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Impacts of a short-interval severe fire on forest structure and regeneration in a temperate Andean *Araucaria-Nothofagus* forest

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Abstract

Background Warmer climate conditions are altering fire regimes globally, eroding the capacity of forest ecosystems to resist and recover from natural disturbances like wildfire. Severe and rapidly repeated wildfires are promoting tree regeneration failure of obligate-seeders and/or fire-sensitive species in temperate forests of the Southern Hemisphere. We collected post-fire field data to evaluate whether forest structure and tree regeneration responses varied between two Andean forest study areas dominated by the threatened Gondwanan conifer *Araucaria araucana* and *Nothofagus* species (southern beeches) — one area burned once, the other reburned after 13 years.

Results Tree mortality was high across species after a single high severity and/or repeated wildfire, although some *A. araucana* trees were able to survive both events. Post-fire seedling regeneration of *A. araucana* and *Nothofagus* spp. was poor in areas affected by severe wildfires, and the latter was absent from reburned plots. A key driver of this regeneration failure was increasing distance to live seed source trees, which was negatively correlated with these species' post-fire seedling abundances. In contrast, species with the capacity to regenerate via resprouting (*A. araucana, N. alpina, N. obliqua*) did so after a single high severity fire; however, only a single *Nothofagus* species (*N. alpina*) resprouted abundantly after a reburn.

Conclusions Our findings suggest that high severity and short-interval fires can drastically change the structure of and limit post-fire tree regeneration in *Araucaria-Nothofagus* forests, promoting alternative post-fire forest ecosystem trajectories. Resprouting species of the *Nothofagus* genus, especially *N. alpina*, exhibit the greatest resilience to these emerging fire patterns. These forests are currently facing an unprecedented climatic shift toward greater fire activity, where resprouting is the favored regeneration strategy. If the occurrence of severe and short-interval fires increases in the coming decades, as predicted, we expect *Araucaria-Nothofagus* forests to shift toward a drier, more flammable shrubland ecosystem state.

Keywords *Araucaria araucana*, Forest fires, Forest regeneration, Monkey puzzle tree, *Nothofagus* species, Post-fire regeneration, Short-interval fires, Southern hemisphere temperate forests

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Resumen

Antecedentes Las condiciones climáticas más cálidas están alterando globalmente los regímenes de incendio, erodando la capacidad de los ecosistemas forestales de resistir y recuperarse de disturbios naturales como el fuego. Los incendios frecuentes y más severos promueven una falla en la regeneración de árboles que se reproducen por semilla y/o en aquellas especies sensibles al fuego en bosques templados del hemisferio sur. Colectamos datos de campo en zonas quemadas para evaluar si la estructura forestal y las respuestas de la regeneración variaron entre dos áreas de estudio en el bosque andino dominado por la especie gondwanica amenazada, *Araucaria araucana,* y especies de *Nothofagus* (hayas del sur). Esto se realizó en un área quemada una vez, y en la otra quemada y vuelta a quemar luego de 13 años.

Resultados La mortalidad de árboles fue alta entre especies luego de un incendio de alta severidad y/o repetido en el tiempo, aunque algunos árboles de *A. araucana* fueron capaces de sobrevivir a ambos eventos. La regeneración por plántulas tanto de *A. araucana* como de las especies de *Nothofagus* fue baja en las áreas afectadas por un incendio severo, y los *Nothofagus* estuvieron ausentes en las áreas quemadas por dos incendios. La causa dominante de esta falla en la regeneración fue la distancia incremental de árboles semilleros vivos, lo que fue negativamente correlacionado con la abundancia de plántulas encontradas en las zonas quemadas. En contraste, las especies con capacidad de regenerar vía rebrotes (*A. araucana, N. alpina, N. obliqua*), lo hicieron luego de un evento de fuego severo; sin embargo, sólo la especie *N. alpina* rebrotó abundantemente luego del segundo evento de fuego.

Conclusiones Nuestros resultados sugieren que los incendios de alta severidad, y repetidos a intervalos de tiempo cortos, puede cambiar drásticamente la estructura y limitar la posterior regeneración en bosques de *Araucaria-Nothofagus,* promoviendo trayectorias alternativas en el ecosistema boscoso. Las especies rebrotantes del género *Nothofagus*, en especial *N. alpina*, exhibe la mayor resiliencia a esos patrones de fuego emergentes. Estos bosques están enfrentando un cambio sin precedentes que tiende hacia una mayor actividad de incendios, donde el rebrote es la estrategia de regeneración favorecida. Si la ocurrencia de fuegos severos y a intervalos cortos se incrementan en las próximas décadas, como ha sido predicho, es de esperar que los bosques de *Araucaria-Nothofagus* cambien hacia estados del tipo de ecosistemas de matorral, más secos e inflamables.

Background

Changes in forest structure and regeneration patterns due to altered fire regimes are raising concern globally surrounding forest ecosystem resilience and persistence. Atmospheric-sea surface temperature oscillations have been reflected by climate-fire interactions across Mediterranean, Temperate, Boreal, and Arctic regions of the Northern Hemisphere (Justino et al. 2022; Zhao et al. 2022), as well as Mediterranean and Temperate regions in the Southern Hemisphere (Kitzberger et al. 2001; Holz et al. 2017; Mariani et al. 2018). The effects of these interactions are resulting in unprecedented droughts, extended fire seasons, and below-average precipitation, promoting ideal conditions for more extreme and widespread fires (Westerling et al. 2006; Jolly et al. 2015; Abatzoglou and Williams 2016; González et al. 2018). These trends are of critical concern due to anticipated changes in fire regimes that promote longer fire seasons (e.g., greater extent of time when fire is likely to occur), greater fire frequency (e.g., short-interval fires), and higher severity of fire effects (e.g., increased magnitude of ecological change), which can alter the resilience of forest ecosystems worldwide (Enright et al. 2015; Johnstone et al. 2016; Coop et al. 2020). Fire regimes characterized by short-interval and

high severity fire patterns, concurrent with or followed by dry post-fire conditions, strongly influence post-fire tree regeneration and understory composition, favoring the persistence of species that most rapidly recover after fire (e.g., resprouting plants; Johnstone et al. 2016; Stevens-Rumann and Morgan 2016; Young et al. 2019; Coop et al. 2020; Davis et al. 2020; Steel et al. 2021; Seidl and Turner 2022).

The capacity of trees to vegetatively regenerate (i.e., resprout) or massively produce and disperse seeds after wildfire may be recognized as resilience traits that benefit species persistence (Pausas and Keeley 2014). There is evidence that expansive high severity fires and/or short-interval fires (i.e., reburns) may promote notable reductions in regeneration or cause outright regeneration failure of obligate-seed tree species (Donato et al. 2009; Enright et al. 2015; Fairman et al. 2015; Harvey et al. 2016; Assal et al. 2018; Stevens-Rumann et al. 2018; Stevens-Rumann and Morgan 2019; Busby et al. 2020) and sometimes even of serotinous (Buma et al. 2013; Turner et al. 2019) and/or resprouting tree species (Fairman et al. 2019). Potentially, there may be large-scale transitions from a mesic and less flammable forest community to a fire-prone, non-forest system dominated by resprouting shrub species, likely as or more flammable

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than obligate-seeding trees, resulting in positive feed-backs that increases the frequency of fires over time (Odion et al. 2010; Paritsis et al. 2015; Tepley et al. 2018; Buma et al. 2020).

In Patagonian-Andean forests in Chile and Argentina, altered fire regimes due to climate change may have critical impacts on ecosystems in the Temperate-Mediterranean climate transition zone, many of which have evolved under mixed fire regimes characterized by frequent surface (i.e., low severity), infrequent severe, or moderately frequent mixed-severity wildfires. These fire regimes have promoted species dominance by both fire-adapted and fire-sensitive species (González et al. 2010b; Paritsis et al. 2015; Mundo et al. 2017b). Fires in these ecosystems may be ignited naturally by lightning or volcanic activity, but most fires are believed to have been ignited by humans and these anthropogenic fires have increased in frequency over the past two centuries (Veblen 1982a; Heusser 1994; González et al. 2005, 2020; Holz and Veblen 2011; Mundo et al. 2013; Holz et al. 2016; Muñoz et al. 2023). European colonization and subsequent changes in land use patterns critically influenced fire regime shifts in southern South America. Although natural ignitions occurred and native communities historically used fire (e.g., for hunting, communication, heating, warfare), the effect of European colonization resulted in an increase of widespread fires during the nineteenth to twentieth centuries, significantly reducing the original distribution of long-lived relict conifer species (Veblen et al. 1999; Lara et al. 1999; González et al. 2020).

In recent years, large-scale events have burned extensive swaths of temperate ecosystems in the Southern Hemisphere (Boer et al. 2020; Le Breton et al. 2022), including *Araucaria-Nothofagus* forests in northern Patagonia (González and Veblen 2007; González and Lara 2015; Assal et al. 2018; Franco et al. 2022). Forests in south-central Chile may already be experiencing altered fire regimes, where the number of fires, severity, and burned area have significantly increased in recent decades (Úbeda and Sarricolea 2016; González et al. 2018). These fire patterns are correlated with unprecedented climatic warming and drying that is linked to anthropogenic climate change (Garreaud et al. 2020; González et al. 2020) and natural climate modes, such as El Niño Southern Oscillation and the Southern Annular Mode in the Southern Hemisphere (Veblen et al. 2008; Holz and Veblen 2012; Holz et al. 2012, 2017; Mariani et al. 2018; Urrutia-Jalabert et al. 2018; Garreaud et al. 2020; González et al. 2020). Exceptionally dry conditions associated with these modes triggered the extreme wildfire year in south-central Chile in 2017, strongly affecting natural and human systems (de la Barrera et al. 2018; Bowman et al. 2019; McWethy et al. 2021). Similarly, wildfires

in 2002 and 2015 are considered the most extensive fires in Andean *Araucaria-Nothofagus* forests in southern Chile over the past 60 years, where large areas were affected by both fire events in a time span of 13 years, potentially indicating an early shift of fire regime due to climate change (González and Veblen 2007; González and Lara 2015; González et al. 2020).

This apparent shift in fire regime is of great conservation concern. *Araucaria araucana* (hereafter Araucaria) is of the utmost value to the local indigenous population because of its spiritual significance, as well as due to the importance of its seeds in the diet of local communities (Sanguinetti et al. 2023). In addition, this paleoendemic Gondwanan conifer is globally considered endangered, and populations are considered regionally threatened despite primarily occurring in protected areas (CITES 2001; Veblen et al. 2011; Premoli et al. 2011; González et al. 2013; Sanguinetti et al. 2023). Although Araucaria (a post-fire facultative resprouter/seeder sensu Prior and Bowman 2020; Supplemental Data S1) and some co-dominant southern beech *Nothofagus* spp. (i.e., *N. alpina, N. obliqua*, post-fire obligate resprouters sensu Prior and Bowman 2020; Supplemental Data S1) have traits allowing some degree of resistance to and/or persistence after fire (e.g., species capable to resprout; Veblen 1982a; Burns 1993; Donoso 1993; González et al. 2010a, b; Mundo et al. 2017a; González et al. 2020), other co-dominant *Nothofagus* spp. (i.e., *N. dombeyi, N. pumilio*, post-fire obligate colonizers sensu Prior and Bowman 2020; Supplemental Data S1) are not well-adapted to recover from high severity fires (e.g., unable to resprout; Assal et al. 2018; Landesmann et al. 2021; Rago et al. 2023), and their recovery capacity following short-interval fires is unknown (Fig. 1). Although the regeneration patterns of Araucaria and *Nothofagus* spp. include a catastrophic mode (sensu Veblen 1992) in the sense that pulses of regeneration occur following infrequent coarse-scale disturbances like landslides, volcanism, and stand-replacing fires (Veblen et al. 1981; González et al. 2010b), decreasing intervals between fire events may compromise their resilience. In similar *Nothofagus* dominated forests further south in Patagonia (i.e., without Araucaria at ca. 40° S), severe wildfires are contributing to the conversion of forests to more flammable non-forest assemblages (e.g., tall shrublands dominated by *N. antarctica* and *Chusquea* bamboos), where positive feedback processes are likely to promote the persistence of fire-prone ecosystems (Mermoz et al. 2005; Paritsis et al. 2015; Kitzberger et al. 2022). In temperate *Araucaria-Nothofagus* forests, Araucaria regeneration may be threatened due to its narrow geographical distribution, short-distance seed dispersal, and slow
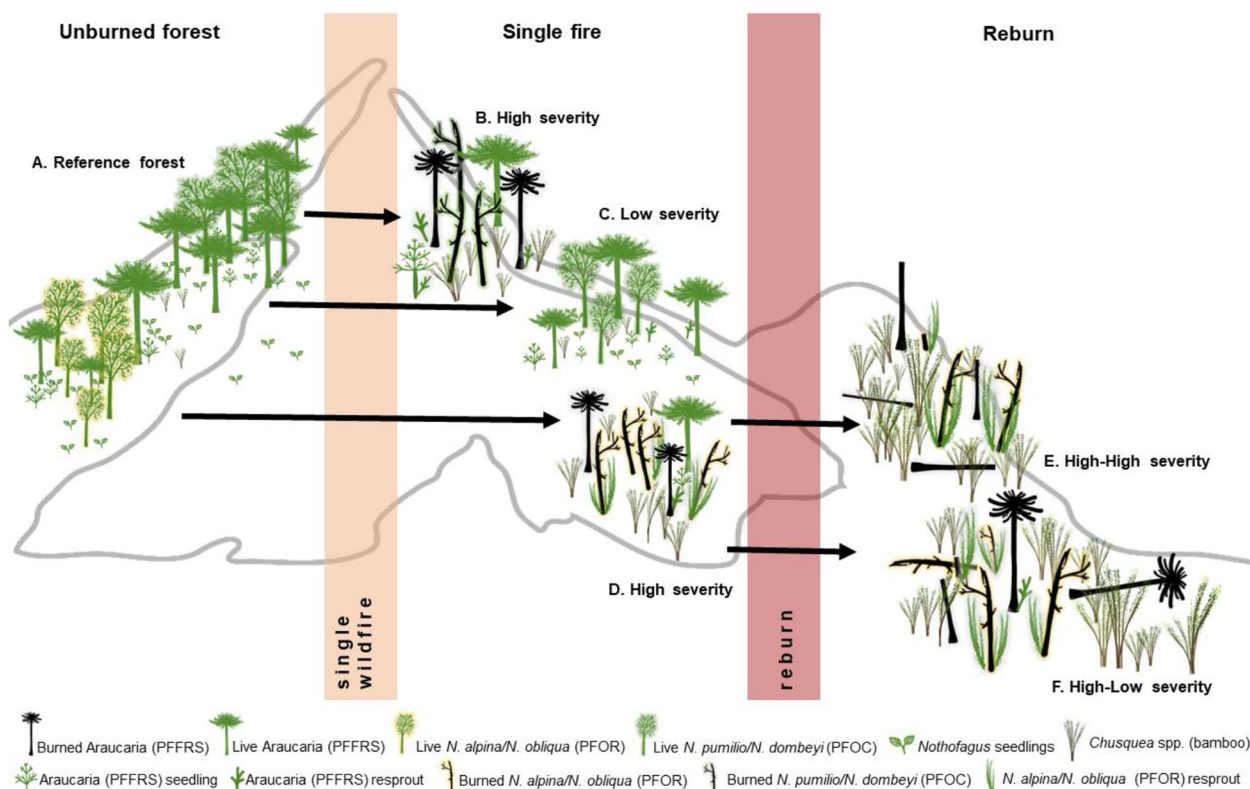
Fig. 1 Conceptual diagram illustrating how Araucaria (post-fire facultative resprouter/seeder traits, PFFRS), *N. pumilio* and *N. dombeyi* combined (post-fire obligate colonizer traits, PFOC), and *N. alpina* and *N. obliqua* combined (post-fire obligate resprouter traits, PFOR) respond to wildfire patterns highlighted in this study and adapted according to species regeneration dynamics. (*A*) Reference forest, where Araucaria and *Nothofagus* occur across a range of size (age) classes and some canopy trees. *Chusquea* bamboo is likely to be present beneath canopy gaps. (*B*) A single high severity fire kills all the adult trees of *Nothofagus* and most of the Araucaria. *Chusquea* bamboo typically resprouts and proliferates under conditions of low canopy tree cover. (*C*) A single low burn severity fire does not affect the adult tree layer but facilitates new post-fire tree seedling establishment. Juvenile Araucarias may survive a single low burn severity, and *Chusquea* bamboo growth and resprouting may be enhanced where openings in the canopy occur. (*D*) Single high burn severity in areas where Araucaria, *Nothofagus* and *Chusquea* bamboo all resprout. (*E*) A second high or (*F*) low burn severity in an area previously burned at high severity eliminates nearby live seed source trees, inhibiting successful seedling establishment. Araucaria may resprout in areas affected by a second low severity fire. In this second case, when PFOR species are present, the more common pathway is widespread resprouting of and dominance by *Chusquea* bamboos. The new configuration is a fire-prone, open and dry non-forest system dominated by more fire prone *Chusquea* bamboos and resprouting shrubs and small trees

post-fire establishment (Fajardo and González 2009; González et al. 2010b). A number of studies associated with post-fire tree regeneration of Araucaria and *Nothofagus* spp. have been conducted in the temperate forests of south-central Chile (Burns 1993; Assal et al. 2018; Arroyo-Vargas et al. 2019; Fuentes-Ramirez et al. 2020). However, substantial uncertainty persists surrounding post-fire and post-reburn recovery and the persistence of species and plant functional traits under emerging high severity and unprecedented short-interval wildfires in these forests.

We address some of this uncertainty by evaluating post-fire sexual reproduction (i.e., seedling establishment) and vegetative (i.e., resprouting) regeneration responses of dominant tree species, aggregated by functional types, and their drivers, within Andean *Araucaria-Nothofagus* forests that were burned once or were reburned during fire events in 2002 and 2015. Specifically, we asked the following research questions:

(1) How are post-fire forest structures and tree regeneration patterns differentially affected by single and short-interval fire events involving low and high fire severities within each fire?

(2) What are the primary biotic and abiotic drivers of post-fire sexual (by seedling establishment) and asexual (by resprouting) regeneration among the dominant tree species when aggregated by functional traits?

We posed these questions to identify what regeneration traits and strategies confer greater or lesser resilience to high-severity fire effects and short-interval

reburning, including fire-sensitive species that did not evolve with a pervasive fire filtering role (sensu Prior and Bowman 2020; see Supplemental Data S1 for further explanation). We hypothesized that following a single fire, we expected significant differences in post-fire forest structure and the abundance of varying functional traits under low versus high fire severities, where the latter would be associated with greater departures from the reference forest compared to the former. We also expected little to no difference in post-fire forest structure between areas that were reburned after 13 years at different burn severity, but we did expect statistically different structure in reburns compared to reference forests (Fig. 1). Furthermore, we hypothesized that drivers of tree regeneration differ distinctly for seedlings versus resprouts among fire severity classes for both single and reburned areas, where seedling establishment is primarily driven by biotic fire legacies and resprouting by abiotic site conditions.

Methods

Study area

We selected two study areas in the Andean mountains of south-central Chile, both dominated by *Araucaria-Nothofagus* forests: China Muerta National Reserve (hereafter single burn; 38.8° S, 71.5° W; Fig. 2), and Malleco National Reserve and Tolhuaca National Park (hereafter reburn; 38.2° S, 71.8° W; Fig. 2). The climate is a transition between cool Mediterranean and warm Temperate, with warm and dry summers and cold winters (Luebert and Pliscoff 2017). Climate conditions vary between study areas due to their geographic locations: China Muerta National Reserve is located at higher latitude and elevation, characterized by mean annual precipitation of 1430 mm (period 1990–2020), where the average annual minimum and maximum temperatures in the coldest (Jun–Aug) and warmest (Dec–Feb) seasons are −1.2 and 24.1 °C, respectively (Lonquimay station; CR2 2023); mean annual precipitation at Malleco National Reserve
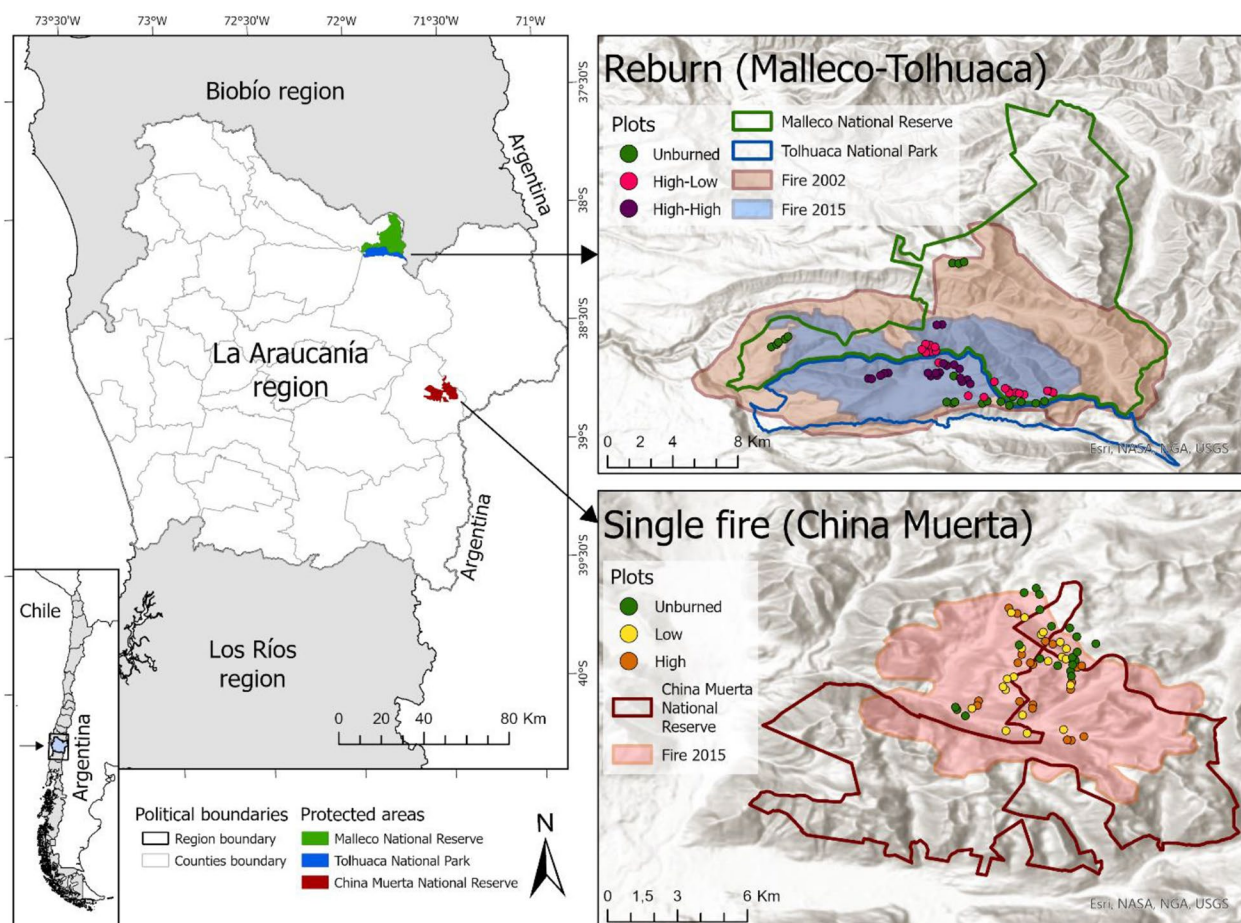
Fig. 2 Locations of Malleco-Tolhuaca and China Muerta study areas in south-central Chile. Maps highlight protected areas, burned areas, and plot locations. Most of the unburned plots are located inside of the fire perimeter in each study site, but in patches that were not affected by wildfires. Plots colors represent the following burn severities (in the associated colors): unburned (green), low (yellow), high (orange), high-low (red), and high-high (purple)

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and Tolhuaca National Park is 2839 mm, where the average annual minimum and maximum temperatures in the coldest and warmest seasons are 0.5 and 22.6 °C, respectively (Laguna Malleco weather station; CR2 2023). Soils in both study areas are Andosols and Histosols, derived from post-glacial deposits of volcanic ash composed of medium to coarse-grained tephras (Wright 1965; CIREN et al. 2010; Casanova et al. 2013).

Temperate forests from the Andean Araucanía region are dominated by the living fossil and threatened conifer *Araucaria araucana* (araucaria, monkey puzzle, pewen), and the angiosperm southern beech species in the *Nothofagus* genus (i.e., *N. pumilio*, *N. dombeyi*, *N. obliqua*, *N. alpina*, and *N. antarctica*). Beneath the canopy gaps of these forests, the understory plant communities are dominated by *Chusquea* bamboo species (Veblen 1982b). The geographical distribution of these species is not homogenous along their latitude and elevation gradient. The reburned study area is characterized by the predominance of *N. obliqua*, *N. alpina* and *N. dombeyi,* and *A. araucana* at higher elevations, whereas the single burn study area is dominated more homogeneously in space by *A. araucana* and *N. pumilio*. The paleoendemic Araucaria is a dioecious slow-growing and long-lived conifer that can reach over 1000 years in age (Tortorelli 1942; Veblen 1982a; Aguilera-Betti et al. 2017). In Chile, Andean Araucaria populations are mostly distributed between 37° 30' S and 39° 40' S, growing between 1000 and 1600 m in elevation, where pure stands form or combine with different *Nothofagus* spp. (Veblen 1982a; González et al. 2013). Mature individuals of Araucaria are fire-resistant trees that develop thick bark, self-prune their lower branches, protect the seeds inside cones situated at the top of the canopy, and resprout from epicormic buds located below their bark (Veblen 1982a; Burns 1993; González et al. 2013). *Nothofagus* spp. have a larger latitudinal and longitudinal distribution range than Araucaria, encompassing the central and southern part of Chile and the Andean Patagonian area of Argentina. *Nothofagus* spp. have shorter lifespans than Araucaria, reaching an age of 150–600 years (Veblen et al. 1981; Burns 1993; Pollmann 2003; González et al. 2010b). These species develop a thinner bark, making them susceptible to fire-induced mortality from moderate-to-high severity fires. However, *N. alpina*, *N. obliqua*, and *N. antarctica* have the capacity to resprout vegetatively after wildfires, whereas *N. domb*eyi and *N. pumilio* are dependent on sexual reproduction and seedling establishment following fires (Veblen et al. 1996).

Some studies indicate that, historically, moderate-to-high severity fires occurred at intervals of multiple decades to a couple of centuries in forests dominated by *A. araucaria* and *N. pumilo* (González et al. 2010b, 2020).

However, China Muerta (CM) and Malleco-Tolhuaca (MT) study areas were affected by large fire events in 2002 (MT only) and 2015 (CM and MT) that have been linked with intense regional drought conditions (Urrutia-Jalabert et al. 2018; Garreaud 2018). The 2002 wildfire in MT was lightning-ignited in mid austral summer (January), burning approximately 12,000 ha (Assal et al. 2018, ca. 70% of the Malleco and Tolhuaca protected areas, combined); 13 years later, the wildfire of 2015 was human-ignited, occurring near the end of the austral summer (March), reburning approximately 5500 ha from the previous wildfire (CONAF 2015; Ortega and Levet 2020). The 2015 wildfire in CM was also human-ignited near the end of the austral summer (March), burning approximately 6600 ha (CONAF 2015). Both 2015 wildfires were facilitated by exceptional drought that has affected south-central Chile since 2010 and were exacerbated by dry foehn winds (i.e., puelche) from the eastside of the Andes range (Garreaud et al. 2017; McWethy et al. 2021).

Sampling design and data collection

We established a total of 120 circular plots (0.07 ha; Fig. 2) in areas burned by a single fire and short-interval reburn during the austral summer of 2020 (Jan–Mar). Our sampling design follows Busby et al. (2020) and was stratified by burn severity and number of fires. In the single burned area, strata included unburned reference, low, and high burn severity classes; in the reburned area, strata included unburned reference, high-low and high-high burn severity classes. We established 20 plots total in each burn severity class. Moderate burn severity classifications were excluded from our sampling design and stratification based on their low accuracy (i.e., wide range of fire effects) and challenges associated with field validation (Franco et al. 2020). Also, other combinations of burn severities (i.e., low-low and/or low–high) were discarded due to their low representation in the study area and/or difficult access in the reburned area. Sample plots were randomly located in accessible areas (i.e., maximum of 4500 m from roads), outside of any previous restoration efforts, with minimal known cattle pressure (i.e., by direct observation in the field), and were no closer than 100 m from other sample plots to minimize spatial autocorrelation (average of 276 m). Burn severity maps for each wildfire event were created using pre-fire and 1-year post-fire Landsat imagery and the relativized delta normalized burn ratio (RdNBR; Miller and Thode 2007; Parks et al. 2014). RdNBR thresholds used to classify burn severity maps were defined according to Assal et al. (2018) and later field verified by direct observation. If any of the plots did not match the remote sensing burn severity classification, we shifted the plot locations at

30-m intervals until field observations matched the target severity map class. Unburned plots were located in both reburn and single fire study areas under similar environmental conditions as those selected for the burned plots.

Within each circular plot, we recorded aspect, slope, elevation, and coordinates at plot center (Table 1). Additionally, we used latitude, slope, and aspect to calculate the heat load index (HLI) for each plot location, a measure of direct incident radiation (McCune and Keon 2002; McCune 2007). All individuals (live and dead trees) were recorded within each plot to obtain basal area by measuring the DBH (diameter at breast height) at 1.3 m from the ground of every individual with a DBH > 4.0 cm. Among trees that were fire-killed and resprouting, we considered the individual as dead (dead above-ground) and counted the resprout as regeneration. If tree individuals were bifurcated below a height of 1.3 m, these trees were tallied as separate individuals. The number of recorded trees within plots was used to calculate live and dead tree densities (Table 1). To identify the species when tree individuals were totally burned, we observed the presence of resprouts, compared bark characteristics, and examined tree bole and branch architecture to identify the species when possible. We established four quadrats (1 × 1 m) at 7 m from the plot center in each cardinal direction (north, east, south, west) to estimate the percent

coverage of coarse (> 7.6 cm diameter) and fine (< 7.6 cm diameter) woody debris, bare ground, and understory vegetation (herbs, shrub, and bamboo; Table 1). Vegetation cover (tall understory vegetation and canopy cover combined) was also measured in each quadrat with a spherical crown densiometer placed at 0.5 m from the ground to evaluate its interaction with seedlings. To accurately quantify tree juvenile abundance while maximizing sampling efficiency, all tree stems < 4.0 cm DBH (hereafter seedlings) per tree species were counted within four variable-width belt transects extending from plot center in each cardinal direction (Busby et al. 2020). First, we estimated seedling abundance within the default four 2×14 m (112 m^2) belt transects; if estimated seedling abundance was greater than 200 or less than 10 individuals, sampled belt transect size was reduced to 1×14 m (56 m^2) or increased to the entire plot area (700 m^2), respectively. Belt-transect sizes were used to expand the seedling counts to the plot level. We also counted the total number of resprouts (individual stems) per tree species in the entire plot area (0.07 ha), which were mostly growing from the base or root of fire-killed trees. Lastly, potentially seed-bearing tree distances of the closest 10 mature live *Nothofagus* spp. (i.e., potential seed-bearing trees since we were unable to identify flower or fruits at a distance and our observations were made 5 years after

Table 1 Field collected and remote sensing data and their methods of measurement at our study sites

Category	Variable	Method of measurement	Unit	Type and range
Biotic	Bare ground cover +	Field measured at quadrat level (4 quadrats, at 7 m from plot center, averaged)	Relative coverage (%)	Continuous; bounded [0 100]
	Coarse woody debris * +		Relative coverage (%)	Continuous; bounded [0 100]
	Fine woody debris +		Relative coverage (%)	Continuous; bounded [0 100]
	Distance to seed-bearing trees *	Field measured (10 closest mature trees; averaged)	Meters (m)	Continuous; bounded [0 200]
	Herbs +	Field estimated at quadrat level (4 quadrats, at 7 m from plot center, averaged)	Relative coverage (%)	Continuous; bounded [0 100]
	Shrubs +		Relative coverage (%)	Continuous; bounded [0 100]
	Bamboos +		Relative coverage (%)	Continuous; bounded [0 100]
	Vegetation cover * +	Field measured at quadrat level (4 quadrats, at 7 m from plot center, averaged)	Relative coverage (%)	Continuous; bounded [0 100]
	Total basal area	Derived from field-measured tree structure at plot level	Area/hectare (m^2/ha)	Continuous; not bounded [0 117.9]
	Live tree basal area of each species-specific trait group *		Area/hectare (m^2/ha)	Continuous; not bounded [0 85.3]
	Dead tree basal area *		Area/hectare (m^2/ha)	Continuous; not bounded [0 33.3]
	Live tree density +		Tree/hectare	Continuous; not bounded [0 3211.4]
	Dead tree density +		Tree/hectare	Continuous; not bounded [0 2716.2]
Abiotic	Elevation *	Field measured at plot level	Meters (m)	Continuous; bounded [988 1745]
	Slope		Degrees (°)	Continuous; bounded [2 42]
	Aspect		Degrees (°)	Continuous; bounded [4 360]
	Heat Load Index *	Derived from field-measured slope, aspect, and latitude	Unitless	Continuous; not bounded [0.53 1.24]

Note that variables used in the permutational multivariate analyses of the variance (PERMANOVA), and variables considered as predictors in the post-fire seedling and resprout regeneration GLM models are indicated by + and * in the table, respectively

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fire) and 10 live Araucaria female individuals (presence of distinct female cones) were measured from the plot center using a rangefinder (TruPulse 200/Laser Technology). Given tree species' limited seed dispersal ranges in our study areas, we did not count any potential seed source individuals if they were further than 200 m from plot center.

Statistical analysis
Forest structure
We conducted multivariate and univariate analyses to detect potential differences in post-fire forest structure across burn severity classes in each study area (single fire and reburn), adapting methods from Stevens-Rumann and Morgan (2016) and Busby et al. (2020). To assess differences in post-fire forest structure, a Permutational Multivariate Analyses of the Variance (PERMANOVA) with 999 permutations and the Bray–Curtis distance dissimilarity index (*vegan* package; Oksanen et al. 2020) was used. For this analysis, we considered nine field-measured variables: percent of ground cover of bare ground, coarse and fine woody debris; relative vegetation cover; abundance coverage of herbs, shrubs, and bamboos; and live and dead tree density (Table 1). Pairwise multilevel comparison was used when significant differences were detected by using burn severity as grouping factor with 999 permutations, distance of Bray–Curtis, and adjusting *p*-values with the Holm method (*pairwiseAdonis* package; Martínez 2017). To identify potential differences in individual components of forest structure across burn severity class in each study area, we conducted a non-parametric univariate Kruskal–Wallis test. If statistical differences were detected, a post hoc Wilcoxon rank sum test was used for pairwise comparisons; the Holm method was used to adjust the *p*-value for multiple comparisons (*stats* package; R Core Team 2022).

Forest regeneration
We used negative binomial generalized linear models (GLM) to identify drivers of post-fire forest regeneration patterns in terms of seedling and resprout counts (*MASS* package; Venables and Ripley 2002) in each study area (single fire and reburn). Individual models were fit on seedling and resprout counts for the primary tree species according to respective post-fire regeneration traits and strategies (sensu Prior and Bowman 2020; detailed explanation in Supplemental Data S1): Araucaria resprouts and surviving trees produce seedlings after fire (post-fire facultative resprouter/seeder, hereafter PFFRS); *N. alpina* and *N. obliqua* resprout, but they are not cued to produce seedlings after fire (post-fire obligate resprouter, hereafter PFOR)—surviving trees however could also colonize from seeds from unburned patches; and *N.*

dombeyi and *N. pumilio* cannot resprout and are not cued to produce seedlings after fire, but they can colonize from unburned patches or surviving seed trees (post-fire obligate colonizer, hereafter PFOC). Before fitting the models, variables were standardized (*z*-score; Table 1). Seedling abundance models were initially fitted with all explanatory variables. For resprout models, we excluded distance to potential seed-bearing trees and vegetation cover as predictors, given that the former attribute is not related to the number of resprouts and the latter attribute captured most of the same resprouts as cover in the understory. To improve model performance and interpretability, a stepwise backward selection procedure was used to reduce full models to their parsimonious version by relative improvements in Akaike Information Criterion (AIC). We evaluated significant outliers with Cook's distance and removed from each model if these distance values exceeded 0.5 (Cook 1979). Furthermore, multicollinearity was assessed via the variance inflation factor (VIF); if any of the predictors had a VIF > 2, we removed it and created a new version of the model to be later compared with the full and reduced models. Full and reduced models were compared using AIC and analyses of the variance by the Likelihood ratio tests of negative binomial models (*stats* package; R Core Team 2022). Model predictive performance was evaluated by comparing Spearman's rank correlation between predicted and observed values. Additionally, we also evaluated the goodness of fit of each model calculating Pearson's chi-squared statistics. Both tests were conducted with *stats* package.

Results
Fire effects on forest structure
We identified a total of 15 tree species present within our study plots (Table S1); however, only the dominant tree species were considered in our results. In severely burned plots (high severity and reburned), only a few Araucaria (PFFRS) and no southern beech *N. pumilio* and *N. dombeyi* (PFOC) individuals were found to have survived the fire, when sampled 5 years post-fire (Fig. S1). The post-fire structure of *Araucaria-Nothofagus* forests was statistically different among burn severity classes in both once burned and reburned plots when all nine variables were considered in each PERMANOVA analysis (pseudo-F: 3.311, *P* = 0.001). The pairwise PERMANOVA indicated that forest structure was statistically different between plots burned by a single fire with high and low (pseudo-F: 1.924, *P* = 0.014) fire severities and high severity and unburned areas (pseudo-F: 2.966, *P* = 0.001); low severity was not statistically different from unburned areas (Table S2). Forest structure in reburned plots was statistically different between unburned and high-low

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(pseudo-F: 2.726, $P=0.001$) or high-high (pseudo-F: 2.196, $P=0.001$), but not between high-low and high-high (Table S2).

When comparing differences among individual forest structure attributes at the single fire study area, live tree density, vegetation cover at 0.5 m, and shrub cover were significantly greater in unburned plots than in burned plots (low and high), while dead tree density and fine woody debris were significantly lower in unburned plots

(Fig. 3). Moreover, dead tree density and shrub cover were statistically lower and greater between unburned and both low- and high-severity burned classes ($P<0.05$, Fig. 3), respectively. Herb, bamboo, bare ground, and coarse woody debris cover were not statistically different between burn severity classes (Fig. 3). In the reburned study area, we found that live tree density and vegetation cover were significantly greater in unburned plots than in reburned plots ($P<0.05$); only dead tree density
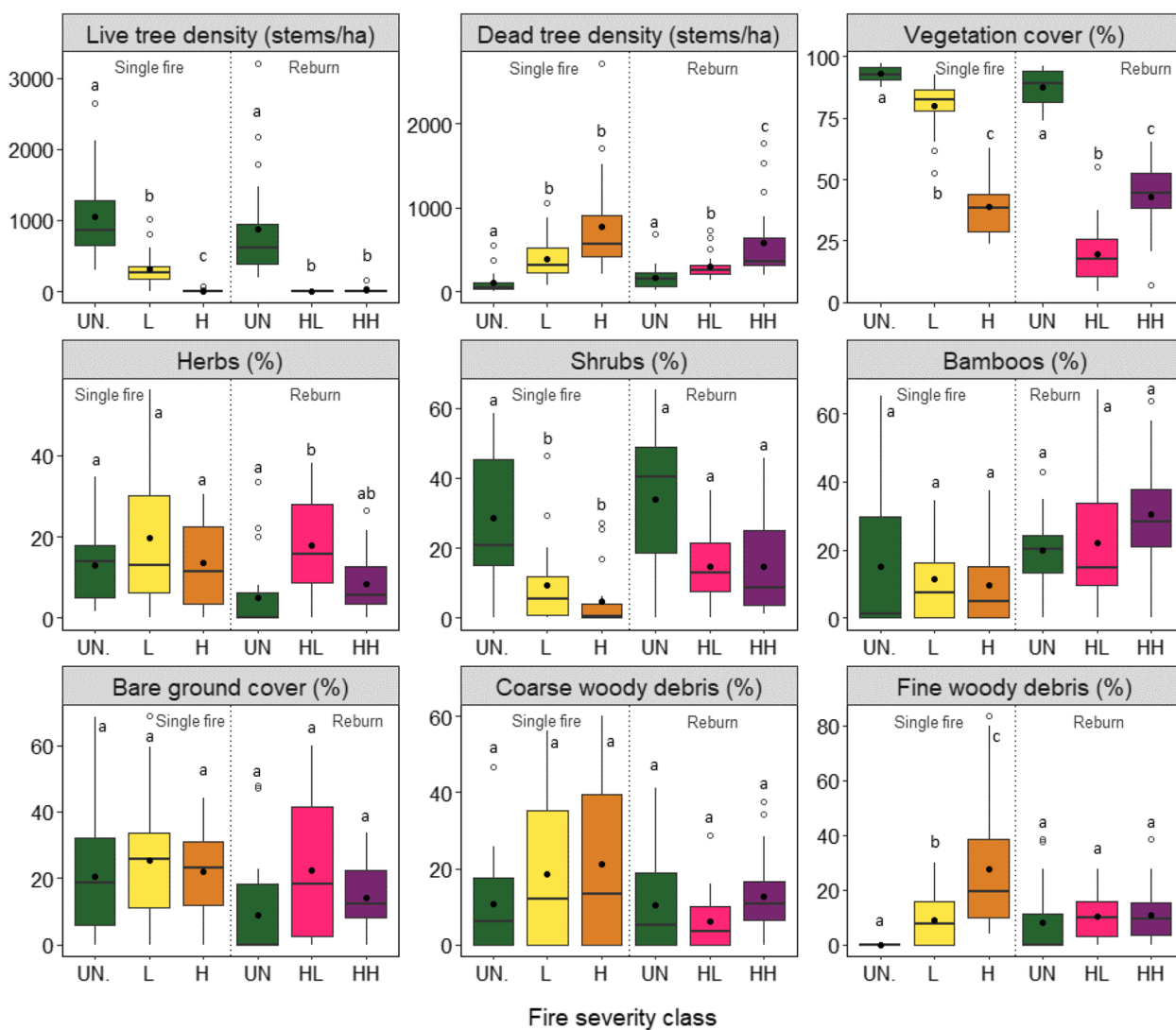
Fig. 3 Boxplots from 9-field measured variables as characteristic of forest structure across fire treatments in areas burned with a single fire (China Muerta: UN, L, and H bars) and reburned (Malleco-Tolhuaca: UN, HL, and HH bars). In each panel, sites affected by single fire (left) and reburned (right) are separated by a vertical dotted line. Vertical lines (whiskers) indicate variability outside of the interquartile range, thick horizontal lines represent the median, black dots indicate the mean, and white dots are outliers. Different lowercase letters indicate statistical difference of each variable along burn severity within each separated study area (Kruskal–Wallis test; pairwise comparison Wilcoxon rank test; Holm *p*-adjust method; $P<0.05$)

was significantly lower in unburned plots (Fig. 3). Furthermore, live tree density and herb cover were not statistically different between high-low and high-high plots, but dead tree density and vegetation cover were greater in high-high compared to high-low plots (Fig. 3). Shrub, bamboo, bare ground, and coarse and fine woody debris cover were not statistically different between burn severity classes in the reburned area (Fig. 3).

Fire effects on tree regeneration

We recorded a total of 12 tree species growing as seedlings (stems < 4.0 cm DBH) within our study areas (Table S1), although our interpretations are focused on

regeneration of the dominant tree species Araucaria and *Nothofagus*.

Considering sexual reproduction by seedling establishment at the once burned study area, seedling abundance was greatest for PFOC, followed by PFOR (Fig. 4A). PFOC and PFOR seedling abundances were not statistically different between unburned plots and those burned at low severity, whereas PFOC seedling abundances were statistically different between plots burned at low and high severities ($P < 0.001$; Fig. 4A). The PFOC *N. pumilio* was the most abundant species at the single burn study area and primarily concentrated in unburned and low severity plots, followed by the PFOR *N. alpina* in low
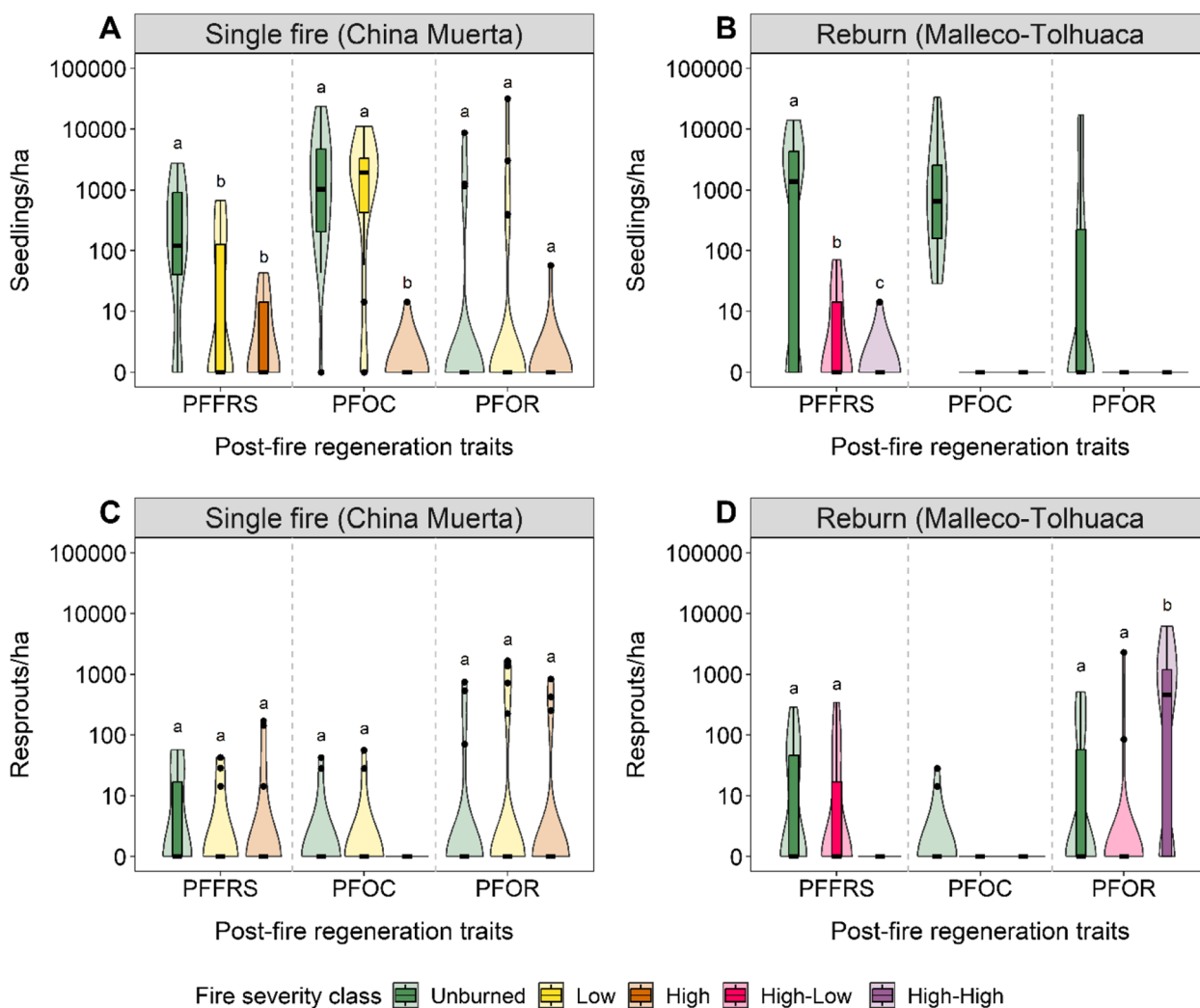

Fig. 4 Boxplot and violin plots of seedling and resprout abundances of PFFRS (post-fire facultative resprouter/seeder: *A. araucana*), PFOC (post-fire obligate colonizers: *N. dombeyi*, *N. pumilio*) and PFOR (post-fire obligate resprouters: *N. alpina*, *N. obliqua*) at China Muerta (single burn; panels **A** and **C**) and Malleco-Tolhuaca (reburn; panels **B** and **D**) study areas. Vertical lines (whiskers) indicate variability outside of the interquartile range, thick horizontal lines represent the median, black dots are outliers. Lowercase letters indicate statistical difference among species within each fire severity in each study area (Kruskal–Wallis test; pairwise comparison Wilcoxon rank test; Holm *p*-adjust method; $P < 0.05$). *Y*-axis represented in $\log_{10}$ scale

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severity plots (Table S3, Fig. S2). Seedling abundances of the PFFRS species Araucaria were statistically different between unburned and burned plots only ($P < 0.05$, Fig. 4A). *Nothofagus* seedling abundance was minimal in plots burned at high severity (Fig. 4A, Table S3). In contrast, in the reburned study area, Araucaria seedling abundance was the greatest across species, and it was statistically different among burn severity classes ($P < 0.05$; Fig. 4B, Table S3). PFOC and PFOR seedlings were also abundant in unburned plots at the reburn, but zero seedlings were found in reburned plots (high-low and high-high; Fig. 4B, Table S3).

In the case of asexual regeneration by resprouts, and considering first the once burned study area, PFOR species were the most abundant and were not statistically different across fire severity classes (Fig. 4C). The PFOR *N. alpina* and *N. obliqua* were the most abundant and primarily concentrated in plots burned at low severity (Table S4). Araucaria resprouts were present across all fire severity classes, with lower and higher abundance than *Nothofagus* characterized by PFOR and PFOC traits, respectively (Fig. 4C, Table S4). Although very scarce, individuals of *N. pumilio* presented basal resprouts in unburned reference forests and at once-burned areas low severity sites. However, resprouts were only rarely observed on a few live trees, and the probability of resprouting being attributed to fire is low. In contrast, in the reburned study area, resprout abundance of PFOR species was significantly greater in plots affected by two high severity fires (high-high, Fig. 4D). The PFOR *N. alpina* resprout abundance was statistically different between high-high and high-low plots and was greatest in high-high plots ($P = 0.004$; Table S4, Fig. S2). Araucaria resprouts were only found at relatively low densities in unburned and high-low severity plots and were not statistically different between those two fire severity classes (Table S4). Finally, the presence of resprouts on a few individuals of *N. pumilio* and *N. dombeyi* was observed in unburned reference forests, but these were very rarely observed.

Biotic and abiotic drivers of tree regeneration

PFFRS (Araucaria) seedling abundance in the single fire study area was significantly and negatively predicted by dead tree basal area (Fig. 5A) and distance from the seed source (Fig. 5B). PFOC seedling abundance was also significantly negatively predicted by distance to seed-bearing trees (Fig. 5C, Table 2). Seedling abundance models were validated with Pearson's goodness of fit (both $P > 0.05$); the PFOC seedling abundance model had greater predictive accuracy than the PFFRS model (Spearman's rho: 0.773 and 0.729, respectively; Table 2). Resprout abundance for PFFRS in this study area was

significantly and positively predicted by live tree basal area (Table 2) and heat load index (Table 2); however, predictive power was weaker (Spearman's rho: 0.474). Seedling and resprout abundance of PFOR could not be fitted, possibly due to the low number of plots with seedlings (13% of the plots) and resprouts (17% of the plots).

In the case of the reburned study area, PFFRS seedling abundance was positively predicted by vegetation cover (Fig. 5E), and elevation (Fig. 5F), and negatively predicted by distance from seed source (Fig. 5D, Table 2). PFFRS resprout abundance was only positively predicted by elevation (Table 2). PFFRS seedling and resprout abundance models were validated with Pearson's goodness of fit (both $P > 0.05$); predictive accuracy was greater in the seedling than in the resprout model (Spearman's rho: 0.778, and 0.591, respectively; Table 2). Seedling abundance models from both PFOC and PFOR groups were not conducted due to the lack of *Nothofagus* seedling establishment in the understory of high-low and high-high burn severity class plots, and in general due to the low number of unburned plots with seedling establishment at the reburn study site. Lastly, the PFOR resprout model could not be fit due to low representation across sampled plots, although resprouts were mostly present in plots at the high-high burn severity class (Fig. 4).

Discussion

Severe and short-interval wildfires shape post-fire structure

Our results on forest structure characterization showed greater combined pre-fire dominance of PFFRS (Araucaria) and PFOC (*N. pumilio* and *N. dombeyi*) at the single burn study area (mostly mixed *Araucaria-Nothofagus* forests), whereas PFOR (*N. alpina* and *N. obliqua*) had greater presence at the reburn study area (mostly Araucaria and *Nothofagus* vegetation belts). We found that post-fire forest structure in areas burned at least once by a single high severity fire was statistically different from unburned or burned by a single low severity fire, with a greater number of dead adult tree species from all functional traits, supporting our first hypothesis. Furthermore, short-interval reburns did not produce statistically different post-fire forest structures among plots burned at high-then-low and at high-then-high severities, where all tree species from both combined burn severities were scorched and dead, also supporting our hypothesis. Across forest types globally, an increasing body of evidence indicates that any high-severity fire in a short temporal period is the primary driver of major shifts in post-fire forest structure (Bowman et al. 2014; Stevens-Rumann and Morgan 2016; Tepley et al. 2017; Turner et al. 2019; Busby et al. 2020; Coop et al. 2020; Steel et al. 2021; Nemens et al. 2022). In *Araucaria-Nothofagus*
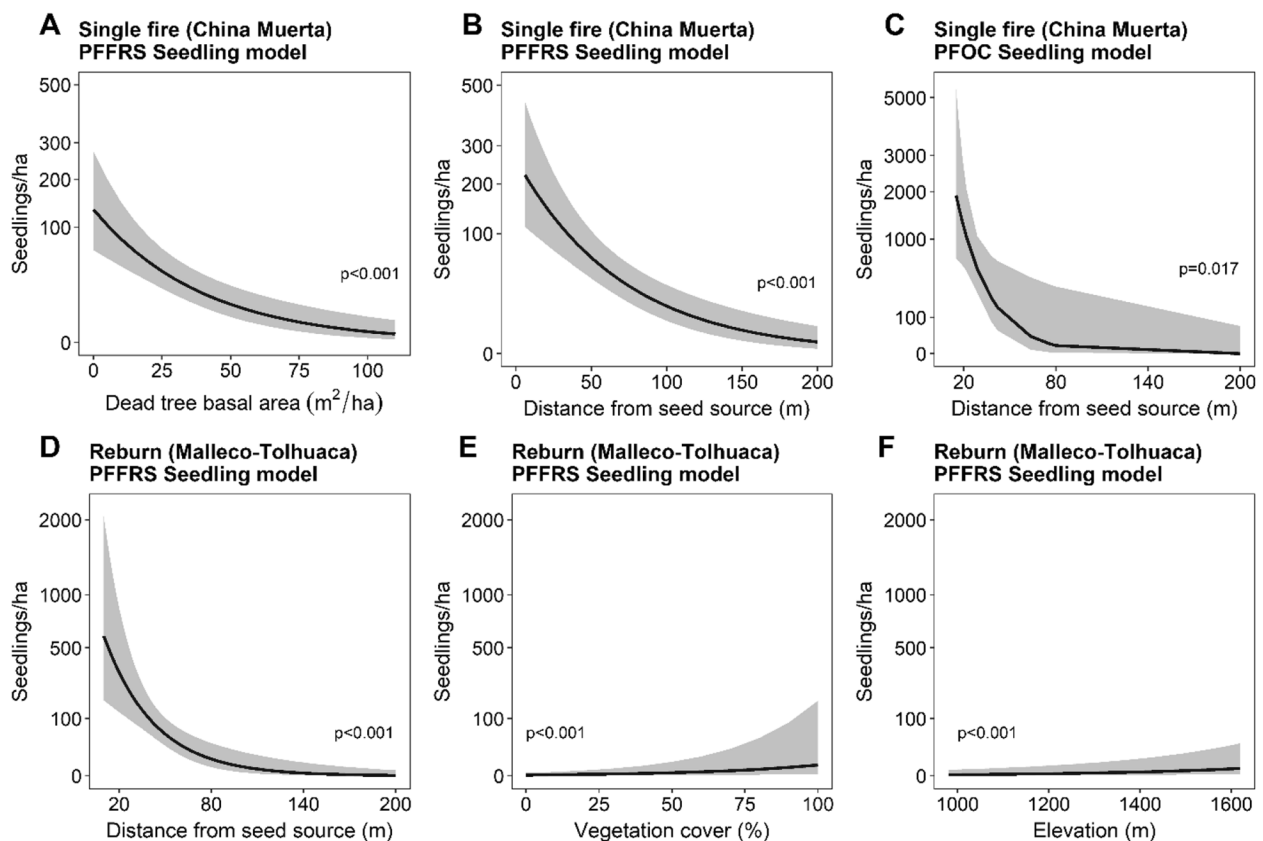
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Fig. 5 Nonlinear regression curves of post-fire seedling and resprout abundances and their confidence intervals (grey shaded area) as a function of significant predictors ($P \leq 0.05$) of the reduced negative binomial GLMs (Table 2) at China Muerta (**A–C**) and Malleco-Tolhuaca (**D–F**) study areas. Panels indicate seedling abundance models of post-fire facultative resprouter/seeder traits (PFFRS; *A. araucana*), and post-fire obligate colonizer traits (PFOC; *N. dombeyi* and *N. pumilio*). *Y*-axis represented in square-root scale

forests of the south-central Chilean Andes, infrequent high-severity fire effects drive massive transfer of live trees into dead standing and downed wood pools, shaping the long-term structure and composition of these forests (González and Veblen 2007; González et al. 2010a, b; Assal et al. 2018). A study conducted in similar *Araucaria-Nothofagus* forests on the eastern side of the Andes (i.e., under drier conditions) found that isolated trees with less connected canopies, as tree size increased, are more likely to burn at high severity (Franco et al. 2022). This may be driven by warmer and drier microsite conditions, influenced by a lack of or poor horizontal canopy connectivity, and exacerbated by the abundant establishment of the highly flammable, shade-intolerant bamboo *Chusquea* spp. that rapidly ignite and spread fire (Cóbar-Carranza et al. 2014; Franco et al. 2022). Our field observations and results indicate that *Chusquea* spp. is widely present in both study areas; it has been documented as a species that abundantly resprouts after fire (Veblen 1982b; González and Veblen 2007; Assal et al. 2018; Fuentes-Ramirez et al. 2020; Arroyo-Vargas et al. 2022).

In the case of forests affected by low severity fire, and in the absence of reburns, forest development will likely continue toward late successional stages, where gap-phase dynamics primarily control new opportunities for tree recruitment (Veblen et al. 1981; Veblen 1982a). In general, understory vegetation cover (e.g., herbs, shrubs, bamboos) showed little change pre- and post-fire across burn severity gradients, suggesting that this vegetation layer is resilient to wildfire in these forests (Fuentes-Ramirez et al. 2020; Arroyo-Vargas et al. 2022). Relatively rapid recovery of the understory plant community was recorded 3 years after the 2002 fire at Malleco-Tolhuaca (González and Veblen 2007), whereas slower recovery of understory plant communities was found in severely burned areas 3 years after the 2015 wildfire at China Muerta (Arroyo-Vargas et al. 2019). Such differences in understory vegetation recovery and composition between study areas may be related to geographic location (China Muerta is located further south and east [stronger continentality effect], and at higher elevation in the Andes [colder] than the Malleco-Tolhuaca study

Table 2 Negative binomial GLM coefficients estimates (β) for the reduced seedling and resprout count models for the PFFRS (post-fire facultative resprouter/seeder: *A. araucana*), and PFOC (post-fire obligate colonizers: *N. dombeyi, N pumilio*)

Site	Category	Predictors	Models		PFOC (*N. dombeyi & N. pumilio*)
			PFFRS (*A. araucana*)		
			Seedlings	Resprouts	Seedlings
China Muerta (single burn)		*Intercept*	**0.770**	**− 0.998**	*− 1.216*
	Biotic	Coarse woody debris			
		Dead tree basal area	**− 1.400**		
		Distance to seed-bearing trees	**− 1.890**	NA	**− 8.874**
		Live tree basal area		**1.017**	− 0.630
		Vegetation cover		NA	
	Abiotic	Elevation		0.792	
		Heat load index	0.389	**1.012**	
	Performance metrics	Spearman's rank (rho)	0.729	0.474	0.773
		Pearson's statistic χ^2	1320	360	1888
		Pearson's statistic p	0.329	0.402	0.450
Malleco-Tolhuaca (reburned)		*Intercept*	*− 3.908*	*− 2.520*	
	Biotic	Coarse woody debris			
		Dead tree basal area			
		Distance to seed-bearing trees	**− 4.674**	NA	
		Live tree basal area			
		Vegetation cover	**1.584**	NA	
	Abiotic	Elevation	**1.027**	**3.530**	
		Heat load index			
	Performance metrics	Spearman's rank (rho)	0.778	0.591	
		Pearson's statistic χ^2	728	469.4	
		Pearson's statistic p	0.359	0.791	

The sample size for each full model was 60 plots. Full seedling models considered distance to seed-bearing trees or live tree basal area and vegetation cover or dead tree basal area due to their high correlation (> 0.7). We did not consider distance to seed-bearing trees and vegetation cover as a predictor in resprout models, which are designated with NA (not applicable). Bold values indicate predictors that were statistically significant ($p < 0.05$) in the reduced models. Spearman's rank correlation indicates the distance between predicted and observed values of the seedling count models. Pearson's statistics indicate the lack of fit if the *p*-values are significant ($p < 0.05$)

area). Despite overall understory vegetation recovery, rare or fire-sensitive native species or the establishment of exotic and invasive species may be either constrained (i.e., due to the lack of post-fire traits of some native species) or facilitated (i.e., due to the livestock presence) in burned areas, respectively (Urrutia-Estrada et al. 2018; Arroyo-Vargas et al. 2019, 2022).

High severity fire events in *Araucaria-Nothofagus* forests that create high dead woody fuel loads and facilitate rapid post-fire recovery of flammable understory vegetation, such as shrubs and bamboos, may increase the risk of short-interval reburns, especially under increasingly warm and dry summer weather conditions (Paritsis et al. 2015; Blackhall et al. 2017; Fuentes-Ramirez et al. 2020; Landesmann et al. 2021; Arroyo-Vargas et al. 2022). In fact, the 2015 fires were preceded by a historic megadrought across central and south-central Chile, with significant precipitation deficits since 2010 (Garreaud et al. 2017, 2020; Boisier et al. 2018); moreover, this region has been under a trend of rising temperatures since the 1950s (Holz et al. 2017). These climatic trends are likely to promote positive fire-vegetation feedbacks that in turn increase fire frequency, extent, severity, and support dominance by flammable, shade-intolerant bamboos, shrubs, and overall, other species that are able to resprout under warmer and drier conditions (Paritsis et al. 2015; Kitzberger et al. 2016; Tiribelli et al. 2018; Landesmann et al. 2021). These feedbacks may lead to long-term conversions of fire-affected *Araucaria-Nothofagus* forests or Araucaria, *N. alpina, N. obliqua* vegetation belts into alternative states dominated primarily by bamboos and shrubs species (Paritsis et al. 2015; Assal et al. 2018; Landesmann et al. 2021; Arroyo-Vargas et al. 2022).

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Burn severity and short-interval fires affect tree regeneration

Species from the *Nothofagus* genus described in this study are all able to colonize areas through seed dispersal and establishment (sexual reproduction) when canopy gaps are created and/or disturbances remove vegetation cover (Veblen et al. 1996). In this study, we separate *Nothofagus* spp. according to their post-fire traits and strategies that emerge post-disturbance (i.e., resprouting capacity after fire; asexual reproduction). Further discussion of the selection of trait and strategy group classifications among main tree species is included in Supplemental Data S1.

In general, *Nothofagus* seedlings belonging to the PFOC (*N. dombeyi, N. pumilio*) and PFOR (*N. alpina, N. obliqua*) groups were rarely found in sites once burned at a high severity and were totally absent from reburned sites involving a high severity fire due to the lack of live adult individuals. *Nothofagus* spp. within the PFOC and PFOR groups are considered fire-sensitive due to a thin bark that largely fails to protect the cambium from heat transfer and thus fire-caused cambium necrosis, especially when younger. In addition, often their canopies are lower in height in comparison to large Araucaria, so the probability of crown fires is higher. Despite exhibiting high sensitivity to fire, surviving *Nothofagus* individuals do produce small and lightweight seeds, fluctuating from 1.8–3.5 mg (*N. dombeyi*; Lusk and Kelly 2003; Donoso et al. 2006) to 10–27.8 mg (*N. pumilio*; Schinelli 2012), which disperse by wind very effectively (especially in the case of *N. dombeyi*) and up to 500 m from a focal tree (less than 100 m for *N. pumilio* and more than 500 m for *N. dombeyi*; Donoso 1993; Kitzberger and Veblen 1999; Assal et al. 2018). In contrast, Araucaria seedlings were found in both once burned and reburned sites that involved a high severity fire, but at lower densities in areas reburned with a second high severity fire. Although most Araucaria survive low-to-moderate fires due to its thick bark and tall canopies, especially at the adult stage, trees are less likely to survive severe fire effects (crown fires). On surviving trees, at the time of the fire if cones are present and survive on female trees, seeds inside of cones are protected and then can be released soon after the fire (González et al. 2013; Fuentes-Ramírez et al. 2019). This may explain why we observed Araucaria seedling establishment directly underneath dead (at the time of sampling) adult Araucaria individuals (González et al. 2013). Araucaria seeds are more tolerant to heat than those of *Nothofagus* (Boberg et al. 2010; Cóbar-Carranza et al. 2015), which allow them to also establish in exposed areas lacking overstory and understory vegetation cover. In addition, Araucaria and *Nothofagus* spp. seed in masting cycles (Donoso 1993, 2006; Veblen et al. 1996;

Sanguinetti and Kitzberger 2008; Fajardo et al. 2016), and thus post-fire seed dispersal (and subsequent seedling establishment) may fail to occur when poor seed crops follow fire. In those cases, seedling establishment may appear temporally protracted—assuming seed sources are still present and spatially proximate. However, when understory vegetation (especially *Chusquea* bamboo) recovery occurs rapidly after fire, as was observed in our study sites, seedling competition with recovering vegetation may limit tree establishment to a short post-fire temporal window, or until bamboo flowering events (González et al. 2002; Holz and Veblen 2006).

Post-fire resprouting regeneration responses were found in different degrees in Araucaria (PFFRS), *N. alpina* and *N. obliqua* (both PFOR) in both single and reburned study areas. Previous studies have documented that these species have the capacity to resprout after fire (Donoso 1993; Assal et al. 2018; Fuentes-Ramírez et al. 2019), responses that were also observed within our study areas. Our results show that tree regeneration in reburned areas occurred primarily by *N. alpina*, which resprouted profusely after two severe wildfires in a short period of time, suggesting this species exhibits high resilience to severe and short-interval fires. In contrast, we did not find Araucaria resprouts after two high burn severity fires in a short period of time, suggesting that increasing frequency and severity of short-interval fire, as projected under climate change, may erode the resilience of this endangered conifer. Conversely, *N. dombeyi* and *N. pumilio* (PFOC) are typically not able to resprout vegetatively after any fire.

Biotic and abiotic predictors differ between seedling establishment and resprouting

Seedling establishment of PFFRS (Araucaria) and PFOC (*N. dombeyi* and *N. pumilio*) may fail when seed-bearing trees are not spatially proximate. As hypothesized, post-fire seedling abundance among these species was primarily driven by distance to live seed-bearing trees (Assal et al. 2018; Arroyo-Vargas et al. 2019). To successfully colonize burned areas, surviving seed-bearing *Nothofagus* trees need to be within a distance of 30–100 m and produce a productive post-fire crop (Kitzberger and Veblen 1999; Assal et al. 2018; Urretavizcaya et al. 2018). To facilitate successful seed germination, establishment, and seedling survival, cool, moist, and protected site conditions are needed. Numerous observational and experimental studies document the sensitivity of successful establishment of *N. pumilio* to protective vegetation or coarse woody cover and adequate soil moisture (Heinemann et al. 2000; Tercero-Bucardo et al. 2007; Pastur et al. 2014).

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In the case of Araucaria, seeds disperse poorly due to their larger size and heavier weight (2–4 cm, and 3.5–5 g/ seed; Fajardo and González 2009; González et al. 2013). These characteristics, in addition to our results, demonstrate that the poor dispersal capacity of Araucaria may critically limit its post-fire regeneration in severely burned areas, particularly when the number of surviving trees is few to none. Moreover, short-interval reburns may truncate post-fire regeneration of Araucaria when wildfires occur in a period shorter than the time required for the tree to sexually mature and produce seeds (e.g., > 30 years and > 20 cm of DBH; Sanguinetti and Kitzberger 2008), resulting in local-scale population collapse (Fig. 1).

The GLM models predicting post-fire asexual regeneration by resprout are generally weaker than seedling abundance models, likely because our resprout models did not consider any below-ground predictor. Mechanisms that drive post-fire resprouting have been shown to involve the allocation of plant resources, which differs between obligate resprouter (shoots and storage tissues) and facultative seeder (shoots) species (Pausas et al. 2004; Lawes and Clarke 2011). This may explain the weaker model performance for Araucaria—or the inability to fit a GLM for PFOR trait species. In the field we found widespread basal resprouting by Araucaria after high-severity fire (consistent with González et al. 2010b, 2013), and our results further suggest that larger-diameter Araucaria may have a higher probability of resprouting after a single fire; drier microsite conditions were also correlated with increased probability of basal resprout after a single fire (Boberg et al. 2010; Cóbar-Carranza et al. 2015). Thus, considering prior work and our results, Araucaria is likely to successfully recover (albeit slowly) after a single high severity fire and even under projected warmer and drier conditions, yet this recovery can be disrupted by repeated short-interval fires.

Forest management implications

While fires have been an intrinsic evolutionary process in our study region, as most clearly reflected by the fire-related traits of Araucaria, our results indicate that frequent, large, and severe fires can threaten the persistence of Araucaria and *Nothofagus* populations in these southern hemisphere temperate forests. Although prescribed and managed fires are known to be an effective method to reduce the risk of high severity fires in many forests that historically have been affected by periodic wildfires elsewhere (USDI, USDA 2014), the implementation of a similar "fight fire with fire" strategy in *Araucaria-Nothofagus* forests is fraught with technical challenges and the likelihood of undesired ecological outcomes. For example, while fuel reduction would be the desired outcome of prescribed or managed fires, the duration of any reduction in flammability is likely to be short-lived where the fire promotes development of fuels dominated by highly flammable resprouting vegetation, including *Chusquea* bamboo species (Mermoz et al. 2005; Kitzberger et al. 2016). Given the rapid post-fire recovery of shrub and bamboo fuels observed in our study area, the application of intentional forest burning to reduce fuel loads is likely to have the undesired outcome of increasing landscape-scale flammability. Additionally, the potential effects of fire on biodiversity, water resources, soil attributes, exotic plant invasions, and CO_2 emissions must be considered before adopting intentional burning as a tool to reduce fuels in these ecosystems. Furthermore, local wildland firefighter training is primarily focused on controlling and extinguishing fire rather than using it as a management tool, at least in forested landscapes. Current policy in our study area (Ortega et al. 2006) limits prescribed burning to agricultural lands and continues to stress prevention of wildfires which is consistent with existing knowledge that burning has been documented to promote conversion from less-fire-prone forests to more-fire-prone shrublands and bamboo thickets (Mermoz et al. 2005; Paritsis et al. 2015; Tiribelli et al. 2018; Landesmann et al. 2021). Moreover, any prescribed fire or "let burn policy" would have to contend with public concern for protection of sensitive ecosystems within protected areas and especially with the cultural and sacred significance of the Araucaria forests for the Mapuche and Pehuenche people (Sanguinetti et al. 2023), who do not apply fire to their forests.

Land managers in this region are increasingly focusing on the need for site-specific research to support management protocols that can better cope with climate change challenges (Donoso et al. 2022; Souza-Alonso et al. 2022). In the context of adaptation to continued climate change, these challenges will intensify and will need to be addressed through management decisions, based on ecological understanding of the pros and cons of a range of adaptive decisions for specific management areas. Toward that effort, our research results, when applied in the Resist-Accept-Direct (RAD) framework (Lynch et al. 2022), can be used to inform decisions made by stakeholders and managers to better adapt to the likelihood of climate-induced increases in fire activity in the studied *Araucaria-Nothofagus* forests. The RAD framework is a useful and pragmatic tool encompassing three adaptive pathways that can be considered for ecosystems facing rapid transformations due to climate change (Schuurman et al. 2020). The results of our study can be applied in a RAD framework by identifying patterns and mechanisms associated with post-fire regeneration failure and success in the *Araucaria-Nothofagus* forests of our study area. For

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example, our findings support the development of forest management plans that *resist* transitions from forest to non-forest by both protection of and planting of trees that have more effective fire resistance and fire recovery traits (e.g., Araucaria, and/or *N. alpina, N. obliqua*). At some other sites with appropriate vegetation attributes, managers, and stakeholders may *accept* a post-fire reduction in abundance of *N. dombeyi* and *N. pumilio,* where it is likely that there would be an acceptable post-fire shift toward dominance by *Chusquea* bamboo and/or other resprouter species. Finally, to *direct* and align forest ecosystems with expected future climatic conditions, managers may consider planting of tree species with resprouting traits at higher elevation than their current range based on their superior tolerance to warmer and drier conditions and demonstrated ability to vigorously recover following fire (e.g., *N. alpina*). Decision-making for adapting to a changing climate—whether promoting resist, accept, or direct pathways—must prioritize societal values while also being informed by ecological knowledge specific to the ecosystems under discussion.

Conclusions

In the *Araucaria-Nothofagus* forests of the Andean region of south-central Chile, the effects of burn severity on forest structure and tree regeneration are distinct for fires of different severity and return intervals when measured 5 years post-fire. A single low-severity fire only slightly alters the structure of the forest, whereas a high severity fire greatly reduces the number of surviving trees, limits post-fire tree establishment, and creates exposed environmental conditions where resprouting shrub and bamboos thrive in following years. If the fire-free interval following a high-severity event is long enough to allow tree species to reestablish and achieve sexual maturity and fire-resistant attributes, however, alternative ecosystem trajectories can be avoided. Yet, even if future climatic conditions are favorable for tree regeneration, it could take decades to centuries to reestablish similar pre-fire conditions. Conversely, increasing fire frequency and severity may shift affected *Araucaria-Nothofagus* forests into persistent, non-forest ecosystem states. Severe short-interval reburns can considerably reduce seedling establishment by the fire-adapted species *A. araucana* and cause regeneration failure among obligate seeding *Nothofagus* species. Overall, warming-mediated changes to these ecosystems' fire regimes will be detrimental for *A. araucana* dominance and regeneration as well as for seedling establishment of all *Nothofagus* species. In contrast, shifting fire regimes will be beneficial for *Nothofagus* spp. that are able to resprout after fire (*N. alpina* and *N. obliqua*) and for resprouting shrub and bamboo species. As fire activity increases, positive fire-climate-vegetation feedbacks may drive severely burned *Araucaria-Nothofagus* forests into dry, exposed, and flammable shrubland ecosystem states. We highlight the importance of identifying the relative success of the key tree species post-fire seedling establishment and regeneration by resprouting that determine post-fire vegetation trajectories under warming-altered fire regimes to provide guidance for adaptive management decision-making and restoration strategies in the face of continued climate change.

Supplementary Information

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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