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Initial response of understorey vegetation and tree regeneration to a mixed-severity fire in old-growth *Araucaria*–*Nothofagus* forests

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Abstract

Questions: Fire is a key factor influencing *Araucaria araucana* forests, but the impact of fire severity on the understorey vegetation is not well understood. In this study we seek to answer the following questions: (a) how do initial plant diversity, composition and spatial distribution of the understorey vegetation change in response to different levels of fire severity; and (b) does the abundance of dominant tree species exhibit different patterns across a fire severity gradient shortly after fire?

Location: Old-growth *Araucaria araucana*–*Nothofagus pumilio* forests in the Andes of south-central Chile (38° S, 71° W) burned in 2015.

Methods: We evaluated the post-fire plant regeneration across a fire severity gradient ranging from unburned forests to areas of high fire severity. One year after fire (in February 2016), we measured woody and herbaceous species richness, abundance, height, origin (native vs exotic species), life forms and the spatial pattern of plant recovery.

Results: Plant species richness and abundance were significantly higher within the unburned forest and low fire severity areas one year after fire, compared to areas of high and moderate fire severity. Overall, nearly 50% of the species present in the unburned forest were not found in areas of high severity, including the tree *Nothofagus pumilio*. Rapid vegetative resprouting of pioneer species such as *Chusquea culeou* resulted in an aggregated spatial distribution of plants after fire.

Conclusions: Plant diversity and the abundance of *Araucaria araucana* and *Nothofagus pumilio* were reduced in areas of high fire severity one year after fire. Exotic species were more abundant within areas of low severity, being likely mediated by cattle browsing. Our research makes clear the potential changes in forest composition and structure if dominant tree species are not capable of recovering after fire. We recommend the exclusion of cattle within fire-affected areas and planting *Nothofagus pumilio* in areas of high fire severity.

KEYWORDS

abundance, *Araucaria araucana*, *Nothofagus pumilio*, plant diversity, post-fire vegetation recovery, severity gradient, spatial distribution, species richness

1 | INTRODUCTION

One of the most striking examples of altered disturbance regimes at a global scale involves changes in the frequency, severity and seasonality of fires (Westerling, Hidalgo, Cayan, & Swetnam, 2006; Littell, McKenzie, Peterson, & Westerling, 2009; Moritz et al., 2012). Fire regimes outside their historical range of variability and exhibiting increased frequency and severity may compromise several key properties of the ecosystem. As a result, fire can alter many ecological patterns and processes including plant composition, functional diversity, and biogeochemical cycles (Westerling & Bryant, 2008; Bowman et al., 2009). Additionally, the “resilience” (i.e., the ability of an ecosystem to return to its original pre-disturbance state after a given disturbance), and the “resistance” (i.e., the ability of an ecosystem to maintain its original pre-disturbance state in the face of disturbance) can decrease when characteristics of a fire regime (e.g., severity) change rapidly (Pickett & White, 1985; Stevens-Rumann et al., 2018).

Climate change is predicted to increase dry and hot conditions across the globe (IPCC,), which is expected to further alter fire regimes and forest ecosystem dynamics. Under scenarios of climate change, increased fire activity will likely promote plant species assemblages that are better suited to harsh drier post-fire conditions (Donato, Harvey, & Turner, 2016). For example, wildfires followed by drought conditions may decrease forest resilience through reduced tree regeneration, potentially resulting in forest ecosystem conversion to states dominated by shrubs or grasses (Enright, Fontaine, Bowman, Bradstock, & Williams, 2015; Paritsis, Veblen, & Holz, 2015; Kitzberger et al., 2016). Indeed, severe drought conditions, partially attributed to anthropogenic origin (Boisier, Rondanelli, Garreaud, & Muñoz, 2016), have been recorded in central and south-central Chile in the last decade (Garreaud et al., 2017). Since year 2010, annual precipitation has decreased 20–30%, promoting the increase in fire frequency and size, including in La Araucanía region (González & Lara, 2015; González, Gomez-Gonzalez, Lara, Garreaud, & Diaz-Hormazabal, 2018).

Forest fires generally result in a heterogeneous mosaic of patches of different fire severities (i.e., a mixed-severity fire) to which vegetation may respond differently. The severity of fire is related to the degree of loss of understorey and soil organic matter caused by fire (i.e., vegetation, soil) and canopy mortality (Keeley, 2009). Thus, the resulting spatial pattern of plants may reflect the effects of fire severity and the underlying abiotic environment being altered (Agee, 2003). As a result, fire severity encompasses a continuum from nearly no effect on the forest to almost complete mortality of the canopy (Fornwalt & Kaufmann, 2014). For instance, high-severity fires that kill most canopy trees are often followed by the establishment of trees of the same or a different species, potentially creating a distinct post-fire plant community. In contrast, low-severity fires result in no or little mortality of canopy trees, and typically do not change the composition of the plant community (Hessburg, Salter, & James, 2007). Also, mixed-severity fires are expected to create fine-scale patchiness in the forest spatial structure. Although still understudied, the spatial and temporal patterns of vegetation affected by different levels of fire severity are important to be assessed from the early beginning after fire, as they can help to better understand the possible pathways for forest recovery.

Fire is recognized to be a key disturbance shaping forests formed by *Araucaria araucana* and *Nothofagus pumilio* (hereafter referred to as *Araucaria–Nothofagus* forests) in the Andean region of southern South America (Burns, 1993; González, Veblen, & Sibold, 2005; Mundo, Kitzberger, Roig Junent, Villalba, & Barrera, 2013; Holz et al., 2017). *Araucaria–Nothofagus* forests are typically shaped by a mixed-severity fire regime that includes surface and crown fires ignited by lightning and anthropogenic sources (González, 2005). Although *Araucaria araucana* is adapted to withstand moderate-severity fires or reestablish following high-severity fires (Burns, 1993), recent large, repeated high-severity fires may have hampered the potential resilience of these forests, especially under changing post-fire climatic conditions (Boisier et al., 2016; Garreaud et al., 2017; González et al., 2018). Furthermore, native plant species associated with *Araucaria–Nothofagus* forests also present strategies and adaptations to tolerate, survive and recover after high-severity fires (e.g., seedling establishment and resprouting), and the degree to which plants are adapted to fire strongly influences the structure and function of forests following a fire (Veblen, Mermoz, Martin, & Kitzberger, 1992; Veblen, Kitzberger, Raffaele, & Lorenz, 2003). Nevertheless, there is still little knowledge of the impact of mixed-severity fires, and how the understorey vegetation associated with *Araucaria–Nothofagus* forests would be affected and respond to different levels of fire severity over the short term.

Old-growth *Araucaria araucana* forests are particularly valuable because of their significant biodiversity and cultural values (Aagesen, 1998; dos Reis, Ladio, & Peroni, 2014). By year 1,500, 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 intentional fires used for land clearance (Lara, Solari, Rutherford, Thiers, & Trecaman, 1999). Currently, *A. araucana* is classified as an endangered species in Chile and it was declared a Natural Monument in 1990, with logging completely prohibited. Despite its legal protection, and its significant social and ecological value, *A. araucana* populations — including national parks and reserves — are still experiencing an increased risk of degradation, being subjected to logging (González & Veblen, 2007), cattle grazing (Zamorano-Elgueta, Cayuela, Gonzalez-Espinosa, Lara, & Parra-Vazquez, 2012) and fire-induced disturbances (González & Lara, 2015; Assal, González, & Sibold, 2018; Fuentes-Ramirez, Barrientos, Almonacid, Arriagada-Escamilla, & Salas-Eljatib, 2018).

Understanding the impacts of fire on the composition and structure of the vegetation requires taking into consideration several factors, such as the spatio-temporal variability in fire severity and differences among plant species in their ability to recover shortly after fire (González, Szejner, Muñoz, & Silva, 2010b; González, Veblen, & Sibold, 2010a). Most of our current knowledge on *Araucaria–Nothofagus* forest dynamics in the Andes of southern Chile is based on inferences from assessments of stand composition and the structure of these stands in response to fire and volcanism (Burns, 1993; Veblen et al., 2008; González, Veblen, et al., 2010a) or

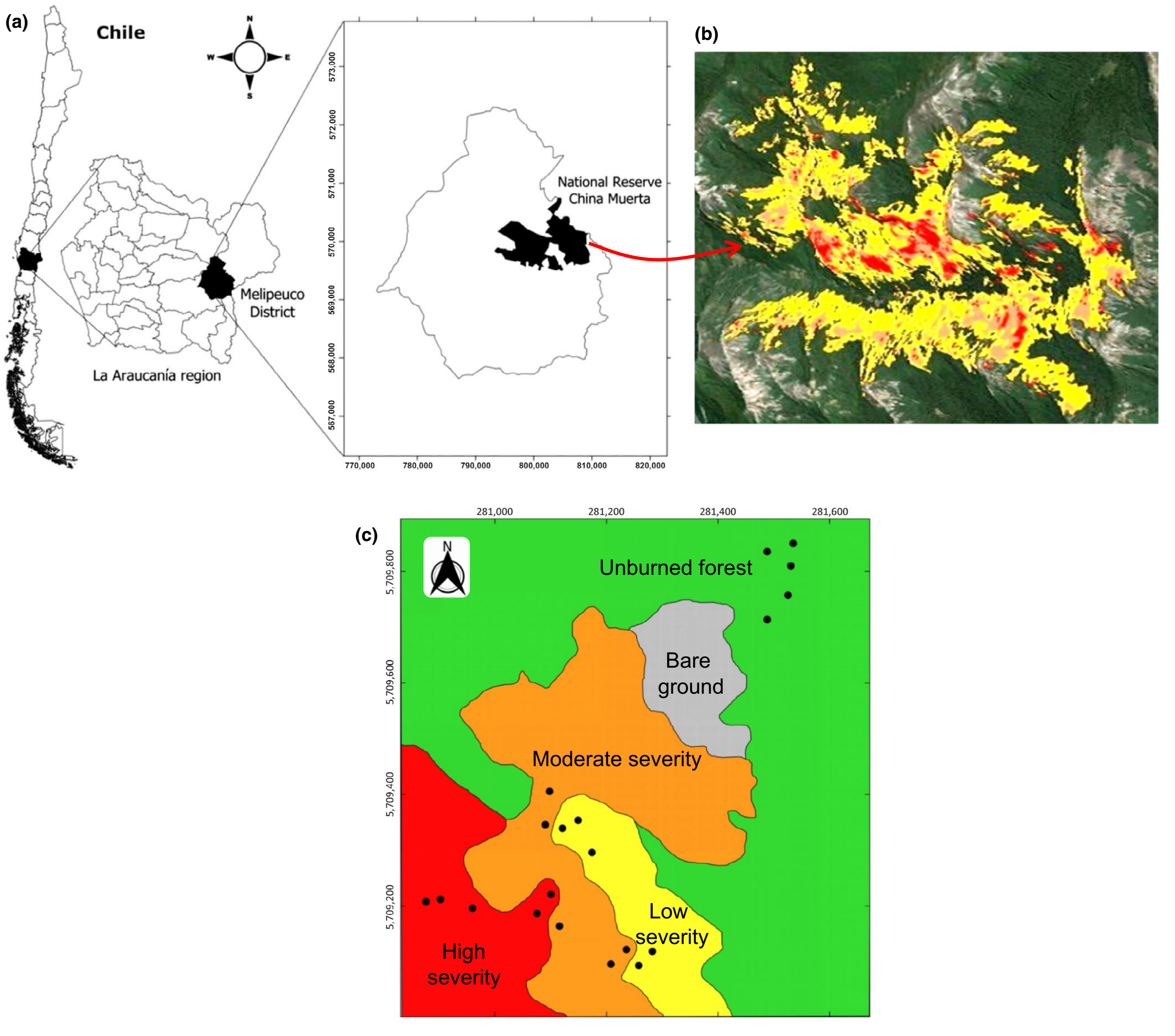

FIGURE 1 (a) Geographic location of the study area in the National Reserve China Muerta, Melipeuco district, La Araucanía region (38° S, 71° W), south-central Chile. (b) Map showing the different levels of fire severity that affected the study area: low (yellow), moderate (orange) and high (red), and (c) location of the actual sample plots within each fire severity level including the unburned forest [Colour figure can be viewed at wileyonlinelibrary.com]

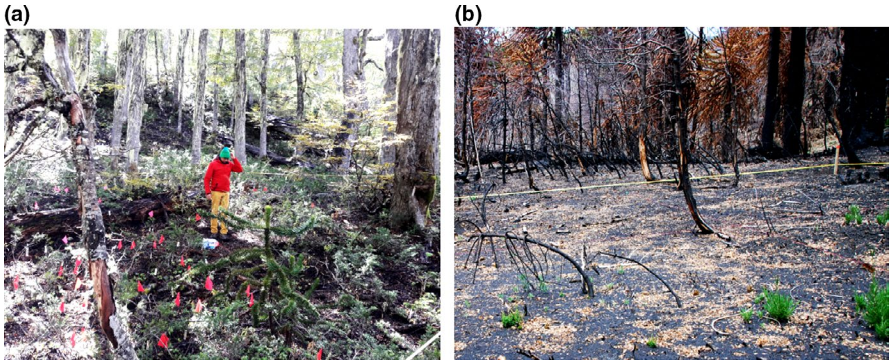

FIGURE 2 Images of the experimental burned area showing our study sites for (a) the unburned forest and (b) areas of high fire severity in *Araucaria–Nothofagus* forests in the Andes of south-central Chile [Colour figure can be viewed at wileyonlinelibrary.com]

surveys of vegetation recovery several years after fire (Assal et al., 2018). Nevertheless, little research has focused on the immediate impact of fire severity on *Araucaria–Nothofagus* forests, and the initial response of tree regeneration and understorey species to different levels of fire severity (González, Szejner, et al., 2010b). This research is fundamental for an appropriate assessment of post-fire plant response, and for better understanding the potential fire-induced changes in forest recovery. Toward that end, the main goal of this study was to assess the initial response (i.e., one year after fire) of vegetation in old-growth *Araucaria–Nothofagus* forests affected by a mixed-severity fire in March of 2015. The specific questions we set out to answer were: (a) how do initial plant diversity, composition and spatial distribution of the understorey vegetation change in response to different levels of fire severity; and (b) does the abundance of dominant tree species (i.e., *Araucaria araucana* and *Nothofagus pumilio*) exhibit different patterns across a fire severity gradient shortly after fire?

2 | METHODS

2.1 | Study area

The study area corresponds to old-growth *Araucaria araucana–Nothofagus pumilio* forests located in the National Reserve China Muerta, in southern Chile (38° S, 71° W; Figure 1). This area had not encountered severe wildfires in recent decades. The climate is temperate and warm, with less than four months of drought and snow because of the effect of altitude (i.e., 1,480 m a.s.l.). Mean annual temperature for summer (December–March) is 19°C, whereas for winter (June to September) it is 5°C. Mean annual rainfall is 2,500 mm, with a dry period between December and March. Precipitation includes abundant winter snowfall, which provides enough moisture for plants during the following growing season. Soils are developed from recent volcanic ashes (Andisols and Histosols orders) and well stratified, deep and dark brown in color, with coarse texture and permeable throughout the profile (CIREN, 2010).

The vegetation in the area is dominated by the native conifer *Araucaria araucana* and the deciduous broad-leaved *Nothofagus pumilio*. Whereas *A. araucana* can regenerate by seeds and vegetative resprouts after low-to-moderate fires, *N. pumilio* is an obligate seeder. This forest belongs to the Andean–Patagonian forests, and to a lesser extent to the Andean deciduous forest (Gajardo, 1994), which occurs mostly in the Andes mountains (37°45′ S to 40°20′ S) including the Chilean and Argentinean range (Veblen, Burns, Kitzberger, Lara, & Villalba, 1995). The understorey vegetation is dominated by the shrubs *Chusquea culeou*, *Maytenus disticha* and *Gaultheria poeppigii*, and the herbaceous layer is represented by *Osmorhiza chilensis*, *Viola magellanica* and *Adenocaulon chilense* (Luebert & Pliscoff, 2006). Within our study area, *A. araucana* populations can occur in pure stands (>90% canopy cover) or mixed with *N. pumilio*. The study area presents signs of cattle activity (mostly cows), with a rather low density (i.e., <50 heads in the entire reserve). The National Reserve China Muerta, along with other areas in the Chilean Andes, forms the UNESCO Araucarias Biosphere Reserve.

2.2 | Wildfire description and burn gradient

During March–April of 2015 an extensive wildfire affected south-central Chile. The wildfire that affected the National Reserve China Muerta was active for 23 days (from March 14 to April 6, 2015), and burned 3,765 ha of *Araucaria–Nothofagus* forests. According to the Chilean Forest Service (CONAF), the fire started as the result of a poorly smothered bonfire that quickly spread throughout the landscape, most likely due to extremely dry conditions, and also favored by several preceding years of drought (Garreaud et al., 2017; González et al., 2018). By using satellite imagery analyses (i.e., Landsat-8/OLI) and the dNBR index (differential normalized burn ratio; Key & Benson, 1999), the Chilean Forest Service (CONAF) defined three levels of fire severity: high, moderate and low. Areas of high fire severity presented a dNBR index >0.6; areas of moderate severity had a dNBR of 0.6–0.35, and areas of low fire severity between 0.35 and 0.1 (Mora & Crisóstomo, 2016). Subsequent to the classification developed by CONAF, we characterized each level of fire severity in the field by describing the damage on trees and the understorey vegetation. Areas of high fire severity suffered crown fires and had trees and understorey vegetation totally charred. Less than 1% of canopy trees survived fire in high fire severity areas. In addition, there was a dense layer of ash in the soil (up to 30 cm in depth) and large holes in the ground caused by tree stumps that were completely carbonized through below-ground combustion

(Figure 2b). In moderate fire severity areas, trees were partially burned, the forest canopy presented some unburned branches, and there was understorey vegetation that survived fire. We defined moderate-severity areas as <50% of canopy tree survival. Finally, areas of low fire severity had a superficial fire, with slight damage in branches and most of the trees survived fire (>90%). The extent of each fire-affected area was ~970 ha in high, 910 ha in moderate and 1,890 ha in low fire severity (Mora & Crisóstomo, 2016). In addition, we used an adjacent unburned forest with no signs of damage caused by fire to serve as reference (i.e., representing the conditions prior to fire). The unburned forest presented a dNBR index <0.1 (Figure 2a). We acknowledge that our study represents a short-term assessment of immediate post-fire regeneration (i.e., one year after fire) which limits our ability to predict long-term post-fire trajectories. In this study, we assumed that the unburned forest was similar in its plant composition to the burned areas before the fire (i.e., space for time assumption).

2.3 | Design and vegetation sampling

Within the burned zone, we selected an experimental area of 1,200 m × 500 m (i.e., 60 ha) that included the three fire severity categories and the unburned forest (i.e., 30 ha of unburned forest, 7 ha of low, 14 ha of moderate and 9 ha of high fire severity), and presented homogeneous site conditions: mean elevation of 1,480 m a.s.l., N–NE aspect, 10–20% slope, and similar neighboring vegetation. This experimental area was the only one that covered the entire burned gradient, where areas of low, moderate and high fire severity were close to the unburned forest. Within the experimental area, we randomly established a total of 20 permanent square sample plots of 100 m^2 (i.e., five per each fire severity level including the unburned forest) following the procedures recommended by Gregoire and Valentine (2008). The fire-affected plots (high, moderate and low fire severity) were located ca. 800 m away of the unburned forest. Within each plot, we surveyed all vascular plants in February 2016, which corresponds to the one-year-after-fire response. We measured species richness, plant abundance (i.e., the number of individuals at the plot scale), plant height, and plant origin (i.e., native or exotic species) and life form (i.e., trees, shrubs and herbs). 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, and also because plants ≥5 cm tall will have increased chance to survive and establish after fire. If shoots from the same species were <5 cm apart from each other, we recorded them as a single individual. Unknown specimens were collected and identified afterwards following specialized literature and available data bases: Matthei (1995) for grasses and forbs, Teillier, Marticorena, Macaya, Bonnemaison, and Delaunoy (2014) for shrubs and trees, and Zuloaga, Morrone, and Belgrano (2008).

In addition, we evaluated the spatial distribution (e.g., attraction or repulsion) of plant individuals establishing after high and moderate fire severity. We focused on these burned areas as we were primarily interested in the spatial pattern of vegetation within the more fire-affected areas, assuming that the spatial dynamics of plant recovery would be more rapid (and easier to detect at smaller scales) in areas of high and moderate fire severity. In these burned areas, two additional 200-m^2 rectangular plots were established, and the Cartesian coordinates of each plant ≥5 cm tall was obtained by traditional measurement procedures, so that the origin (i.e., coordinate $x = 0$, $y = 0$) was set at the southwestern corner of each plot, and the x–y coordinates for each individual were determined using metric tapes measuring from the origin of the plot.

2.4 | Data analyses

We analyzed plant recovery along the fire severity gradient by computing the accumulated species richness and by comparing it among fire severity levels (including the unburned forest). We performed a randomization test (using 999 randomizations and $\alpha = 0.05$), computing the quantiles at $p = 0.975$ and $p = 0.025$ that correspond 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 between fire severity levels is much larger than expected under the null hypothesis of "no difference between sites". This test was computed using the "*rich*" package (Rossi, 2011) implemented in the statistical software R (R Core Team, 2019). We also computed the Shannon–Wiener diversity index for each fire severity level and performed a non-metric multidimensional scaling (NMDS) ordination analysis for assessing the compositional variation of vegetation across the fire severity levels. We also carried out a similarity percentage analysis (SIMPER) to establish the intra-group floristic similarity and the inter-group floristic dissimilarity. The analysis also assessed the average contribution of each species to the similarity or dissimilarity among severity levels (Clarke, 1993). The Shannon–Wiener index, the NMDS and the SIMPER analyses were performed using the R package "*vegan*" (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). For assessing the effect of fire severity on plant abundance and plant height, we used a one-way ANOVA and performed a posteriori Tukey's tests for pairwise comparisons among the different fire severity levels. The response variables were log-transformed in order to fulfill the assumptions of normality and homoscedasticity of residuals.

The spatial distribution of plant recovery was studied by using point pattern analysis. Given that we were interested in the overall spatial pattern of plant recovery within high- and moderate-severity burned areas, and some species had low abundances, we pooled together all resprouting species. We used the univariate pair correlation function, $g(r)$ (Stoyan & Stoyan, 1996) for characterizing the spatial distribution as a function of distance, rather than as a function of neighborhood point density (Wiegand & Moloney, 2014). We used complete spatial randomness (CSR) as the null model for detecting aggregation or inhibition among plants. For a complete random distribution of plants, $g(r) = 1$; meanwhile, values >1 indicate aggregation, and values <1 indicate segregation among plants. Significance tests were calculated

TABLE 1 Cumulative species richness across sample plots, Shannon–Wiener diversity index (*H*'), number of native and exotic species, life form composition (in %) and unique and common species by fire severity level

	Fire severity level			
	Unburned	Low	Moderate	High
Total species richness	31[a]	34[a]	16[b]	14[b]
Plant origin				
Native species	30[a]	26[a]	15[b]	13[b]
Exotic species	1[a]	8[b]	1[a]	1[a]
Diversity index *H*'	1.61	1.80	0.75	0.74
Life forms				
Trees (%)	12	17	5	3
Shrubs (%)	71	55	73	78
Tall shrubs (%)	42	48	11	12
Small shrubs (%)	58	52	89	88
Herbaceous (%)	17	28	22	19
Broad-leaved (%)	96	97	98	93
Graminoids (%)	4	3	2	7
No. of unique species	8	10	1	4
No. of common species	6			

Note: Life form composition is represented in percentage relative to the total abundance recorded in each fire severity level. Shrubs are split into small and tall shrubs and herbs are split into broad-leaved and graminoids. Note that different letters indicate statistically significant differences at α = 0.05 for species richness computed using a randomization test.

by computing 95% confidence envelopes for the null model using 199 Monte-Carlo simulations. We used the "*spatstat*" R package (Baddeley & Turner, 2005) for carrying out the spatial analyses.

3 | RESULTS

One year after fire, we found that fire severity greatly affected the composition of the understorey vegetation in old-growth *Araucaria–Nothofagus* forests. Species richness was significantly higher in the unburned forest and low-severity areas, compared to areas of moderate and high fire severity (all $p < 0.01$; Table 1; additional information showing the species accumulation curves for each fire severity level can be found in Appendix S1). Likewise, richness of native species was significantly higher in the unburned forest and low-severity areas, compared to high and moderate fire severity areas ($p < 0.01$; Table 1). Exotic species richness, however, was significantly higher within low-severity areas, compared to the unburned forest, moderate and high fire severity areas ($p < 0.01$; Table 1). Overall, we found 50 vascular plant species establishing across the entire severity gradient in the following year after fire (see the floristic list in Appendix S1). From these, two species corresponded to trees (4%), 14 were shrubs (28%), and 34 were herbs (68%). From the herbaceous species, only six were graminoids (18%). Graminoids had low abundances overall, but they were present in all fire severity levels (see Appendix S2).

Unique species (i.e., those that appeared within a given fire severity level only) are represented by eight species in the unburned forests (including *Codonorchis lessonii* and *Sisyrinchium arenarium*), 10 in low severity (including *Calceolaria valdiviana* and *Phacelia secunda*), one in moderate fire severity (the exotic *Agrostis capillaris*) and four in high severity (including *Adesmia emarginata* and *Rhodophiala andicola*; see Table 1 and Appendix S1). The species that were common to the entire fire severity gradient were *Alstroemeria aurea*, *Araucaria araucana*, *Berberis microphylla*, *Chusquea culeou*, *Gaultheria poeppigii* and *Vicia nigricans*, which represent 12% of the all recorded richness. Regarding plant origin, most of the vegetation was native, with only eight exotic species representing 17% of all the recorded richness (Table 1).

Plant abundance within the unburned forest (expressed as mean number of plants per hectare) was significantly higher than in low-, moderate- and high-severity areas ($p < 0.001$), with a mean difference

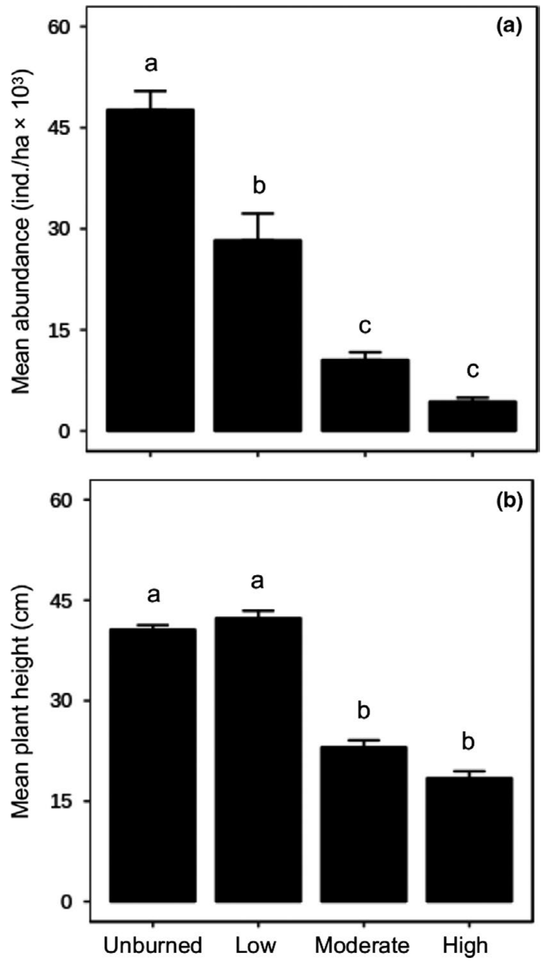

FIGURE 3 Initial plant response in terms of (a) mean plant abundance (+*SE*) expressed as individuals per hectare, and (b) mean plant height (+*SE*) according to fire severity levels within *Araucaria–Nothofagus* forests. Note that different letters above bars indicate statistically significant differences for the means at α = 0.05 using Tukey's tests

of 19,360, 37,100 and 43,300 plants, respectively (Figure 3a). Plant abundance was significantly higher in low-severity than in moderate- and high-severity areas ($p < 0.01$), with a mean difference of 17,740 and 23,940, respectively. However, plant abundance did not differ between high and moderate fire severity ($p > 0.05$; mean difference = 6,200 individuals). The most abundant species found across all severity levels were *Maytenus disticha*, *Gaultheria poeppigii*, *Chusquea culeou*, *Alstroemeria aurea*, and *Nothofagus pumilio* (the latter only present in low-severity areas and the unburned forest). These five species by themselves comprised >65% of the total recorded abundance. While abundance of *Araucaria araucana* was four times greater in the unburned forests than in the severely fire-affected areas, *Nothofagus pumilio*, the other dominant tree species in the forest, was completely absent from areas of high fire severity (Table 2). When looking at the abundance of life forms (i.e., trees, shrubs and herbs), we found that shrubs were the most abundant across the entire fire severity gradient (i.e., in high, moderate and low fire severity; 69% on average). Herbaceous species accounted for 23% of the total abundance on average, and trees only reached 8% (Table 1).

Mean plant height across all species was significantly higher within the unburned forest and low-severity, compared to moderate- and high-severity areas ($p < 0.001$; Figure 3b). One year after fire, and within areas of high fire severity, the tallest species were *Solanum valdiviense* (mean height = 66.5 cm) and resprouting culms of *Chusquea culeou* (mean height = 27.5 cm). In moderate severity, the tallest resprouts and/or surviving seedlings were from *Araucaria araucana* (mean height = 59.8 cm) and *Nothofagus pumilio* (mean height = 51.2 cm). From the species that were common across the entire fire severity gradient, *Chusquea culeou* was far more abundant within areas of moderate and high fire severity, whereas *Gaultheria poeppigii*, *Araucaria araucana* and *Vicia nigricans* were more abundant within the unburned forest (Figure 4a). Overall, these common species presented greater mean heights within the unburned forest and low fire severity areas than areas of high and moderate fire severity (Figure 4b).

The NMDS ordination analysis showed distinct plant assemblages that were associated with different fire severity levels, ranging from the unburned forest and low severity to areas of moderate and high fire severity (Figure 5). The average similarity within each fire severity level ranged from 61% in the unburned forest down to 37% in highly fire-affected areas. The species that most contributed with similarities within each fire severity level were *Maytenus disticha* in the unburned forest, *Alstroemeria aurea* in low severity and *Chusquea culeou* in moderate and high fire severity (see the rest of the species contributions in Appendix S3). The highest dissimilarity was found between the unburned forest and high fire severity areas (88% dissimilarity), where *Maytenus disticha*, *Gaultheria poeppigii*, *Adenocaulon chilense*, *Nothofagus pumilio* and *Ribes magellanicum* accounted for >50% of the dissimilarity between the unburned forest and high fire severity areas (see the rest of species contributions to dissimilarity in Appendix S4).

3.1 | Spatial distribution of plant recovery

We recorded a total of 173 and 74 individuals in the moderate and high fire severity 200-m^2 plots, respectively (Figure 6a,b). Within areas of moderate fire severity, the spatial structure of plant recovery evidenced an aggregated pattern at distances <1.2 m, with a random distribution at broader distances (Figure 6c). This means that the groups of plants had a maximum size of 1.2 meters in diameter, containing 17 individuals on average. Within areas of high fire severity, the spatial distribution of plants showed a more intensely aggregated pattern at very short distances, <0.5 m, but a random spatial distribution at broader distances (Figure 6d). This pattern evidenced small-sized groups with a maximum of 0.5 meters in diameter, and having 20 individuals on average.

4 | DISCUSSION

4.1 | Vegetation response to fire severity

One year after fire, the unburned forest and areas of low fire severity showed significantly higher richness, abundance and plant height than moderate and high fire severity areas. Consistent with other studies (Morgan et al., 2015; Blair, McBurney, Blanchard, Banks, & Lindenmayer, 2016), our results show a heterogeneous post-fire plant composition, in which species richness decreases from low to high fire severity. Severe fires can increasingly exclude fire-sensitive plant species (Hoffmann & Moreira, 2002), leading to a decreased richness, and ultimately to a less diverse plant community. We reported that 17 and 15 species were absent — or could not be detected inside or nearby our sampling plots — from areas of high and moderate fire severity, respectively, compared to the unburned forest. This represents a potential decrease of half the species richness found in unburned forests in the first year after fire. Among the species that were not found in areas of high fire severity, are the tree *Nothofagus pumilio*, the shrub *Ribes trilobum*, and the herbaceous species *Adenocaulon chilense* and *Codonorchis lessonii*. Considering that our results represent the plant community only one year after the fire, long-term trajectories for these species are difficult to ascertain.

Despite the fact that fire is an intrinsic ecological process in *Araucaria araucana* forests (González et al., 2005), our research showed a significant impact of severe wildfires — at least in the short term — on the understorey vegetation associated with *Araucaria–Nothofagus* forests in the Andes of south-central Chile. What is less certain, though, is whether the forest itself will recover toward its pre-fire conditions. We found that one year after fire, the abundance of *A. araucana* and *Nothofagus pumilio*, the two dominant tree species in these forests, was significantly reduced because high-severity fire killed all (or almost all) the trees. *N. pumilio* is a thin-barked and obligate seeder tree that cannot resprout after fire, and therefore, the risk of being killed by a severe fire is much higher than for *A. araucana* that has thicker bark and resprouts (González, Veblen, et al., 2010a; Mundo et al., 2013; Fuentes-Ramirez,

TABLE 2 Plant abundance at plot level and plant height for the dominant tree species *Araucaria araucana* and *Nothofagus pumilio* across fire severity levels in burned forests of National Reserve China Muerta one year after fire

	Araucaria araucana		*Nothofagus pumilio*	
Fire severity level	Mean abund. Ind./ha (±*SE*)	Mean height (±*SE*) (cm)	Mean abund. Ind./ ha (±*SE*)	Mean height (±*SE*) (cm)
Unburned	2,120 (881)[a]	62.3 (6.1)[a]	3,680 (2,224)[a]	54 (2.8)[a]
Low	160 (40)[b]	105.7 (56.3)[a]	4,680 (2,206)[a]	79.6 (4.1)[b]
Moderate	200 (67)[b]	54.8 (28.2)[a]	1,800 (NA)[a]	54.5 (9.1)[a]
High	120 (95)[b]	10 (5.2)[b]	0	–

Note: Different letters indicate statistically significant differences at α = 0.05 for mean abundance and mean height at α = 0.05 using Tukey's test.

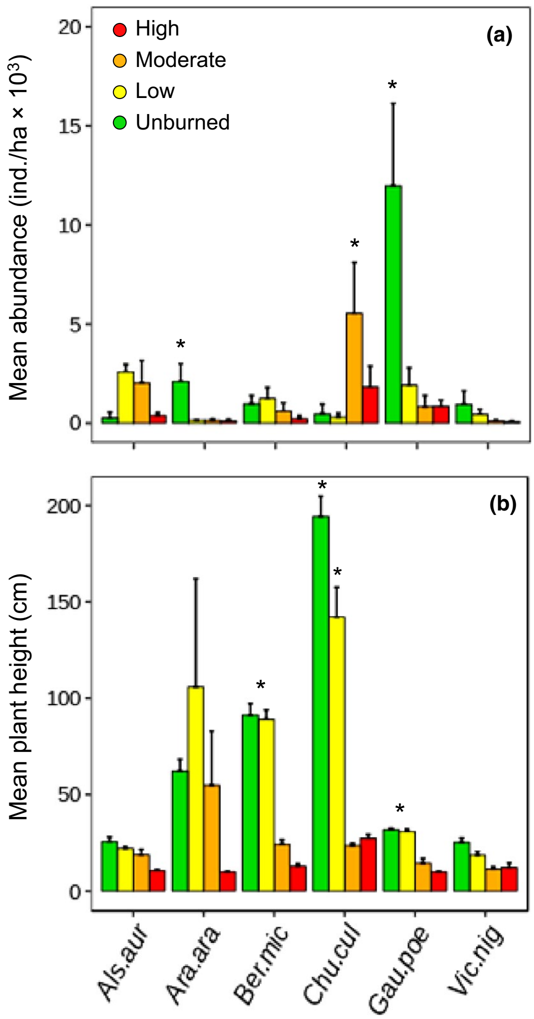

FIGURE 4 (a) Mean abundance (+*SE*), and (b) mean height (+*SE*) for the six common species according to fire severity levels. Als.aur = *Alstroemeria aurea*; Ara.ara = *Araucaria araucana*; Ber.mic = *Berberis microphylla*; Chu.cul = *Chusquea culeou*; Gau.poe = *Gaultheria poeppigii*; Vic.nig = *Vicia nigricans*. Note that asterisks indicate statistically significant differences at α = 0.05 for mean abundance in (a) and mean height in (b) using Tukey's tests [Colour figure can be viewed at wileyonlinelibrary.com]

Arroyo-Vargas, Fierro, & Perez, 2019). Our results coincide with other studies which show that species that primarily reproduce by seeds experience limited post-fire establishment in moderate- to high-severity fires due to the lack of seed-sourcing trees in nearby areas (Maia et al., 2012). For *N. pumilio*, it has been shown that surviving trees in areas severely affected by fire are key for its successful post-fire recovery (González, Veblen, et al., 2010a). Unfortunately, most of the area affected with high fire severity in our study site did not present any surviving trees of *N.s pumilio*, implying a lack of regeneration.

In a recent study, Assal et al. (2018) found that regeneration densities of *Araucaria araucana* and *Nothofagus pumilio* were lower in areas of high severity 10 years after a forest fire in Tolhuaca National Park (ca. 50 km northwest of our study site), with a negative effect of high fire severity nearly twice as great for *N. pumilio*. We predict that *N. pumilio* will find it difficult to recover after a severe fire, since its establishment, survival and growth depend on seed-sourcing trees present in the area, and also on site conditions after the fire, which can change from a light- to a water-limited system (Heinemann, Kitzberger, & Veblen, 2000; Paritsis et al., 2015). Moreover, *N. pumilio* requires a partial canopy protection for establishing purposes, so the shade of surviving trees after fire may protect seedlings from extreme changes in temperature and humidity (Veblen, Donoso, Schlegel, & Escobar, 1981). Regarding *A. araucana*, the study of Assal et al. (2018) highlights that post-fire establishment of this conifer is limited under increasing fire severity, suggesting that frequent, high-severity fires could lead to a decrease in post-fire forest resilience. For *A. araucana*, we noticed a great resprouting capacity in the first year after fire, which is consistent with other studies (González, Szejner, et al., 2010b). Within our study area, *Araucaria*'s recovery primarily comes from root and stump buds found in burned juvenile individuals, and to a lesser extent, survival and re-greening of upper branches in older trees (Fuentes-Ramirez et al., 2019).

Our results also revealed that *Chusquea culeou*, which is a bamboo species that commonly resprout from rhizomes, was fairly abundant in moderate and high fire severity areas (see Figure 4a), implying that species without damage in their root system (due to below-ground fires), and with high capacity for vegetative regrowth (i.e., *Chusquea culeou*), can rapidly reestablish after fire (Bond & Midgley, 2003; González, Szejner, et al., 2010b; González, Veblen, et al., 2010a). While vegetative resprouting of *Araucaria araucana* was abundant in moderate to high fire severity areas, it is still unknown whether the initial survival of *A. araucana* will persist over time. A fast recovery of *Chusquea culeou* (that takes advantage from the canopy removal caused by fire) can increasingly contribute with higher abundance of

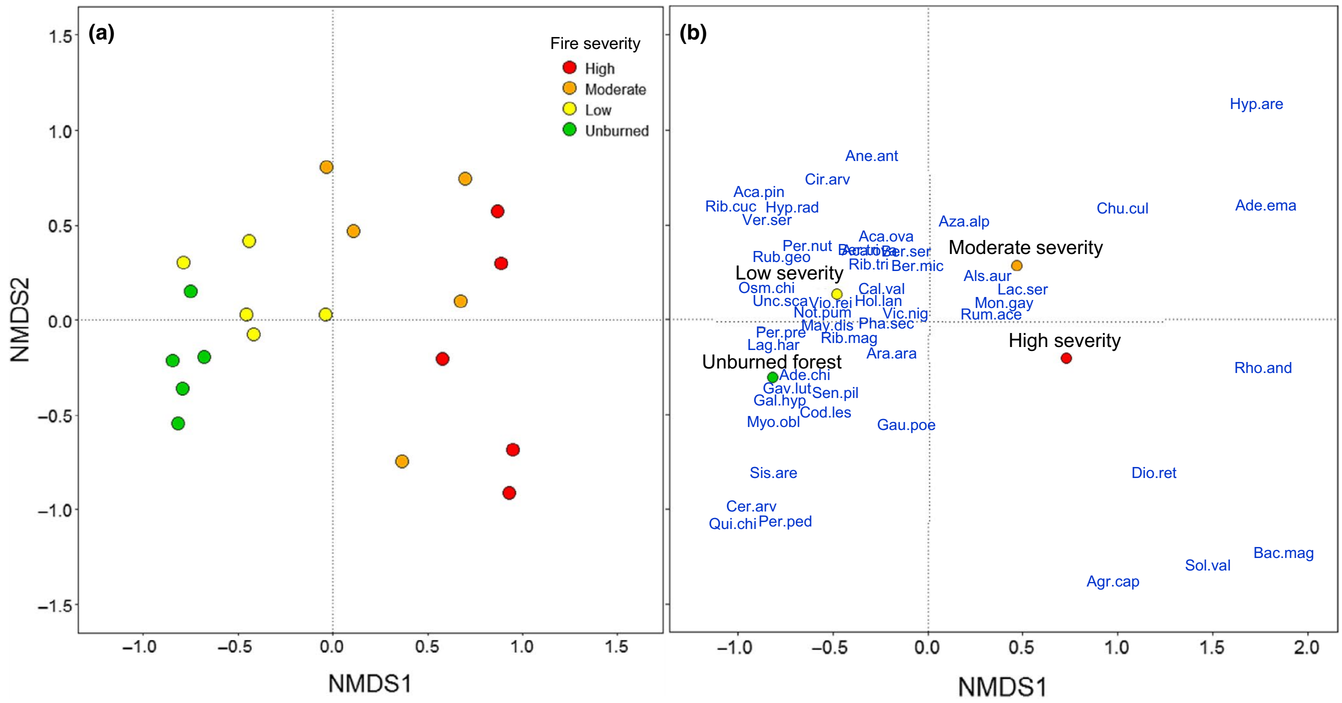

FIGURE 5 Non-metric multidimensional scaling (NMDS) ordination plot of Bray–Curtis similarities showing (a) sample plots and (b) the association of plant species with the fire severity levels studied in *Araucaria–Nothofagus* forest understorey one year after fire (2D stress value = 0.11). Note that the species codes shown in (b) are explained in Appendix S1, and the color-coded circles correspond to the centroid of each severity level based on the distances among the plots shown in (a) [Colour figure can be viewed at wileyonlinelibrary.com]

fine fuels, potentially promoting larger and more frequent fires, and consequently continue to limiting the recovery of *Nothofagus pumilio* and *A. araucana* in the long term (Veblen & Lorenz, 1988; Paritsis et al., 2015).

Although still with low abundances, we found that exotic species were more frequent in low-severity areas, which might be also related to other factors such as cattle grazing that is exerted more intensively over areas with more surviving vegetation (Zamorano-Elgueta et al., 2012). As vegetation was very scarce within the areas more severely burned, cattle would probably have more presence in areas with surviving vegetation, and consequently would promote the dispersal of exotic species. In this sense, we hypothesize that it is a matter of time before some exotic species arrive more abundantly into the most severely burned areas if cattle are not excluded after fire. Indeed, the most abundant exotic species found in our study was *Rumex acetosella*, a highly invasive forb that rapidly establishes following fire and cattle grazing (Fuentes et al., 2014).

4.2 | Spatial patterns

We found larger (but less dense) groups of plants within moderate fire severity areas compared to areas of high fire severity, which could be explained by the high capacity for resprouting of pioneers species, such as *Chusquea culeou*, *Gaultheria poeppigii* and *Alstroemeria aurea* from below-ground rhizomes and roots. Overall, these species were abundant, but more spread-out within moderate fire severity areas, leading to larger groups of plants, compared to areas of high fire severity, where plants were less abundant, but tightly clumped, exhibiting denser, small-sized groups. The spatial pattern of plants within high fire severity areas is likely explained by the close proximity in which species like *Chusquea culeou* and *Gaultheria poeppigii* resprout from below-ground, but also by other resprouter species like *Adesmia emarginata* and *Baccharis magellanica* that only appeared in high-severity areas, forming small-sized groups (A. Fuentes-Ramirez, pers. communication). In this sense, our study reveals that, even at a short-term scale (one year since fire), there are significant changes in the spatial distribution of vegetation between areas of high and moderate fire severity.

5 | CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT

One year after fire, plant diversity, abundance and plant height decreased within areas of high and moderate fire severity compared to adjacent, low fire severity areas and unburned forests. Most of the vegetation recovering across the fire severity gradient were native species (85%). Exotic species (15%) were more abundant in low fire severity areas, suggesting that their establishment is mediated by fire, but also likely by cattle grazing. The findings from our study provide valuable information that can help to design and implement

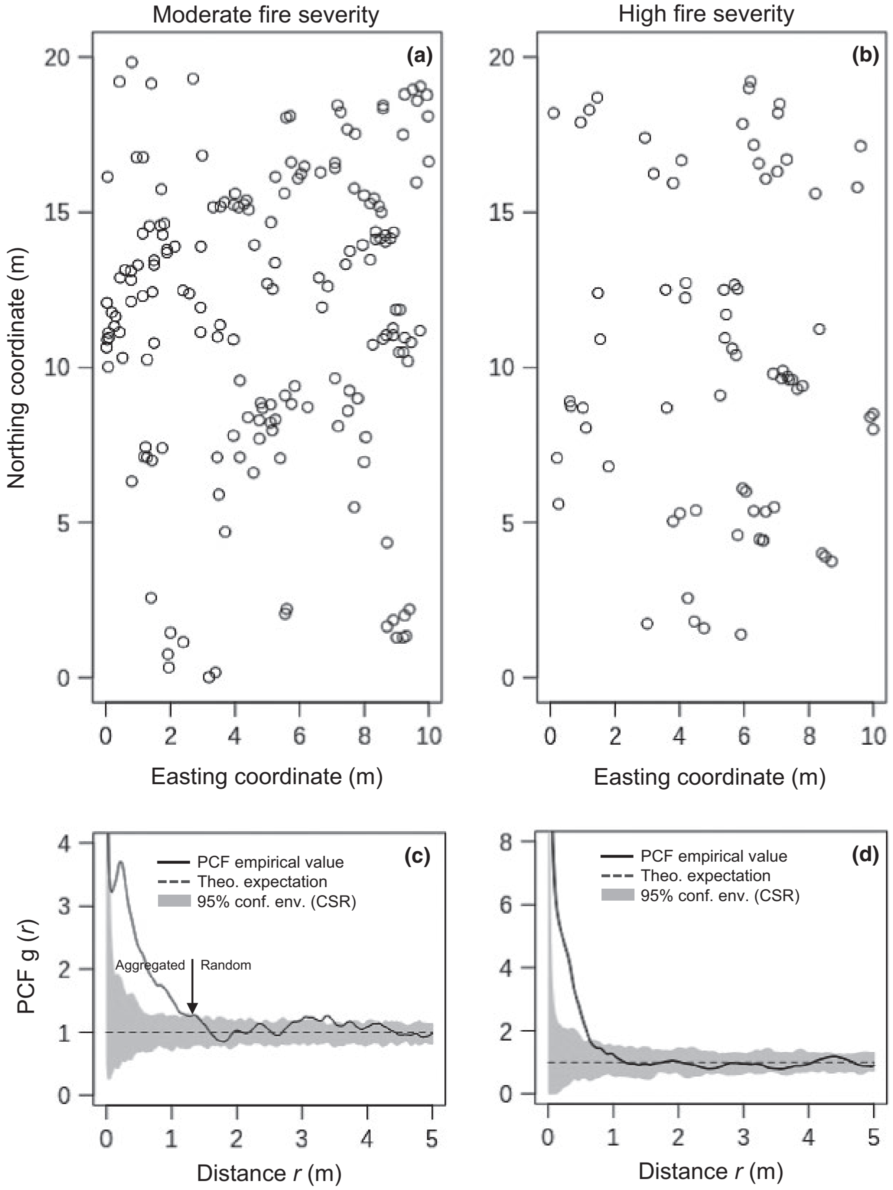

FIGURE 6 Spatial pattern of plant individuals resprouting within (a) moderate-severity (n = 173) and (b) high-severity (n = 74) areas. Pair correlation function (PCF) within areas of (c) moderate and (d) high fire severity. Note that when the solid black line in (c, d) intersects the gray-shaded area the spatial distribution changes from aggregated to random

management plans. With the goal of supporting long-term recovery of *Araucaria–Nothofagus* forests, and increasing plant diversity over time, we recommend: (a) limit the access of cattle into burned areas to prevent the spread of exotic species. Studies have shown a great impact of cattle activity in *Araucaria araucana* forests, mainly because of the negative effect of browsing and trampling on the native vegetation (Zamorano-Elgueta et al., 2012), but also because cattle are effective vectors of exotic invasive species (Amiri, Ariapour, & Fadai, 2008); and (b) planting with the native tree *Nothofagus pumilio* in areas of high fire severity due to its unsuccessful recruitment. Despite that our study represents a short-term assessment of vegetation after fire, we visualize a potential change in forest composition and structure if the dominant tree species are not capable of recovering after fire. This will ultimately depend on the successful recovery of *Araucaria araucana*, the arrival of propagules that can promote the establishment of *N. pumilio* and actions to prevent further disturbances caused by cattle.

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AUTHOR CONTRIBUTIONS

AFR designed the study, collected data, performed statistical analyses and drafted the manuscript. CSE, JUE and PAV helped with data analysis. PS and PAV helped with fieldwork. MEG contributed to interpret results. All authors collaborated to write the final manuscript draft.

DATA AVAILABILITY STATEMENT

Available from the corresponding author upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Species accumulation curves for each fire severity level.

Appendix S2. List of all vascular plant species found in burned *Araucaria–Nothofagus* forests.

Appendix S3. Summary table of similarity percentages within each fire severity level.

Appendix S4. Summary table of dissimilarity percentages between each severity level.

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