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Short-term response of soil microorganisms, nutrients and plant recovery in fire-affected *Araucaria araucana* forests

Andres Fuentes-Ramirez[a,d,*], Marcia Barrientos[a], Leonardo Almonacid[b], Cesar Arriagada-Escamilla[b], Christian Salas-Eljatib[c,a]

[a] *Laboratorio de Biometría, Departamento de Ciencias Forestales, Universidad de La Frontera, Casilla 54-D, Temuco, Chile*
[b] *Laboratorio de Biorremediación, Departamento Ciencias Forestales, Universidad de La Frontera, Casilla 54-D, Temuco, Chile*
[c] *Centro de Modelación y Monitoreo de Ecosistemas, Facultad de Ciencias, Universidad Mayor, Santiago, Chile*
[d] *Instituto de Ecología y Biodiversidad (IEB), Santiago, Chile*

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ABSTRACT

Soil contains a wide variety of microorganisms that are responsible for fundamental ecological processes. However, increased frequency and severity of fires reduce microbial diversity and alter soil nutrient availability, affecting vegetation recovery. By using a large-scale wildfire that burned endangered *Araucaria araucana* forests in south-central Chile (38°S), we assessed the short-term post-fire response of microorganisms, soil nutrients, and plant recovery. One year after fire, we sampled soils from burned and unburned areas, and measured the number of bacterial and fungal colony forming units, and the microbiological activity of the soil. We also measured soil nutrients (N, P, and K), organic matter content and species richness, abundance and plant diversity after fire. We found a significant increase in microbiological activity in burned soils (BS) compared to unburned soils (UBS), with bacteria and fungi being four and seven times greater in BS than in UBS, respectively. Concentrations of N, P and K were also greater in BS than in UBS. Plant species richness was two times higher in unburned than in burned areas, with a drastic reduction of the dominant tree species *Araucaria araucana* and *Nothofagus pumilio* after fire. The changes in soil properties after fire may be related to organic matter mineralization, the contribution of nutrients from ashes, or due to post-fire conditions (e.g., increased soil temperature after canopy removal by fire). Overall, our study shows a positive, short-term response in soil microorganisms abundance and nutrient content, but a rapid initial reduction of plant diversity of the main dominant tree species in these forest ecosystems after a severe fire. Further research is necessary as vegetation results are only preliminary and they can vary in the short-to-medium term. Our study provides insightful clues to delve into more applied research aimed at the post-fire restoration of the endemic, long-lived *Araucaria araucana* forests.

1. Introduction

Disturbances are important components of ecosystem dynamics, but increased variations in their regimens can greatly alter their structure and functioning (Hobbs and Huenneke, 1992, Mouillot et al., 2013). Some of the most striking examples of altered disturbance regimes involve changes in the frequency, severity, and seasonality of fires (Littell et al., 2009; Moritz et al., 2012). Fire can affect the composition of ecological communities through reductions in plant density and cover, as well as producing alterations in the chemical and biological properties of soil, such as pH, organic matter and nutrient contents, edaphic fauna and soil microorganisms (Certini, 2005; Hart et al., 2005; Neary et al., 1999). Among these, soil microbes are key for fundamental ecological processes that occur underground, including organic matter decomposition and nutrient cycling (Baldrian, 2017; Schulz et al., 2013). Fire can directly affect the abundance and diversity of microorganisms due to soil overheating, or indirectly by changing their physical and chemical environment (Banning and Murphy, 2008). Overheating of the soil can result in a significant reduction of microbial biomass, which in turn can affect the structure and diversity of the microbial community (Acea and Carballas, 1999; Guo et al., 2015). In this sense, forest fires can have an immediate and long-lasting impact on soil microorganisms, and therefore on the ecosystem services they provide (Whitman et al., 2014).

The effects of fire on soil are mostly related to frequency, severity, temperature peaks and duration of the wildfire (Gongalsky, 2006;

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* Corresponding author.
E-mail address: andres.fuentes@ufrontera.cl (A. Fuentes-Ramirez).

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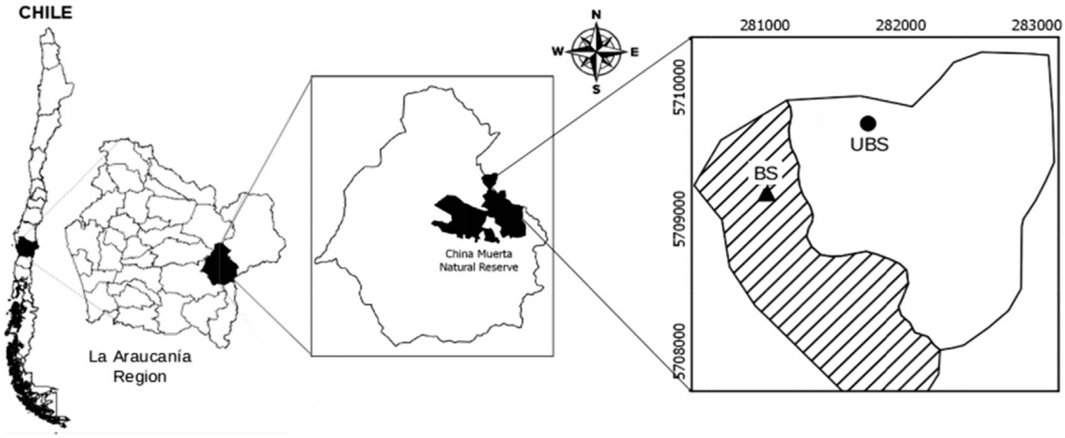

Fig. 1. Geographic location of the study area in the National Reserve China Muerta, La Araucanía region (38°S, 71°W), south-central Chile. The far right panel shows the burned (dashed) and the unburned areas. The burned sampling plots are located ca. 800 m apart from the unburned plots. Within each soil condition (i.e., BS and UBS) the sampling plots are located ca. 30 away from each other.

Williams et al., 2012). High-severity fires cause significant removal of organic matter, deterioration of structure and porosity of the soil, considerable nutrient losses (e.g., nitrogen) and a severe alteration of the amount and composition of microorganisms (Certini, 2005). On the other hand, low-severity fires can have positive impacts on ecosystems, such as increased mineralization of organic matter (Soong and Cotrufo, 2015), diversity maintenance in ecosystems (Velle et al., 2012) and prompting the early successional stages in forest ecosystems. Since wildfires are becoming increasingly frequent and severe worldwide (Krawchuk et al., 2009; Moritz et al., 2012; Stephens et al., 2014), it is crucial to understand their ecological impacts on soil microorganisms and the potential changes in ecosystem-related functions (e.g., biodiversity maintenance). Furthermore, understanding the effect of fire on the forest soil–plant system is critical for predicting potential feedbacks between climate change, wildfires, nutrient and soil microorganisms dynamics with the broader aim of ecosystem conservation and management (Singh et al., 2017).

The increased frequency and severity of fires worldwide has received a growing interest from the scientific community for assessing their impacts on soil microorganisms and biogeochemical cycles (Knelman et al., 2015; Velasco et al., 2009). However, rather few studies have examined the initial response of soil microorganisms and nutrients to fire in natural forests, particularly within old-growth forests of high ecological value. Such is the case of the patrimonial *Araucaria*-dominated forests in the Andes of southern South America. *Araucaria araucana* (Mol.) K. Koch is an endemic, long-lived native conifer from Chile and Argentina. Forests formed by *A. araucana* are particularly valuable because of their significant biodiversity and cultural values (Aagesen, 1998; dos Reis et al., 2014). By 1500, prior to the Spanish colonization, *A. araucana* forests covered ca. 500,000 ha in Chile, but during the 1920–1970s the area covered by the species was reduced by almost 50% due to logging and fires (Lara et al., 1999). In fact, *Araucaria araucana* populations outside national parks and reserves are still experiencing an increased risk of degradation, being subjected to logging (González and Veblen, 2007), cattle grazing (Fuentes-Ramirez et al., 2011), increasing and unsustainable harvesting of its edible seeds and fire-induced disturbances (Cóbar-Carranza et al., 2014; González et al., 2013). Currently, *A. Araucana* is classified as an endangered species in Chile; it was declared *Natural Monument* in 1990, with complete prohibition of logging, even of a single tree. Nowadays, *A. araucana* is considered an emblematic species because of its ecological and social importance (Aagesen, 1998; dos Reis et al., 2014).

Regarding the impacts of fire on soil properties in *A. araucana* forests, Rivas et al. (2016) studied the impact of fires on protein production by soil mycorrhizal fungi four years after fire. To this end, knowledge on the initial response (i.e., one year after fire) of soil microorganisms and nutrients in *A. araucana* forests is lacking. In the short term, studies have shown that soil microbial abundance can increase, decrease or remain unchanged after a fire (Bowker et al., 2004; Neary et al., 1999), whereas nutrients availability (i.e., N and K) generally tend to decrease after fire because of high combustion temperatures and volatilization (Esque et al., 2010). The ability of the soil microbial community to recover after a fire disturbance is crucial for plant recovery and for the functioning of the entire ecosystem. For instance, metabolic activity from microbial soil communities is responsible for most of carbon (C) mineralization and other soil nutrient cycling processes (Knelman et al., 2015; Mikola and Setala, 1998).

To date, most of studies dealing with fire in *A. araucana* forests in the southern Andes have focused on forest dynamics (e.g., using dendrochronological studies) or have assessed specific soil properties several years after fire (Rivas et al., 2012). However, an initial assessment and the interplay involving soil microorganisms, nutrients and vegetation after fire remains unclear. Therefore, we assessed the initial response (i.e., one year after fire) of soil microorganisms and nutrients within *Araucaria araucana* forests that were affected by a severe, large-scale fire in 2015 in the Andes of south-central Chile. Given the high severity of the fire, we hypothesize that the microbial activity and abundance of bacteria and fungi, as well as the availability of soil nutrients will decrease in burned soils, compared to adjacent unburned soils. Specifically, this research aimed at: (i) determining the abundance of soil bacteria, fungi and soil biological activity within burned and unburned soils; (ii) evaluating the impact of the fire on the availability of soil nutrients (i.e., N, P and K) and soil organic matter; and (iii) assessing the initial response of vegetation recovery and its relationship with microorganisms and nutrients in the first year after fire. Improving our understanding of the initial response of microorganisms, soil nutrients, and vegetation after fire is crucial for providing ecological insights to be taken into account when designing and implementing early conservation and restoration actions for the endangered *A. araucana* forests.

2. Materials and methods

2.1. Study area

The study area is located in the National Reserve China Muerta, in the Andes of south-central Chile (38°S, 71°W; Fig. 1). The Reserve encompasses 11,170 ha, mainly covered by the endemic, long-lived conifer *Araucaria araucana*. According to the vegetational classification of Gajardo (1995), the *A. Araucana*-dominated forests belong to the

Andean-Patagonian and deciduous forests. Within our study area, *A. araucana* populations can occur as pure stands or as mixed-species forests with *Nothofagus pumilio* and *Nothofagus dombeyi* (González et al., 2013). The understory vegetation is dominated by *Chusquea culeou*, *Maytenus disticha* and *Gaultheria poepigii*, whereas the forest floor is represented by *Osmorhiza chilensis*, *Viola magellanica* and *Adenocaulon chilense* (Luebert and Pliscoff, 2006). Over 90% of the study area is covered by *A. araucana* forests, which along with other areas in the Chilean Andes, belongs to the UNESCO *Biosphere Reserve Araucarias*. The study area has an irregular and scarped topography, ranging from 800 to 1850 m a.s.l of elevation. The climate is temperate and warm, with less than four months of drought and snow because of the effect of altitude. Mean annual temperature for summer (December to March) is 19 °C, whereas for winter (June to September) it is 5 °C. Mean annual rainfall is ca. 2500 mm, with a dry period between the months of December and March. Precipitation also includes abundant winter snowfall, which provides enough moisture for plants during the following growing season. The soils are from the Andisol order (Soil Survey Staff, 1999), developed from recent volcanic ashes. These soils are deep, well-stratified, and dark brown in color, with coarse texture and permeable throughout their profile with abundant gravel in their layers (CIREN, 2010).

2.2. Description of the fire

The Chilean Forest Service (CONAF) reported that the wildfire that burned the study area began as the result of a poorly smothered bonfire in March 14, 2015, and it was brought under control 23 days later, on April 6, 2015. The fire spread rapidly throughout the landscape due to extreme dry fuels accumulated from several preceding dry years as a result of La Niña cycle. After fire extinguishing, and using the normalized burn ratio (NBR index; Key and Benson, 1999), CONAF carried out satellite imagery analyses to determine the degree of fire severity in the burned areas. The most-fire-affected areas presented a NBR index > 0.66, whereas unburned areas had a NBR < 0.1 (Mora and Crisóstomo, 2016). Excluding the high summit lands stripped of vegetation and incombustible areas (rock bluffs and sand banks), 3765 ha were affected by the fire (equivalent to 34% of the National Reserve).

2.3. Sampling design

We focused on the following surface soil conditions: a soil completely affected by the fire (burned soil, BS), and an adjacent forest with unburned soil (UBS) (Fig. 2). The BS was located within a forest exposed to a fire of high severity (NBR > 0.66), resulting in a complete consumption of the organic horizon ($O_i + O_e$ layer) and almost complete mortality of the forest vegetation, with trees completely charred from base to crown and a layer of ash in the soil. Another feature within BS was the presence of large holes in the ground, where tree stumps that previously existed were completely consumed due to underground fires that scorched the roots of the trees. The UBS corresponded to a remaining adjacent forest with no signs of damage caused by the fire (NBR < 0.1). In our study area, the BS is located about 800 m away from the UBS, but at the same elevation range (1400 m.a.s.l.), aspect (N and NE), slope (10–20%), and similar neighboring vegetation, therefore, the site variables where we collected the soil and vegetation data were similar between BS and UBS conditions.

One year after fire, in early April 2016, we collected samples of soil from the first 10 cm of the mineral soil horizon. The recognizable plant material, as well as the ash and the charred organic matter were removed before conducting the soil sampling. Each sample (of approximately 1 kg) consisted of a mixture of six sub-samples collected at six random locations within each of the 20 permanent sampling plots (25 m^2 in area). The samples were collected from the BS and UBS areas using a soil corer (10×12 cm in diameter and height, respectively). Thus, the design consisted in one (composite) soil sample per 20 permanent plots per two burn conditions (i.e., $1 \times 20 \times 2 = 40$ samples in total). The sampling plots within each of the fire conditions (i.e., BS and UBS) were ca. 30 m away from each other, and preliminary spatial analyses showed no spatial autocorrelation among the plots. The collected samples were labeled in plastic bags and stored at 4 °C. Whereas a sub-sample from the field-collected soil was used for carrying out microbial analysis, the rest of soil was processed for nutrient analyses.

2.4. Microorganisms analyses

We used the serial dilution method to determine the colony forming units (CFU) of bacteria and fungi. Although the use of more advanced techniques (e.g., molecular biology based on DNA analysis) can allow us to obtain a greater amount of data, they do not provide much information about the activity of soil microorganisms (e.g., because of incorporating DNA from dead microorganism or in latency state). The assessment of CFU in culture in plates and enzymatic activity determination have the advantage of providing information of the actual active microorganisms (Braun et al., 2006), most likely involved in processes of nutrient recycling and recovery of the ecosystem through their metabolic activities at the moment of sampling (Vale et al., 2005).

To allow the assessment of CFU, sub-samples (of approximately 100 g each) of field-collected soil were sieved to 2 mm and air dried to a constant weight. Then, we took a small sub-sample (of ca. 1 g of soil) from the sieved and dried soil and proceed with the serial dilution. Five serial dilutions in sterilized distilled water for fungi and bacteria were performed: from 10^1 to 10^5. After dilutions were completed, 100 μL of diluted samples were evenly spread in the surface of potato dextrose agar (PDA) and Luria-Bertani (LB) agar in triplicate. After three (for bacteria) and seven (for fungi) days of incubation at 28 °C and in

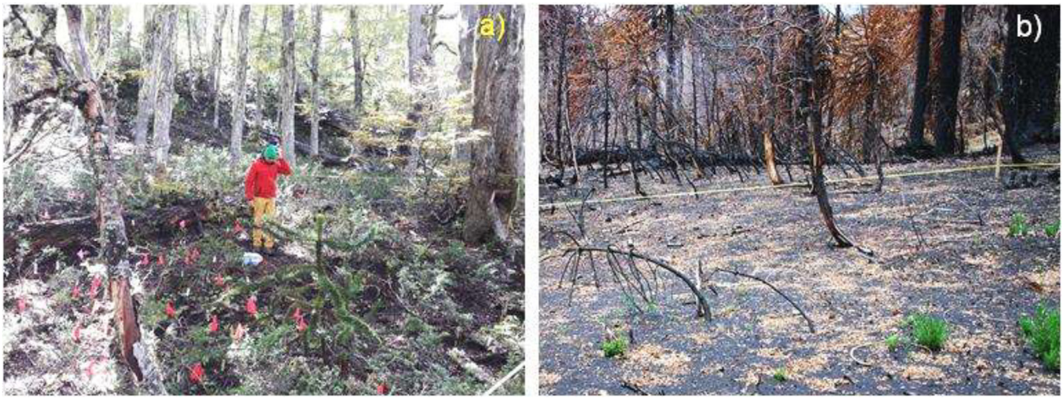

Fig. 2. Pictures of the soil surface conditions: a) unburned (UBS) and b) burned (BS) soils within *Araucaria araucana* forests. Picture b) was taken one year after fire, at the same time of data collection in early April 2016.

darkness, CFU of bacteria and fungi were determined and counted by visual observation and presented as numbers of CFU per gram of dry soil.

We also evaluated the hydrolysis of fluorescein diacetate (FDA), which is a sensitive indicator of the potential microbiological activity in the soil (Adam and Duncan, 2001). For this analysis, another small subsample (of ca. 2 g and 20 samples from BS and 20 from UBS, $n = 40$) from the same sieved and dried soil used in the previous step were incubated with 15 mL of 60 mM KH_2PO_4 buffer pH 7.6. Then, fluorescein diacetate (0.2 mL), dissolved in acetone, was added. The samples were later incubated for 1 h at 30 °C in the dark. After this, acetone (15 mL) was added to stop the reaction, and the samples were centrifuged at 3500*g* for 15 min. Finally, we used a spectrophotometer (TU-1810 Split Beam UV–VIS, Electronic Co. Ltd, Shanghai, China) to measure the absorbance of the supernatant at 490 nm, and the results were expressed as µg of fluorescein per g of dry soil. In this analysis, a high amount of FDA is associated with an increased biological activity in the soil.

2.5. Soil nutrients analyses

To determine the content of soil nutrients, we used the 40 originally field-collected samples (20 from BS and 20 from UBS, $n = 40$) that were used for the previous microbial analyses, and processed them for nutrient content determination. The soil variables considered in the analysis were nitrogen (N), phosphorus (P), and potassium (K) and the content of organic matter (OM). The soil nutrients N, P and K are essential for plant growth and for the development of soil microorganisms, especially after major disturbances, such as wildfires (Neary et al., 1999). Soil microbes, like bacteria and fungi are capable of increasing the availability of nutrients in soil through different mechanisms (Marschner et al., 2011), and in turn, higher nutrient and organic matter content can modulate the microbial biomass and their enzymatic activity (Lladó et al., 2017).

The N content was determined by the Kjeldahl method (Kjeldahl, 1883). The available P content was determined by extraction with $NaHCO_3$ at pH 8.5 (Olsen and Sommers, 1982). The OM was determined by the method described by Walkley and Black (1934). The available K was determined by the methodology developed by Mingorance (2002). Results for the nutrient analysis are expressed in mg per kg of soil for N, P and K and percentage for OM.

2.6. Vegetation sampling

We surveyed post-fire vegetation recovery at the same time we collected the soil samples (i.e., one year after fire) and from the same locations: the 40 permanent 25 m^2 plots (i.e., 20 in BS and 20 in UBS). Within each plot, we assessed species richness and plant abundance at the plot-level. We recorded all plant individuals with height ≥5 cm. This decision was made based on the difficulty to correctly identify seedlings at the very early stage of establishment in the BS area. If shoots from the same species were < 5 cm apart from each other, we recorded them as a single individual. Plant abundance is presented as number of individuals in 25 m^2. Plant taxonomy (i.e., for species identification) followed Matthei (1995) for grasses and forbs and Teillier et al. (2014) for shrubs and trees.

2.7. Statistical analyses

For assessing the effect of the fire on the abundance of soil microorganisms (bacteria and fungi) and on the soil biological activity (FDA activity), we computed the non-parametric paired Mann-Whitney *U* test (with 5% of significance level) between the burn conditions (BS and UBS). The decision of using a non-parametric analysis was made because of the response variables (i.e., CFU count and FDA activity) did not follow a Gaussian distribution. The effect of fire on the availability of soil nutrients (i.e., N, P, K and OM) was assessed using paired *t*-tests due to that nutrient data met the assumptions for parametric analyses (i.e., normality and equal variances of residuals). All the statistical analyses for microbial and nutrient data were carried out in the statistical software R (R Core Team, 2017).

For analyzing plant recovery after fire, we compared plant species richness between BS and UBS by carrying out a randomization test. This analysis computes the quantiles at $P = 0.975$ and $P = 0.025$, corresponding to a global interval of 95%. If the observed difference in species richness is well above the upper quantile value, this indicates that the observed difference is much larger than expected under the null hypothesis of "no difference between sites". We used the R package *rich* (Rossi, 2011) for computing the randomization test between BS and UBS. In addition, we computed the Shannon-Wiener diversity index and determined statistical differences between BS and UBS using a paired *t*-test. Finally, we assessed the effect of fire on the mean plant abundance at the plot-level by conducting a paired *t*-test between BS and UBS.

3. Results

One year after a severe wildfire burned *Araucaria* forests, our results showed that fire had a significant effect on the abundance of bacteria ($P < 0.01$), fungi ($P < 0.0001$) and the soil biological activity ($P < 0.01$). We found a significantly higher abundance of bacteria (W = 750.5; $P < 0.01$, Fig. 3a) and fungi (W = 1768.5; $P < 0.0001$,

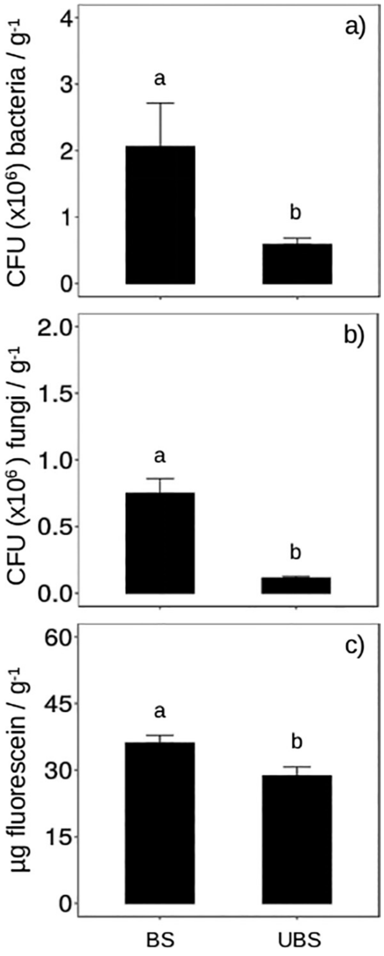

Fig. 3. Mean value (+S.E.) of colony forming units (CFU) for a) soil bacteria, b) soil fungi and c) biological activity of the soil (Fluorescein diacetate activity) at both burned (BS) and unburned (UBS) soils. Note that different letters above bars indicate statistically significant differences at α = 0.05 for the means using the Mann-Whitney *U* test.

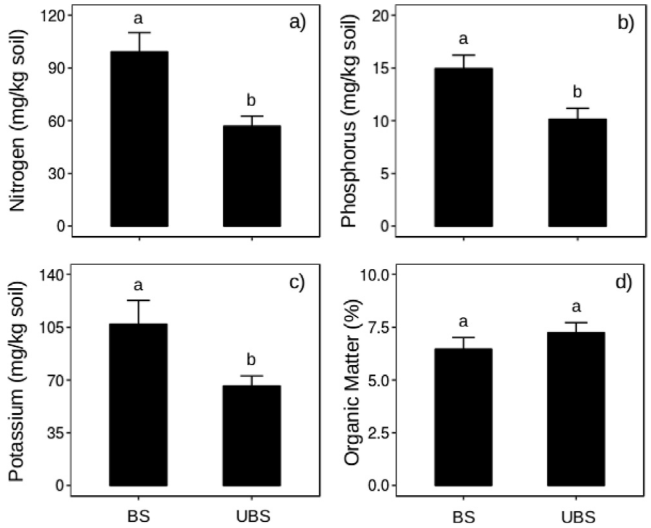

Fig. 4. Mean value (+S.E.) of soil nutrients within both burned (BS) and unburned (UBS) soils for a) nitrogen, b) phosphorus, c) potassium and d) organic matter. Note that different letters above bars indicate statistically significant differences at α = 0.05 for the means using paired *t*-tests.

Fig. 3b) in burned soils (BS) than in unburned soils (UBS). Abundance of bacteria was almost four times greater in BS than in UBS, averaging 2.06×10^6 and 0.59×10^6 CFU, respectively. Soil fungi were almost seven times greater in BS than in UBS, with an average of 0.75×10^6 and 0.11×10^6 CFU, respectively. Regarding to soil biological activity, we found that the greater activity of microorganisms appeared in the burned area with an average of 36.09 µg of fluorescein per g of dry soil, being this significantly higher than at unburned sites ($W = 729.5$; $P < 0.01$, Fig. 3c).

We found a statistically significant effect of fire ($P < 0.001$) on soil nutrient availabilities. Greater concentrations of N, P and K were found in BS than in UBS ($P < 0.01$ for all these nutrients). Nitrogen was almost two times higher in BS than in UBS, with an average of 99.2 and 56.9 mg kg^{-1}, respectively (Fig. 4a). For P, an average of 14.95 and 10.15 mg kg^{-1} was found in BS and UBS, respectively (Fig. 4b). Meanwhile, K was almost two times higher in BS than in UBS, with an average of 107.13 and 66.07 mg kg^{-1}, respectively (Fig. 4c). There was no statistically significant difference in OM between burned and unburned soils ($t = -1.11$, df = 19, $P = 0.28$; Fig. 4d).

The assessment of vegetation showed that species richness was significantly lower in BS (14 species) than in UBS (31 species) ($P < 0.01$; Table 1). A total of 37 species were recorded across the burned and unburned plots, from which only eight species were present in both fire conditions (ca. 21% of common flora). On the other hand, we found that 15 plant species were absent in the BS one year after fire, including the co-dominant tree *Nothofagus pumilio*. Only six species were unique to burned forests, vs. 23 species found uniquely in unburned conditions. These results are directly related to the Shannon-Wiener diversity index, which was also significantly lower ($t = 6.15$, df = 19, $P < 0.0001$) within BS (mean = 0.75) than in UBS (mean = 1.61). Likewise, plant abundance at the plot scale was more than ten times lower in BS compared to UBS ($t = 14.08$, df = 19, $P < 0.0001$), averaging 11 and 119 individuals per plot (of 25 m^2), respectively (see Table 1).

Table 1
Species richness, mean plant abundance at plot-level (25 m^2), mean Shannon-Wiener diversity index (H'), mean abundance for *Araucaria araucana* and *Nothofagus pumilio* within unburned soil (UBS) and burned soil (BS). Note that different letters indicate statistically significant differences at α = 0.05 for each variable.

	UBS	BS
Plant species richness	31 a	14 b
Mean plant abundance per plot	119.1 a	11.9 b
Shannon-Wiener index	1.61 a	0.75 b
Araucaria araucana mean abundance	6.2 a	1.5 b
Nothofagus pumilio mean abundance	11.5	0

4. Discussion

One year after a severe fire burned *Araucaria*-dominated forests in the Andes of south-central Chile, we found a positive effect associated to fire on the abundance of CFUs of bacteria and fungi, and also on the biological activity of the soil measured as hydrolysis of fluorescein diacetate (FDA). Although the CFU method for quantifying soil microorganisms has potential limitations (e.g., biased towards microorganisms which are able to grow under specific culture conditions), it has the advantage of providing information of the actual active microorganisms most likely involved in the recovery of the ecosystem (Braun et al., 2006). Studies, though, have generally found negative effects of fire on soil microorganisms (Banning and Murphy, 2008; Goberna et al., 2012). Severe fires can eliminate a high proportion of bacteria and fungi from the soil as a result of the high temperatures generated during combustion (Banning and Murphy, 2008; Mabuhay et al., 2006). High-severity fires, like the one that burned our study area, also tend to modify the balance of soil nutrients, which also modify the post-fire abundance of microorganisms (Certini, 2005).

The greater abundance of microbes and increased biological activity (FDA activity) in burned soils found in this research might be related to distinct factors. First, both fungi and bacteria can present fire-resistant structures or metabolic features with which they can withstand high-severity fires, for later to begin a recovery process and become abundant after fire. For instance, Vázquez et al. (1993) found a significant increase in microorganisms one month after fire in forest ecosystems of northwestern Spain. In the long term, though, soil microbes continue to be greater only for spore-forming bacteria and cyanobacteria and for ammonium-oxidizing fungi. This emphasizes that the response to fire by soil microorganisms largely depends on the functional groups and the metabolic characteristics of the microorganisms themselves. Secondly, factors associated with the time elapsed since the fire (e.g., soil temperature and humidity) can also favor the increase of microorganisms post-fire (Knicker, 2007; Liu et al., 2017). For example, reduced crown coverage in BS sites can allow more direct sunlight into the forest floor and raise the soil temperature, thereby increasing the abundance of microorganisms and biological activity in the soil (Hart et al., 2005). In fact, soil temperature at the time of sampling was 1.7 °C higher in BS then in UBS (18.7 vs. 17 °C in average at 10 cm in depth, respectively).

Fire also has a considerable impact on soil nutrients and their availability for both plant growth and microbial activity. Nutrients variability after fire is mainly related to the combustion process that causes significant nutrient losses due to volatilization (Wittkuhn et al., 2017), or due to mineralization of the organic matter that causes an increase of soil nutrients (Knoepp and Swank, 1993). We found a significant increase of the soil N, P and K contents after fire, findings that are consistent with other studies (DeLuca and Zouhar, 2000; Turner et al., 2007). The availability of nutrients after a fire is variable, and can increase or decrease, depending on site factors (Neary et al., 1999), fire severity, or on the time elapsed since fire (Gimeno-García et al., 2000; Knicker, 2007). The study of Litton and Santelices (2003) showed an increase in exchangeable N and P two and 14 months after a fire in *Nothofagus glauca* forests in central Chile, respectively. In this sense, the organic matter mineralization that occurs as a result of fire can increases the amount of soil nutrients for both plants and microorganisms. Therefore, an increase in the nutritional quality of the soil may be directly related to an increase in the number of soil microbes. Studies conducted within *Araucaria* forests are scarce, but Rivas et al. (2012) showed variable results for soil nutrients three years after a fire that occurred in 2002 in south-central Chile. Whereas P did not change between burned and unburned areas, N (in NO_3^- form) significantly increased. We noted that the BS condition in our study site had a thick, dark and extensive layer of ash covering the soil. According to Pereira et al. (2012) and Badia and Marti (2003), ashes are an important source of nutrients shortly after fire. The accumulation of ash in the soil could also be related to a proliferation of microorganisms (Knicker, 2007; Noyce et al., 2016). Both of these studies also argue that once nutrients are incorporated into the soil after fire, they would become readily available for plant growth. In our research we also found an increasing trend (although non-significant) of soil organic matter within unburned soils that is potentially attributable to the standing biomass and the necromass on the ground that did not burn (Certini et al., 2011).

We also examined the post-fire response of vegetation, and generally found a reduction of species richness and plant diversity within burned *Araucaria araucana* forests. From the results presented here, we argue that despite the negative impact of the fire on vegetation in the first year since fire (which is expected to occur), plant recovery should tend to gradually improve over time as a result of the increase of nutrients and microbial activity in the soil, both key components for plant recovery after fire (Bond and Midgley, 2003; Maia et al., 2012). Nevertheless, other important factors that govern post-fire vegetation recovery include germination of seeds from the seed bank (when conditions are favorable) and the resprouting capability of vegetation. It should be noted that the feedbacks between soil microorganisms, nutrients and plant growth might become highly variable as time since fire goes on (Ginzburg and Steinberger, 2012). Soil nutrients losses within burned areas could increase over time as a consequence of soil erosion due to the lack of plant cover (Gimeno-García et al., 2000). Our study shows that areas of BS are slowly recovering its vegetation cover, which in turn will help to keep the plant litter layer over time, and thus, maintaining the microbial activity and the nutrient cycling after fire.

However, our study revealed that one year after fire, the abundance of key trees *Araucaria araucana* and *Nothofagus pumilio*, the two dominant tree species in these forests, was drastically reduced in areas of high fire severity. Indeed, the tree *N. pumilio* and other 14 species were completely absent from BS areas (at least one year after fire). Whereas *A. araucana* can reproduce by both seeds and vegetative resprouting after fire (González et al., 2010), *N. pumilio* is an obligated seed-reproducer. Seed dispersal for *N. pumilio* could be limited after fire if parental trees are killed by fire or if their locations are far away from the burned areas (Raffaele et al., 2011). Although still a very initial response of vegetation to fire, and further research is needed, our results line up with previous studies, showing that a reduction of key tree species in *A. araucana* forests could affect the post-fire development of forest structure (Hoffmann and Moreira, 2002; González et al., 2010; Paritsis et al., 2015).

5. Conclusion

One year after fire, we found a significant increase in the abundance of bacteria and fungi, as well as in the microbial activity of burned soils (BS) compared to unburned soils (UBS) of *Araucaria araucana* forests. Our results showed that, in average, bacteria and fungi were four and seven times greater in BS than in UBS, respectively. Also, a significant increase in the soil nutrients N, P and K was found in areas affected by fire compared to unburned forests. During the same period of time, however, plant richness, diversity and abundance significantly decreased within areas of high fire severity compared to adjacent, unburned forests. Moreover, our study revealed that *Araucaria araucana* and *Nothofagus pumilio*, the two dominant tree species in these forests, drastically reduced their abundance within fire-affected areas, with the latter being absent from the severely burned areas. However, further research is necessary as vegetation results are only preliminary and they can vary in the short-to-medium term. This research is the first attempt to understand the short-term relationship between fire, soil properties and vegetation recovery within *A. araucana* forests. Finally, and more importantly, our study provides an early baseline that should be useful for determining longer-term ecosystem recovery, and to delve into more applied research aimed at the post-fire restoration of the endemic, long-lived *Araucaria araucana* forests.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.apsoil.2018.08.010.

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