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RESEARCH ARTICLE

Early vegetation recovery following a mid to high-severity fire in the Andean-Patagonian forests

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Abstract
A change in fire regimes is occurring worldwide, affecting post-fire succession. Under this context, there is an increasing need to prioritize restoration areas and focus on their particular goals. To assess the emergent understorey represents the first approximation of post-fire re-vegetation, necessary to establish appropriate restoration guidelines. In this study, we aimed to assess the initial post-fire response in a mid to high-severity fire in the Andean-Patagonian forests. We (1) compared plant community structure among fire severities, (2) evaluated the response of plant community structure to the interaction between fire severity and forest type, (3) compared plant composition among fire severity-forest type categories and (4) evaluated woody species regeneration after fire. We found that the vegetation cover of the lower stratum began to recover early after the fire and to a greater extent in mid than in high severity, whereas the upper stratum was incipient in the mid and nil in high severity. Native species predominated in burned and unburned plots, although they were less in the burned plots. Among the growth form, shrubs and trees were similarly affected by fire, independently of the forest type. Plant community composition varied among most fire severity-forest type categories. The frequency of woody species regenerated by re-sprouts and by seeds was lower in burned than unburned plots. These results suggest that although there is an early recovery of vegetation, the high cover of exposed soil and the loss of the upper vegetation stratum may favour erosion and difficult tree establishment. Besides, tree species that only regenerate from seeds will probably not recover naturally. In addition, the presence of exotic species with high invasive risk may need control. Thus, since fire severity and forest type may drive different post-fire natural recovery scenarios, different restoration actions should be taken to promote resilient systems for the future.

KEYWORDS
climate change, post-fire, restoration, succession, understorey

INTRODUCTION

Fire regimes are changing worldwide due to multiple interacting stressors, most notably climate change, large-scale changes in land cover and vegetation structure and direct human influence on ignition sources (Rogers et al., 2020). Recently, mega-fires with unprecedented high severity burned areas, have occurred across forest regions globally (Collins et al., 2021; Higuera & Abatzoglou, 2021; Silveira et al., 2020). Particularly in the Patagonian-Andean region, an increase in fire activity is expected, driven by an increasing trend in temperature and drought (Kitzberger et al., 2022; Veblen et al., 2011). Also, an increase in extend and severity is expected, driven by multiple causes such as fuel wood accumulation as a consequence of fire suppression and fuel type changes promoted by the introduction and spread of fire-prone exotic conifers and other productive activities (Veblen et al., 2011). Under this situation, there is an increasing interest to promote and develop ecological restoration following fires, with efforts in setting the most appropriate ecological restoration strategy for each situation (de Paz et al., 2019; Souza-Alonso et al., 2022). The first step to select the most appropriate ecological restoration strategy is to know the initial stage of the ecosystem after the disturbance and visualize the possible future scenarios considering ecological, social and economical aspects (Souza-Alonso et al., 2022).

The re-vegetation after a fire depends on resprouting capability, seed resistance and propagules dispersion from surrounding unburned areas (Falk et al., 2022). So, fire profoundly impacts successional trajectories in the different ecosystems. Moreover, different responses may occur in the same ecosystem depending on variables such as fire severity and post-fire use (Blackhall, Raffaele, & Veblen, 2015; Cohn et al., 2015; Doherty et al., 2017). Thus, successional stages may revert to the pre-disturbance condition or alternative states may persist, especially under the influence of climate change and non-native species (Falk et al., 2022; Nolan et al., 2021).

The temperate forests of Patagonia, also called Andean-Patagonian forests, are located in a narrow strip between latitudes 37° and 54° south (Cabrera, 1971), covering around 3.2 million ha (Mohr Bell et al., 2019). These forests are composed of different forest types with a diverse understory that varies with elevation and location along a west–east gradient of precipitation (Donoso, 1993; Kitzberger et al., 2016). Fire has been recurrent for millennia in this region, modulating plant community structure and dynamics (Veblen et al., 2003). Whereas many shrubs, perennial herbs and some of the main tree species have the capability of resprouting, most of the main tree species do not, relaying on remanent seeds in the soil or seed arrival from unburned individuals (Dimitri, 1983; Urretavizcaya & Defossé, 2004). In the early stages after a fire, resprouters usually dominate, and in the mid stages, tree colonization may occur especially close to unburned patches or at low severity, returning to a forest system in the long term (Cavallero et al., 2015). However, as the main trees present a transient seed bank and limited dispersion from unburned areas, forests may be unable to recover if fire severity is moderate to high since the more severe the fire, the greater the loss of litter and duff layers and thus the transient seeds accumulated in the surface soil (Cuevas & Arroyo, 1999; Landesmann et al., 2021; Landesmann & Morales, 2018; Urretavizcaya et al., 2022; Urretavizcaya & Defossé, 2004). In those cases, shrublands establish as alternative states (Rusch et al., 2016, 2017). However, resprouter species can also be affected by fire severity, with less survival at higher severity (Wright & Clarke, 2007).

As more land is affected by wildfires, the need to prioritize restoration areas based on the particular goals of each of them (e.g. ecological, productive, recreative, urbanistic) grows. Lately, more frequent ignition points are occurring in wildland-urban interface areas (Godoy et al., 2019, 2022). These fires spread to the surrounding forests, which have important functions for society, such as the regulation of water directly used by the population, used as recreation areas and providing income through livestock activity, among others. In addition, in the surrounding areas, some native forests were converted into exotic conifer plantations that have not been properly managed. Therefore, restoration strategies may include a wide variety of actions, from sowing and plantation of native species to the extraction of invasive species. Through the analysis of the emergent understorey, it is possible to obtain a first approximation of the post-fire re-vegetation, which is necessary to establish appropriate action guidelines. In this study we aimed to assess the emergent post-fire understorey and associated structural variables, considering fire severity and forest type. We tested the hypotheses that (1) fire severity determines the initial recovery of post-fire vegetation, due to its different impact on the survival of individuals that could regenerate vegetatively and/or sexually, and on the seed present in the soil, (2) the effect of fire severity on the initial recovery of post-fire vegetation depends on forest type, due to pre-fire composition and variable resprouting capability, seed resistance and dispersion among species. Specifically, our objectives were to (1) compare plant community structure among fire severity conditions for all native forests, (2) evaluate the response of plant community structure to fire severity and forest type interaction for a subset of native forests, (3) compare plant composition among combined fire severity-forest type categories and (4) evaluate woody species regeneration after fire. We expected to find an early recovery of vegetation cover and richness, both of them gradually related to fire severity. Further, we expected certain variations in the magnitude of change of these variables among forest types. In addition, we expected to find differences in plant community composition among the combined fire severity-forest type categories, that would lead to different post-fire natural recovery scenarios. Finally, we expected less regeneration of woody species with greater fire severity. This would imply that different restoration strategies are required for each situation.

METHODS

Study area

The study area is located in northwestern Chubut province, Patagonia, Argentina (Figure 1). It presents a typical Temperate-Mediterranean climate with cold and wet winters, and dry and warm summers (Köppen & Geiger, 1936). Mean annual precipitation is between 750 and 1000 mm (Fick & Hijmans, 2017), 75% of which falls during the autumn and winter months. Soils of the region derive from volcanic ashes, with Andisols in the

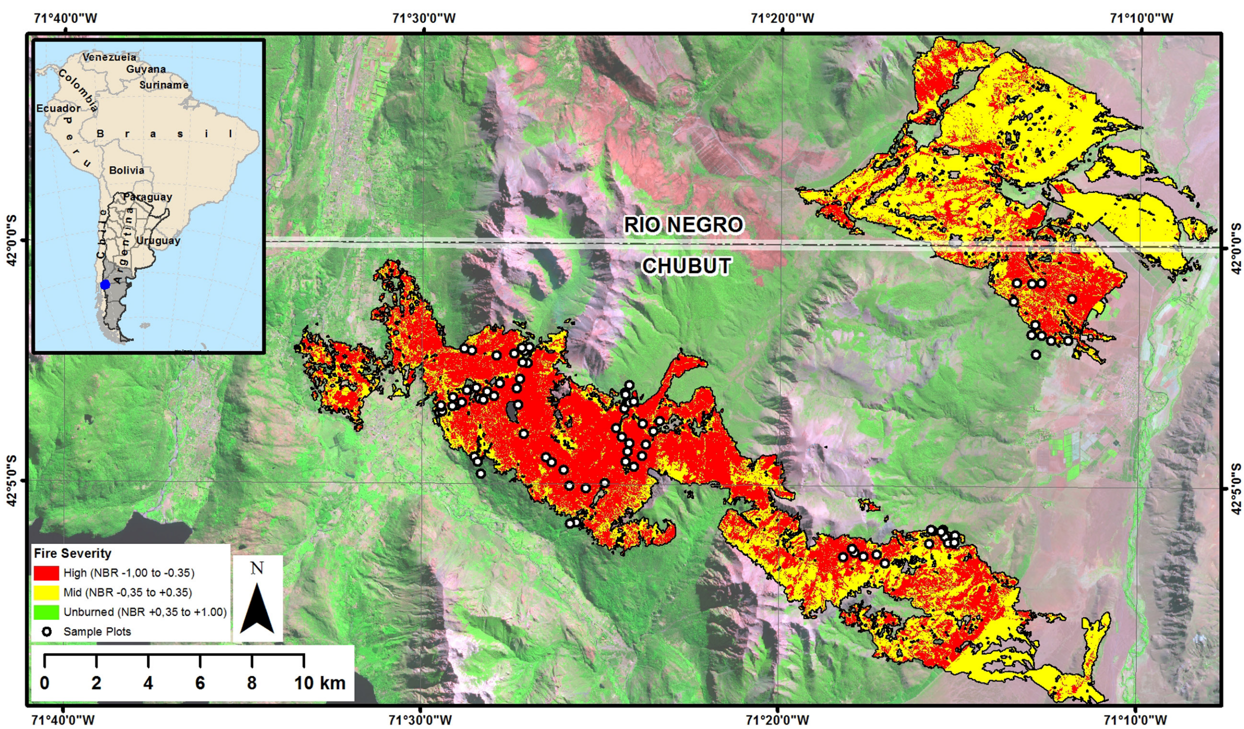

FIGURE 1 Study area “point blue” located in Patagonia “grey area”. In the main map, the burned area is delimited by black lines, with the fire severity classification based on NBR thresholds.

areas of higher humidity and transitional to Mollisols in the drier areas of the study area (Etchevere, 1972; La Manna et al., 2020). At the beginning of March 2021, two wildfires, called "Las Golondrinas" and "El Boquete", burned approximately 18 500 ha (9340 ha of native forests, 1680 ha of exotic conifer plantations, and the remnant surface mainly of native shrublands and steppes) in just a few days, part of which developed giving rise to the most complex interface fire in the history of Patagonia (Mohr Bell, 2021). The affected area is mountainous, with gentle and steep slopes. According to slope classes, approximately 20% of the affected area corresponded to class I (0%–3% slope), 25% to class II (3%–10%), 39% to class III (10%–25%), 15.5% to class IV (25%–45%) and 0.5% to class V (>45%) (Mohr Bell, 2021).

Fire severity analysis

We carried out a preliminary classification of the fire severity, through the analysis of satellite images for the affected area. We based the classification on the method adjusted for the post-fire analysis carried out for the "Cholila" fire, which occurred in 2015, which showed that the post-fire Normalized Burn Ratio (NBR) had the best correlation with field observations (SSB et al., 2015). The NBR is a normalized ratio between Near Infrared (NIR) band (~785 to 899 nm, Landsat-8 band #5, Sentinel-2 band #8) and Short Wave Infrared 2 (SWIR2) band (~2100 to 2280 nm, Landsat-8 band #7, Sentinel-2 band #12). We used a Sentinel-2 MSI Level 2A Surface Reflectance (Copernicus Sentinel data 2021) satellite image taken on March 26, 2021. The NBR was calculated using bands 8 and 12 which correspond to NIR and SWIR 2, respectively.

$$\mathrm{NBR} = (\mathrm{b8} - \mathrm{b12}) / (\mathrm{b8} + \mathrm{b12}).$$

We obtained a map of fire severity classified into three classes, using NBR thresholds: High severity (NBR −1.00 to −0.35), mid severity (NBR −0.35 to +0.35) and unburned (NBR +0.35 to +1.00) (Figure 1).

Field sampling

Within the study area, we established 84 circular plots of 400 m^2, distributed in different fire severities and forest types. The plots were at least 100 m apart from each other. We based the selection of the plots on the map of fire severity and the forest-type cover of the area (Mohr Bell et al., 2019) (Figure 1, Appendix S1). In the field, we classified each plot based on the modified US Forest Service classification (Lutes et al., 2006; SSB et al., 2015), which rates the severity of damage on the ground and four vegetation strata divided by height, obtaining three severity levels: unburned, mid and high. Unburned plots were not affected by the fire. Mid-severity plots were affected by fire and included those with all trees dead but scorched foliage remaining at the canopy or on the floor, or with some trees remaining alive. High-severity plots were affected by the fire and included those with all trees dead and litter and duff completely consumed (Figure 2). Field classification was coincident with satellite classification (Figure 1). Since fire severity was mainly high throughout the study area, most surveyed plots presented this condition, whereas the number of mid-severity plots was low. We established most unburned plots at the edge of the fire perimeter due to the lack of unburned patches. The forest types sampled were those dominated by *Nothofagus pumilio* (Np), *Nothofagus*

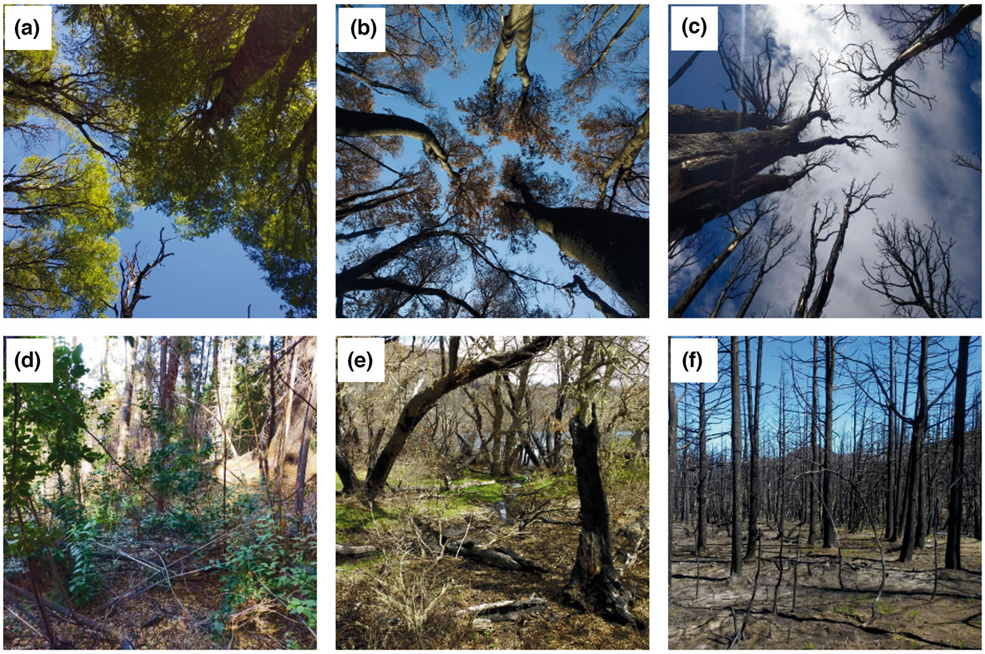

FIGURE 2 Characterization of the canopy and understorey of the unburned (a, d), mid (b, e) and high (c, f) severity.

dombeyi (Nd), *Nothofagus antarctica* (Na), *Austrocedrus chilensis* (Ac), mixed of *A. chilensis* and *N. dombeyi* (Ac–Nd) and exotic conifer plantations of *Pinus ponderosa*, *Pseudotsuga menziessi* or *Pinus contorta* var. *murrayana* (P) (Figure 1, Table 1, Appendix S1).

We recorded all plant species at each 400 m^2 circular plot and identified them according to Correa (1969–1999) and Zuloaga et al. (2022). In a 50 m^2 concentric circular plot, we estimated the vegetation cover of the lower stratum (0–50 cm height), that of the upper stratum (50–300 cm height), the canopy cover of dead or alive trees (>300 cm height) and in four 1 m^2 plots, we estimated exposed soil cover. For woody species, we identified the mechanism of regeneration (resprouting or seedling) in the burned plots. In the case of tree species, we also recorded dead individuals as they remained as snags. This was not possible for shrub species since those completely consumed by fire could not be identified. We concentrated the sampling of burned plots during spring (October–December 2021) to reduce the variability of vegetation between post-fire plots that could be caused by the course of the growing season, which usually lasts from October to March, and the sampling of unburned plots during summer (January—February 2022), since we assumed that their variation during the growing season would be minimal and not influence the comparison with burned plots.

TABLE 1 Plots sampled at each fire severity and forest type.

Forest type/fire severity	Unburned	Mid	High
Nothofagus pumilio	7	5	12
Nothofagus dombeyii	3	3	7
Nothofagus antarctica	1		11
Austrocedrus chilensis	5	3	11
A. chilensis and *N. dombeyii*	1		8
Exotic pine plantations			7

Analyses

Plant community structure among fire severity

We classified the identified species by nativity as native/endemic, and adventive/introduced, and by growth form as annual herbs, perennial herbs, shrubs and trees, according to Zuloaga et al. (2022). With this information, we calculated the total richness and richness of each nativity and growth form for each 400 m^2 plot.

To compare plant community structure among fire severity conditions we focused on native forests (i.e. we excluded exotic conifer plantation plots). We used generalized linear models with Poisson distribution (function glm, package stats), and we treated fire severity as a fixed effect with three levels (unburned, mid and high). Response variables were lower stratum vegetation, upper stratum vegetation, canopy and exposed soil covers, as well as total, native/endemic, adventive/introduced, annual herbs, perennial herbs, shrubs and tree richness. When differences in fire severity were significant ($p < 0.05$), we performed Tukey contrasts (function glht, package multcomp) (Torsten et al., 2008). These analyses were performed in the software R (R Core Team, 2021).

Plant community structure between fire severity and forest type

To compare plant community structure among fire severity and forest type, and their interaction, we focused on the forests that presented burned and unburned plots. We used a factorial design (3×3), with the factors fire severity (levels: unburned, mid and high) and forest type (levels: Np, Nd and Ac) as fixed effects. Response variables were the same and the analyses procedure was similar as described for plant community structure among fire severity.

Plant community composition

To compare plant community composition among the combined fire severity-forest type categories, we performed a permutational multivariate analysis of variance (PERMANOVA) (function adonis, package Vegan) (Oksanen et al., 2020). We excluded the unburned plots of Na and Ac–Nd since there was only one replicate for each of them. We used Bray's distance, based on species presence at the plot level. When differences were significant ($p < 0.05$), we carried out pairwise comparisons (function pairwise. adonis, package pairwiseAdonis) (Martinez Arbizu, 2017). To visualize the results, we displayed plant community data graphically in ordination space using a non-metric multidimensional scaling (NMDS) based on species presence with Bray's distance (function metaMDS, package Vegan). We added a dummy variable to include plots with zero presence in the analysis, and we excluded unidentified species.

To identify characteristic species of each fire severity and their combination, we used indicator species analysis, based on species presence (function multipatt, package indicspecies) (De Cáceres & Legendre, 2009). This analysis is based on species specificity and sensibility to a particular habitat (Dufrêne & Legendre, 1997). Besides, to assess characteristic species after the fire, and since the largest burnt area showed high severity, we carried out an indicator species analysis to identify characteristic species of each forest type and their combination at high severity.

These analyses were performed in the software R (R Core Team, 2021).

Woody species regeneration

To characterize woody species regeneration at each fire severity, we identified the regeneration strategy (resprouting and/or regeneration by seeds) of each species, and for each regeneration strategy detected, we estimated the species frequency (i.e. the number of times a species occurs in a given number of plots) in each fire severity, as follows: For shrubs, we calculated the percentage with respect to the total plots of the corresponding fire severity, whereas for trees, we calculated the percentage with respect to the total plots with the pre-fire presence of that species at the corresponding fire severity. We considered trees less than 5 cm in diameter at breast height as regeneration, thus it may include individuals not affected by fire in those plots not completely burned, whereas it characterizes the natural regeneration in unburned plots.

RESULTS

Plant community structure among fire severity

We detected significant differences among fire severity for lower stratum vegetation cover ($p < 0.001$, $D^2 = 0.27$), upper stratum vegetation cover ($p < 0.001$, $D^2 = 0.85$) and canopy cover ($p < 0.001$, $D^2 = 0.53$). The three variables showed the highest value in the unburned plots, followed by mid-severity and the lowest value in high severity. We did not record any upper stratum vegetation cover for high severity. Exposed soil also showed significant differences ($p < 0.001$, $D^2 = 0.78$), with the highest value in high severity, followed by mid-severity and with the lowest value in unburned plots (Figure 3).

We detected significant differences between burned and unburned plots for total richness ($p < 0.001$, $D^2 = 0.07$), and that of native/endemic ($p < 0.001$, $D^2 = 0.19$), shrubs ($p < 0.001$, $D^2 = 0.32$) and trees ($p < 0.001$, $D^2 = 0.32$), with the highest value in the unburned plots (Figure 4).

Plant community structure between fire severity and forest type

We detected significant interactions between fire severity and forest type for lower stratum vegetation cover ($p < 0.001$, $D^2 = 0.46$), upper stratum vegetation cover ($p < 0.001$, $D^2 = 0.88$), canopy cover ($p < 0.001$, $D^2 = 0.82$) and exposed soil ($p < 0.001$, $D^2 = 0.73$). For all those variables, differences among fire severity were detected at all forest types. For lower stratum vegetation cover, Np showed a gradual decrease from unburned to high severity, Nd showed the highest values in unburned plots and no differences between burned plots, and Ac showed the lowest values in high severity and no differences between unburned plots and mid-severity. For upper stratum vegetation cover, all forest types showed the highest values in unburned plots, and no cover in burned plots, except for Ac, which showed a lower cover in mid-severity. For canopy cover and exposed soil, in general, differences were significant among fire severity in the three forest types analysed, with variation in the magnitude of the effect (Figure 5).

We detected significant interactions for total richness ($p < 0.001$, $D^2 = 0.44$), native/endemic ($p < 0.001$, $D^2 = 0.45$) and perennial herbs ($p < 0.001$, $D^2 = 0.40$). For total richness, only Np showed lower values in high severity than mid-severity and unburned plots. This response was also observed for native/endemic, for which also Nd showed differences

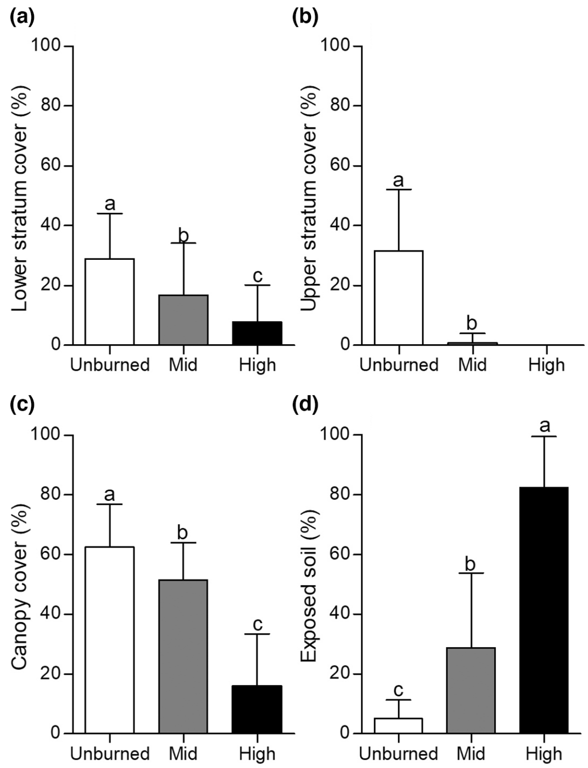

FIGURE 3 Mean vegetation cover of the lower stratum (a), upper stratum (b), canopy cover (c) and exposed soil cover (d) of the three fire severity conditions. Error bars indicate SE. Different letters indicate significant differences among fire severity conditions ($p < 0.05$).

among fire severity, but with mid severity lower than unburned plots. For perennial herbs, no differences were detected among fire severity for any forest type. For shrubs, trees, adventive/introduced and annual herbs no significant interactions were detected, but they showed significant differences in one of the main effects. The main effect of fire severity was significant for shrubs ($p < 0.001$, $D^2 = 0.46$) and trees ($p < 0.001$, $D^2 = 0.51$), with the highest values in the unburned plots, which differed from high severity. The main effect of forest type was significant for adventive/introduced ($p < 0.001$, $D^2 = 0.47$) and annual herbs ($p < 0.001$, $D^2 = 0.37$), with the highest values in Ac, which differed from both Nd and Np (Figure 6).

Plant community composition

We documented a total of 85 taxa, belonging to 43 families. We identified 71 taxa at the species level, eight at genus level and six at family level. Some herbs could not be identified and were grouped as unidentified herbs.

Species composition was different among the combined fire severity-forest type categories ($p < 0.001$), which explained 35% of the composition variability. The three unburned forests analysed showed differences among them (always $p < 0.05$). Differences were also detected among all the unburned forests and all high-severity forests. Most of the high-severity forests showed differences among them, especially Np that differed from all the other high-severity forests. The three mid-severity forests analysed did not show differences among them, but there were differences among some of them with some unburned and high-severity forests (Appendix S2, Figure 7).

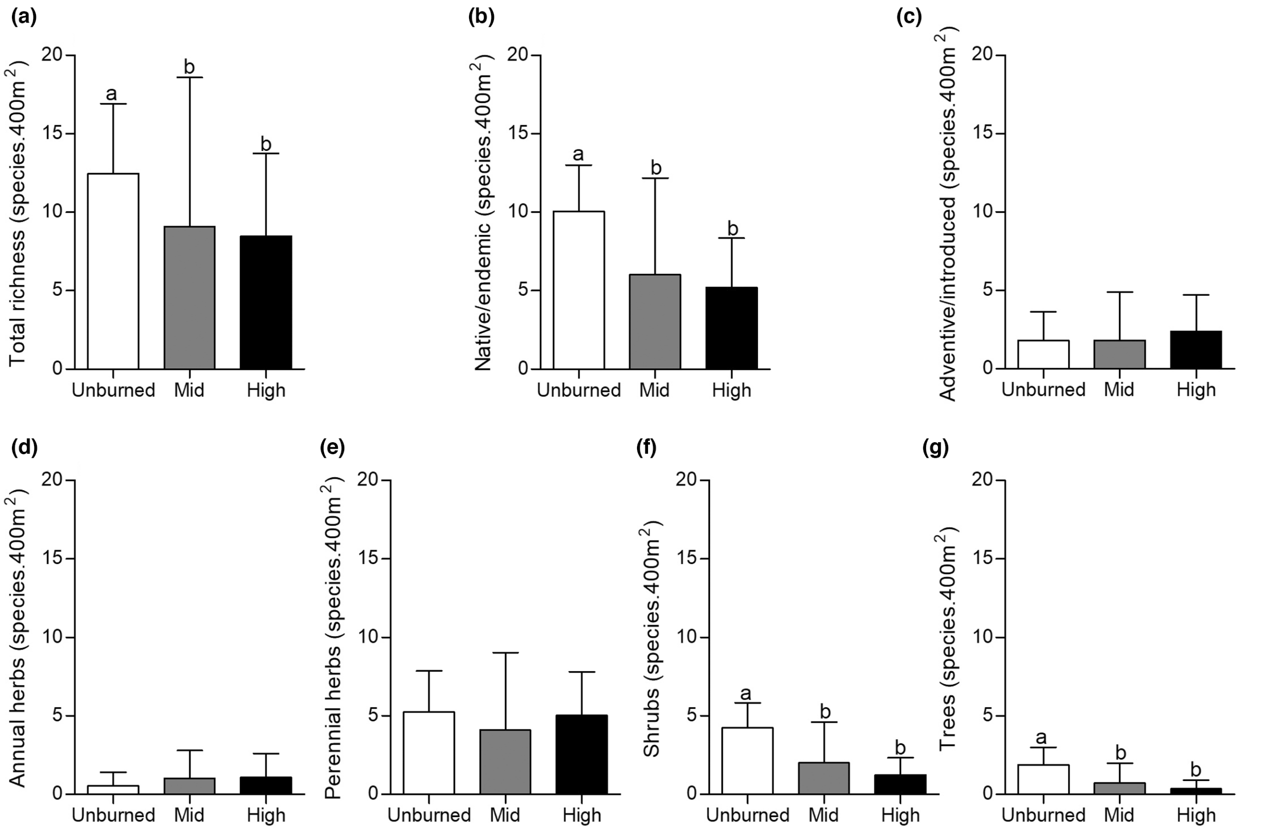

FIGURE 4 Mean total richness (a), and that of native/endemic (b), adventive/introduced (c), annual herbs (d), perennial herbs (e), shrubs (f), trees (g) for the three fire severity conditions. Error bars indicate SE. Different letters indicate significant differences among fire severity conditions ($p < 0.05$).

Considering all forest types together, many species characterized the unburned and the combination of unburned and mid-severity conditions, whereas few species characterized the mid, or mid and high severity conditions. Those species were all native/endemic and mainly shrubs and trees (Table 2). Regarding only the high severity condition, some species characterized the different forest types or their combination. Many of them were adventive/introduced, and mainly herbs (Table 3).

Woody species regeneration

The only regeneration strategy detected for shrubs in burned plots was resprouting. Many shrubs began to resprout early after the fire, both in mid and high severity, although in most cases their frequency was lower than shrubs detected in the unburned condition (Table 4).

For tree species, we detected both resprouting and regeneration by seeds in burned plots. Among the three native trees that only regenerate by seeds, *Austrocedrus chilensis* and *Nothofagus dombeyi* showed regeneration in the mid-severity condition, which corresponded to a Np plot not completely burned and due to their size of the saplings they were probably individuals not affected by fire. In most unburned plots we detected tree regeneration. The exotic conifers only regenerated by seeds and showed post-fire regeneration in both mid and high-severity conditions, and probably most of them germinated after fire since they were at the seedling stage. The resprouter trees showed incipient resprouts in the high-severity condition. No mid-severity plots were detected with the presence of *Nothofagus*

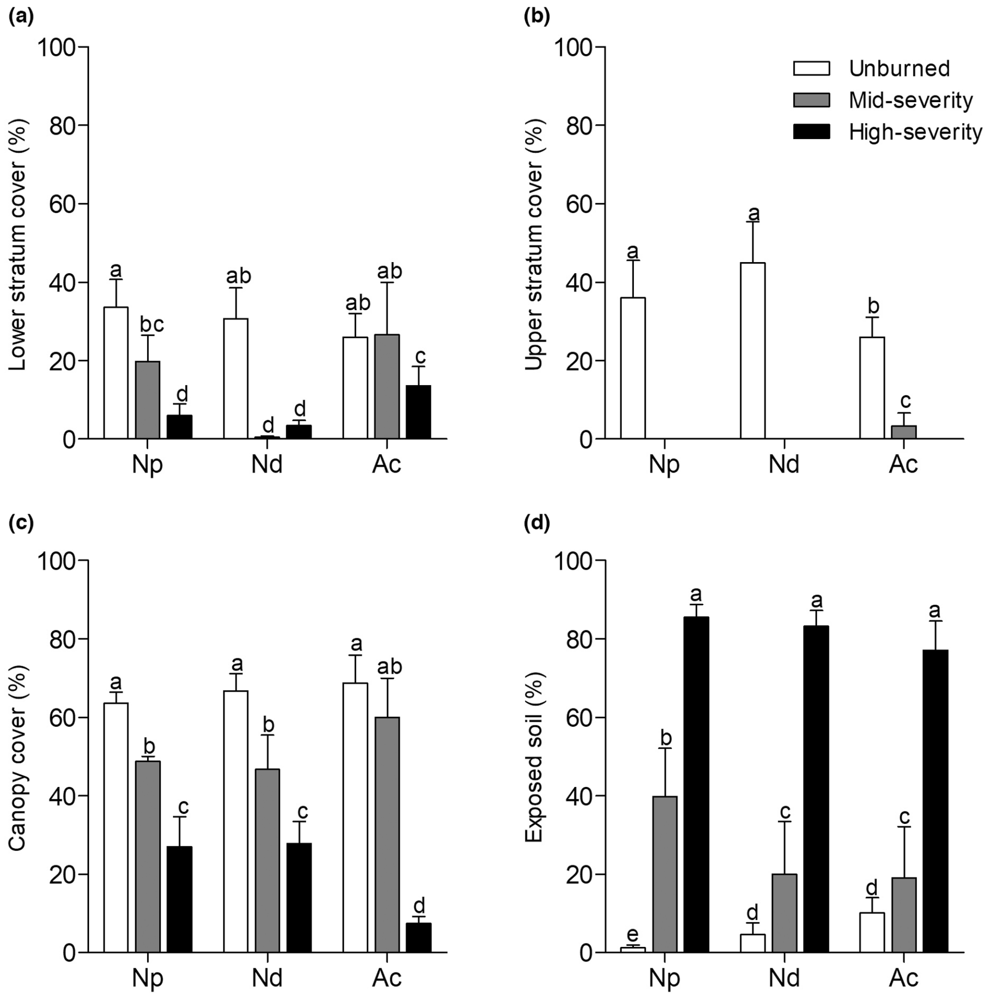

FIGURE 5 Mean vegetation cover of the lower stratum (a), upper stratum (b), canopy cover (c) and exposed soil cover (d) of the three fire severity conditions at each forest type (Ac, *Austrocedrus chilensis*; Nd, *Nothofagus dombeyi*; Np, *Nothofagus pumilio*). Error bars indicate SE. Different letters indicate significant differences among treatments ($p < 0.05$).

antarctica, and only two were detected with presence of *Lomatia hirsuta* (Table 5).

DISCUSSION

As we expected and consistent with the general fact that ecosystem recovery capability decrease as fire severity increase (Keeley, 2009), the vegetation cover of the lower stratum began to recover early after the fire and to a greater extent in mid-severity than in high severity. Richness was affected by fire, and this, as well as other structural variables of the plant community, varied in its response when analysed among forest types. Besides, plant community composition was different among most fire severy-forest type categories (Fuente-s-Ramirez et al., 2020) and many woody species showed early post-fire resprouting regeneration, although with variable frequency among species and fire severity, suggesting different post-fire natural recovery scenarios.

The recovery of the vegetation cover in the initial stage of post-fire plays an important role in soil nutrient stabilization and soil erosion reduction (Neary et al., 2005; Urretavizcaya, 2010). In addition to the higher cover of the lower vegetation in mid-severity compared to high severity, we detected

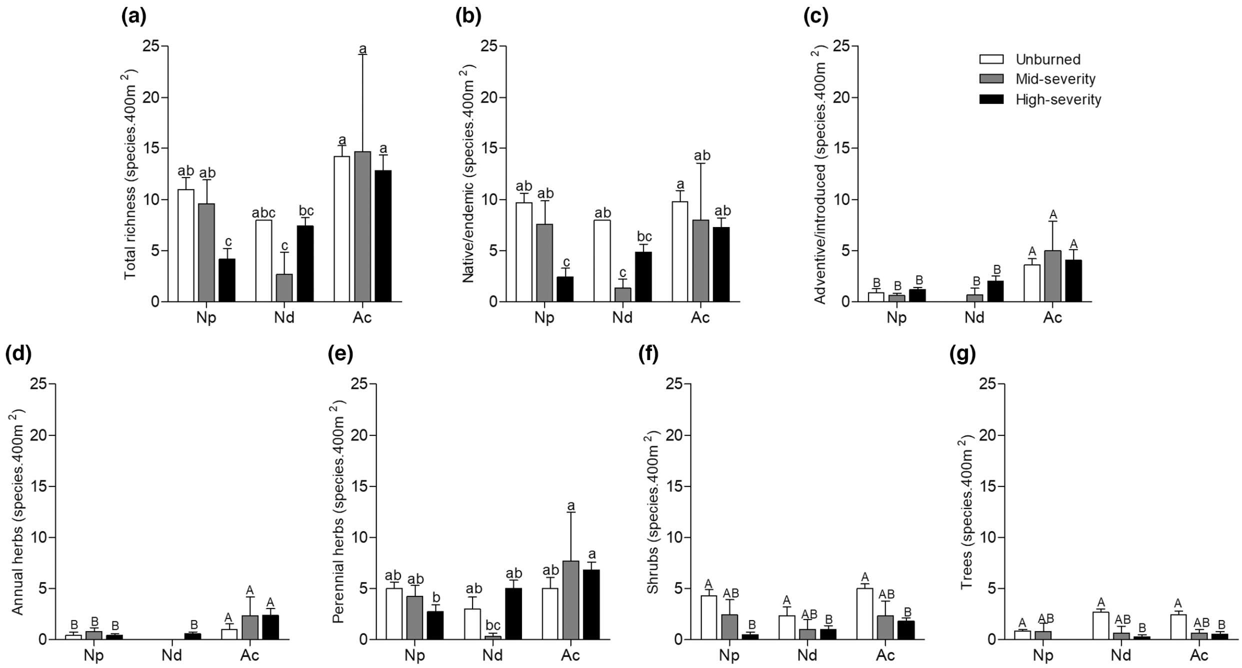

FIGURE 6 Mean total richness (a), and that of native/endemic (b), adventive/introduced (c), annual herbs (d) perennial herbs (e), shrubs (f), trees (g) of the three fire severity conditions at each forest type (Np—*Nothofagus pumilio*, Nd—*Nothofagus dombeyi*, Ac——*Austrocedrus chilensis*). Error bars indicate SE. Different letters indicate significant differences among treatments ($p < 0.05$), with capital letters for main effect differences.

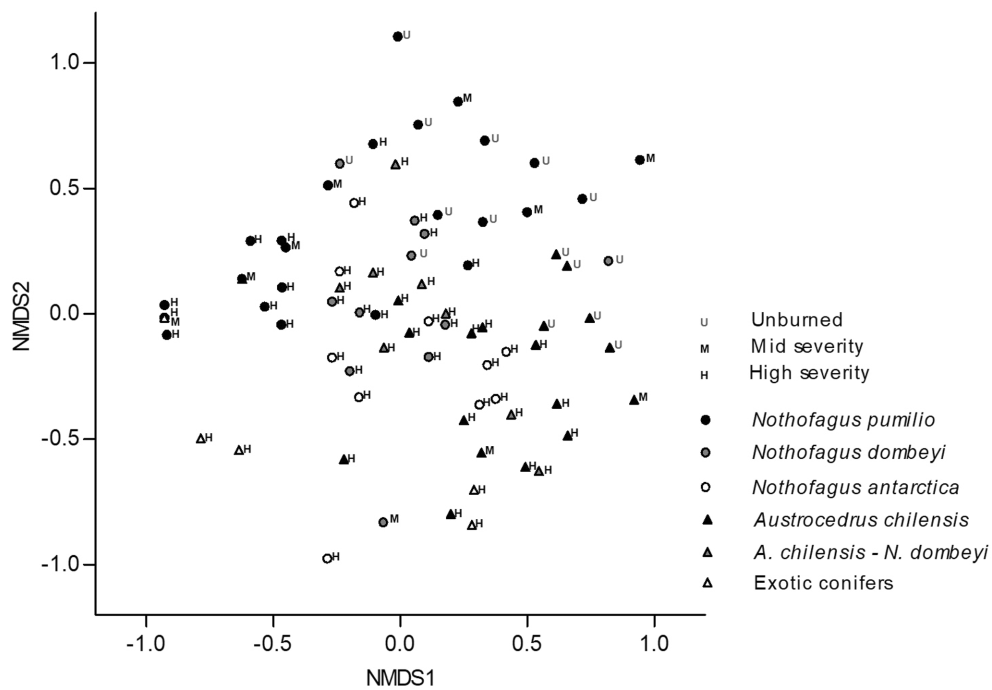

FIGURE 7 Two-dimensional non-metric multidimensional scaling (NMDS) ordination of vegetation representing the combined fire severity-forest type categories. Ordination is based on species presence at the plot level, using Bray's distance (stress = 0.25).

a lower cover of the exposed soil caused by the fall of some scorched leaves from trees. These leaves might be contributing to the reduction of heat stress and soil erosion by acting as mulching (Girona-García et al., 2021). However, in the short term after the fire, the vegetation cover

TABLE 2 Characteristic species at each fire severity or their combination based on indicator value (IV) analysis.

Characteristic species by fire severity	Growth-form	IV	*p*-Value
Unburned			
Maytenus disticha	S	0.79	0.002
Berberis microphylla	S	0.53	0.007
Nothofagus pumilio	T	0.53	0.003
Lomatia hirsuta	T	0.51	0.007
Berberis serratodentata	S	0.49	0.004
Ribes magellanicus	S	0.49	0.007
Austroblechnum penna-marina	PH	0.46	0.024
Anemone multifida	PH	0.45	0.03
Acaena splendens	PH	0.34	0.047
Unburned + mid			
Osmorhiza berteroi	PH	0.73	0.001
Austrocedrus chilensis	T	0.63	0.001
Nothofagus dombeyi	T	0.42	0.027
Embothrium coccineum	S	0.41	0.040
Mid			
Azorella prolifera	S	0.47	0.009
High + mid			
Phacelia secunda	PH	0.57	0.027

Abbreviations: PH, perennial herb; S, shrub; T, tree.

of the lower stratum was less than two-thirds in mid-severity and less than one-third in high severity of the cover detected in the unburned. Thus, early herb sowing may be necessary to favour slope stability, important in mountainous areas (Abbate et al., 2019; Löbmann et al., 2020; López Alaniz, Gobbi, Quinteros, & Puntieri, 2018). Remnant trees and leaves in the trees also conferred canopy cover, which might be contributing to reduce the high radiation and temperatures common after a fire, and that limit tree establishment and development (Urretavizcaya et al., 2006; Urretavizcaya & Defossé, 2019).

While plant species richness generally recovers early after a fire, plant community composition usually remains variable among fire severities since different reproductive strategies and traits may be favourable in each situation (Fernández-García et al., 2020; Giorgis et al., 2021; Morgan et al., 2015; Wang & Kemball, 2005). Our results showed that initial richness was different between the unburned and burned conditions, but no differences were detected between mid and high severity. However, this general pattern was considering all forest types together, but different responses to fire severity were detected for Np, Nd and Ac. Besides, these forest types were the most sampled, so they may have impacted on the pattern observed. Thus, in future studies, it would be important to focus more on the forest types less represented. Further, richness increment might become evident in the coming years. Regarding native/endemic species, although they were lower in mid and high severity compared to unburned, they predominated in all conditions because they probably also predominated before the fire. This result suggests an early recovery of native/endemic plant species, mainly perennial herbs. Among them, *Phacelia secunda* characterized the burned conditions, as it was also detected after other fires in the region (Gobbi et al., 1995; Urretavizcaya et al., 2018). Although perennial

TABLE 3 Characteristic species at each forest type or their combination at the high severity condition based on indicator value (IV) analysis.

Characteristic species by forest type at high severity	Growth-form	IV	*p*-Value
Np			
Cerastium arvense	PH	0.55	0.027
Ac			
Lactuca serriola	AH	0.52	0.014
Stellaria media	AH	0.52	0.018
P			
Fabiana imbricata	S	0.54	0.025
Pinus ponderosa	T	0.54	0.035
Rubus ulmifolius	S	0.54	0.025
Ac + Ac–Nd			
Orchidaceae	PH	0.66	0.003
Myosotis stricta	PH	0.51	0.036
Na + Ac–Nd			
Nothofagus antarctica	T	0.63	0.005
Ac + Ac–Nd + P			
Collomia biflora	PH	0.56	0.030
Na + Ac + P			
Rosa rubiginosa	S	0.62	0.007
Nd + Na + Ac + Ac–Nd			
Rumex acetosella	PH	0.75	0.003
Phacelia secunda	PH	0.74	0.002
Alstroemeria aurea	PH	0.72	0.017
Np + Nd + Na + Ac + Ac–Nd			
Vicia nigricans	PH	0.89	0.001
Nd + Na + Ac + Ac–Nd + P			
Schinus patagonica	S	0.75	0.035

Note: Adventive/introduced species are underlined.

Abbreviations: Ac, *Austrocedrus chilensis*; AH, annual herb; Na, *Nothofagus antarctica*; Nd, *Nothofagus dombeyi*; Np, *Nothofagus pumilio*; P, exotic conifer plantations; PH, perennial herb; S, shrub; T, tree.

herbs did not show differences among fire severity, when we analysed the interaction among fire severity and three forest types it was significant, suggesting that forest type is conditioning the initial post-fire response of perennial herbs. This growth-form group also contributed the most to the lower stratum cover, thus, it would be important to further study how different perennial herb species respond to fire in each forest type. Regarding adventive/introduced species, although present in burned conditions, they remained at values similar to those of the unburned forests. However, it is important to continue monitoring their regeneration and, if necessary, to manage it, since the seed bank may contain mainly adventive/introduced species that probably spread, especially if cattle is present (Gobbi et al., 1995; Varela et al., 2006). This might be especially important for Ac since it showed a greater richness of adventive/introduced species than Np and Nd, which might be associated with its proximity to settlement (see Appendix S1), making it an area of greater accessibility for human activities (i.e. productive and recreative) and therefore to exotic species spread (Liedtke et al., 2020). There were mainly adventive/introduced species that characterized the different forest types with high severity. However, they

TABLE 4 Frequency of resprouter shrubs at each fire severity.

	Frequency (% of presence)		
	Unburned ($n=17$)	Mid ($n=11$)	High ($n=56$)
Schinus patagonica	82	36	52
Maytenus disticha	76	18	0
Rosa rubiginosa	41	18	23
Aristotelia chilensis	35	9	16
Embothrium coccineum	24	9	2
Berberis darwini	18	18	13
Chusquea culeaou	6	9	0
Ribes cucullatum	6	9	11
Discaria chacaye	6	0	5
Diostea juncea	0	9	2
Rubus ulmifolius	0	0	4

Note: Frequency is based on the plots with the presence of the species related to the total number of plots (*n*) of the corresponding fire severity. Adventive/introduced species are underlined.

TABLE 5 Frequency of tree regeneration by seeds and resprouters at each fire severity.

	Frequency (% of presence)		
	Unburned (*n*)	Mid (*n*)	High (*n*)
By seeds			
Austrocedrus chilensis	75 (8)	20 (5)	0 (26)
Nothofagus dombeyi	75 (4)	17 (6)	0 (13)
Nothofagus pumilio	29 (7)	0 (4)	0 (12)
Exotic conifers	– (0)	50 (2)	40 (10)
Resprouters			
Lomatia hirsuta	100 (5)	0 (2)	11 (18)
Nothofagus antarctica	100 (1)	– (0)	71 (17)

Note: Frequency is based on the plots with the presence of the species related to the total number of plots (*n*) with the presence (dead or alive) of the corresponding species. Adventive/introduced species are underlined.

were also common and frequent in unburned forests, such as *Rumex acetosella*, *Stellaria media* and *Myosotis stricta*. Adventive/introduced shrubs, such as *Rosa rubiginosa*, which characterized the burned Na, Ac and P forests, as well as *Rubus ulmifolius*, which characterized the burned P forest, should be monitored since they can generate invasive processes (Cavallero & Raffaele, 2010). The regeneration of exotic conifer trees, which characterized the burned P forest, may develop in post-fire exotic conifer forest. Besides, surrounding native forests may deserve special attention, since burned environments are susceptible of conifer invasion, especially of serotinous species such as *Pinus contorta* (Franzese & Raffaele, 2017; Raffaele et al., 2016).

Shrubs and trees generally are the growth forms most affected by fire, showing a lower cover in burned areas in many environments (Giorgis et al., 2021). Our results showed that the lower richness of shrubs and trees detected in both mid and high severity was coincident with a lower resprouting frequency for many species, and a minimum or nil upper stratum cover. This might be due to the effect of soil burn severity on the moisture content of the surface soil, which can affect resprouting vigour and individual survival (Fernández et al., 2013; Wright & Clarke, 2007). Vegetation cover of the upper stratum plays an important role in nursing most of the native tree seedlings established naturally or through plantation (Kitzberger et al., 2005; Urretavizcaya et al., 2006, 2018; Urretavizcaya & Defossé, 2013) especially in places with salvage logging (Urretavizcaya & Defossé, 2019). Thus, although it is possible that they recover in the coming years, the plantation of shrubs species early after a fire might be an option to reduce erosion and to act as nurse species for following tree plantations. Besides, some species that characterized the unburned, such as *Maytenus disticha*, *Berberis microphylla*, *Lomatia hirsuta*, *Berberis serrato-dentata* and *Ribes magellanicum*, are capable of resprouting. Thus, it would be important to evaluate their presence and abundance in the burned area in the following years, since they might need more time to resprout.

Initial plant regeneration after fire may occur from resprouting of damaged individuals, as we detected in this study, but also from the remnant seed banks, and seed dispersion from surrounding unburned areas (Falk et al., 2022). Although we did not assess herb regeneration mechanism, on-site observations of native herb seedlings such as *Phacelia secunda*, *Mutisia decurrens*, *M. spinosa*, *Osmorhiza berteroi*, *Vicia nigricans* and exotic herb seedlings such as *Cardus nutants* also indicate regeneration from seeds. Besides, as we evaluated the emergent understory early in the growing season, it is possible that we did not detect species that germinate late. Among the detected species, a positive effect of ashes on *Phacelia secunda* germination (López Alaniz, Gobbi, & Puntieri, 2018), may explain why it characterized the burned conditions. *Vicia magellanica*, a species related to *V. nigricans*, have shown a high percentage of germination with and without ashes (Blackhall et al., 2021). In addition, these two species have been detected in abundance early after fire (Gobbi et al., 1995; Varela et al., 2006). So, fire could have a positive effect on *V. nigricans*, which explains why it characterized all native forests with high fire severity. It would be interesting to delve into the reproductive strategies of other herb species after different fire severity conditions in the field and laboratory to complement the existing studies. The great extent of the fire and the lack of unburned patches suggest that the regeneration from seeds was mainly from the remnant seed banks. However, seed rain might be an important input, mainly for anemochorous and zoochorous species, contributing to the initial post-fire re-vegetation (Cavallero et al., 2013; Rodrigo et al., 2012). Regarding native trees that only regenerate by seeds, the only burned plots where we detected tree regeneration were those with living trees, which probably corresponded to individuals not affected by fire, as it was also found by Landesmann et al. (2021). Considering the sensibility and limited dispersion of these species (Cuevas & Arroyo, 1999; Landesmann & Morales, 2018; Urretavizcaya et al., 2022; Urretavizcaya & Defossé, 2004) and the great extent of high severity of the fire, it might take many years or, most probably, the forest ecosystem will not return if tree plantations are not carried out.

This study shows the basal line of the post-fire state in the Andean-Patagonian forests affected by mid- to high-severity fires and some possible future scenarios from which different actions should be taken. In the actual context of climate change, it may not be practical or even desirable to restore conditions to the historical reference ecosystem, but rather there must be a proper balance between rebuilding past systems and attempting to build resilient systems for the future (Simonson et al., 2021). Our main results show that native species predominated in all fire severity conditions suggesting a good recovery of the understorey. However, vegetation cover and resprouting capability were affected by fire, so, herbs sowing, and shrubs plantations in the short term and subsequently tree plantations may be needed, mainly in high-severity areas. Monitoring possible invasion processes and their mitigation, especially in exotic conifer plantations and the surrounding native forests, may also be needed. More studies focusing on these multiple aspects are fundamental. In addition, it is important to consider social aspects, since productive activities, such as livestock and salvage logging are common in these areas (Blackhall, Raffaele, & Veblen, 2015, Blackhall, Veblen, & Raffaele, 2015; Urretavizcaya & Defossé, 2019). Finally, as wildfires, especially those spreading from wildland-urban interface areas, generate a great social mobilization, this is an opportunity to engage the community in restoration actions that promote resilient systems for the future.

AUTHOR CONTRIBUTIONS

Maria Melisa Rago: Conceptualization (equal); formal analysis (lead); investigation (equal); methodology (equal); visualization (equal); writing – original draft (lead); writing – review and editing (equal). **María Florencia Urretavizcaya:** Conceptualization (equal); formal analysis (supporting); methodology (equal); visualization (equal); writing – review and editing (equal). **Pablo Morelli:** Conceptualization (supporting); investigation (equal); methodology (equal). **Diego Mohr Bell:** Conceptualization (supporting); formal analysis (supporting); investigation (supporting); methodology (supporting); visualization (supporting); writing – review and editing (supporting). **Mario Guzmán:** Conceptualization (equal); funding acquisition (lead); investigation (supporting); methodology (equal); project administration (lead).

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CONFLICT OF INTEREST STATEMENT

The authors have no competing interests to declare that are relevant to the content of this article.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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