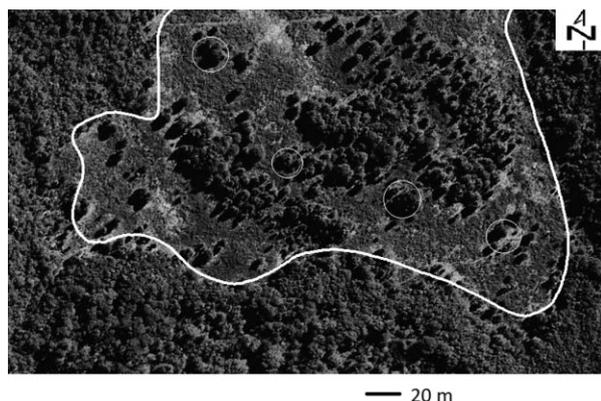

Fig. 2. Aerial photograph of the post-fire regeneration patches. The white line circumscribes the post-fire successional area, and circles indicate four of the 40 regeneration patches studied.

nubigena (Podocarpaceae), *Drimys winteri* (Winteraceae) and *Nothofagus nitida* (Nothofagaceae), with an understorey of *Tepualia stipularis* and other myrtaceous tree species (Gutiérrez *et al*. 2004). The work was conducted within an area of approximately 5 ha that was burned deliberately to open land for grazing before the site was a field station, approximated 50 years ago (Holz & Veblen 2011). Because the area became waterlogged, it was never used as a pasture and forest recovery has continued without human intervention until today (Fig. 2). Forest regeneration pattern has been characterized as nucleated succession (Albornoz *et al*. 2013), where 117 regeneration patches varying in size and level of development are embedded in a matrix of low shrubs (such as *Gaultheria mucronata* and *Myrteola nummularia*, less than 1.5 m tall), prostrate ferns (*Blechnum penna-marina* and *Gleichenia* spp.), with scattered *Sphagnum* moss mounds, over seasonally waterlogged soils.

Regeneration patches

We selected 40 of the 117 regeneration patches of varying size and complexity to represent the entire range of observed variation in the regeneration process defined by Albornoz *et al*. (2013). In these 40 patches, we evaluated tree species richness and abundance (i.e. number of individuals per species), and measured patch area and tree basal area of each patch. Basal area for a patch was calculated as the ratio of the sum of the Diameter at breast height (DBH) of all individuals with a DBH > 5 cm divided by patch area, representing the area of patch covered by trees.

Soil and leaf nutrient analysis

To assess possible changes in soil nutrient concentrations during post-fire secondary succession, soil samples (20 cm deep, mineral soil horizon, A) were collected within each of the 40 selected patches. Three soil subsamples were collected within each tree patch and pooled for chemical analyses. In addition, we collected at least 10 fully expanded fresh leaves of all trees present within each patch and collected litter right under the canopy of trees in the patches. Fresh leaves were collected in the middle of the growing season (i.e. December and January) and freshly fallen litter was collected in late autumn (April–May) during the peak of litter production (Pérez *et al*. 2003). Soil samples were obtained during the late autumn. Samples were taken to the lab, dried for 72 h at 60°C, and ground for chemical analyses. Total carbon (C) and N determinations of soil and plant material were made by flash combustion in a Carlo Erba NA 2500 Elemental Analyser. We used acid extraction for soil P (i.e. total P) and foliar tissue concentrations. For this, 0.25 g of sample was digested in concentrated sulphuric acid–water–peroxide solution in a Digesdahl Digestion machine and concentrations were determined colorimetrically with molybdenum blue (Steubing & Fangmeier 1992). All chemical analyses were conducted in the Biogeochemistry Laboratory at the Pontificia Universidad Católica de Chile. We considered litter nutrient concentrations as estimates of NRP (*sensu* Killingbeck 1996). Foliar N:P ratios for the tree community within each patch were also calculated to evaluate nutrient limitation or co-limitation (Koerselman & Meuleman 1996).

Statistical analyses

To detect soil nutrient changes during the regeneration process, we correlated indicators of patch succession status, such as patch area, tree basal area of the patch, woody species abundance and tree species richness, with total N and P concentrations for the patch soils. For this analysis, we used the Pearson product-moment correlation coefficients. Similarly, we used Pearson's correlations to test the relationship between soil nutrient availability and leaf nutrient contents of trees at the patch level, measured by foliar and litter nutrient concentrations. Nutrients in litter were considered indicators of NRP. Finally, to diagnose nutrient limitation changes during the regeneration process, we ran linear regressions of

foliar N:P *versus* soil N and soil P respectively. All analyses were conducted in R v. 2.7.1 (R Development Core Team, 2011).

RESULTS

Soil nutrients *versus* patch succession

Across the 40 tree regeneration patches sampled over the entire successional area, total soil P ranged from 367 to 591 mg kg^{-1} with a mean of 467.8 ± 9.3 mg kg^{-1} (±1 Standard Error of the Mean; SEM), and total soil N ranged from 451.8 to 2052 mg kg^{-1} with a mean of 1433 ± 51.6 mg kg^{-1}. Post-fire soil P concentrations were negatively correlated with patch regeneration status indicators (Table 1), that is, soil P tends to decline with patch recovery progress. In contrast, post-fire soil N concentrations did not change significantly during the regeneration process and were unrelated to any of the indicators of patch regeneration status (Table 1).

Foliar nutrient concentrations

Foliar P concentrations of trees per patch ranged from 0.04% to 0.87%, with a mean of 0.05 ± 0.001% of leaf dry mass, and foliar values were unrelated to soil P concentrations ($R^2 = 0.09$, $F_{1,36} = 3.53$, d.f. = 36, $P > 0.06$). Similarly, foliar N of trees per patch varied from 0.81% to 1.85 %, with a mean value of 1.06 ± 0.03%, and foliar N contents were unrelated to soil N in the patches ($R^2 = 0.01$, $F_{1,36} = 0.42$, d.f. = 36, $P = 0.52$). Foliar N:P ratios varied among successional patches from 16.6 to 25.9, indicating that tree communities in all post-fire regenerating patches could be P limited. Foliar N:P of trees in patches was negatively related to total soil P in the patch ($R^2 = 0.28$, $F_{1,36} = 15.75$, d.f. = 36, $P < 0.001$; Fig. 3a), but it was unrelated to total soil N ($R^2 = -0.02$, $F_{1,36} = 0.27$, d.f. = 36, $P = 0.6$; Fig. 3b).

NRP

In our successional area, NRP was greater for P than for N. Litter P at the patch level varied from 0.01% to 0.038%, with a mean of 0.02 ± 0.001%, and litter P content was positively correlated with total soil P in the patch ($R^2 = 0.23$, $F_{1,36} = 12.0$, $P < 0.01$; Fig. 4a). Litter N concentrations per patch varied from 0.44% to 1.03%, with a mean of 0.72 ± 0.02%, and litter N contents were negatively correlated with soil N content per patch ($R^2 = 0.15$, $F_{1,36} = 7.5$, $P < 0.01$; Fig. 4b). These extremely low litter P values strongly suggest that trees in these regeneration patches have very high resorption proficiencies (<0.04% litter P in evergreen tree species) regardless of total soil P values (Fig. 4a). Some litter *P* values recorded in this study represent the lowest concentrations at which a plant can reduce nutrient contents in senesced leaves (0.01% litter P, or ultimate potential resorption, *sensu* Killingbeck 1996). Such values were recorded in 15% of the regenerating tree patches where total soil P was <526 mg kg^{-1}. Complete proficient N resorption (<0.7% litter N, *sensu* Killingbeck 1996) was also recorded in 45% of the regenerating patches in our successional area for the whole range of total soil N concentrations. Ultimate potential resorption of N was not observed in any of the patches (Fig. 4b).

DISCUSSION

Our study shows that in a relatively short period of about 50 years, following anthropogenic forest burning in this area of southern South America, tree growth within regeneration patches may become P limited. The negative relationship between soil P and the area of regenerating patches (Table 1), as well as between soil P and tree species richness (Table 1), suggest that plant uptake is depleting the soil pools of mineral P over successional time. This is further confirmed by the trends in P resorption proficiency, which reached 'complete resorption' in all

Table 1. Relationships between soil nutrients and post-fire regeneration in tree patches in a secondary succession in Chilean temperate rain forests

Successional status indicators	Soil P		Soil N	
	r	t	r	t
Patch area (m^2)	−0.33	2.2*	−0.12	0.76
Patch basal area (m^{2}ha^{-1})	−0.33	2.1*	0.04	0.24
Woody species richness	−0.48	3.4*	−0.18	0.83
Woody species abundance	−0.47	3.3*	−0.13	1.18

Significant values *$P < 0.05$. r: coefficient value of Pearson's product moment correlation. t: value of the test statistic. Values in the table are for Pearson correlations between total soil concentrations of nitrogen (N; mg kg^{-1}) and phosphorus (P; mg kg^{-1}) and patch regeneration status indicators ($n = 40$ patches).
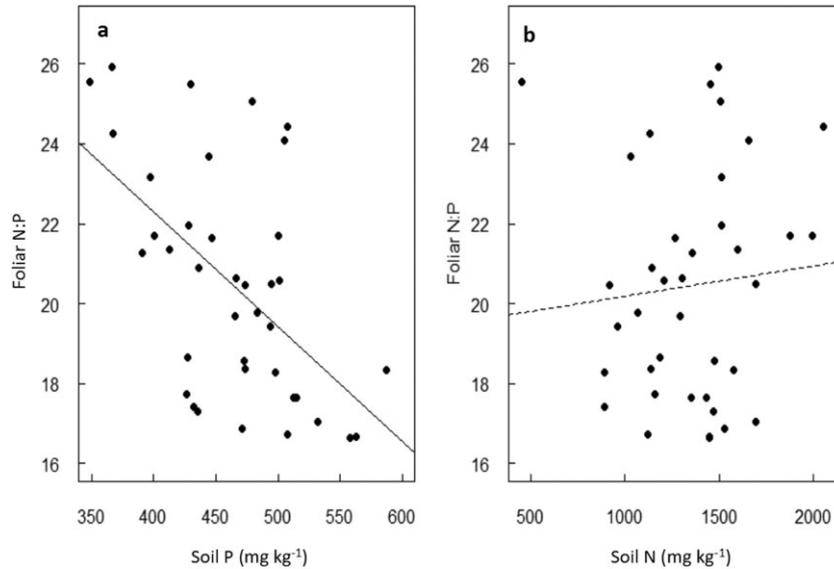
Fig. 3. Foliar N:P ratio for the tree community within each patch in relation to (a) total soil P and (b) total soil N concentrations of each patch. Foliar N:P ratios were significantly decreased with total soil P. Solid line indicates significant relationship, and the dashed line indicates non-significant relationship. Foliar N:P ratios > 16 indicate potential P limitation for plant growth according to Koerselman and Meuleman (1996) and Güsewell (2004).
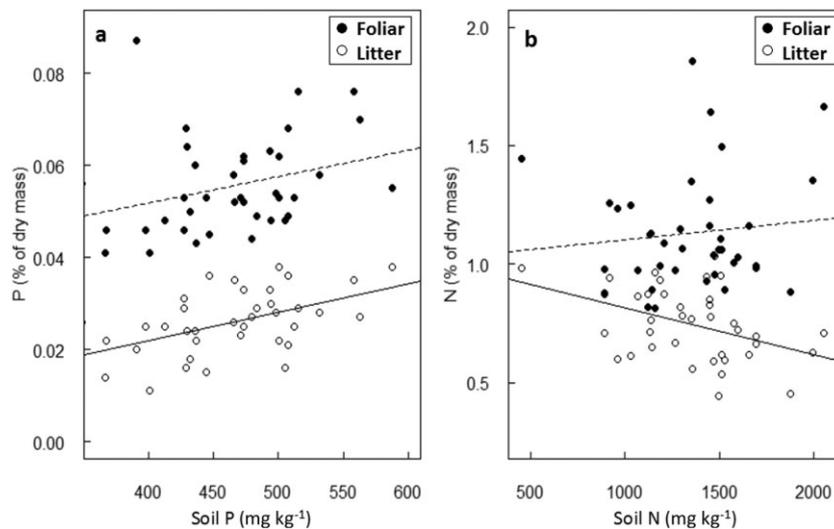

Fig. 4. Foliar and litter nutrient concentrations and their relationship with total soil nutrient concentrations among 40 post-fire regenerating tree patches that differ in size and age. (a) Litter P significantly increased with total soil P, but no relation was found between foliar P and soil P among patches. All litter P concentrations represent very high P resorption (less than 0.04% of litter dry mass); (b) Significant decreases in litter N with soil N, but no significant relation between foliar N and soil N among patches. Solid lines indicate significant relationships and dashed lines indicate non-significant relationships ($P > 0.05$). See text for more statistical details.

regenerating tree patches in the burned area. Taken together, these two observations indicate that post-fire soil P can become rapidly sequestered in plant biomass during the early phases of forest recovery. In contrast, our results for soil N over the successional area indicate that plenty of N is available for plant use in all regeneration patches, as we found no indication of changes in soil N concentrations with any variable associated with patch regeneration status. Further, we found foliar N:P ratios above 16 for trees in the patches (Fig. 3), which are indicative of P-limited plant growth (Koerselman & Meuleman 1996). Based on these relatively high foliar nutrient ratios, we could assume that trees growing in these regenerating tree patches are becoming limited by P and less likely by N (Fig. 3).

Total soil P concentrations in the regeneration patches studied (i.e. 367–591 mg kg^{-1}) are similar to the lowest values recorded for temperate forests in southern Chile. Previous studies in Chiloé forests measured total soil P contents that ranged between 400 and 1000 mg kg^{-1} (Ruthsatz & Villagrán 1991) and between 357 and 413 mg kg^{-1} (Thomas *et al.* 1999) both estimates for old-growth, temperate forests of Cordillera de Pichué, coastal range of Chiloé Island. Likewise, soil P values for several old-growth rainforests in the vicinity of the burnt area ranged between 300 and 500 mg kg^{-1} (Gaxiola *et al.* 2014 unpubl. data), values that are very close to those measured in our early secondary successional patches (Table 1). We infer from these data that plant growth and tree establishment following the forest fire have reduced soil P during regeneration to levels that are similar to old-growth undisturbed stands in the region. This is further supported by the strong negative correlation between total soil P and tree species richness and abundance in the developing patches (Table 1) that suggest further declines in soil P through subsequent secondary succession. Consequently, as regenerating patches expand and trees grow over time, soil P in this successional area becomes immobilized in above-ground plant biomass. Since we know of no other source to replenish P in the soil pool in this post-fire regenerating area, it is most likely that P depletion in successional soils could hamper further tree growth and establishment and become a factor that slows down or even arrests successional progress.

Tree growth in Chilean old-growth temperate forests is generally considered to be N limited (Thomas *et al.* 1999; Vann *et al.* 2002); however, in contrast to our present knowledge of changes in N availability during secondary succession (e.g. Pérez *et al.* 2004), P limitations for tree growth in young successional forests, have not previously been examined. Vann *et al.* (2002) calculated both annual P and N requirements for growth of adult trees in old-growth, evergreen rainforests and found that P pools in soil exceed by several fold the annual requirement based on current annual biomass increments. However, these authors also showed that more than 60% of the total P pool in these old-growth forests was stored in the above-ground biomass, in contrast to only 15% of the total N pool. This means that after a fire, or complete tree removal, around 60% of all the P is removed from the system. According to Vann *et al.* (2002), on these grounds, it seems likely that nutrient requirements of old established trees in undisturbed forests are satisfied by current nutrient availability and internal nutrient cycling. However, we must take into account that adult trees allocate most nutrients to maintenance and reproduction rather than growth, whereas nutrient requirements of young, actively

growing trees may be much higher in early successional sites.

Although we measured total soil P and not plant available P, it is known that a large fraction of P in soil P Chilean temperate forest is found in forms that cannot be readily used by plants, predominantly bound to cations or as organic P, because of the volcanic origin of most soils (Thomas *et al.* 1999; Borie & Rubio 2003). Accordingly, Pinochet *et al.* (2001) measured soil P fractions in volcanic soils from southern Chile and described that soil P varied between 354 and 1414 mg kg^{-1}, 53% to 82% of which was bound in organic compounds. Similarly, Borie and Rubio (2003) reported that forest soils from southern Chile could contain more than 50% of total P in organic forms. Indeed, soil organic P can occur in a broad spectrum of compounds that vary in their degree of availability to plants. Some plants can use organic P via the synthesis of phosphatase enzymes, or assimilation can be assisted by the presence of mycorrhizal fungi (Attiwill & Adams 1993). Our current measures of soil P could overestimate the degree of P limitation for tree growth during post-fire succession. Therefore, further studies of soil P fractions, as well as tree species capacity to produce phosphatases, organic acids, or develop associations with mycorrhizal fungi that enhance uptake of organic P are required to improve our understanding of P limitation and dynamics during succession in these temperate ecosystems. Similarly, fertilization experiments can provide more conclusive results on the role of nutrient limitation in these temperate forests.

We present an important example of how anthropogenic fire disturbances could produce long-term consequences for biogeochemical cycles in successional forests, because a forest fire consumes more than 60% of the P pool, most of which is present in the tree trunk, branches and leaves (Vann *et al.* 2002). Nonetheless, the fairly constant soil N concentrations found in regenerating patches suggest a rapid recovery of N pools (Pérez *et al.* 2004), presumably due to the profuse activity of N fixers, such as heterotrophic bacteria, free-living in litter and soils, associated with liverworts, or in symbiotic lichens. N availability can be built up to near pre-fire values within decades of secondary succession in Chilean temperate rainforests (Aravena *et al.* 2002; Pérez *et al.* 2004). In the present study, foliar N:P ratios were sensitive indicators of changes in soil P concentrations in post-fire regenerating patches (Fig. 3). According to the literature, N:P values tend to be primarily driven by changes in soil P rather than soil N (Koerselman & Meuleman 1996; Güsewell 2004). Thus, high foliar N:P ratios can be strong evidence of declining P availability over successional time, while soil N continues to be available for plant growth. Similarly, our current foliar N:P values are similar to data previously reported for different

tree species from surrounding old-growth forests (see Table S1).

On the other hand, tree communities in regenerating patches efficiently reduce litter P and N concentrations, keeping community foliar N:P at values lower than 26 (Fig. 3) despite the low soil P availability observed among patches. Richardson *et al.* (2008) also showed that high NRP along soils with low P availability promoted low foliar N:P at the community level (i.e. foliar N:P ranged from 10 to 22). Furthermore, NRP was 0.04% on soils with soil P of ~600 mg kg^{-1} (Richardson *et al.* 2005) and we report here NRP of 0.04% at soil P of 580 mg kg^{-1} which is the highest total P value reported in the regeneration patches. Hence species from temperate forests from New Zealand and Chile growing at low soil nutrient availability seem to share similar nutrient conservation strategies independently of the origin of nutrient limitation. In terms of nitrogen, species in New Zealand, growing at soil N values of 2000, had NRP of 1% (Richardson *et al.* 2005), whereas in Chile for the same soil N value, community level NRP was 0.7%. In contrast to expectation, we found that nitrogen NRP tended to increase with increasing soil N (Fig. 3b); however, we notice in Fig. 3a by Richardson *et al.* (2004) that community level litter N decreased with increasing soil N (i.e. from 1.2% to 0.6% at soil values ranging between 2000 and 4000 mg kg^{-1}). Therefore not only our range of soil N (i.e. 500–2000 mg kg^{-1}) after 50 years of forest succession seems to mirror soil N values of the early stages of ecosystem development of the Franz Josef chronosequence in New Zealand, but also the pattern of nitrogen resorption proficiency. An explanation for these counterintuitive patterns could be associated with species N uptake strategies. As suggested by Aerts and Chapin (2000), at very low N levels plants N uptake strategies are related to nitrate or ammonium absorption via the roots; therefore, it is likely that at intermediate soil N availabilities, plant uptake strategies switch towards internal N cycling. This, however, requires further investigation.

We provide evidence that NRP can be an effective mechanism to promote P use efficiency at the tree community level during post-fire succession. Litter concentrations previously reported for other evergreen Chilean temperate forests (Lusk *et al.* 2003) ranged from 0.04% to 0.12%, while in this post-fire successional area, values are remarkably smaller (i.e. 0.01 to 0.04; Fig. 4a). These low values seem to be expected for juvenile growing trees in successional patches, rather than for adult trees in pristine forests. During post-fire succession, greater nutrient retranslocation may be required to maintain tree growth rates. Additional work will be necessary to fully understand how tree species adjust to variable soil nutrient conditions during their life cycle.

We show here that in ecosystems where nutrients are stored primarily in above-ground biomass (i.e. oligotrophic ecosystems, *sensu* Boerner 1982), removal or loss of above-ground biomass (due to fire or logging) represents a major pathway of nutrient loss with consequences for subsequent succession. Thin, organic-rich soils such as those found in Chilean temperate forests in the coastal range (Vann *et al.* 2002) can support large amounts of living biomass, based on efficient nutrient uptake and retention (e.g. Pérez *et al.* 1998), but the resilience of forests is limited to fairly small-scale disturbances such as single or multiple tree falls, with infrequent large disturbances (Veblen *et al.* 1981; Armesto & Fuentes 1988; Gutiérrez *et al.* 2004). Furthermore, we provide evidence that element retranslocation is a key nutrient conservation strategy for regenerating tree communities after fire. High retranslocation may consequently reduce P returns to the soil via litter, further enhancing soil nutrient limitation for establishing tree seedlings. We predict that, once abiotic barriers for tree seedling establishment such as seasonal waterlogging (Albornoz *et al.* 2013) are overcome, these seedlings have to further endure nutrient limitation in secondary successional patches scattered over a matrix of shrubs, sedges and ferns. Further studies of tree seedling survival and juvenile growth rates in soil chronosequences could improve current models of secondary succession and restoration strategies following anthropogenic disturbances in southern temperate forests. The warming and drying of the climate expected for this region of southern South America in the coming decades is likely to increase the risk of large anthropogenic fires (Veblen *et al.* 2011), which may cause massive losses of nutrients stored in above-ground biomass and therefore enhance P limitation, preventing the progress of succession over large areas of the landscape.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Foliar N:P mean values of the three dominant tree species.