Combined effects of anthropogenic fires and land-use change on soil properties and processes in Patagonia, Chile

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Alex Fajardo [a,*], Michael J. Gundale [b]

[a] Centro de Investigación en Ecosistemas de la Patagonia (CIEP) Conicyt-Regional R10C1003, Universidad Austral de Chile, Camino Baguales s/n, Coyhaique 5951601, Chile
[b] Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, SE901-83 Umeå, Sweden

A B S T R A C T

Fire and land-use change are two major types of disturbances that strongly affect the structure and function of forest ecosystems around the world, although their impacts can be difficult to quantify due to concomitant changes in climate or other land-use change factors. In this study we examined how fire and subsequent land-use conversion impacted soil properties (i.e. organic matter (OM), total available pools of carbon (C), nitrogen (N), and phosphorous (P)), and processes (i.e. N cycling inferred through δ^{15}N) in each of six different land cover types, including old- and second-growth native Nothofagus pumilio, ~50 year old exotic conifer plantations, and grassland pastures. We selected six land cover types, including unburned old-growth (MF), and post-fire second-growth (SG) forests of N. pumilio, post-fire afforestations of Pinus contorta (PC), P. ponderosa (PP) and P. sylvestris (PS), and post-fire grassland (GR), in three watersheds in the Aysén Region, Chilean Patagonia. In one growing season, at each of 5–7 sampling locations within each site, two 10 cm deep soil cores were removed using a 12.4 cm diameter PVC soil-corer. From each soil core, organic matter content, total C and N concentrations, availability of NH_4^+, NO_3^-, and PO_4^-, and δ^{15}N were determined. Additionally, we collected foliage of Osmorhiza chilensis, a forb that was present in every tree-cover condition, for δ^{15}N determination. Unburned old-growth Nothofagus forests showed significantly higher stocks of OM, C, N and P than the P. contorta and P. sylvestris afforestations but not higher than Nothofagus second-growth forests and P. ponderosa afforestations. Conifer afforestations showed significantly lower NH_4^+ values than unburned Nothofagus forests, whereas no differences in NO_3^- were found among the land cover types. Contrary to expectations, conifer afforestations showed significantly higher plant and soil δ^{15}N values than the unburned Nothofagus forests. Although most land cover types resulted in significant alteration of soil properties and processes relative to the mature, unburned N. pumilio forests, we highlight that P. ponderosa afforestations generated the most similar characteristics, suggesting a utility of this species to restore some ecosystem properties.

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1. Introduction

Fire is the dominant type of natural disturbance in many forest ecosystems around the world. In many cases they occur at large scales, and have a strong control on forest dynamics by burning existing forests and initiating a new regeneration cycle (Veblen et al., 2011). Many early-successional tree species are able to persist only because of large-scale fires, and are dependent on the post-fire regeneration environment. One well known way that fire influences forest ecosystem dynamics is through its effects on soil properties and processes (Neary et al., 1999). Fire can strongly influence soil structure and nutrient availability, as well as ecosystem nutrient and carbon (C) budgets (Neary et al., 1999; Chapin et al., 2002; MacKenzie and DeLuca, 2006), with magnitude of change depending on the intensity, frequency or evenness of fire (Gundale et al., 2006; Bond-Lamberty et al., 2007). For example, nitrogen (N) availability can sharply increase following fire due to the conversion of organic to inorganic N, as well as enhanced mineralization and nitrification rates (e.g. Covington and Sackett, 1992; Davidson et al., 1992; Gundale et al., 2005). Although, in other cases, N availability has proved to decrease with time since fire (e.g. DeLuca et al., 2002; MacKenzie et al., 2004). While much is known about the short-term impact of fire in systems where fires commonly occur, relatively little is known about the long term impact of fire in forest systems where fire is uncommon, and is accompanied by land-use change.

* Corresponding author.
  E-mail addresses: alex.fajardo@ciep.cl (A. Fajardo), michael.gundale@slu.se (M.J. Gundale).

Humans have intentionally used fires in many forest ecosystems throughout the world as a tool to convert native forests to a variety of other land-uses (Mooney et al., 2005). Land-use change involves alterations of the way humans use the land that modifies the physical and biotic properties of a system, including the soil, the relative abundances of natural habitats and the introduction of new land-cover types (Turner et al., 2001). One of the most common motivations for using fire is to convert native forests to grassland for the purpose of livestock production; this conversion in particular is known to have detrimental impacts, such as reduction in native biodiversity (Vitousek, 1994; Foley et al., 2005). In many cases, however, land-use change has actually occurred as a land-cover change, i.e. native forests have been replaced by fast-growing tree species; this conversion has the potential to greatly alter ecosystem properties and processes over long time scales. For instance, differences in the quantity and quality of C inputs associated with different cover species may lead to differences in key soil properties and processes, such as C stocks or nutrient availability (Dube et al., 2009; Wardle et al., 2011; McIntosh et al., 2012). Quantification of these changes is relatively rare in temperate ecosystems throughout the world because land-use changes have usually occurred many centuries ago, and have involved a wide range of change factors (e.g. N atmospheric deposition, climate change, management activities associated with multiple forest rotations, etc.) that have been difficult to disentangle.

The southern Andes region of Chile and Argentina constitutes a temperate forest ecosystem that has relatively recently been subjected to wildfire and land cover conversion. The region has been historically dominated by *Nothofagus* forests, which have been influenced by large-scale natural disturbances such volcanic eruptions, landslides and wind. These disturbances, as well as small-scale gap disturbances are important in the establishment, recruitment and growth of *Nothofagus* species (Donoso, 1993; Veblen et al., 1996; Rebertus et al., 1997; Fajardo and González, 2009). Fire was not historically an important disturbance in *Nothofagus* forests in the Patagonia region of Chile (Veblen et al., 2008), particularly because lightning ignition is almost completely lacking in this region (Christian et al., 2003). Large-scale, anthropogenic fires were started in this region between 1930 and 1950 with the objective of establishing livestock pastures where *Nothofagus* forests existed. This initiative resulted in the destruction of ca. 3 million hectares of *Nothofagus pumilio* old-growth forests and other less common companion species (Quintanilla Pérez, 2008). Remnant patches of old-growth *N. pumilio* forests served as a seed source for regeneration on the burnt landscape, which occurred primarily around the margins of burned areas. Within decades, natural regeneration of *N. pumilio* resulted in dense second-growth forests around the margins of the burned areas (Fajardo and McIntire, 2010; McIntire and Fajardo, 2011), whereas a majority of burned area transitioned to grassland-herb communities consisting of a mix of native and non-native species (Sánchez-Jardón et al., 2010). In other areas deforested by fire, local authorities initiated afforestation (the intentional planting of woody species) projects using fast-growing, non-native coniferous species in the 1960s and 1970s, including *Pinus contorta*, *P. sylvestris* and *P. ponderosa*. Thus, with the combination of historical land clearing fire and land-cover changes, the Patagonian landscape has been transformed from contiguous old-growth *N. pumilio* forests to a mosaic of land-cover types with remnant native forest adjacent to second-growth native forest, grasslands and coniferous plantations (Fig. 1). After nearly a century since anthropogenic fires first occurred in the region, little is known about how soil properties and processes differ among these different land-use trajectories.

The objective of the present study was to determine the combined effect of historical fire and subsequent shift in vegetation cover type on soil properties and processes in the Chilean

Fig. 1. Depiction of Mano Negra area (Coyhaique Province, Aysén Region, Chile), where it can be seen (from south toward north) the landscape mosaic resulting from the action of human-provoked fires and land-use change. In particular, old-growth and second-growth, post-fire native *Nothofagus pumilio* forests appear in rusty orange (the picture was taken in April, Austral autumn). Dark green patches correspond to post-fire, pine afforestations (*P. contorta*, *P. ponderosa*, and *P. sylvestris*). Finally, treeless areas correspond to post-fire grasslands with varied degrees of management intensity; only low-intensity managed grasslands were used in the current study. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Patagonia landscape. The Chilean Patagonia region is one of the last temperate regions on Earth to be transformed by humans, while at the same time has experienced very little influence from historic agricultural activities or global change factors, such as climate warming or atmospheric N deposition (Weathers and Likens, 1997). Thus, this region provides an ideal opportunity to assess the impacts of land-use activities on key ecosystem properties, which is substantially more difficult in the northern hemisphere, where human disturbances and management have a long history. In this study we evaluated the impact of 6 different land cover types on soil properties and processes, including: old-growth, unburned *N. pumilio* forest; adjacent highly dense second-growth *N. pumilio* forest naturally re-established after fire; ~50 year old post-fire afforestations of exotic conifers of *Pinus contorta*, *P. ponderosa*, and *P. sylvestris*; and post-fire grassland. In each of these vegetation cover conditions we assessed total stocks of C and N in surface soils, extractable pools of key nutrients (NH_4^+, NO_3^-, and PO_4^-), and the foliar and soil natural abundances of stable N isotopes (i.e. $\delta^{15}N$), which can provide insights into both long term changes in N cycling, as well as factors currently affecting plant nutrient acquisition. We hypothesized: (1) that all cover types would exhibit lower stocks of total soil organic matter (SOM), C, and N relatively to native old-growth *N. pumilio* forests due to combustion and volatilization losses that would have occurred during the historical fires used to clear the landscape in the region; (2) that the establishment of forest cover (either native or exotic tree species) would lead to recovery of these pools, because of their *similar* production of litter and woody debris. We thus predict forested sites would exhibit the most similar total soil C, and N stocks relative to old-growth *N. pumilio* forests, particularly for *P. ponderosa*, which achieves the highest rate of production in the region (Hernández et al., 2013); (3) that nutrient availability would differ among the cover types, with conifer species exhibiting lower concentrations of available nutrients because they are known to produce more recalcitrant litter and exhibit higher growth and thus nutrient uptake rates; and (4) that the land cover types exhibiting the highest concentrations of inorganic N availability would exhibit the highest plant and soil $\delta^{15}N$ values, because N would be less tightly conserved in these cover types, leading to greater losses of isotopically lighter N (i.e. ^{14}N relative to ^{15}N).

Testing these hypotheses in combination will provide valuable knowledge into how divergent land cover trajectories in the Patagonia region have impacted key soil properties and processes.

2. Methods

2.1. Site description

Our study utilized six land cover types, including old-growth (MF) and second-growth (SG) forests of *N. pumilio*, plantations of *Pinus contorta* (PC), *P. ponderosa* (PP) and *P. sylvestris* (PS), and open grassland (GR), and 3 replicates of each cover type (i.e. 18 sites in total). The sites occurred at three different areas in the Coyhaique Province of the Aysén Region, Chile: Mano Negra (45°26′S, 71°58′W, 910 m a.s.l.), Coyhaique Reserve (45°33′S, 71°59′W, 600 m a.s.l.), and Cerro Castillo Reserve (45°59′S, 71°59′W, 850 m a.s.l.). The annual precipitation in these areas is on average 890 mm (Coyhaique National Reserve weather station, Dirección General de Aguas, 2004–2013, 400 m a.s.l.). The dominant understory species in MF and, in lower density, in SG are *Acaena ovalifolia* (Asteraceae), *Berberis serratodentata* (Berberidaceae), *Empetrum rubrum* (Ericaceae), *Fuchsia megellanica* (Onagraceae), and *Ribes magellanicum* (Saxifragaceae). In the three pine afforestations, the understory was mostly represented by *Alopecurus magellanicus* (Poaceae), *Berberis microphylla* (Berberidaceae), *Cerastium arvense* (Caryophyllaceae), *Leontodon saxatilis* (Asteraceae), and *Veronica serpyllifolia* (Plantaginaceae). Lastly, in GR we mostly found *Acaena intergerrima*, *Erigeron leptopelatus* (Asteraceae), *Festuca gracillima* (Poaceae), *Phacelia secunda* (Hydrophyllaceae), and *Senecio patagonicus* (Asteraceae). *Osmorhiza chilensis* (Apiaceae), a common forb, was the only species found in all 18 sites.

In order to assure that all site conditions within each area were affected by the same fire event, we selected sites that were not more than ∼3 km apart, and no more than a 75 m difference in elevation. We note here that all three areas were covered by a single cover type—i.e. fuel type (*N. pumilio*)—when large-scale fires occurred. Thus, it is more likely that any variation in fire severity across the study areas was likely spatially random rather than consistently varying with elevation. We also ensured that sites had not experienced any fire or intensive management activities for the last 30 years. Fires in Mano Negra and Coyhaique Reserve occurred in the mid-1940s and in the mid-1960s for Cerro Castillo Reserve. Each fire resulted in a complete mortality of the native *N. pumilio* forest vegetation. Soils associated with historical *N. pumilio* in the region are Andosols (Piper et al., 2013), derived from the ash of some active volcanoes in the region, and usually exhibit a loam or sand–loam texture, and a pH between 4.5 and 5.8 (Schlatter, 1994).

2.2. Soil and plant sampling

The collection of all soil and plant tissue samples was conducted in January 2011. All sampling was done at least 100 m away from the edge of each forest. For each site a list of 5–7 sampling point coordinates was created using a random walk design with a random start point (Underwood, 1997), where bearing directions (constrained to 180°) and distances (constrained from 10 to 30 m) were randomly generated using a spread sheet program. At each of these sampling locations, two 10 cm deep soil cores were removed using a 12.4 cm diameter PVC soil-corer with a stainless steel serrated edge (volume = 1207.627 cm^3). Before collecting each core, we removed all recognizable litter from the soil surface (O_i horizon). After collection, each core was placed in a labelled Ziploc bag that was immediately sealed and maintained in a cooler in fresh conditions (<15 °C air temperature) for ca. 2 h

to minimize nutrient mineralization, then they were placed in a refrigerator (3 °C). The first soil core collected from each sampling location was used for determination of organic matter content, total C and N concentrations, and availability of NH_4^+, NO_3^-, and PO_4^-. The second soil sample was oven-dried at 72 °C for 48 h, after which it was weighed (for bulk density determination), sieved (4 mm), and ground to a fine powder with a mill for $\delta^{15}N$ analysis. Furthermore, we characterized the canopy openness of each site by taking digital hemispherical photographs of the above canopy from a height of ∼50 cm at 20 sampling points (including the 5–7 used for soil sampling). For this we used a 7-mm Nikon f 7.4 fisheye lens (the lens has an orthographic projection of 180° angle of view), mounted on a Nikon Coolpix 5000 digital camera (Nikon Corporation, Tokyo, Japan). Photographs were taken under cloudy sky conditions or late in the day to avoid the direct exposure to sun. Photographs were also under-exposed by two stops, to increase contrast between the sky and foliage (Zhang et al., 2005). From these digital photographs we computed canopy openness for each sampling point using the Gap Light Analyzer (GLA ver. 2) software (Frazer et al., 2000).

2.3. Soil physicochemical analyses

After collection, the first soil sample collected from each sampling location was refrigerated at 3 °C for two days, and then shipped to a soil testing laboratory (Universidad de Concepción, Chillán, Chile), where a portion of the sample was oven dried, and analyzed for moisture content, soil organic matter (SOM) content (% of soil dry weight basis, d.w.), total C (%), total N (%), and the remaining field moist portion was analyzed for nitrate (NO_3^-, mg kg^{-1} soil d.w.), ammonium (NH_4^+, mg kg^{-1} soil d.w.), pH, Olsen-P (mg kg^{-1} soil d.w., a standard protocol to measure available P), and C/N ratio. Total N was analyzed by the direct nesslerization semi micro-Kjeldahl method (Middleton, 1960) and organic matter content was estimated by the rapid dichromate oxidation method (Walkley and Black, 1934). Mineral N (i.e. NH_4^+ and NO_3^-) was extracted using a 5:1 proportion of K_2SO_4 solution:soil, after which the extracts were analyzed for NH_4^+ and NO_3^- using standard colorimetric methods (Longeri et al., 1979; Robarge et al., 1983). Olsen-P was extracted using a 20:1 proportion of pH 8.5 NaHCO$_3$ solution:soil, as described in Steubing et al. (2002). In order to scale total element pool values up to an area basis, we first measured the mass of the air-dried soil cores collected in each site (0–10 cm depth, the second soil sample). These mass values were converted to a surface area basis using the surface area of the soil corer. Percent SOM, C, and N values were then multiplied by the estimated soil mass values in order to scale their masses to a per hectare basis.

With the aim of providing insights into how N cycling differs between the stand types, we measured $\delta^{15}N$ values on the oven dried soil cores, as well as one plant species that consistently occurred in every site, *Osmorhiza chilensis* Hook. & Arn. (Apiaceae). This species is a perennial forb that is a very common understory component of the southern Andes deciduous *Nothofagus* forest; it can reach 0.8 m of height (Silva, 2010). We were cautious to avoid collecting foliar tissue coming from different species because it is known that species with different mycorrhizal types can exhibit different isotopic signatures. Thus the N isotopic signal from the single species present in all sites (*O. chilensis*) served as the best proxy to assess long term shifts in N cycling among the cover land types. The $\delta^{15}N$ measurements of *O. chilensis* were performed on leaves, which were collected as close as possible to each soil sampling location (<2 m). For leaf $\delta^{15}N$ analyses, samples were oven-dried for 48 h at 72 °C, and afterwards, ground to a fine powder. Isotopic analysis of soil and leaf material was then performed (Center for Stable Isotope Biogeochemistry,

University of California-Berkeley, CA, USA), using a continuous mass spectrometer. The $\delta^{15}N$ signature of plant and soil samples was computed as the deviation of the sample material (R_{sample}) from the isotopic standard (R_{std}), where R denotes the ratio of stable N ($^{15}N/^{14}N$) isotopes, expressed in δ notation:

$$\delta^{15}N(\permil) = (R_{sample}/R_{std} - 1) \times 1000$$

2.4. Statistical analysis

Because some soil variables (e.g. total C, total N, NO_3^-, NH_4^+) did not show a normal distribution in their residuals, variables were all log-transformed to meet this assumption of the analysis of variance. To correct for potential biases in the leaf $\delta^{15}N$ (*O. chilensis*) values because of site-specific differences in background bulk soil $\delta^{15}N$, a relative $\delta^{15}N$ value was calculated for all systems as the difference between $\delta^{15}N$ of *O. chilensis* and $\delta^{15}N$ of soil (Amundson et al., 2003). Differences between the six land cover types were then compared using one-way ANOVAs, with the three areas serving as random blocks. This analysis allowed us to control for site-specific effects of soil nutrients on leaf N contents. Given that sites within areas had slightly different elevations, we first considered this variable in the models; however, elevation had not a significant effect ($P > 0.05$) on soil and plant variable, therefore we took it out from posterior analyses. When significant differences were detected, post-hoc Tukey–Kramer Honest Significant Difference (HSD) tests were performed to evaluate pair-wise differences between land cover types. All statistical tests were performed with R (R Development Core Team, 2012).

3. Results

3.1. Total soil C and N stocks

Soil organic matter (SOM), total C and N stocks within the surface 10 cm significantly varied among the land cover types (Fig. 2). For SOM, MF showed the highest values on a per hectare basis (42.92 Mg ha^{-1}, SE = 5.00), which was significantly greater than PC (29.38 Mg ha^{-1}, SE = 4.47) and PS (27.35 Mg ha^{-1}, SE = 3.44 tons ha^{-1}), but not GR, PP and SG cover types (Fig. 2a). Similarly, the different land cover types strongly differed for total

N ($F = 3.985$, $P = 0.003$) and total C ($F = 6.547$, $P < 0.001$, Fig. 2b–c). In particular, variation in total N differed significantly with the highest values found in MF (1.17 Mg ha^{-1}, SE = 0.14), GR (1.12 Mg ha^{-1}, SE = 0.07) and PP (1.14 Mg ha^{-1}, SE = 0.09, Fig. 2b), and significantly lower values found in PC (0.88 Mg ha^{-1}, SE = 0.09) and PS (0.86 Mg ha^{-1}, SE = 0.11, Fig. 2b). Variation in total C was higher than for total N among canopy covers, being highest in MF with 24.89 Mg ha^{-1} (SE = 2.90) and lowest in PC with 13.88 Mg ha^{-1} (SE = 1.65), with intermediate values for GR, PP and SG (ca. 19 Mg ha^{-1}).

3.2. Soil C, N and P concentrations

C and N concentrations (in percentage basis) also differed significantly among land cover types (Table 1). In particular, GR and PP had the highest C concentrations, while SG had the lowest, with MF having intermediate values (Table 1); PP has the highest N concentrations, while PS had the lowest, and *Nothofagus* forest types had intermediate values (Table 1). Values of pH were significantly lower for native vegetation (old- and second-growth *N. pumilio* forests) than for exotic pine cover types and grassland (Table 1). Finally, the C/N ratio was significantly higher in MF (21.62) than PC, PP and GR (16.21, 17.39, and 16.89, respectively, Table 1).

Across systems, we found a high variation of NO_3^- within land cover types, which led to a non-significant difference among systems ($F = 1.111$, $P = 0.362$, Fig. 3a). The different land cover types did show significantly different NH_4^+ concentrations ($F = 9.018$, $P < 0.001$, Fig. 3b), where MF (24.88 mg kg^{-1}, SE = 5.67) and SG (23.32 mg kg^{-1}, SE = 4.84, Fig. 3b) presented the highest values. The remaining cover types had significantly lower NH_4^+ values when compared to the native systems; in particular, the three pine systems were very similar to one another (Fig. 3b). Lastly, Olsen-P significantly differed between the land cover types ($F = 16.146$, $P < 0.001$, Fig. 3c); SG, MF, PC and PP presented significantly higher concentration values than GR and PS.

3.3. N isotope composition

We found that both soil ($F = 6.976$, $P < 0.001$, Fig. 4a) and foliar *Osmorhiza* ($F = 17.528$, $P < 0.001$, Fig. 4b) $\delta^{15}N$ signatures varied significantly among the land cover types. Soil $\delta^{15}N$ values were
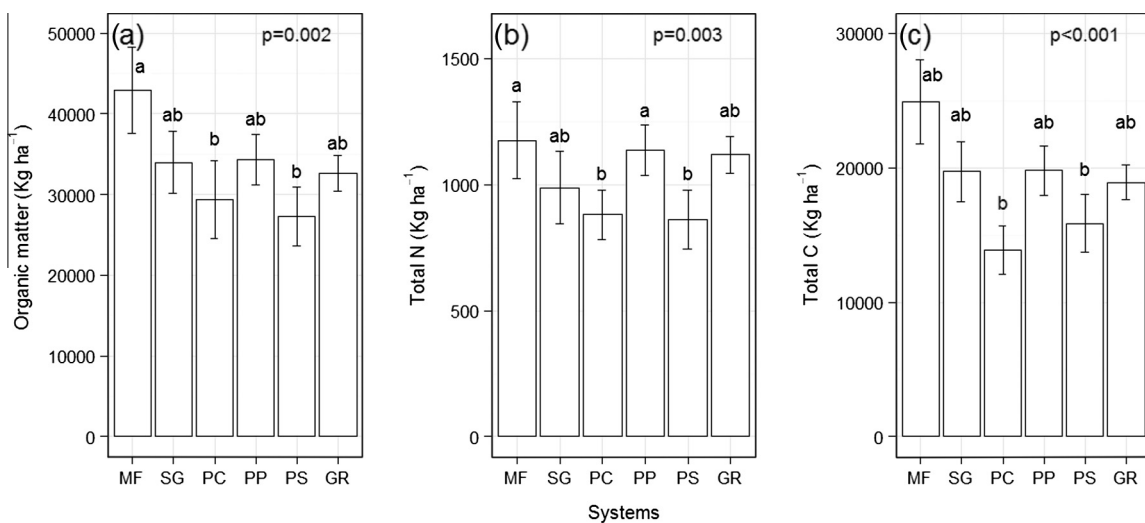

Fig. 2. Organic matter (SOM), C and N pool (kg ha^{-1}) mean values (±1 CI) of the soil surface (0–10 cm) of different land cover types in Patagonia, Chile. The different land cover types are: old-growth (MF) and second-growth (SG), post-fire native *Nothofagus pumilio*, *Pinus contorta* (PC), *P. ponderosa* (PP), and *P. sylvestris* (PS) post-fire, pine afforestations, and treeless, post-fire grasslands. Different letters represent significant different ($P < 0.05$) means between land cover types.

Table 1
General characteristics of the different land cover types surveyed in the present study, including old-growth of *Nothofagus pumilio* not affected by fire (MF), second-growth, post-fire forest of *N. pumilio* (SG), post-fire forest plantations of *Pinus contorta* (PC), *P. ponderosa* (PP), *P. sylvestris* (PS), and post-fire grassland (GR) in Patagonia, Chile.

Canopy condition	Canopy openness (%)	Bulk density (tons m^{-3})	pH	C (%)	N (%)	C/N
	$F = 341.36$	$F = 10.624$	$F = 5.783$	$F = 4.216$	$F = 4.691$	$F = 6.437$
	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P = 0.003$	$P < 0.001$	$P < 0.001$
MF	9.03 (0.70) *bd*	0.44 (0.02) *bc*	5.25 (0.11) *b*	40.33 (0.31) *ab*	1.91 (0.11) *ab*	21.62 (0.75) *a*
SG	7.27 (0.30) *d*	0.41 (0.07) *c*	5.36 (0.08) *b*	39.48 (0.25) *b*	2.04 (0.05) *ab*	20.53 (0.93) *ab*
PC	12.19 (0.64) *b*	0.43 (0.02) *bc*	5.53 (0.04) *a*	40.84 (0.28) *ab*	1.96 (0.15) *ab*	16.21 (1.15) *b*
PP	10.82 (1.68) *b*	0.54 (0.07) *a*	5.63 (0.06) *a*	40.92 (0.95) *a*	2.32 (0.07) *a*	17.39 (0.48) *b*
PS	18.18 (1.76) *c*	0.50 (0.07) *ab*	5.59 (0.05) *a*	40.67 (0.57) *ab*	1.83 (0.16) *b*	18.26 (0.77) *ab*
GR	77.46 (0.92) *a*	0.50 (0.01) *a*	5.63 (0.04) *a*	41.17 (0.53) *a*	1.89 (0.13) *ab*	16.89 (0.40) *b*

Different letters represent significant different ($P < 0.05$) means between land cover types.
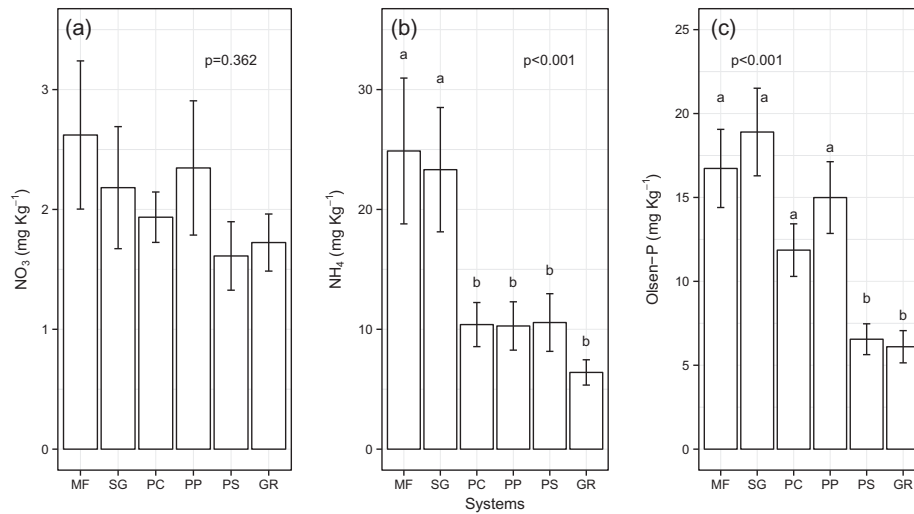

Fig. 3. Mean (±1 CI) concentrations of NO_3^-, NH_4^+, and Olsen-P in the soil surface (0–10 cm, dry weight) of different land cover types in Patagonia, Chile. The different land cover types are: old-growth (MF) and second-growth (SG), post-fire native *Nothofagus pumilio*, *Pinus contorta* (PC), *P. ponderosa* (PP), and *P. sylvestris* (PS) post-fire, pine afforestations, and treeless, post-fire grasslands. Different letters represent significant different ($P < 0.05$) means between land cover types.
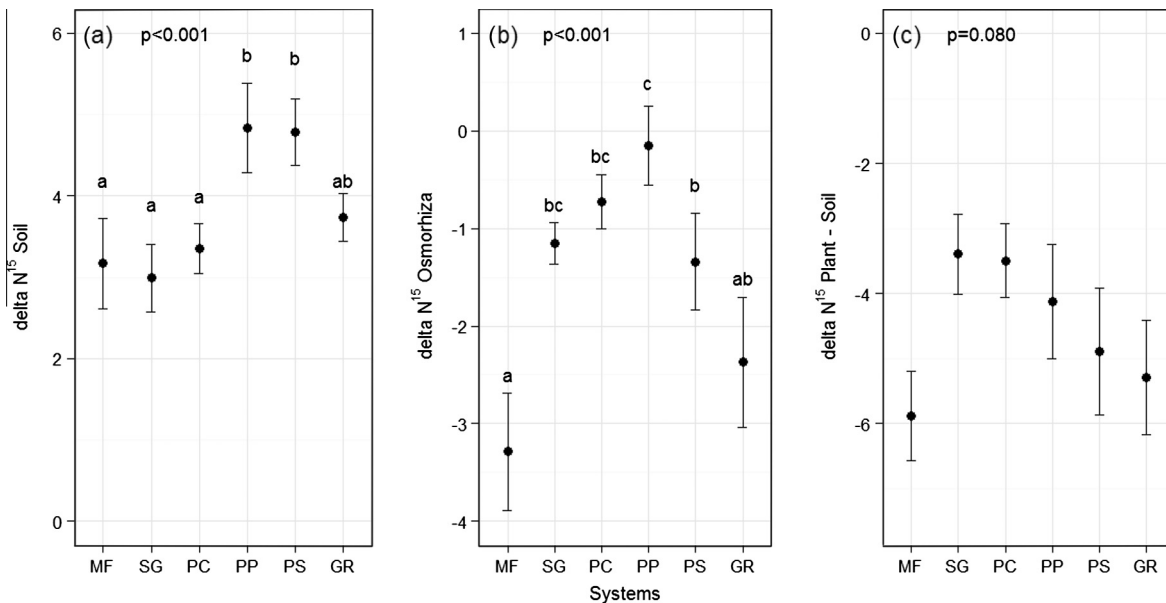

Fig. 4. Mean (±1 CI) $\delta^{15}N$ signature of soil (a), *Osmorhiza chilensis* leaves (b), and the difference between leaf and soil $\delta^{15}N$ signatures (c) in response to six different land cover types in Patagonia, Chile. The different land cover types are: old-growth (MF) and second-growth (SG) post-fire native *Nothofagus pumilio*, post-fire *Pinus contorta* (PC), *P. ponderosa* (PP), and *P. sylvestris* (PS) afforestations, and post-fire treeless grasslands. Different letters represent significant different ($P < 0.05$) means between land cover types.

positive and higher (more enriched) than those found for *Osmorhiza* foliar $\delta^{15}N$. Soil $\delta^{15}N$ values were significantly higher in PP (4.83‰) and PS (4.78‰), compared to MF (3.17‰), PC (3.35‰) and SG (2.99‰, Fig. 4a). *Osmorhiza* foliar $\delta^{15}N$ values were markedly different among all canopy cover types, being lowest for MF (−3.29‰) and GR (−2.37‰) and highest for PP (−0.15‰, Fig. 4b). Finally, the net difference between soil and leaf relative $\delta^{15}N$ values (i.e. $\delta^{15}N$ *O. chilensis* – $\delta^{15}N$ soil) did not vary across canopy cover types ($F = 2.115$, $P = 0.080$, Fig. 4c).

4. Discussion

The burning of almost 3 million hectares in the last century in the Aysén Region of Chile signified a catastrophic ecological disturbance. Our study showed that land-use change, more so than fire, significantly modified total nutrient stocks and extractable pools, as well as plant and soil isotopic N composition. In particular, our data did not provide support to our first hypothesis; although undisturbed old-growth *N. pumilio* forest showed the highest total organic matter and C stocks in the surface 10 cm of the soil, it did not differ from the second-growth post-fire *Nothofagus* forest (SG). In addition, the old-growth *N. pumilio* forest was among several cover types with the highest total N stocks, especially when compared to *Pinus contorta* and *P. sylvestris* plantations; although total N stocks did not differ significantly from the second-growth forest of *N. pumilio* and *P. ponderosa*. In this respect, our results are partially consistent with Rivas et al. (2012) who found that historic large-scale fires in *Araucaria–Nothofagus* in northern Patagonia, Chile, had no significant legacy effects on soil total C and N. We did not find support for our second hypothesis that sites planted with different forests cover types would show the most similar total soil OM, C, and N pools relative to the old-growth forest. Although we found that the second-growth, post-fire *N. pumilio* forest and, as expected, afforested *P. ponderosa* sites appeared to be most similar to old-growth *N. pumilio* forests, *Pinus contorta* and *P. sylvestris* sites had significantly lower stocks of OM, total C, and N than the old-growth sites. Treeless grasslands showed an intermediate pattern, not differing significantly from the old-growth *N. pumilio* forest in OM, total C and N. In combination, these data highlight that the rate of soil OM and element pool accumulation following fire is highly dependent on the specific identity of the species a site is planted with. This is because fire in our system was a discreet anthropogenic land clearing event with no fire occurring either before or after this event. Thus, our study-design positions us very well to differentiate whether the vegetation cover type or the historical fire is the main driver of variation in soil properties.

Although afforestations with fast-growing conifer species have been highly advocated for C sequestration (i.e. C gains) in many parts of the world (particularly in undeveloped countries), we show evidence that not all pine species would necessarily promote increases in soil C, which should be considered in ecosystem C budgets. For example, with the exception of pH, the soil under *P. ponderosa* afforestations appeared to be the most similar to pre-fire conditions, i.e. old-growth *N. pumilio* forest. Among the three pine species, *P. ponderosa* is the one that achieves the highest growth rates in the region. Because of this, almost 25,000 ha have been planted in Chilean Patagonia (Hernández et al., 2013), and nearly 70,000 ha in northwest Patagonia, Argentina (Laclau, 2003). Its relatively high growth rate in the region is likely due to the very similar climatic and edaphic conditions to the region east of the Cascades Mountains (USA), where the genotype planted in Patagonia originally came from. The potential benefit of *P. ponderosa* soil characteristics is, however, contingent on other potential negative aspects of its introduction being investigated: e.g.

potential for invasiveness, increase in wildfire (Paritsis et al., 2015). On the other hand, soil characteristics under *P. contorta* afforestations showed to be the most different when compared with the old-growth *N. pumilio* forest. This is consistent with Dickie et al. (2010), who found that naturalized *P. contorta* in New Zealand caused net soil C losses rather than gains relative to grasslands. Hence, *P. contorta* not only constitutes an aggressive invasive species in many parts of the world (Gundale et al., 2014), but can sometimes have deleterious effects on ecosystem properties (i.e. soil C).

We did find support for our third hypothesis, that afforestation with exotic conifers would be associated with reduced soil nutrient availability due to their recalcitrant litter and relatively high rate of nutrient uptake associated with their fast growth rates. Although we did not find significant differences among cover types for NO_3, we did find significant differences for NH_4^+ concentrations, as well as inorganic N. In particular, the data showed that all three conifer cover types showed significantly lower NH_4^+ concentrations compared to either *Nothofagus* cover type. It is well established that fire can initially increase inorganic N availability for a variety of reasons, including its thermal conversion of organic to inorganic N, as well as enhanced mineralization and nitrification rates (Covington and Sackett, 1992; Gundale et al., 2006). However, over decadal time scales the direct effect of fire on soil processes diminishes, and characteristics of the dominant vegetation serve as the primary control on nutrient cycling and availability (Hart et al., 2005). Our results support this suggestion, by showing that differences were more strongly linked to the identity of the tree species occupying a site, rather than to direct legacy effects of the fire. One major factor that could explain this pattern is the differences in litter quality produced by the contrasting plant communities. Litter quality and decomposition rates may be a major distinction between native deciduous *N. pumilio* forests and evergreen pine species. The litter produced by the three exotic conifers is known to be relatively more recalcitrant compared to *N. pumilio* litter (Hess and Austin, 2014), which likely results in slower decomposition and mineralization rates (Gelfand et al., 2012). An additional factor that likely contributed to differences in NH_4^+ availability among the forest cover types was soil nutrients uptake by trees, which would likely have been higher in the fast-growing exotic conifers and grassland communities relative to the slower growing *Nothofagus* forests.

Similar to NH_4^+, differences in P-availability among the cover types appeared to be driven by differences in species rather than differences in legacy effects of fire. Here, all forests (except *P. sylvestris*) showed significantly higher concentrations compared to the grassland. Young, volcanic soils of the southern Andes are known to have a high total P content (Borie and Rubio, 2003), but several studies using similar methodology have suggested P availability is low (Diehl et al., 2003; Piper et al., 2013; Fajardo and Piper, 2015), because PO_4^- is readily precipitated by aluminum- and iron-complexes (Borie and Rubio, 2003; Piper et al., 2013). The high P availability in 4 of the 5 forest types may be due to their interference with these PO_4^- binding reactions, or enhanced weathering associated with their ectomycorrhizal fungi (Diehl et al., 2003; Chen et al., 2008; Gundale et al., 2008).

For our fourth hypothesis, we predicted that land cover types exhibiting the highest extractable N concentrations would exhibit the highest plant and soil $\delta^{15}N$ values, because higher inorganic N concentrations are often symptomatic of more rapid N cycling, where both N inputs and losses are greater (Pardo et al., 2002; Compton et al., 2007; Evans, 2007). Because ^{14}N is lost via leaching and gaseous fluxes at a higher rate than ^{15}N, more rapid nutrient cycling can lead to an upward drift of ^{15}N signatures over time (Compton et al., 2007; Evans, 2007). Also, due to a potential increase in plant N demands in conifer afforestations, N would

potentially be more conserved compared to native *Nothofagus* forests and grasslands (Hess and Austin, 2014), and thus we expected plant and soil $\delta^{15}N$ values of conifer plantations to be lower compared to *Nothofagus* forests and grasslands. However, contrary to our hypothesis, soils within *P. ponderosa* and *P. sylvestris* sites showed the highest soil $\delta^{15}N$ values, but were among the cover types exhibiting the lowest concentrations of NH_4^+ availability. This result is consistent with Hess and Austin (2014), who also found higher $\delta^{15}N$ values for *P. ponderosa* than for *N. antarctica* shrublands and forests in northern Patagonia, Argentina.

In addition to measuring soil $\delta^{15}N$ signatures, we evaluated foliar $\delta^{15}N$ of a single herbaceous plant species, *O. chilensis*, which was present in all cover types in order to further infer differences in N cycling. In contrast to soil $\delta^{15}N$ signatures and inconsistent with our fourth hypothesis, we found foliar signatures to be most depleted and different in old-growth *N. pumilio* forests and grasslands relative to the other cover types. We can offer two opposing explanations for this pattern. First, the lower $\delta^{15}N$ values of *O. chilensis* growing in the old-growth *N. pumilio* forests could be due to greater acquisition of inorganic N relative to organic N (i.e. the former being isotopically lighter than the latter) (Högberg, 1997; Dawson et al., 2002; Evans, 2007; Gundale et al., 2012), which is possible given that our data showed that NH_4^+ concentrations were higher relative to most of the other land cover types. Alternatively, it is well known that mycorrhizae disproportionately retain the heavier isotope, and give a depleted signature to the plant, causing their signatures to be more depleted relative to soils (Hobbie and Högberg, 2012). This mechanism, in addition to preferential uptake of inorganic N, could explain why plant $\delta^{15}N$ signatures were lower than soil signatures in all stand types. Further, it may explain the relatively lower $\delta^{15}N$ signature of *O. chilensis* in the grassland environment, where dependence on mycorrhizae may have been greater as a result of lower nutrient availability and more intense competition with grasses and other herbaceous species with a similar growth habit. Regardless of the mechanism underlying the shift in $\delta^{15}N$ signature of *O. chilensis*, we think our data point to the different cover types causing a change in N cycling processes in the region.

5. Conclusions

Few other regions in the world can provide an opportunity to evaluate the effects of fire and land-use change on ecosystem properties and processes like western Patagonia in the southern Andes. This is because this region has minimally experienced concomitant environmental changes, such as anthropogenic N deposition, climate change, and other disturbances that occur widely in a majority of northern hemisphere temperate regions, where landscape transformation began much earlier. Here we found that the legacy of large-scale, human-provoked fires that occurred ca. 70 years ago had few consistent effects across stand types where historical burning occurred; whereas differences in land cover significantly impacted many of the measured variables. Time may be an important factor explaining these differences: fires were very intense but occurred once in time, whereas vegetation cover influences processes continuously. The establishment of some fast-growing conifer afforestations in these burned areas, such as those planted with *P. ponderosa*, appears to have some beneficial impacts because it causes some soil properties to more closely resemble pre-fire conditions. Indeed the recovery of some soil properties and processes by planting *P. ponderosa* may be useful for restoring native forests in this region, as many previous forest restoration attempts have failed on these disturbed sites due to altered soil properties (Fajardo and McIntire, 2011). While other potential aspect of *P. ponderosa* introduction certainly need to be considered

(e.g. potential as an invader, enhancement of regional fire regime, etc.), afforestations with this species may potentially serve as a useful transitional tool in restoration programs by promoting the recovery of the soil organic layer, which can eventually be thinned to allow establishment of native forest species, which require a thick soil organic horizon for establishment. Further studies should cover the effects of the fire and land-use change combination on plant and animal biodiversity and plant functional trait distributions to establish a more integral picture of ecosystem properties and functioning in these young disturbed landscapes.

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