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Fire effects on diversity patterns of the understory communities of *Araucaria-Nothofagus* forests

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Abstract Short-interval and high-severity fires combined are emerging as a catalyst of major reorganization of understory plant communities. In temperate forests of south-central Chile, concern exists about the resilience of threatened *Araucaria-Nothofagus* forests, including its understory community following extensive and severe fires. In this study we use an array of diversity indices and functional traits as proxies of community resilience. We ask if the species and communities are affected by wildfires, and how these responses are mediated by burn severity and frequency, and other biophysical variables. First, we explore the hypothesis that fire is the major driver of community changes, and that burn severity is the main factor that shifts compositional attributes of communities. Secondly, we hypothesize that a reburn will lead to a greater shift than a single burn in understory compositional attributes, where resprouting species replace obligate seeders, reducing local diversity. We established 120 field plots across a burn severity gradient in two study sites: one affected by a single (burned 2015), and the second by two fires (burned 2002 and 2015), where vascular plant species abundance, among other biotic, abiotic, and topographic variables were estimated. We found that burn (high) severity is the main driver of post-fire understory assemblages, resulting in communities less competitive and heterogeneous, with an increasing number of exotic species. Also, post-fire responses are resulting in communities in which the high abundance of flammable taxa and post-fire resprouter species at the early-seral stage may lead to large-scale transitions from mesic forest ecosystems to dry, open forest and fire-prone shrublands in reburned areas. Our results highlight the ecological importance of short-interval and severe wildfires as leading factors in the transition of post-fire understory communities of *Araucaria-Nothofagus* forests to a system dominated by post-fire obligate resprouters, where tree species are less represented compromising the recovery of these ecosystems. These findings improve the understanding of the current post-fire processes that affect flammability feedbacks and contribute to a baseline of the current patterns in a world of altered fire regimes.

Keywords Understory composition · *Araucaria-Nothofagus* forests · Species diversity · Post-fire traits · Generalized linear models

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Introduction

The combined impact of climate change and direct human activities is resulting in altered fire regimes that are triggering rapid plant community reorganizations, where high-severity and short-interval fires increasingly select for traits that best resist fire or recover from fire (Enright et al. 2015; Johnstone et al. 2016; McDowell et al. 2020; Steel et al. 2021). Rapid post-fire reorganization involves changes in successional trajectories due to fire effects on structure and understory composition (Stevens-Rumann and Morgan 2016; Holz et al. 2020; Davis et al. 2020). This reorganization and change in post-fire composition has been observed in ecosystems exposed to extensive high-severity fires (i.e., widespread fires) and/or unprecedented short-interval fires (i.e., reburns), where even species with traits adapted to high-severity burns fail to survive or recover from a second fire (Donato et al. 2009; Enright et al. 2015; Harvey et al. 2016; Busby et al. 2020). An extensive body of research has shown that in some temperate forest ecosystems in Tasmania (mixed evergreen conifer and angiosperms; Holz et al. 2015), northwestern Patagonia Argentina (evergreen conifers; Kitzberger et al. 2016), and northwestern of the US (evergreen angiosperms; Tepley et al. 2017), the post-fire nature of the plant community can be externally forced by climate change (i.e., longer drought and dry seasons) and mediated by local topographic settings (i.e., aspect and microsite conditions; Su et al. 2019). Once shifts have been initiated, internally stabilizing mechanisms (e.g., fire trait effects on positive feedbacks), can favor post-fire community transitions from a pyrophobic (cooler and shadier microclimate, less flammable, fire inhibiting) forest to a pyrophytic (drier and sunnier microclimate, fire-prone) shrubland community (Holz et al. 2015; Kitzberger et al. 2016; Tepley et al. 2017; Landesmann et al. 2021; Furlaud et al. 2021).

In the context of potential fire-driven forest conversion to more flammable vegetation, the effects of wildfire on the diversity of understory communities (i.e., shrubs and herbaceous species) have been understudied. The understory community characterizes the early post-fire environment and thus contributes to the successional trajectory of a forest ecosystem (Nilsson and Wardle 2005; Su et al. 2019), maintains forest structure and function by facilitating the regeneration of the dominant tree species (Gilliam 2007), contributes resistance to and constrains abundance of existing invasive species (Levine et al. 2004; McGlone et al. 2011), and overall provides most of the species diversity in temperate forest communities (Roberts 2004). Recently burned ecosystems may experience a reduction or sometimes an increase in native understory richness due to wildfire, depending on burn severity, site productivity, post-fire competition and/or climatic conditions (Connell 1978; Romme et al. 2016; Richter et al. 2019; Holz et al. 2020; Brodie et al. 2021). Increased diversity has been observed following low-to-moderate severity fires (Burkle et al. 2015), as reduced competition favored the abundance of pre-fire non-dominant taxa (Huston 2014). In contrast, ecosystems affected by severe and/or by frequent fires may exhibit a decrease in species abundance and richness, reducing the capacity of the community to absorb new disturbances without compromising its functioning (Fairman et al. 2017; Turner et al. 2019). Thus, reduced post-fire diversity has the potential to be used as a proxy to identify resilient plants from the community (Johnstone et al. 2016; Moreno-Mateos et al. 2017; Richter et al. 2019) or compromised ecosystem functioning (Hooper et al. 2005). Moreover, a functional and ecological perspective is needed to understand and broadly predict and generalize the effects of fire and associated biophysical drivers on post-fire diversity responses (Noble and Gitay 1996; Reich et al. 2004; Lu et al. 2016). Only a handful of post-fire classification response systems exist that consider a plant functional trait approach, most of which were developed for fire-prone environments (Pausas et al. 2004; Pausas and Keeley 2014; Clarke et al. 2015), with only few recent efforts to include frameworks that consider ecosystems that historically experienced relatively little fire pressure (McWethy et al. 2013; Prior and Bowman 2020). This recent effort is of critical importance, as fire continues to expand into pyrophobic temperate forests under warming trends and land use change practices (Mariani et al. 2018).

Temperate forests of the southern hemisphere have evolved under varying degrees and types of fire activity, shaping landscapes and distributions of plant communities from the most (SE Australia) to the least (New Zealand) affected by fire as a selective pressure (Whitlock et al. 2015; Gilliam 2016; Kitzberger et al. 2016). Intermediate in this fire exposure gradient lies southern South America, where in recent decades *Araucaria-Nothofagus* forests (monkey puzzle – southern beech forests) in the northern Patagonia region of Chile and Argentina have been severely affected by fire (González et al. 2005, 2020; Mundo et al. 2017). The frequency of severe and extensive fires has increased over recent decades, which is attributable to anthropogenic impacts and climate change (González et al. 2005; González and Veblen 2007; Mundo et al. 2013), with studies mostly focused on post-fire responses of tree or shrub species (Franco et al. 2022). Studies conducted in northern Patagonia in similar forest types but lacking the fire-resistant *Araucaria araucana* (monkey puzzle tree or pehuén; Veblen 1982a; Supplement 1) have shown how positive feedbacks emerge and stabilize burned forests, where resprouting shrub species (e.g., *Chusquea* spp.; Supplement 1) replace fire-intolerant forests dominated by obligate seeder species (Cavallero and Blackhall 2020). The *Chusquea* genus is also recognized as one of the most flammable taxa in the understory of these forests and their proliferation is favored by canopy openings, included those resulting from fire (Veblen 1982b; Blackhall and Raffaele 2019; Cavallero and Blackhall 2020). Overall, these studies have reported a shift from pyrophobic to pyrophytic (more flammable, fire promoting) communities (Mermoz et al. 2005; Paritsis et al. 2015; Kitzberger et al. 2016; Landesmann et al. 2021).

Less is known however about the effect and drivers of fire on the understory functional traits and their post-fire dynamics in *Araucaria-Nothofagus* forests (González and Veblen 2007; Urrutia-Estrada et al. 2018; Arroyo-Vargas et al. 2019). The current research seeks to fill this gap through the evaluation of post-fire understory community responses and interactions with the effects of short-interval fires, burn severity and environmental factors. Specifically, we address two key research questions:

(1) What are the effects of fire on species richness composition of the *Araucaria-Nothofagus* understory communities? We hypothesize that a) there is a decrease of species that establish in areas affected by fire, and b) that increased fire severity will lead to community homogenization in pyrophobic ecosystems.

(2) How are these responses mediated by burn severity, site, topographic predictors, and burn frequency (single versus a double [reburn])? We hypothesize that fire will lead to major community changes and that the primary factors behind landscape-scale shifts in the compositional attributes of these forests toward a more fire-prone (i.e., resprouting-dominated) community is a) burn severity, and b) a shorter fire interval (i.e., regardless of reburn severity).

In this study, we examine post-fire plant community responses in *Araucaria-Nothofagus* forests in two study sites, one that burned in 2002 and reburned in 2015 and another that burned once in 2015, both located in the Andes in south-central Chile. In addition, we quantified the recruitment of all tree species to identify the potential for shifts in dominance among species and vegetation types and overall community reorganization, including changes from obligate seeding tall forest to resprouter-dominated shrubland (*matorral*).

Methods

Study area

The study areas, located in the Andes of south-central Chile (Araucanía district), were burned by a single and second event: the China Muerta National Reserve (hereafter CM study site; 38.8°S, 71.5°W) burned in 2015, and the Malleco National Reserve and Tolhuaca National Park (hereafter MT study site; 38.2°, 71.8°W) burned in 2002 and reburned in 2015 (Fig. 1). The regional climate is a transition between warm temperate and cool Mediterranean, characterized by dry and warm summer seasons and cold winters (Luebert and Pliscoff 2017). The mean annual (30-years: 1990–2020) precipitation at CM is 1,430 mm, with average maximum and minimum temperature in the warmest (Dec-Feb) and coldest (Jun-Aug, with higher snow proportion) seasons of 24.2 °C and 5.2 °C, respectively (Lonquimay station; CR2 2021). At the MT site, the mean annual

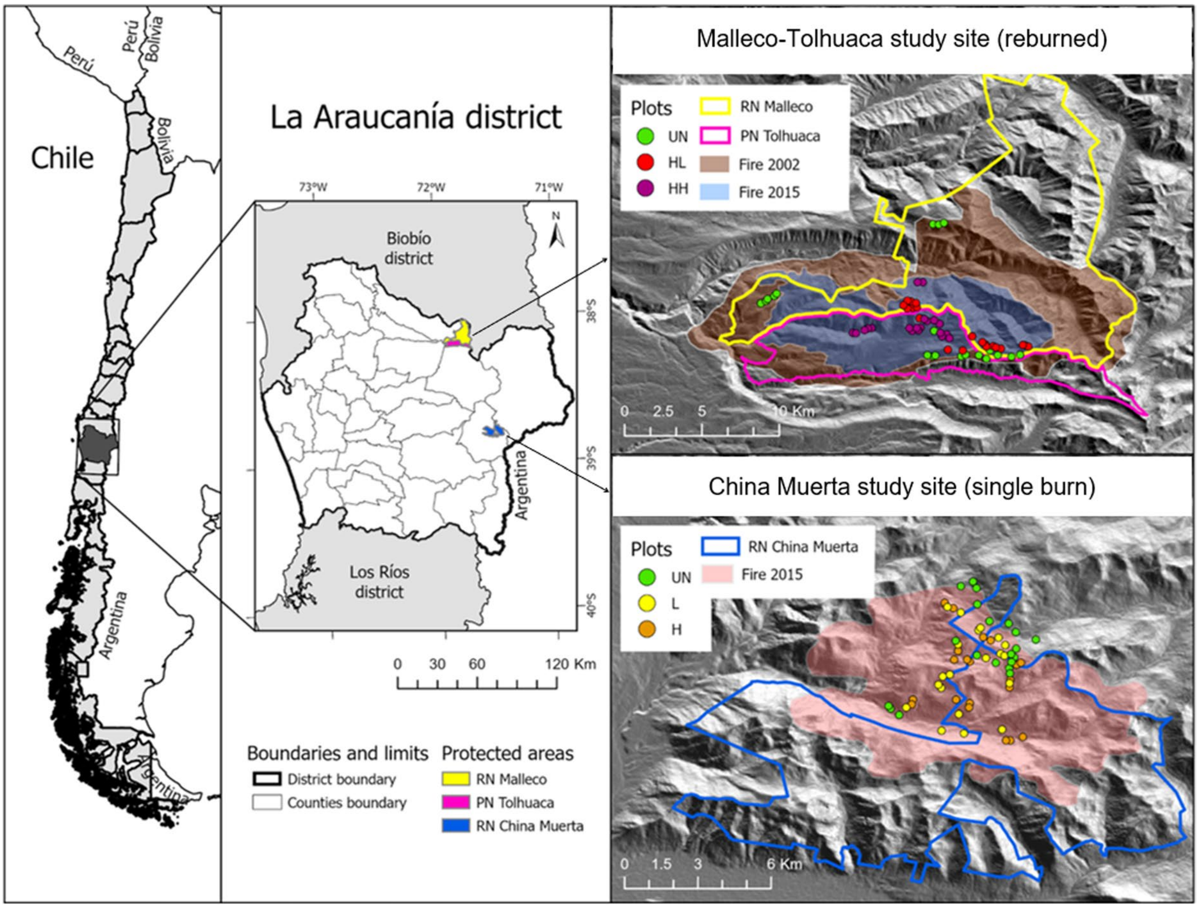

Fig. 1 Locations of China Muerta (single burn) and Malleco-Tolhuaca (reburned) study sites in the Araucanía district, south-central Chile. Maps highlight protected areas and wildfire boundaries, and plot locations in each study site. UN, HL, HH, L, and H stand for unburned, high-low, high-high, low, and high-severity fires, respectively. A total of 60 plots per study area was placed according to burn severity maps (20 per condition in each study site), based on relativized delta normalized burn ratio (RdNBR), and field observations. 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. RN and PN stand for the Natural Reserve and National Park, respectively

precipitation is substantially higher at 2,839 mm, with a colder average maximum and warmer minimum temperature in summer (Dec-Feb) and winter (Jun-Aug) temperature of 22.6 °C and 5.9 °C, respectively (Laguna Malleco station; CR2 2021). While the CM area is slightly higher in both latitude and elevation, it is also slightly eastward and exposed to a more continental (drier and cooler) climate than the MT area. Both study areas are characterized by coarse-textured volcanic soils, which are derived from medium to coarse-grained tephras (Casanova et al. 2013). The forests studied are dominated by *Araucaria araucana* (pehuén; monkey puzzle) and southern beech species, including *Nothofagus dombeyi* and *N. pumilio* (Supplement 1). At lower elevations, the forests also include *N. alpina*, *N. obliqua* and in some cases *N. antarctica*, which are capable of resprouting. Forest understories are characterized by *Chusquea* bamboo spp. (i.e., *C. culeou,* and *C. quila*; Poaceae), *Maytenus disticha* (Celastraceae), *Gaultheria* spp. (i.e., *G. poeppigii,* and *G. phillyreifolia*; Ericaceae), and the herbs *Alstroemeria aurea* (Alstroemeriaceae)*, Senecio* spp., and *Adenocaulon chilense* (Asteraceae), among others (González and Veblen 2007; Arroyo-Vargas et al. 2019).

Araucaria-Nothofagus forests have important cultural, subsistence and economic values for the Pehuenche indigenous communities in the Andes of south-central Chile (Aagesen 1998; Reis et al. 2014). The increase of the human population at the end of the XIX century due to the arrival of Euro-Chilean settlers increased anthropogenic disturbances, especially cattle grazing and logging of large individuals of pehuén and southern beech; timber extraction intensified during the first half of the XX century simultaneously with intentional forest burning to open forested areas for livestock raising (Aagesen 1998; Lara et al. 2012). It is estimated that the distribution of *Araucaria* forests has been reduced to 50% during the XX century (~250.000 ha), of which half is within a protected area (~130.500 ha; González et al. 2006). During the second half of the same century, following the establishment of protected status for the pehuén in 1976 as a Chilean Natural Monument (Veblen 1982a), and gradually better administration of several protected areas, both selective logging, silvicultural experiments and intentional burning ceased under a fire suppression policy (CONAF 1996; González et al. 2005, 2020; González and Veblen 2007). However, cattle grazing is a cultural and economic activity of local communities that it is still practiced in these protected ecosystems including moderate levels of pervasive grazing in the areas sampled in the current study (Zamorano-Elgueta et al. 2012). According to local land managers and our own observations other introduced herbivores (e.g., red deer, wild boar, hare) were not common in our study sites.

Dendrochronological studies indicate that the *Araucaria-Nothofagus* forests have been shaped by both frequent low-to-moderate fires and infrequent large, stand-replacing fire events (i.e., a mixed-severity regime; González et al. 2005, 2020; Mundo et al. 2013). Under the policy of fire suppression, no large fires were recorded from the beginning of official records in 1976 until 2002 (CONAF dataset; http://conaf.cl/). Recently, these forests have experienced an increase in the frequency and severity of wildfires as reflected by the 2002 and 2015 fire events in our study sites. The MT site was affected by two widespread wildfires in 2002 and 2015, which were from lightning and human origin, respectively. Fine-scale wildfires were previously recorded in 1960, and later in 1987, both of which had minor impacts (González and Veblen 2007). The 2002 fire burned an area of approximately 17,000 ha (ca. 70% of the MT protected area), of which 30% corresponded to *Araucaria-Nothofagus* forests (González and Veblen 2007). At MT, the 2015 fire burned a surface of approximately 5450 ha, fully overlapping the 2002 burned area (Table 1; Mora and Crisóstomo 2016). In the case of the CM study site, the 2015 wildfire was human originated and burned an area of approximately 3750 ha of the reserve (Table 1; Mora and Crisóstomo 2016). There is no record of previous wildfires since the creation of the CM protected area

Table 1 Description of the wildfires at China Muerta (CM; single burn) and Malleco-Tolhuaca (MT; reburned) study sites considering the year, total burn area (protected areas and surrounding areas), relative burn severity level and the origin of the wildfire

Study site	Wildfire year	Total burned area (hectares)	RdNBR-derived classes	Area burned severity (%)	Fire origin	No of Field plots	Plot elevation range (masl)
CM	2015	6,355	Low	37.3	Accidental, human-caused	20	1053–1705
			Moderate	31.4		20	
			High	31.3		20	
MT	2002	16,751	Low	16.4	Natural, lightning	NA	–
			Moderate	23.5		NA	
			High	60.1		NA	
MT (reburn)[a]	2015	6,814	Low	20.2	Accidental, human-caused	20	988–1621
			Moderate	36.1		20	
			High	43.8		20	

The burn severity maps and areas were calculated and based on relativized delta normalized burn ratio (RdNBR). In addition, the number of sampling plots and plot elevation range are given (*masl* indicates meters above sea level)

[a] All reburn sampling was conducted on areas burned at high severity in the 2002 wildfire at MT

in 1968. The 2015 wildfires started near the end of the austral summer (March), and rapidly propagated thanks to a severe regional drought due to low precipitation and high temperatures throughout central and south-central Chile since 2010, and the influence of the warm and dry foehn (*puelche*) winds coming from the eastside of the Andes (Garreaud et al. 2017; González et al. 2018; McWethy et al. 2021).

Sampling design and data collection

A stratified random sampling, accounting for burn severity and field accessibility (max 4500 m), minimal cattle presence (direct observation of browsing and dung), and areas outside of the 2002 post-fire restoration efforts, was employed. In each study area a total of 60 circular plots (radius = 15 m, ca. 0.07 ha), spaced apart at least 100 m (average distance of 279 m at CM with a range of 117–822 m; and 273 m at MT with a distance range 126–700 m), were set in the 2020 austral summer ($N = 120$ plots, Fig. 1). Burn severity maps for each wildfire were created using the relativized delta normalized burn ratio (RdNBR; Miller and Thode 2007), with pre-fire and 1-year post-fire Landsat imagery. Burn severity thresholds (i.e., low, moderate and high-severity levels) were defined according to Assal et al. (2018) and field verified. For the areas that burned in 2002 at MT, and due to inaccessibility and post-fire logging and restoration, only those burned at high severity were available for sampling, which were reburned at low- and high severity during the 2015 fire (hereafter burn severity classes at MT as High-Low: HL; and High-High: HH). At the CM study site, plots were established in areas that burned at low- and high severity in 2015 (hereafter at CM as Low: L; and High, H). Areas burned at moderate severity (31.4% at CM and 36.1% second burn at MT) were excluded from our study due to low-accuracy and poor field-validation (Franco et al. 2020). For comparison with burned sites, 20 circular plots (radius = 15 m) were established in unburned forests (hereafter UN) in each study site. Within each plot, 4 quadrats (1 m^2), distanced 7 m from the plot center to each cardinal direction were located. Within each quadrat all vascular species were identified and abundances (% cover) were directly estimated. The abundance of tree species was estimated independently if the regeneration strategy was from seeds or resprout. Also, the coverage of coarse woody debris (CWD; stems > 7.6 cm diameter), fine woody debris (FWD; plant litter < 7.6 cm diameter) and bare ground were estimated in the same quadrats. In addition, average canopy cover was recorded, by the same person throughout the campaign, in each of four quadrats, with a spherical crown densiometer placed at 50 cm above the ground. Coordinates, elevation, aspect and slope were recorded at the center of each plot. A Heat Load Index (HLI), which is an integrated metric of direct incident radiation according to latitude, slope, and aspect at each plot (McCune and Keon 2002; McCune 2007), was later computed as a proxy of long-term moisture availability (Littlefield 2019; Busby et al. 2020; Brodie et al. 2021).

Finally, to evaluate post-fire traits of woody species, we adopted Prior and Bowman (2020)'s post-fire trait classification because it best represents the traits of the affected taxa and applies to pyrophobic communities (e.g., Paritsis et al. 2015; Kitzberger et al. 2016). The post-fire trait classes are: post-fire obligate resprouter (i.e., survives complete defoliation by resprouting and does not produce seedlings; PFOR), post-fire obligate seeder (i.e., regenerates [often profusely] from seeds, but does not resprout; PFOS), post-fire facultative resprouter/seeder (i.e., resprouts and produces seedlings; PFFRS), and post-fire obligate colonizer (i.e., neither resprout nor produce seedlings, but able to gradually recolonize burned areas by dispersal from outside the high-severity burned area; PFOC). Although in our study areas no taxa were classified as it, Prior and Bowman's (2020)'s classification also includes a fire-intolerant (FI) class, where post-fire populations are unable to recover by post-fire resprouting, seeding or colonization and thus collapse at the event scale. Woody species were classified into one of these categories (Supplement 2) based on the available literature, field observations, or consultations with local experts (Raffaele and Veblen 1998; Montenegro et al. 2003; Paritsis et al. 2006; González and Veblen 2007; Kitzberger et al. 2016; Blackhall and Cavallero 2018). In the field, species were classified according to their response to fire disturbance rather than from the perspective of their attributes in the absence of fire (e.g., in the unburned stands). In addition to FI, no woody species was classified as PFOS class in our study area. Additionally, we defined bamboos as a separate life form classification that encompasses several *Chusquea* species (i.e., identified only at the generic level due to the scarcity of inflorescences except during rare masting event) due to their distinct flammability, and their unique capacity to resprout after fire from above and belowground meristems, even when the above biomass is fully consumed (i.e., due to their widespread and tough horizontal rhizome; Veblen 1982b; Cavallero and Blackhall 2020).

Statistical analysis

Post-fire species diversity and composition

To evaluate post-fire diversity and understory composition, we first calculated alpha diversity in terms of species richness (S; number of species), antilogarithm of Shannon's entropy index (eH'; number of species if they were equally distributed), inverse Simpson index (inverse D; which measures a species' dominance), and Pielou's evenness index (J; which considers diversity along with species richness) at plot level (Richter et al. 2019). To test for statistical differences in the post-fire response of understory diversity indices, we compared the mean values of S, eH', inverse D and J indices among the burn severity classes and the reference forest within each site using the nonparametric Kruskal–Wallis rank-sum test. The post hoc pairwise Wilcoxon rank-sum test was used to identify differences considering the Bonferroni correction for multiple tests among groups. Normality and homoscedasticity of the variance were verified with the Shapiro–Wilk Normality test and Levene's test, respectively, which were not met. Thus, all tests were performed in the *stats* R package (R Core Team 2020). In addition, we calculated two beta diversity indices using Whittaker's species turnover metric, or compositional change in a habitat gradient in the same geographical region, to evaluate species composition change ratio among plots within each burn severity class (i.e., beta diversity = gamma diversity/alpha diversity-1; Whittaker 1972; Tuomisto 2010), and Jaccard dissimilarity (1-J) as a proxy to identify species homogenization between plots within burn severity classification in each study site (Richter et al. 2019) using *vegan* R package (Oksanen et al. 2020).

We used non-metric multidimensional scaling (NMDS) ordination with Euclidean distance and 2 dimensions (k = 2) to summarize and explore the post-fire understory responses to burn severity from three different perspectives: (1) vascular plant species; (2) life forms (i.e., herbs [graminoids and forbs], vines, shrubs, bamboos, and trees; adapted from Raunkiær 1934); and (3) fire traits of the woody plant taxa (adopted from Prior and Bowman 2020). The NMDS ordination analyses and plots were conducted in the *vegan* R package (Oksanen et al. 2020). Finally, we conducted a permutational multivariate analysis of the variance (PERMANOVA) to identify statistically difference among fire severity groups. We considered 999 permutations and Bray–Curtis distance using the *vegan* package (Oksanen et al. 2020). Then, a pairwise multilevel comparison procedure was conducted when significant differences were detected among fire groups. Permutations were set in 999 and *p*-values were adjusted to reduce type I error of multiple comparisons with Holm method using *pairwiseAdonis* R package (Martínez 2017).

Interaction of life form and post-fire trait class responses with environmental factors

We used *mvabund*, an R package designed to relate environmental predictors to community data, to independently fit generalized linear models (GLMs; with a negative binomial distribution and a log-link function) with both multivariate (community) and univariate (individual classification levels used in the NMDS) abundance data (Wang et al. 2021). Because we expected local-to-landscape-scale biophysical factors to affect our response variables, model predictors include burn severity classes (i.e., disturbance treatments), and fine-scale site and meso-scale topographic variables. This model-based analysis framework uses the deviance explained statistic (i.e., pseudo-R^2) to assess each GLM's goodness of fit and reported results from models with the lowest maximum likelihood, and unlike traditional distance matrix based methods this approach avoids inflation of type 1 and type 2 errors (Warton et al. 2012; Wang et al. 2012). Assumptions of these GLMs were met and include independence of sites, mean–variance

Table 2 Predictor variables included in multivariate and univariate post-fire abundance models* and their methods of measurements

Category	Variable	Method of measurement	Unit	Type	Range
Fire	Burn severity	Relativized delta Normalized Burn Ratio (RdNBR) and field verified	Unitless	Categorical	Unburned, low, high, high-low, high-high
Abiotic	Bare ground	Field measured at quadrat level	Relative coverage (%)	Continuous	Bounded [0 100]
	Slope	Field measured at plot level	Degrees (°)	Continuous	Bounded [0 42]
	Aspect		Degrees (°)	Continuous	Bounded [4 360]
	Elevation		Meters (m)	Continuous	Bounded [988 1745]
	HLI	Derived from field-measured slope, aspect, and latitude (McCune and Keon 2002; McCune 2007)	Unitless	Continuous	Not bounded [0.53 1.24]
Biotic	Coarse woody debris	Field measured (4 quadrats at 7 m from plot center; averaged)	Cover (%)	Continuous	Bounded [0 100]
	Fine woody debris				
	Canopy cover				

*Response variables are life form (herbs, shrubs, bamboos, vines and trees) and wood species trait (post-fire obligate resprouters, post-fire facultative resprouter/seeders, and post-fire obligate colonizers, following Prior and Bowman 2020)

and log-linear relationships between mean abundance and the environmental variables. These were visually checked by plotting residual and fitted values and trends in size of residuals at different fitted values (Wang et al. 2012). The *anova.manyglm* function was used to generate an analysis of deviance table, which summarize the statistical significance of the fitted model regarding to the effects of burn severity and other predictors on mean abundance of community and individual classes. We corrected for multiple tests using the *p.adjust* (*method* = *"adjusted"*; Table 2; Wang et al. 2012). Multicollinearity was assessed in each model using the variance inflation factor (VIF) measure in *car* package in R (Fox and Weisberg 2019).

Table 3 Diversity indices in response to burn severity classes at China Muerta (CM; single burn) and Malleco-Tolhuaca (MT; reburned) study sites

Study site	Burn severity	Alpha diversity (α)				Beta diversity (β)		Total species richness (S)	% Non-native (N)
		Mean S (SE)	Mean eH' (SE)	Inverse D index (SE)	Mean J (SE)	Whittaker β_W	Mean Jd (SE)		
CM (single burn)	Unburned	9.5 (0.8)^{a}	40.8 (5.7)^{a}	3.4 (0.2)^{a}	0.70 (0.02)^{a}	3.32	0.787^{a}	41	9.8% (4)
	Low	8.1 (0.5)^{a}	39.0 (6.7)^{a}	3.6 (0.3)^{a}	0.72 (0.03)^{a}	5.34	0.853^{b}	51	17.6% (9)
	High	5.3 (0.5)^{b}	17.6 (4.0)^{b}	2.6 (0.3)^{b}	0.68 (0.04)^{a}	4.32	0.877^{c}	28	37.9% (11)
MT (reburned)	Unburned	8.4 (0.8)^{a}	54.1 (10.7)^{a}	4.2 (0.4)^{a}	0.78 (0.02)^{a}	3.76	0.769^{a}	40	0% (0)
	High-Low	6.8 (0.6)^{a}	35.1 (8.2)^{ab}	3.5 (0.4)^{ab}	0.72 (0.05)^{a}	4.44	0.777^{a}	37	15.8% (6)
	High-High	7.0 (0.6)^{a}	26.8 (5.4)^{b}	3.0 (0.3)^{b}	0.67 (0.04)^{a}	4.14	0.729^{b}	36	16.2% (6)

Mean values of vascular plant species richness (S), antilogarithm of Shannon's entropy index (eH'), inverse Simpson index (D), Pielou's evenness (J) and their respective standard errors (SE) are presented. In addition, Whittaker's species turnover (Beta; β_W), mean Jaccard dissimilarity index (Jd), total species richness (S), and the relative and absolute (N) number of non-native species are reported

Lowercase letters indicate statistical difference in each study site among burn severity levels according to each diversity index (Kruskal–Wallis test, $p < 0.05$)

*The Whittaker beta diversity was computed as gamma diversity/alpha diversity-1 (Whittaker 1972; Tuomisto 2010)

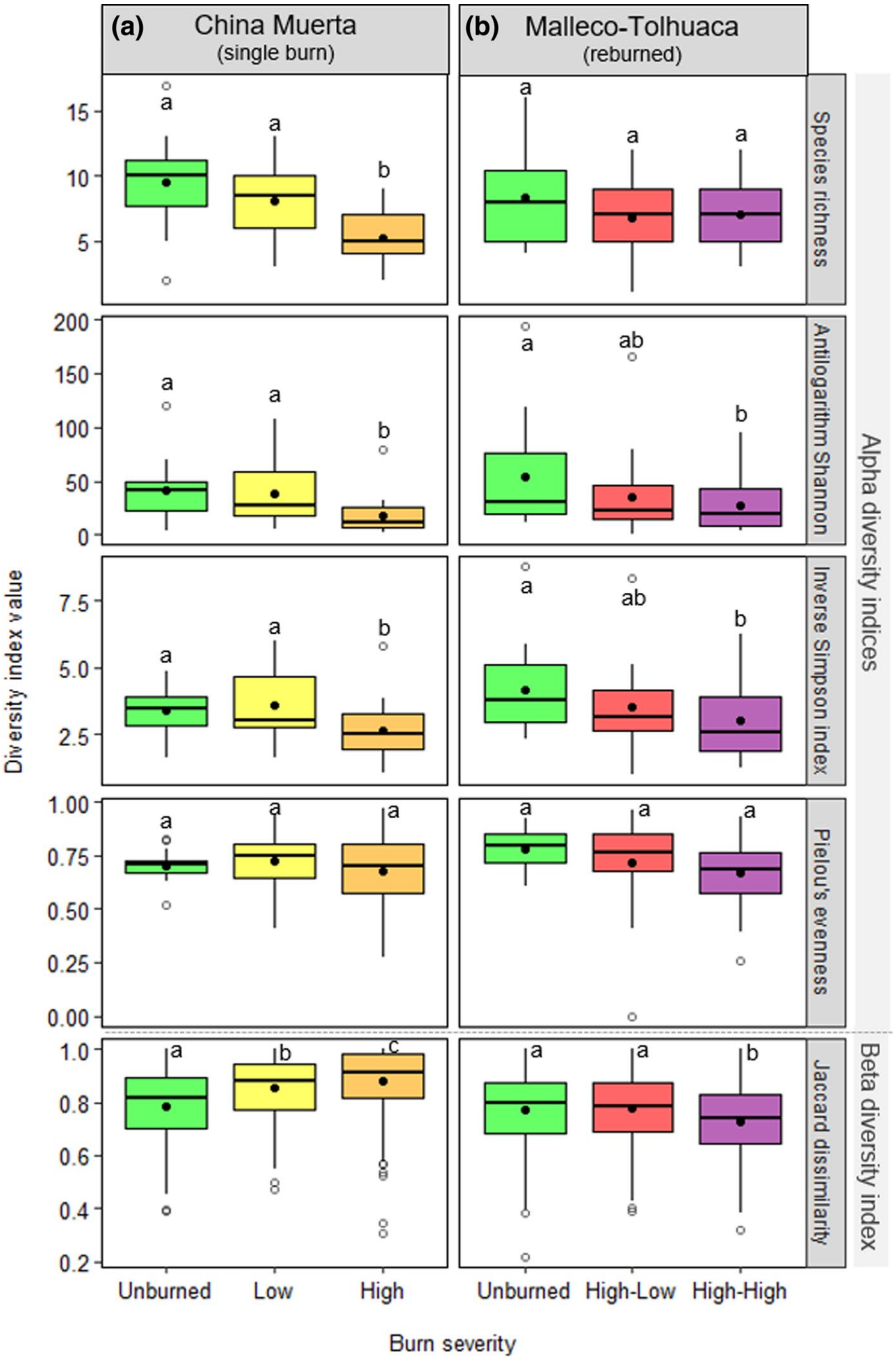

Fig. 2 Boxplots representing the diversity indices in responses to burn severity classes include mean antilogarithm of Shannon's entropy index (eH'), inverse Simpson index (D), Jaccard dissimilarity, Pielou's evenness (J), Species richness (S) and their respective standard errors (± SE) across burn severity classes and the unburned reference forest at **a** China Muerta (CM: single burn) and **b** Malleco-Tolhuaca (MT; reburned) study sites. Colored boxes represent the interquartile range of the data (middle spread, 50% of the data), thick horizontal lines and black dots represent median and mean species richness, respectively. Vertical lines (whiskers) indicate the species richness variability outside of the interquartile range, and uncolored dots are outliers. Means with different letters in the same panel are statistically different from each other (Kruskal–Wallis test; $p < 0.05$)

Results

Post-fire species diversity and composition response

We found a total of 71 and 69 vascular plant species at CM and MT study sites, respectively (Supplement 2). Total and mean species richness decline as burn severity increases: at CM site the mean species richness at the H plots was significantly lower than at the L and UN plots (Table 3, Fig. 2a); but at the MT site mean richness was not statistically different among severity classes 5 years after the 2015 reburn ($p > 0.05$, Table 3, Fig. 2b). The other diversity indices used here—including mean antilogarithm of Shannon's, inverse Simpson, and Pielou's evenness indices—also decrease at both study sites as burn severity increases. The mean values of the former two indices showed differences between the UN and the high-severity class (i.e., H at CM, and HH at MT; $p < 0.05$, Table 3, Fig. 2), but no statistical differences were found between low-severity and either the unburned and high-severity class (i.e., L at CM, and HL at MT; $p > 0.05$, Table 3). The mean values of Pielou's evenness index were not statistically different among burn severity classes in any of the study sites ($p > 0.05$, Table 3, Fig. 2). The Whittaker beta diversity index indicated that diversity among plots declined in burned areas, as the lowest burn severity class (L and HL at CM and MT sites, respectively; Table 3), but the Jaccard dissimilarity increases with the fire severity in areas burned once and sightly decreases in areas severely burned twice with HH (Fig. 2). The number of non-native species increases, but at different rates, with burn severity: at MT no exotic species were found in UN sites and similar values were found in HL and HH class severities (ca. 16% in each; Table 3). At CM, more than a third of the species identified in H burn severity plots were exotic species (ca. 38%), in comparison to half this number at L, and a third this number at the control (Table 3). Among the 18 exotic species recorded in both study sites across burn severity classes, 14 are categorized as invasive species (Supplement 2; Fuentes et al. 2013). Eighty-nine percent of non-native species were herbs, and the rest were woody species (including *Rosa rubiginosa* found in the UN and H burn severity class at CM and in the HL class at MT, and *Pseudotsuga menziesii* sparsely found in UN plots at the CM study site).

In general, the NMDS results at the CM site, post-fire response patterns were statistical different and distinguished according to the burn severity class in all three NMDS analyses ($p < 0.05$), with H severity and UN plots at opposite extremes of the NMDS axis 1 (Fig. 3a–f). In contrast to MT, the separation between the UN condition and either burn severity class was clearer and statistically significant from the other classes ($p = 0.001$). The NMDS plot based on life forms showed a shorter distance among the severity classes (Fig. 3b, e), with bamboo, vines and herbs aligned around the zero value (Fig. 3b), where L and H are not significantly different. Higher overlap among classes and flatter (negative kurtosis) curves along axis 1 were observed in the fire trait NMDS, where PFOC and PFOR overlapped the most with all three burn classes (Fig. 3c, f); however, the UN plots were statistically different from each of the other severity classes (Supplement 3). At the MT site show that UN plots were different from plots affected by fire; the PERMANOVA tests show that all the evaluation criteria (plant composition, life forms and post-fire traits) are statistical different at CM and MT study sites ($p < 0.05$; Supplement 3). The aggregation pattern by severity was most pronounced and significant when all vascular plant species were included in the NMDS (Fig. 3g). When species were represented by their life forms, UN plots are statistically different but closer to both classes of burn severity ($p = 0.001$), which is mostly due to the overlapping of bamboo along the NMDS axis 1 (Fig. 3h, k). HL and HH were statistically different in the life form PERMANOVA, but with higher significance ($p = 0.025$). In contrast, the post-fire response of woody plant species along axis 1 placed the HH burn severity in between the HL and the UN condition. However, UN is statistically different from HL and HH, but burned areas are not significant different ($p = 0.115$; Supplement 3). In part this is due to the shared association of HL and HH severity burn classes with both PFOR and PFOC species, which were common in areas burned at both burn severities and in the reference stands (Fig. 3i, l).

Post-fire life form and trait responses to burn severity

Abundances of post-fire responses varied across burn class at each site, but in general vines and trees were consistently the least and shrubs the most abundant post-fire life form. PFOR was the most abundant woody species fire trait. At the CM site, the abundance of the herb, shrub, and bamboo life forms (median = 13.8, 7.8, 5.0, respectively) were higher than those of trees and vines (median = 0.8 and 0.0, respectively, Fig. 4b). Shrubs reached highest abundance values under UN conditions (median = 20.9, Fig. 4a), as did trees, which were practically absent from the H severity class (median = 0.0, Fig. 4a).

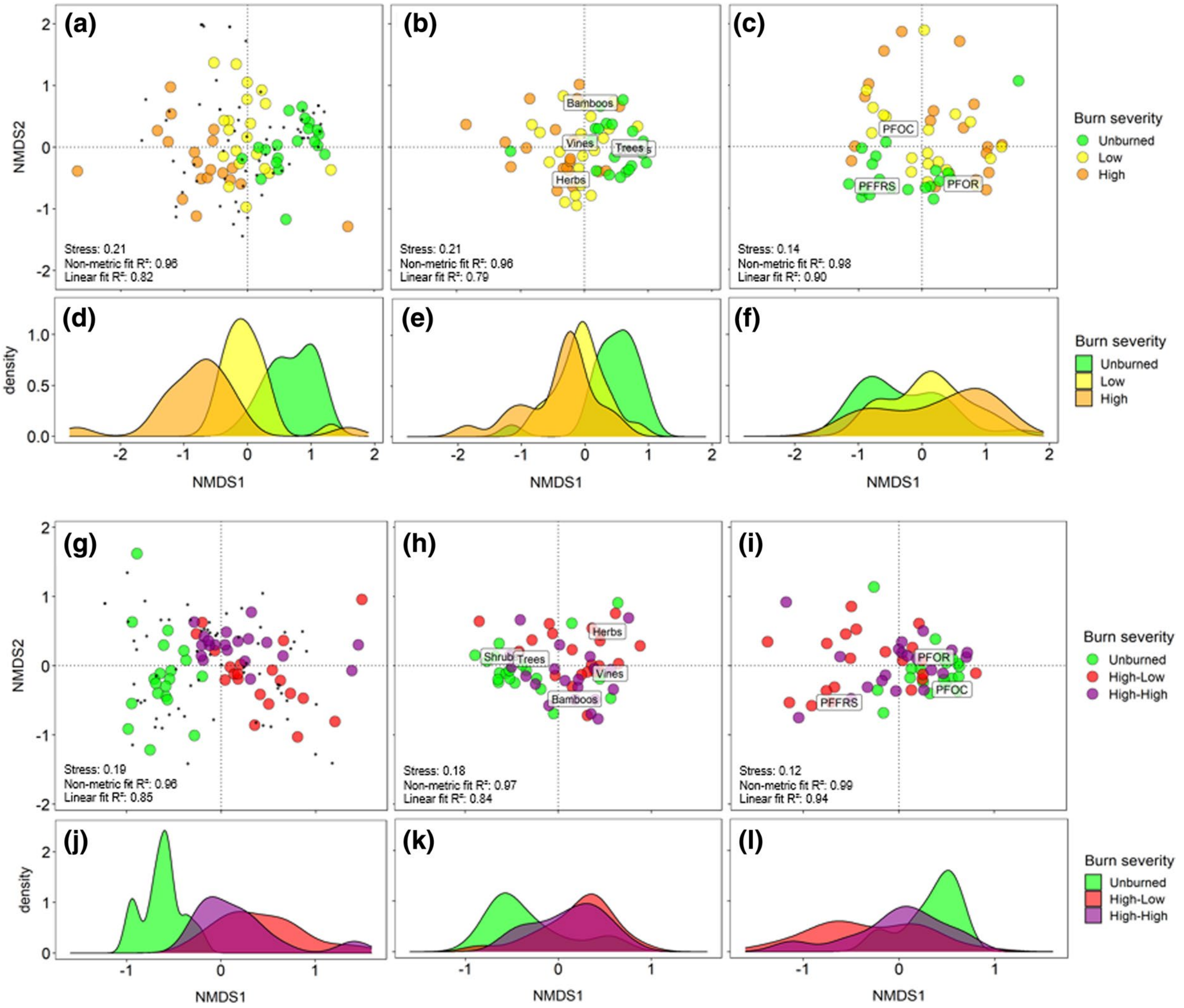

Fig. 3 Non-metric multidimensional scaling (NMDS) diagrams for the China Muerta (CM; **a**–**c**) and Malleco-Tolhuaca study sites (MT; **g**–**i**), where each circle represents the location of unburned (green), low (yellow), high (orange), high-low (red) and high-high (purple) severity plots. Colors between MT and CM differ to differentiate single fire vs. reburn severity classes. China Muerta NMDS ordination plots represent **a** vascular plant community (71 species, black dots), **b** life forms (71 species), and **c** post-fire response of woody plant species (26 species). Malleco-Tolhuaca NMDS ordination plots represent **g** vascular plant community (69 species, black dots), **h** life forms (69 species), and **i** post-fire response of woody plant species (36 species). Density plots derived from NMDS axis 1 are shown below each respective NMDS ordination plot (**d–f** at CM, and **j–l** at MT). PFFRS, PFOC, and PFOR indicate post-fire facultative resprouter/seeder, post-fire obligate colonizer, and post-fire obligate resprouter, respectively. Stress, non-metric and linear fit R^2 values are reported

Herbs and vines had opposite abundance patterns; the former was the most and the latter the least common life form (median = 13.8 and 0.0, respectively, Fig. 4b) at the CM site, with the same pattern repeated in the L severity class (median = 13 and 0.1, respectively, Fig. 4a). The abundance of PFFRS species at CM was highest (median = 8.8, Fig. 4d), especially in the unburned forest (median = 19.4, Fig. 4c). PFOC species were the least abundant species across the gradient (median = 2.1, Fig. 4d) and poorly represented in H severity sites (median = 0.0, Fig. 4c). PFOR species were more abundant in the L severity class (median = 10.3, Fig. 4c). At the MT site, the bamboo and shrub life forms were most abundant, especially in HL (median = 14.6 and 12.9, respectively, Fig. 4e), and mostly in HH plots for the former

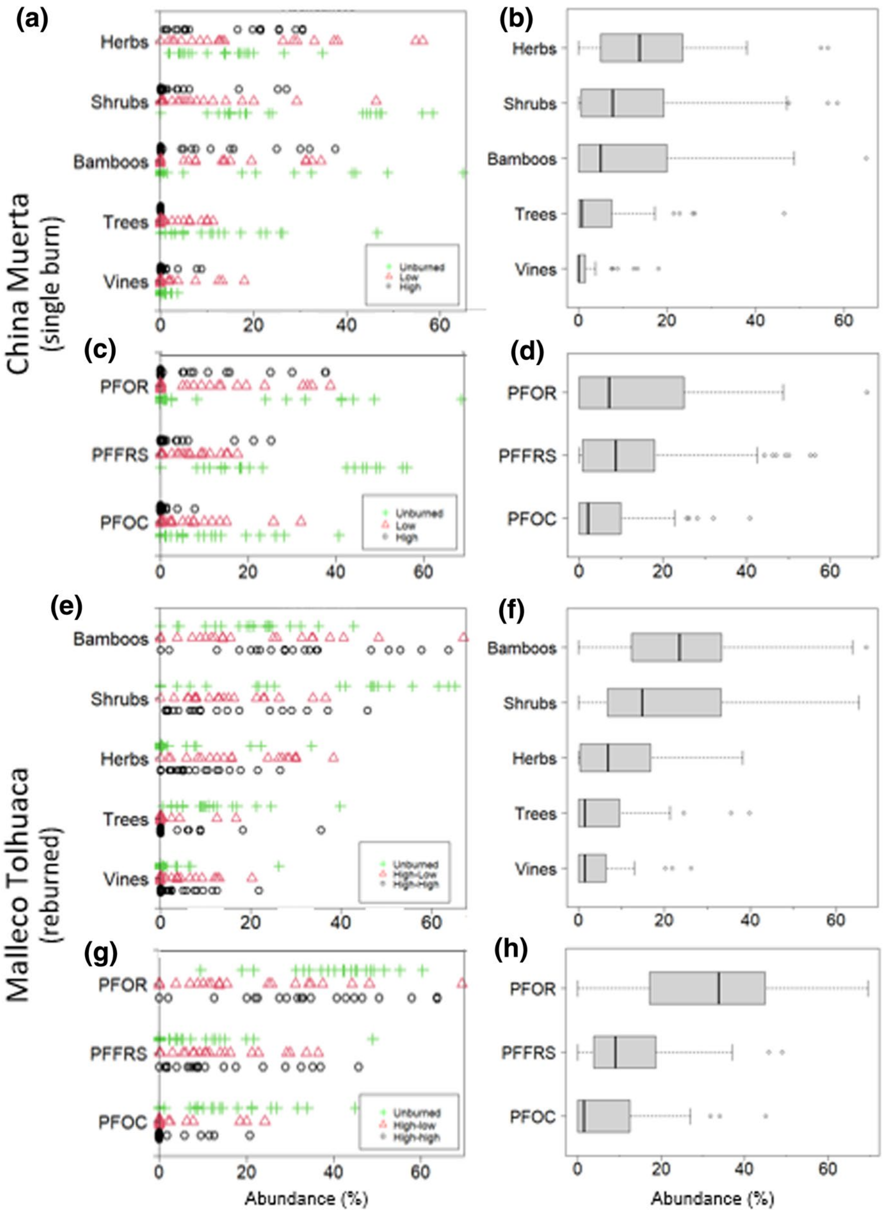

Fig. 4 China Muerta (single burn) abundance plots against burn severity class (**a**, **c**) and their corresponding boxplots (**b**, **d**) for life forms and post-fire response. Malleco-Tolhuaca (reburned) abundance plots against burn severity class (**e**, **g**) and their corresponding boxplots (**f**, **h**) for life forms and post-fire response. PFFRS, PFOC, and PFOR stand for post-fire facultative resprouter/seeder, post-fire obligate colonizer, and post-fire obligate resprouter, respectively. Boxplot diagrams represent the interquartile range of the abundance data (middle spread, 50% of the data), thick vertical lines represent median abundance. Horizontal dashed lines indicate the abundance variability outside of the interquartile range, and uncolored dots are outliers

(median = 28.4, Fig. 4f) and in UN plots for the latter (median = 40.4, Fig. 4f). Finally, PFOR was by far the most abundant post-fire response trait in the MT site (median = 33.8, Fig. 4h) and was found in all severity classes (median = 43.4, UN; 14.6, HL; 32.8, HH; Fig. 4g). In contrast, PFOC had the lowest estimated plant cover (median = 1.5, Fig. 4g), with greatest abundance in the unburned understory of MT site (median = 13.3, UN, Fig. 4g).

The multivariate abundance models indicate that burn severity and bare ground are the predictors that best explain differences in the relative abundances of post-fire life forms and trait responses among plant communities (Table 4), whereas only burn severity best predicts most of the post-fire life forms and post-fire traits individually (Table 5). Topographic predictors were not statistically significant for any of the species' classifications in either study sites (Table 4). Burn severity, bare ground, CWD and

Table 4 Multivariate analyses of deviance (pseudo-R^2) from China Muerta (CM; single burn) and Malleco-Tolhuaca (MT; reburned) studies sites according to their post-fire life forms and post-fire trait classifications. Bold values indicate the statistical significance (p<0.05).

	China Muerta (single burn)				Malleco-Tolhuaca (reburned)			
	Residual Degrees of freedom	Degrees of freedom difference	Deviance	Probability (> deviance)	Residual Degrees of freedom	Degrees of freedom difference	Deviance	Probability (> deviance)
	Life form multivariate analysis				*Life form multivariate analysis*			
Intercept	58				59			
Burn severity	56	2	78.38	**0.001**	57	2	37.07	**0.001**
Slope	55	1	4.35	0.4	56	1	3.28	0.582
Aspect	54	1	2.31	0.762	55	1	2.56	0.703
Elevation	53	1	1.08	0.942	54	1	5.49	0.305
Bare ground	52	1	14.03	**0.023**	53	1	22.59	**0.001**
Coarse woody debris	51	1	16.33	**0.007**	52	1	10.31	0.088
Fine woody debris	50	1	24.21	**0.001**	51	1	9.53	0.125
Mean canopy cover	49	1	6.62	0.299	50	1	12.23	0.055
Heat Load Index	48	1	2.19	0.861	49	1	6.23	0.326
	Post-fire trait response multivariate analysis				*Post-fire trait response multivariate analysis*			
Intercept	57				59			
Burn severity	55	2	45.36	**0.001**	57	2	17.72	**0.002**
Slope	54	1	2.66	0.354	56	1	2.47	0.367
Aspect	53	1	1.17	0.687	55	1	2.62	0.387
Elevation	52	1	0.19	0.984	54	1	1.99	0.474
Bare ground	51	1	14.53	**0.004**	53	1	23.96	**0.001**
Coarse woody debris	50	1	11.34	**0.016**	52	1	11.26	**0.01**
Fine woody debris	49	1	19.18	**0.002**	51	1	14.84	**0.007**
Mean canopy cover	48	1	4.34	0.297	50	1	14.52	**0.013**
Heat Load Index	47	1	3.95	0.331	49	1	1.97	0.59

FWD (Dev = 78.4, 14.03, 16.3, 24.2, respectively, $p < 0.05$) are predictors that differentiate the communities according to the composition of the post-fire life forms in CM study site (Table 4). The univariate model indicates that only burn severity positively predicts the abundance of shrubs, but it declines in strength across the fire gradient (Table 5). This model also shows that tree abundance is positively associated with UN and low-severity fire but is negatively affected by high-severity fires ($p < 0.05$; Table 5). Post-fire life form communities at MT were best differentiated by burn severity (Dev = 37.1, $p = 0.001$) and bare ground (Dev = 22.6, $p = 0.001$; Table 4). The univariate analysis (Table 5) shows that the greater

Table 5 Univariate analyses of deviance (adjusted for multiple testing) from China Muerta (CM; single burn) and Malleco-Tolhuaca (MT; reburned) study sites according to their post-fire life forms and post-fire trait classifications. Bold values indicate the statistical significance (p<0.05) between both the life forms and the post-fire traits against predictors.

China Muerta (single burn)			Predictor coefficient		
Response variable	Deviance	Probability (> deviance)	Burn severity class		
			Unburned	High-Low	High-High
Life forms					
Bamboos	0.51	0.590	– 0.02	1.59	4.68
Herbs	2.59	0.282	2.69	3.64	4.19
Shrubs	18.76	**0.001**	1.64	0.75	0.60
Trees	50.44	**0.001**	5.98	4.90	– 11.53
Vines	6.05	0.099	– 4.79	– 2.14	– 0.43
Post-fire traits					
Post-fire obligate resprouter (PFOR)	0.73	0.496	1.05	2.30	4.93
Post-fire facultative resprouter/seeder (PFFRS)	24.35	**0.001**	1.06	– 0.27	– 0.41
Post-fire obligate colonizer (PFOC)	20.27	**0.001**	– 2.93	– 1.34	– 1.04
Malleco-Tolhuaca (reburned)			Predictor coefficient		
Response variable	Deviance	Probability (> deviance)	Burn severity class		
			Unburned	Low	High
Life forms					
Bamboos	3.29	0.210	2.99	4.30	4.25
Herbs	9.91	**0.007**	0.87	1.86	1.57
Shrubs	12.19	**0.007**	2.91	1.76	2.20
Trees	9.78	**0.007**	– 3.92	– 4.30	– 3.31
Vines	1.91	0.320	6.73	6.68	6.49
Post-fire traits					
Post-fire obligate resprouter (PFOR)	6.75	**0.034**	3.91	4.77	4.60
Post-fire facultative resprouter/seeder (PFFRS)	2.38	0.237	1.28	0.90	1.76
Post-fire obligate colonizer (PFOC)	8.59	**0.021**	1.23	0.50	0.93

the severity of the second burn the greater the mean abundance of shrubs at the MT site. The opposite is true for mean tree species abundance: the lower the severity of the second burn the higher its impact on mean tree abundance. The variance inflation factors (VIF) of these explanatory variables were < 2.0.

In both study sites, burn severity, bare ground, CWD and FWD were the main predictors of the multivariate abundance of post-fire trait responses. At CM, burn severity, bare ground, CWD, and FWD (Dev = 45.4, 14.5, 11.4, 19.2, respectively, $p < 0.05$) were the best predictors of post-fire traits in the multivariate analysis (Table 4), and the univariate model clarifies that burn severity (either high or low) negatively predicts the abundance of PFOC, and PFFRS species (Table 5). The abundances of PFOC species are negatively associated with the unburned class, whereas PFFRS species are positively associated with the unburned class at CM site (Table 5). At MT, the multivariate abundance model indicated that burn severity, bare ground, CWD, FWD and canopy cover (Dev = 17.7, 24.0, 11.3, 14.8, 14.5, respectively, $p < 0.05$) were strong predictors of post-fire trait abundance (Table 4). Here, the univariate analysis confirms that fire of any severity favors PFOR species and less so for PFOC, which are dispersed from, and are more abundant in the reference forest of the MT site (Table 5).

Discussion

Our findings in *Araucaria-Nothofagus* temperate forests show that in general high burn severity was the main sampled driver of changes in post-fire diversity and understory species assemblages. In the study areas sampled, the community parameters were less susceptible to being modified by a second burn, regardless of its severity, in comparison to the effects of the first burn. The abundance of herbs responded positively to single fire, and along with that of shrubs, PFOC, and PFOR responded positively to short-interval fire. Single fire and reburn negatively affected the abundance of PFOC and PFFRS and of trees, respectively, while trees were also negatively affected by single, high-severity fire. The bamboo life form showed a slight, non-significant positive trend in its response to any fire. Shrubs responded positively to any fire.

Post-fire species diversity and compositional response

Wildfires that burned *Araucaria-Nothofagus* forests in both study sites had a significant effect on the species richness and composition of the understory community. At CM and MT sites approximately 58% and 56% of the species were found in UN plots, respectively. Of the species that were established only in unburned conditions, 10 and 18 were found at CM and MT, respectively, whereas 30 at CM and 29 at MT were found in burned areas. Species more sensitive to fire, like some native herbs, were unique to unburned areas (Supplement 2). In addition, all exotic species that we recorded in MT, and most of them in CM site, were mostly herbaceous and were found in burned areas exclusively (Supplement 2). These exotic species are mostly considered (shade-intolerant) invasives, and as they continue to be introduced to these protected areas by livestock, we expect them to persist in these burned systems until they are shaded and outcompeted by the native and aggressive shade-intolerant bamboo and/or by canopy closure. The high number of exotic invasive species recorded indicates a high vulnerability of the *Araucaria-Nothofagus* understories to shifts species composition. High-elevation ecosystems, including some we studied here are generally regarded as harsh environments less suitable for the establishment of exotic species (Pauchard et al. 2016; Lembrechts et al. 2016). However, the combined effects of disturbance (natural and anthropogenic) and climate change can favor the growth of these populations in high-elevation ecosystems (Pauchard et al. 2009; Alexander et al. 2016). Livestock grazing was observed across the burn severity gradient in both study sites, which would be expected to promote the spread of exotic species as well as potentially negatively influencing tree regeneration (Raffaele et al. 2011; Zamorano-Elgueta et al. 2012; Blackhall et al. 2017). Previous research in Patagonian *Nothofagus* forests has highlighted the role of livestock in promoting the abundance of exotic forb species which in turn increase flammable fine fuels potentially contributing to transitions to fire-prone shrublands (Raffaele et al. 2011).

Our results indicate that fire reorganizes plant communities by reducing competition in burned areas, which is reflected by the increase of species richness relative to the reference forests. This type of disturbance facilitates the establishment of species that were absent prior to fire, which diversifies the site conditions for plant establishment (Huston 2014; Burkle et al. 2015). One of the common short-term impacts of wildfire is nutrient enrichment on disturbed sites (Caon et al. 2014), which also promotes the initial establishment of exotic species (Brooks 2003; Liu et al. 2018). Five years since the 2015 wildfire, mean species richness within areas burned at high severity appeared to be recovering but was still below the reference condition, especially at the CM site. Our findings show that total species richness is higher in areas affected by low-severity fires (compared to high-severity fires) at both study sites, consistent with our expectation and with theory (i.e., but only partially with the Intermediate Disturbance

Hypothesis, which proposes highest richness and diversity values at intermediate disturbance; Connell 1978). Reburned areas experienced even further declines in alpha diversity metrics (i.e., Shannon's entropy, inverse Simpson, and Pielou's evenness), especially in areas reburned at high severity. However, we did not find a significant shift of species dominance. Although these results were not corrected for spatial autocorrelation, we believe a mean plot-to-plot distance of ca. 275 m reduced this noise. Similar results have been found in the Rocky Mountains in the western US, where density and richness were reduced in the understory of subalpine temperate conifer forests after a short-interval fire (Hoecker and Turner 2022), and in repeatedly burned sagebrush ecosystems (Mahood and Balch 2019). In those studies, only a few species were able to persist abundantly after frequent fires, either exotic species or fire-tolerant species. However, the beta diversity (dissimilarity) practically did not change in our reburned areas, and it increased in areas burned once, contrary to our hypothesis. The homogenization pattern was not found in the studied understory composition, where we should expect a significant decrease of the diversity indices when fire severity increases in areas affected by infrequent fires (Richter et al. 2019). Dendrochronological studies indicate that fire is not naturally a frequent disturbance in a short-to-medium period of time (González and Veblen 2007; González et al. 2020). However, paleoecological studies show that volcanic events have been part of the dynamic of these ecosystems periodically at long time scales (Dickson et al. 2021; Nanavati et al. 2021), suggesting fires have shaped these ecosystems and that the understory community may have evolved with these disturbances. We also highlight that these trends in our study sites agree with initial surveys conducted after one (Urrutia-Estrada et al. 2018) and three years (Arroyo-Vargas et al. 2019) post-fire at the CM site, and therefore indicate that early surveys are good predictors of mean richness of understory communities burned at high-severity five years post-fire. Similarly, a survey conducted at MT in 2005 (three years after the initial 2002 fire), reports that richness was also lowest in areas burned at high severity (González and Veblen 2007).

The dimensions of the NMDS plots, based on species abundance, show that the reference conditions remained separated from sites affected by an initial fire at CM, yet these distances shrunk after a second fire at MT, even when reburned at low severity. These findings are not conclusive to suggest that high-severity burn and reburn have a homogenization effect on the understory community, which has been found in other forest ecosystems affected by severe wildfires (da Silva et al. 2018; Richter et al. 2019). Research in wetter temperate forests in Tasmania found that short-interval fire also resulted in the homogenization of the overstory taxa, but in contrast to our findings it increased richness of the understory plant community (Holz et al. 2020). Furthermore, and in contrast to our expectations, mean species richness did not vary between the UN and either HL severity at MT or L severity class at CM. These findings may be reflecting that the reference sites may not fully represent pristine conditions due to anthropogenic influence at MT; and similarities in the species composition following a single low-severity event with the reference conditions is consistent with the evolution of *Araucaria*-*Nothofagus* forests under a history of a mixed-severity fire regime (González et al. 2005; Mundo et al. 2017; Nanavati et al. 2021).

The use of the life forms and post-fire traits classification scheme allowed us to hone in on the various strategies to resist and/or recover from wildfire. For instance, while PFOR species from Poaceae (*Chusquea* spp.) were more abundant in the understory, and Nothofagaceae (*N. obliqua* and *N. alpina*) were more abundant in the forest structure of MT study site, species from the PFFRS group were more persistent in burned areas at the understory of CM site. However, we did not record any individual of *N. obliqua* in the understory of MT, which can partially underrepresent the PFOR results. The PFFRS and PFOR groups have bud protection structures that facilitate their growth after wildfires (Montenegro et al. 2003; Clarke et al. 2013; Kitzberger et al. 2016). Some *Nothofagus* tree species (e.g., *N. dombeyi* and *N. pumilio*) are fire-intolerant at the individual tree level but as PFOC species are fire-tolerant at the meta-population level (Prior and Bowman 2020). Moreover, they are dominant components of unburned forests that regenerate in both unburned canopy gaps and can colonize even severely burned sites from bordering seed trees and from remnant survivors in the interior of burned patches (Veblen et al. 1996; González et al. 2010; Tiribelli et al. 2018). Similarly, species classified as PFFRS belong to the Fabaceae, Araucariaceae, Berberidaceae, among other families (Supplement 2), were mostly found in burned plots but also in lower abundance in the UN sites. The species from this fire response class can resprout and also have the capacity to produce abundant seeds (Raffaele and Veblen 1998; Montenegro et al. 2003; Paritsis et al. 2006; Clarke et al. 2013; Kitzberger et al. 2016); thus, even though individuals do not survive fire, seeding allows them to persist at a population level in more flammable environments (Prior and Bowman 20202020).

Post-fire life form and trait responses to burn severity

Whether we evaluate post-fire life forms or trait response classification of the species, our results indicate that burn severity is the factor that best predicts and selects for responses of the post-fire community of *Araucaria-Nothofagus* forests. Most species lacking fire adaptations within understory communities in these forests are able to recover to a similar abundance following a single low-severity fire (González et al. 2005). Previous studies after the 2002 wildfire at Tolhuaca National Park indicate that *Chusquea* spp. was the genus that recovered most rapidly following fire (González and Veblen 2007). Although these species were still abundant 5 years after the 2015 reburn, their response was not predicted by burn severity. In the same line, we observed that PFOR species (e.g., Nothofagaceae, Proteaceae families, among others) were not significant in areas affected by single fire, presumably by the higher elevation and lower temperatures in the cold season, which are exacerbated by the synergetic effects with droughts that are affecting south-central Chile since 2010 (Garreaud et al. 2020; González et al. 2020; Nolan et al. 2021).

The severity of our single burn negatively affected the abundances of PFOC species (i.e., *N. pumilio* and *N. dombeyi*). *Nothofagus pumilio* was found in unburned forests and in stands burned at low severity at CM (mean abundance: 13.7% ± 2.8 at UN, and 4.1% ± 1.3 at L), but only in unburned stands at MT (8.6% ± 2.5). *Nothofagus dombeyi*'s seedlings were rarer, with a presence at unburned reference forests at MT of only (7.7% ± 1.6) but only scarcely found at CM in the low-severity class (0.6% ± 0.1). Although *N. pumilio* and *N. dombeyi* are considered post-disturbance colonizers (Veblen et al. 1981; Donoso 2006), we did not find juveniles in areas burned at high severity, nor in those plots burned twice at any reburn severity. These results are consistent with positive fire-vegetation feedbacks under which high-severity or severe wildfires reduce the abundance and seed sources of the tree colonizer species while promoting the abundance of resprouting flammable shrubs (Paritsis et al. 2015; Kitzberger et al. 2016; Assal et al. 2018; Tiribelli et al. 2018; Landesmann et al. 2021). The scarcity of post-fire regeneration of these species may reflect limitations of seed availability due to distance of live *N. pumilio* and/or *N. dombeyi* adult individuals (distance ≥ 60 m) from sample sites or may reflect other factors such as effects of high-severity fire on post-fire microsites, not matching masting cycles between fire events, and/or unfavorable climatic conditions for seedling establishment.

Although limited in replication, our findings indicate that high burn severity and short-interval fires, can catalyze a rapid shift toward less diverse and fire-prone shrubland communities, especially when resprouter species dominate and promote fire-vegetation feedbacks that persist over time (Paritsis et al. 2015). Previous studies in the Patagonian-Andean ecoregion have reported that woody, resprouting shrub species have a greater propensity to burn compared to tall *N. pumilio* forests (Mermoz et al. 2005; Paritsis et al. 2013), thus increasing the likelihood of subsequent burning due to fuel arrangements and environmental conditions (Paritsis et al. 2015; Kitzberger et al. 2016; Landesmann et al. 2021). Under projected warming, water stress, longer drought seasons and increased fuel aridity for NW Patagonia (Boisier et al. 2018), an increase in high-severity, short-interval fires are expected. However, these results are taken with precaution because our study sites differ in their fire histories and replication was not feasible. Only the Malleco-Tolhuaca study site presented the option to evaluate the effect of short-interval fire. Our results are consistent with the change of the composition across study sites, and the China Muerta study site has shown that high-severity fires are causing these changes as well. However, more studies of reburned areas in this forest type will be needed to establish consistent patterns of effects of short-interval fires.

Conclusion

This study assessed the effects of single fire, and (for the first time in Patagonia) reburns, on the post-fire response of understory communities of *Araucaria-Nothofagus* forests. Although findings vary based on the response variable (i.e., plant community composition, life forms, or fire-related trait), overall, we found comparable understory community responses following a single severe event as well as a second burn that reburned a high-severity event 13-years later. Fire triggered both a reorganization of the plant community and the establishment of species absent in the reference forests. Our findings confirm that *Araucaria-Nothofagus* understory communities are able to absorb a single low-severity event, but that reburning after a short-interval can affect the understory composition by favoring post-fire resprouters and/or facultative resprouter/seeder that quickly and extensively respond. More broadly, our study highlights the role of short-interval fires as a catalyst that reinforces the persistence of pyrophytic communities that quickly resprout, leading to landscape-scale losses of species less tolerant to fire. However, our results do not demonstrate a homogenization of the plant community after a single fire or reburn.

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Author contributions All authors contributed to the conceptualization and design of the study. Data collection and analysis were performed by PAV. The first draft of the manuscript was written by PAV and all authors revised the previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated and analyzed during the current study are available from the corresponding author based on appropriate request.

Code availability Not applicable.

Declarations

Conflict of interest The authors have no conflicts of interest to declare in this work.

Appendix 1

See Fig. 5.

Fig. 5 Images from Malleco-Tolhuaca (reburned; (**a**–**c**)) and China Muerta (single burn; (**d**–**f**)) study sites. Note the presence of livestock in burned areas in Malleco-Tolhuaca (**c**) and China Muerta (**f**) sites and the variable mounts of resprouting *Chusquea* bamboo

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