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Recovery of Chilean Mediterranean vegetation after different frequencies of fires

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ABSTRACT

Post-fire recovery of sites in the Chilean Mediterranean vegetation were evaluated 20–30 years after the last fire. We mapped all fires that occurred between 1985 and 2015 in Central Chile using Landsat images. In order to conduct a spatial analysis of vegetation recovery and field sample, we chose sites burned between 1985 and 1995 that retained native vegetation and cover until 2015. In a sampled of these sites, richness and abundance of woody vegetation, and herbaceous richness were recorded. We contrasted our results from field sampling with control (unburned) sites at the species level. Generalized linear models (GLM) were used to evaluate the relationship between the percentage of vegetation recovered with fire frequency, pre-fire cover, topographic and geographic factors. In addition, GLM were used to evaluate the effects of fire frequency on species richness, abundance, and cover. We found that the proportion of dense and semi-dense vegetation cover were similar in sites burned once and twice, and higher than sites burned three times. Besides, the proportion of dense and semi-dense vegetation cover were higher in lower elevation sites, in those with higher slopes, and far from population centers. The richness and abundance of adult woody species, richness of regeneration and richness of native herbs, were greater in sites that had lesser fire frequency. Mean species richness of native herbaceous species decreased as fire frequency increased, exotic herbaceous cover had no relation with fire frequency, and both native and exotic herbaceous cover were greater at driest latitudes but were not related to fire frequency. Mean species richness after one fire was higher than in unburned sites, but some plant species were found only at unburned sites. We conclude that the Mediterranean vegetation of Chile is able to regenerate to pre-fire conditions after one and two fires, but three consecutive fires reduced its cover, richness and abundance, even 20 years after the fire.

1. Introduction

Frequency of fire is likely to increase in many regions due to climatic change (IPCC, 2019). Scientists are concerned about whether vegetation recovery under heightened frequency of fire will reach the same levels as it has in the past (Pausas et al., 2008), even in areas prone to fires with fire-adapted species, such as in Mediterranean-type ecosystems. Vegetation recovery after repeated fires with short interval years among them has been studied in the Mediterranean vegetation of South Africa, Australia, USA, and Europe, but not yet in Chilean sclerophyllous

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shrublands and forests. Fynbos vegetation in South Africa demonstrated that repeated short-interval fire occurrence (≤6 years) reduce plant cover, height and biomass, but increased species richness (van Wilgen, 1981). In Banksia woodland in Australia, successive short-interval fires have been found to produce a decline in native cover, richness, diversity and replacement of native species by exotics (Fisher et al., 2009). In Californian chaparral it was found that two consecutive, short-interval fires are required to diminish native species composition and cover (Keeley and Brennan, 2012; Lippitt et al., 2013). In Mediterranean maquis (northern Israel) areas burned once, twice and three times were analyzed, and results showed that species composition was dramatically altered when fire frequency increased (Malkisnon et al., 2011; Tessler et al., 2015); however, vegetation cover was not always affected (Wittenberg et al., 2007). In Spain, a general pattern of simplification of species richness has also been found after repeated fires (Vilà-Cabrera et al., 2008), similar to the results from Banksia vegetation in Australia. Herbaceous species cover increased with repeated fires in almost all the areas studied (van Wilgen, 1981; Vilà-Cabrera et al., 2008). The effects cited above of short-interval recurrent fires on vegetation cover and richness were assessed from four to 14 years after a fire occurred, and in many of these cases some changes were expected to occur. However, there is a lack of studies that assess vegetation properties at mature postfire stages.

Different mechanisms have been associated with the reduction in species richness and abundance, especially in woody species, after fires with short-intervals. A first possibility is the depletion of seedbanks, in case the fire intervals are shorter than the time required to produce new seeds following initial fire (Keeley and Brennan, 2012); Second, is the depletion of stored carbohydrate resources that resprouted species require (Pate et al., 1991; Drewa et al., 2002; Pausas et al., 2008; Paula and Ojeda, 2009). Another synergistic mechanism could be soil loss and lack of nutrients after frequent fires; however, in some cases, soil characteristics did not show any clear trend toward fertility loss after recurrent fires (Ferran et al., 2005). In the case of herbs, one of the mechanisms of native vegetation loss is the replacement of these species by exotics or native invasive species, as occurred in several burned Mediterranean areas (Zedler et al. 1983, Vilà-Cabrera et al., 2008).

Compared to other Mediterranean regions, relatively little is known about vegetation dynamics following fire in central Chile. There have been no studies of vegetation recovery after successive fires, nor is the quantity of successive fires in a same stand is known. The Chilean Mediterranean ecosystem is considered a biodiversity hotspot, that mean has high endemism and critically threatened status at the ecosystem and species level (Myers et al., 2000; Olson and Dinerstein, 2002; Alaniz Alberto et al., 2016). The sclerophyllous shrublands and forests in Northern Chile that contains Mediterranean vegetation (30–34°S) is mainly distributed on western- and southern-facing slopes, along creeks, and in some flat areas of coastal hills; currently only 17% of the original cover remains (Salazar et al., 2015). Agriculture, logging, fires, and urbanization have been degrading this vegetation for centuries (Armesto et al., 2010).

Few species of Chilean Mediterranean vegetation have lignotubers, but many of them have the ability to sprout after fire (Montenegro et al., 2004; Figueroa, 2017; Droguett, 2019). A few species have seeds that remain viable, but only after low-intensity fires (Gómez-González and Cavieres, 2009; Gómez-González et al., 2017). Despite the high capability of some woody vegetation to recover after one fire, it is unknown if this occurs at the landscape level after frequent fires. In fact, a field study after one fire showed that the ability of woody vegetation to regain coverage 10 years after a fire was low (Becerra et al., 2018). In contrast, herbaceous cover is able to rebound after fires (Gómez-González et al., 2011; Droguett, 2019): it is more accurate to state that recently burned sites give rise to both native and exotic herb species, which are normally displaced by shrubs or trees if regeneration is successful. Anthropogenic fires seem to favor both exotic and native annuals, with no change in the exotic/native ratio (Gómez-González et al., 2011). However, it is

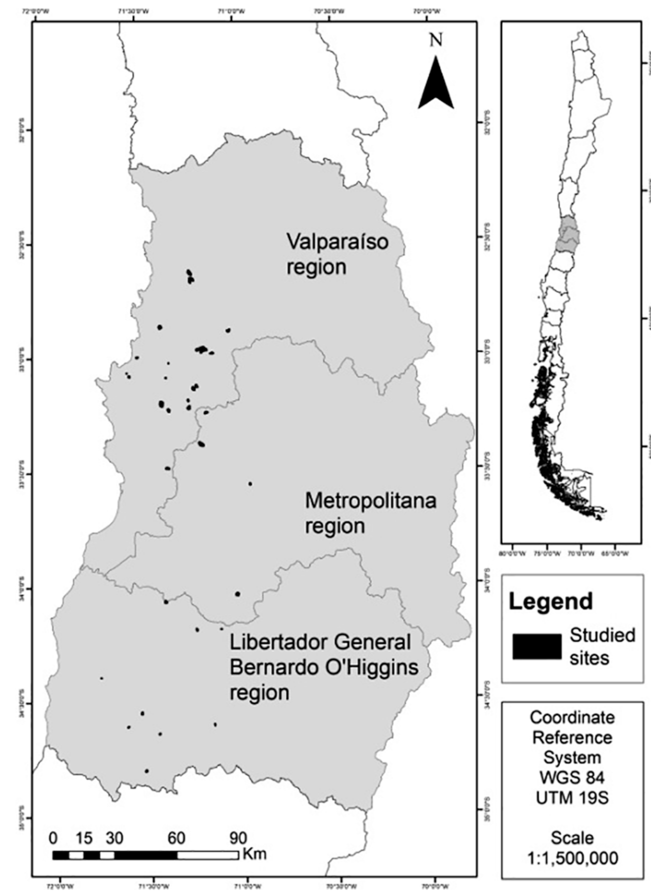

Fig. 1. Study sites, which span three Administrative Regions of Chile, are shown as black dots.

unknown how different fire frequency affects long-term recovery capability of native and exotic herbs in this region. In this paper we assessed: 1. vegetation recovery at the landscape level after different fire frequencies, and 2. richness and abundance of woody and herbaceous vegetation after short-interval fires that occurred once, twice, and three times between 1985 and 1995. We studied short-interval fires because they are more stressing for plant recovery and because we expect short-interval fires are common in Chilean Mediterranean areas. Because recovery of Chilean dryland vegetation is slow (Fuentes-Castillo et al., 2012), we studied the effect of fires on vegetation over the long term, 20 or more years after the last fire. We expect that a higher frequency of short-interval fires reduces the capability of woody vegetation to recover in its cover, richness and abundance, and instead allow exotic herbaceous species to increase in cover and richness. To do this study, we used two approaches: spatial images to assess recovery percentage of woody vegetation after fire, and field studies to evaluate richness and abundance of regeneration and adult individuals of woody species, as well as richness and cover of herbaceous species. It bears highlighting that these kinds of studies are usually published separately; however, we integrated GIS analysis and field work methods because they facilitate integrative inferences at species and landscape levels. We also explored the influence of pre-fire vegetation cover, slope percentage, elevation, proximity to populated centers, and latitude on the vegetation variables analyzed. Elevation has been documented as the best variable explaining vegetation recovery after fire in other Mediterranean areas (Keeley and Brennan, 2012, Storey et al. 2020a). Latitude in central Chile is strongly related to climate, especially precipitation (Becerra, 2016), which may also modulate vegetation recovery.

Table 1
Characteristics of the burned sites studied in central Chile.

Fire frequency	Site	Surface (ha)	Minimun elevation (m)	Maximun elevation (m)	Mean elevation (m)	Minimun slope (%)	Maximum slope (%)	Mean slope (%)	Distance to population centers (m)	Fire year		
										1	2	3
1	1	119.31	195	507	351	10	41	25.5	4184	1990		
	2	370.14	211	805	508	8	57	32.5	0	1990		
	3	32.05	538	827	682.5	12	55	33.5	1585	1990		
	4	206.88	324	859	591.5	4	39	21.5	1153	1991		
	5	59.21	331	598	464.5	12	55	33.5	14,349	1990		
	6	54.95	490	831	660.5	10	65	37.5	7256	1989		
	7	49.15	584	764	674	8	45	26.5	2710	1994		
	8	97.83	294	695	494.5	8	64	36	352	1985		
	9	152.56	315	850	582.5	15	45	30	3396	1985		
	10	108.78	270	650	460	0	50	25	468	1985		
	11	17.26	141	204	172.5	0	26	13	0	1985		
	12	235.7	316	560	438	3	45	24	2000	1985		
	13	27.86	305	408	356.5	8	35	21.5	742	1985		
	14	73.65	640	795	717.5	5	20	12.5	15,100	1985		
	15	97.83	340	700	520	9	55	32	300	1985		
	16	11.14	406	547	476.5	0	55	27.5	6325	1985		
	17	42.62	495	820	657.5	9	45	27	7350	1995		
	18	56.85	220	461	340.5	8	60	34	2796	1995		
	19	106.22	340	770	555	35	60	47.5	1500	1995		
	20	46.98	286	757	521.5	9	57	33	0	1995		
	21	86.94	832	1000	916	0	32	16	9871	1995		
2	1	43.21	491	619	555	1	45	23	1218	1990	1991	
	2	74.92	648	1024	836	11	49	30	4463	1988	1991	
	3	21.85	620	929	774.5	25	55	40	18,249	1989	1990	
	4	35.79	325	467	396	8	36	22	1451	1985	1986	
	5	77.66	350	586	468	1	37	19	3076	1989	1994	
	6	32.68	179	478	328.5	2	79	40.5	1331	1989	1994	
	7	5.44	433	645	539	22	76	49	616	1991	1994	
	8	31.53	325	497	411	14	40	27	13,622	1989	1994	
	9	9.88	146	239	192.5	7	43	25	641	1990	1995	
3	1	6.02	196	254	225	14	30	22	166	1989	1992	1993
	2	4.13	452	514	483	5	40	22.5	11,616	1986	1987	1993
	3	1.31	232	246	239	0	0	0	1572	1985	1989	1994
	4	1.05	190	210	200	0	0	0	136	1991	1993	1995
	5	2.02	199	218	208.5	0	0	0	271	1985	1988	1993

2. Methods

2.1. Study area

The area of study includes three Administrative regions of central Chile: Valparaíso, Santiago Metropolitan, and L. G. B. O'Higgins, spanning 32°02′ to 34°45′S and 69°40′ to 72°10′W (Fig. 1). This study area includes the northern part of the Mediterranean sclerophyllous shrublands and forests of Chile. The climate of this area is Temperate Mediterranean with seasonal rainfall, characterized by mild, rainy winters and warm, dry summers (di Castri and Hajek, 1976, Aschmann, 1984). The historic annual precipitation is about 650 mm coastal hills where we focused our study, but the precipitation has strong interannual oscillations produced by ENSO phenomena. In the last 10 years a severe drought decreased precipitation in 25–45% (Garreaud et al. 2017). The average temperature is 14.5 °C, in summer the temperature can be more than 35 °C (Luebert and Pliscoff, 2006). Still remain 400,000 ha of shrublands and forests in the study area, distributed across two million hectares (CONAF, 2020). This area is the most populated in the country, close to 9.7 million of people, with a rate of annual population increase of 1.1–1.4 depending of the Administrative Region (INE, 2018, www.memoriachilena.gob.cl).

2.2. Satellite image processing

In order to determine the frequency of fires in one site over a specific period of time, all the fires that occurred in the Chilean Mediterranean vegetation between 1985 and 2015 were identified and mapped using Landsat images (TM and OLI sensors), which were obtained from Earth Explorer (https://earthexplorer.usgs.gov). All images were corrected geometrically, radiometrically and atmospherically (Chuvieco et al., 2002; Heilmayr et al., 2016). The oldest cloud free image in our study area was available from 1985, hence it was the earliest year of our study period. A maximum likelihood statistics of the supervised classification method (Chuvieco et al., 2002) was used to classify native forest, scrub, pasture/cropland, urban areas, exotic plantations, water bodies, bare soil and burned areas. We used approximately 500 training points for each classified image, which were acquired through two sources, (a) cadastre of the native plant resources of Chile (CONAF et al., 1999) and its updates to classify images prior to 2002, and (b) Google Earth (specifically its "time slider") to obtain input to classify images after 2002.

For the supervised classification, in addition to the information provided by the six Landsat spectral bands, two indices were used to improve the identification of the burned scars (that we call "sites"): NDVI (Normalized Difference Vegetation Index) (Chuvieco et al., 2002; Heilmayr et al., 2016) and NDWI (Normalized Difference Water Index) (Gao, 1996), which helped to spatially identify the areas in which there were strong changes in the state of vegetation and humidity, respectively. The validation of the classifications was carried out by confusion matrices through 250 points for each image. These validation points were obtained from the same sources of information as the training points.

We used two methods to increase the precision in the identification of burned sites and separated them from those areas where the loss of vegetation was due to other anthropic activities, such as deforestation and land clearance for agriculture. (1) We identified the loss of vegetation cover through spatial analysis (image algebra using the Spatial Analyst extension of ArcGis 10.2) and (2) we created false-color images from spectral bands, which improved the visibility of the areas where the wildfires occurred. These two analyzes were carried out in parallel as a validation method for the identification of burned areas and the regeneration of woody vegetation over time.

2.3. Criteria to choose sites by spatial and fieldwork analysis

From the total burn scars found we decided to only include in our analysis sites with fires up to 1995 in order to focus on sites that have had a long time to recover (20–30 years). The maximum frequency of fires between 1985 and 1995 at the same site was three. For the sites burned twice and three times, we chose fires that occurred with a recurrence interval of less than five years, which is considered in literature as a short fire frequency period (Lippitt et al., 2013; Meng et al., 2014). Besides, for our field analysis, we choose sites that had not burned and converted to other land by 2015, the time of our fieldwork (Table 1). Most of the areas burned during the period we considered had been converted to other land uses, mainly agricultural. These control sites had the same location characteristics of burned site, that is more than 80% of dense vegetation cover, and also no presence of charcoal, at least in areas where we set up the transects. We estimate that the control sites have not been burned for at least 50 years (at least 20 years before 1985), based on the dense cover of woody vegetation present in the 1985 image. The mean distance among control and burned sites was 57.98 km. We could not use control sites in the border of sites burned, because all the natural vegetation was transformed into other land uses. Chilean Mediterranean forests has been the most transformed to other uses in South America (Salazar et al., 2015).

All the burned sites we selected were located on hills of the Coastal Range because they had a higher number of total fires compared to the Andean foothills. All of our sites are located on western-, southern- and southwestern-facing slopes, because this is where the Mediterranean shrublands and forests is mainly distributed.

2.4. Spatial analysis

We chose 21 once burned sites, nine twice burned sites and only five sites that were burned three times because those were rare given our criteria for slopes (and time elapsed between fires (Fig. 1; Table 1). We determined the percentage of vegetation cover of all extension of the chose sites using Google Earth Pro and ArcGis (10.2). We classified the vegetation cover either as Dense vegetation (75–100% of woody vegetation cover), Semi-dense vegetation (50–75%), Open vegetation (1–50%), Burned wood or charcoal, Bare soil, or Other land cover (roads, houses, agricultural crops, bodies of water, among others). The sites had a 69 ha area (ranging from 1 to 370 ha) on average. In the case of sites burned three times, we included small sites because it was difficult to find large burned areas. A total area of 157,780 ha of shrublands and forests, burned different numbers of times between 1985 and 1995 was analyzed.

2.5. Field work

We surveyed and quantified the composition, richness and abundance of woody and herbaceous species in four once burned sites in 1985, in four once burned sites in 1995, in four twice burned sites, and four three times burned sites between 1985 and 1995. These sites were 16 burned sites out of the 35 we studied with satellite images. In addition, we sampled four unburned control sites. In all areas we checked for charcoal in the field in order to know if some fires could have occurred before that year.

Vegetation sampling was conducted between October and November 2015. The elevation and geographical coordinates were recorded for each site using a GPS, and linear distance to the nearest populated center (more than 10,000 people; INE, 2018) was calculated using Google Earth. At each site, we walked the area and chose a representative place (physionomically similar in species composition and cover) then installed four parallel transects 20 m apart with similar slope. Each transect was 50 m long by 2 m wide. Along each transect, we recorded all individuals of woody species >2 2 m high in plots (considered as an adult). We also recorded the seedlings of woody species (individuals less than 2 m tall) in 10 plots of 0.25 m^2 (0.5 × 0.5 m) separated by 10 m from each other along each transect (40 plots per site). Herbaceous composition, species richness and absolute cover (%) per species was also recorded in each plot. Unidentified woody species in the field were collected and identified later using herbarium specimens. Because transects were located in areas representative of the cover at each site, and hence of the recovery level after fire, we expect that the total surface sampled per site (400 m^2) effectively represents the attributes of the plant communities present within each site. We checked for the presence of charcoal or burned logs in both burned and unburned sites, in and around the transects. The composition and abundance of woody and herbaceous species in the burned and control sites are shown in Appendices A and B.

2.6. Statistical analysis

To determine if there were significant differences in the percentage of vegetation cover (dense, semi-dense, and open) between sites with different fire frequencies, an ANOVA was performed. ANOVAs were also performed to determine if there were significant differences in richness and abundance of woody species, and in richness and cover of native and exotic herbaceous species, between sites with different fire frequencies. If the assumptions of the ANOVA were not fulfilled, a Kruskal-Wallis test was performed. If there were significant differences, a post hoc test was performed.

Generalized linear models (GLM) were used to evaluate the effects of different fire frequencies (1, 2 and 3 fires between 1985 and 1995) (Ff), slope (average, maximum and minimum) (Sl), elevation (average, maximum and minimum) (E), distance to population centers (P), latitude (L) and type of pre-fire coverage (exclusively shrub, exclusively forest and a mix of both) (C) on the percentage of native vegetation cover. We used closeness to population centers (towns and cities) as a proxy for perturbation by logging conducted by rural people, and by use of land for cattle pasture, and road density. We used latitude as a proxy of precipitation, due to in Chile latitude decreases in almost the same way that precipitation increases (Luebert and Pliscoff, 2006), and there is not complete data for precipitation from 1985 to 1995 period in part of the study area. We also included the surface of the burned area as an independent variable; however, it was not significant in any model, hence we do not show these results. Severity of fire was not included as an independent variable because it did not influence long-term recovery (more than 15–20 years) in Chilean Mediterranean vegetation (Becerra et al., 2018). The slope exposure was not used as an explicatory variable because we sampled only two types of exposures. The response variables studied were the proportion of dense vegetation (in relation to total area of the burned site) (Dv), proportion of semi-dense vegetation (Sdv) and proportion of open vegetation (Ov). We used a binomial error distribution and a logit link function in GLM. We chose the model with lowest AIC (Akaike criteria) since that indicates the best fit. In all models, control sites increased AIC, so we decided to remove this information from the models, and we used unburned control sites only to discuss results and detect species that not recover after fires. We also calculated the deviance (D^2), which indicates the proportion of the variance that the model explains. The GLM models used were: 9.

Model a: $Y = B_0 + B_1 * Ff\, B_2 * Sl(mean) + B_3 * E(mean) + B_4 * P + B_5 * L + B_6 * C$

Model b: $Y = B_0 + B_1 * Ff + B_2 * Sl(min) + B_3 * E(min) + B_4 * P + B_5 * L + B_6 * C$

Model c: $Y = B_0 + B_1 * Ff + B_2 * Sl(max) + B_3 * E(max) + B_4 * P + B_5 * L + B_6 * C$

Model d: $Y = B_0 + B_1 * Ff$

where $B_{0,1,2,3,4,5,6}$: estimated coefficients, Y: proportion of Dv or DSv or Ov, min: minimum and max: maximum.

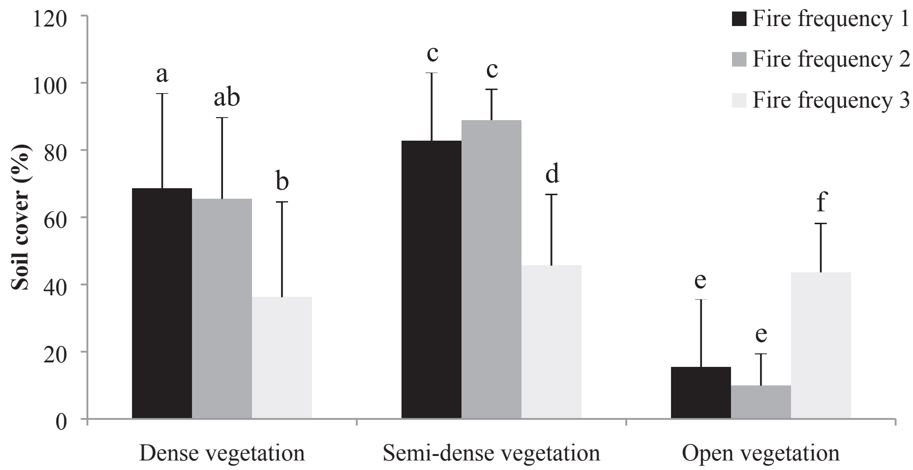

Fig. 2. Percentage of vegetation cover recovered by 2015 (X ± SD) in sites burned once, twice, and three times between 1985 and 1995. Unburned (control) vegetation sites had mainly dense vegetation cover, and were not included in these analyses. Letters indicate significant differences ($p \leq 0.0.075$).

Table 2
Significant variables for GLM analysis on the percentage of vegetation recovered after different number of fires, slope, elevation, latitude, pre-fire coverage and distance to populated center in Central Chile.

Percentage of vegetation cover	Model	Significant terms	AIC	D^2
Dense vegetation	b	(−0.5772) Ff + (+0.0759) Sl (min) + (−0.0044) E (min) + (+0.00008) P + (+9.305) C(forest) + (−1.337) C(shrub) + (−0.3932) C(both)	846.16	46.83
Semi-dense vegetation	a	(−04547) Ff + (+0.0604) Sl (mean) + (−0.0030) E (mean) + (+0.0006) P + (+0.000003) L + (−17.34) C(forest) + (−0.8899) C(shrub)	680.95	44.16
Open vegetation	a	(+0.7737) Ff + (−0.0162) Sl (mean) + (+0.0048) E (mean) + (−0.0005) P + (+1.381) C(shrub) + (−0.6104) C(both)	680.46	36.39

Ff: fire frequency, Sl: slope, E: elevation, P: distance to population centers, L: latitude, C: pre-fire coverage (exclusively shrub or forests or a mix of both), AIC: Akaike Information Criterion, D^2: deviance.

GLMs were used to evaluate the effect of fire frequency (one, two, and three fires) (Ff), elevation at which transects were placed (E), linear distance to population centers (P), latitude (L) and type of pre-fire coverage (forest, shrub or both) (C) on: (a) richness of adult woody species, (b) abundance of adult woody species, (c) richness of regeneration of woody species, (d) abundance of regeneration of woody species, (e) richness of native herbaceous species, (f) richness of exotic herbaceous species, (g) native herbaceous cover (%) and (h) exotic herbaceous cover (%). In the case of the richness and abundance of woody species and herbaceous species richness, we used a Poisson error distribution and a logarithmic link function in GLM since the response variables were counts. For herbaceous cover, a binomial error distribution and a logit link function were used. The models were:

Model a: $Y = B_0 + B_1 * Ff + B_2 * E + B_3 * P + B_4 * L + B_5 * C$
Model b: $Y = B_0 + B_1 * Ff$

where $B_{0,1,2,3,4,5}$: estimated coefficients, Y: richness or abundance of adults and regeneration of woody species, or herbaceous richness or herbaceous cover. We did two exploratory GLM analyses, one using control sites and one without them. We chose the model with lower AIC. A P value less than 0.05 was considered significant, and a value between 0.05 and 0.1 was considered marginally significant.

3. Results

3.1. General information of fires

We found a total of 1586 fires that occurred between 1985 and 2015. The maximum number of burns (that we call frequency of fires) at the same site was seven in the period of 30 years studied, with an average of 1.29 fires per site. The most common number of burns in the same site was two (40.65% of all fires), followed by one fire (30.32%), three fires (17.74%) and four fires (5.80%). The least common frequencies were five to seven fires (5.84%).

3.2. Spatial analysis

The results of the validation of the all-land use/cover maps indicate that an average of 87.8% classifications accuracy was obtained. The land use/cover that obtained the highest accuracy was the water bodies with 97.3%, followed by crop areas with 93.8%. Conversely, the coverage that obtained a lower precision was scrub with 81.4%, followed by urban areas with 86.9%.

Considering the 35 burned sites without land use change that we chose for spatial analysis, we found that 64.6% of the burned vegetation recovered by 2015 (as dense plus semi-dense vegetation). Differences in dense vegetation cover between different fire frequencies were marginally significant (ANOVA $F = 2.88$, $df = 2$, $p = 0.07$; Fig. 2). Specifically, dense vegetation cover was higher in sites burned once than in sites burned three times (Post-hoc pairwise test $p = 0.07$). Also, semi-dense vegetation cover was significantly higher (Kruskal-Wallis chi-squared = 9.08, $df = 2$, $p = 0.01$; Fig. 2) in sites burned once (Post-hoc Nemenyi test $p = 0.02$) and twice (Post-hoc Nemenyi test $p = 0.01$) than sites burned three times. Open vegetation was significantly higher (Kruskal-Wallis chi-squared = 8.21, $df = 2$, $p = 0.02$; Fig. 2) in sites burned three times than sites burned once (Post-hoc Nemenyi test $p = 0.009$) and twice (Post-hoc Nemenyi test $p = 0.005$). These results indicate that with higher number of burns, dense and semi-dense cover decrease while open vegetation increases.

GLM analyses show that fire frequency was negatively and

Table 3
Total species richness and abundance in the burned sites (1 to 3 times) and non-burned control sites in Central Chile.

Origin	Species	Richness (number of species)				Abundance (number of individuals)			
		Fire frequency			Control	Fire frequency			Control
		1	2	3		1	2	3	
Native	Adult woody	14.63 ± 2	13.75 ± 4.35	8.5 ± 3.11	13.75 ± 2.22	105.13 ± 41.32	88 ± 19.18	56.75 ± 15.31	79.25 ± 21.96
	Regeneration woody	9 ± 2.83	6.75 ± 1.5	4.75 ± 3.59	6 ± 3.46	81.25 ± 55.15	25.5 ± 13.18	33.75 ± 56.18	60.5 ± 46.98
	Herbaceous	17.13 ± 3.64	15 ± 3.16	10.5 ± 7.14	14 ± 8.64	–	–	–	–
Exotic	Adult woody	0.25 ± 0.46	0	1.25 ± 1.89	0	0.38 ± 0.74	0	8.5 ± 15.07	0
	Regeneration woody	0	0	0.25 ± 0.5	0.25 ± 0.5	0	0	6.25 ± 12.5	0.25 ± 0.5
	Herbaceous	13.25 ± 5.85	19.25 ± 8.3	9.25 ± 10.11	14.5 ± 6.24	–	–	–	–

Table 4
Significant variables for GLM analysis of woody species richness (number of species) and abundance (number of individuals) for both adult individuals and regeneration in sites burned 1 to 3 times in Central Chile.

Response variable	Model	Significant terms	AIC	D^2
Richness of adult woody species	b	(−0.1651) Ff	271.5	14.9
Abundance of adult woody species	a	(−0.1686) Ff + (+3.773) C(forest) + (−0.3911) C(both)	502.68	30.6
Richness of regeneration woody species	b	(−0.4180) Ff	227.26	21.17
Abundance of regeneration woody species	a	(−0.00007) P + (+0.0004) L + (−11.35) C(forest) + (−0.6953) C(shrub) + (−1.514) C(both)	934.59	37.25

Ff: fire frequency, E: elevation, P: distance to populated centers, L: latitude, C: pre-fire coverage (exclusively shrub, forest or a mix of both), AIC: Akaike Information Criterion, D^2: deviance.

significantly related to dense and semi-dense vegetation, and positively related to open vegetation (Table 2). Also, dense and semi-dense vegetation cover was higher in sites with a greater slope, farther from towns and cities, and at lower elevation (Table 2). In contrast, open vegetation cover was higher in sites with a lesser slope, closer to population centers and at greater elevation. Dense vegetation recovered was significantly higher in sites with pre-fire forest cover, and lower in sites where had shrublands and when it was covered by both (a mix of shrublands and forests). Semi-dense vegetation recovered was significantly lower in sites where had shrublands and forests, and was not significant when the sites had both. Open vegetation recovered was significantly higher in sites with pre-fire shrub cover and lower when it was covered by both (a mix of shrublands and forests). It was not significant when the sites had forests.

3.3. *Fieldwork*

We found pieces of woody charcoal within the transects of all the burned sites, totaling 116 pieces. In total, we recorded 54 native and six exotic woody species in burned and unburned sites. The total abundance of native and exotic woody species was 2860 and 63 individuals, respectively. Adult exotic species were rare (2.2%). One of these species, *Eucalyptus globulus*, was likely planted, and almost half of the records of this tree (N = 31) were found in only one site (Appendix A). The greatest richness and abundance of native woody species in adults and regeneration were found at sites that had been burned once (Table 3).

The most abundant adult woody species in unburned sites were *Cryptocarya alba*, *Peumus boldus* and *Lithrea caustica* (Appendix A). In sites burned once, the three most abundant species were *P. boldus*, *C. alba* and *Retanilla trinervia*. In sites burned twice, dominant species were *C. alba*, *Acacia caven* and *R. trinervia*, and in sites burned three times they were *R. trinervia*, *A. caven* and *Colliguaja odorifera* (Appendix A). In the case of woody seedlings at unburned sites and sites burned once, the most abundant species were *C. alba*, *Maytenus boaria* and *P. boldus*; *Quillaja saponaria*, *C. alba* and *M. boaria* in sites burned twice, and *M. boaria*, *C. alba*, and the exotic species *Teline monspessulana* in sites burned three times (the latter was present in only one site; Appendix A).

In total, combining burned and unburned sites, we recorded 75 and 66 native and exotic herbaceous species, respectively. The greatest richness in both native and exotic herbaceous species was found at sites that had been burned once (Table 3). The most abundant herbaceous species in the control sites were *Anthriscus caucalis* (exotic), *Euphorbia peplus* (exotic) and *Loasa triloba* (Appendix B); in sites burned once, the most abundant were *Adiantum chilense* var. *chilense*, *Alstroemeria* sp. and *Euphorbia peplus* (exotic); in sites burned twice, *Alstroemeria* sp., *A. caucalis* (exotic) and *E. peplus* (exotic) dominated, and in sites burned three times *Amsinckia calycina*, *F. agraria* (exotic) and *Lolium multiflorum* (exotic) were most abundant (Appendix B).

The richness and abundance of adult woody species differed significantly among sites with different fire frequencies (ANOVA F = 10.06, df = 2, p = 0.002 for richness and ANOVA F = 5.96, df = 2, p = 0.005 for abundance). Specifically, the richness and abundance of adult woody species was significantly higher in sites burned once (Post-hoc pairwise test p = 0.012 for richness and Post-hoc pairwise test p = 0.007 for abundance) than in sites burned three times. The woody species richness in regeneration was significantly higher (Kruskal-Wallis chi-squared = 18.459, df = 2, p = 0.0001) at sites burned once than at sites burned twice (Post-hoc Nemenyi test p = 0.002) and three times (Post-hoc Nemenyi test p = 0.001). The abundance of regeneration of woody species was significantly higher (Kruskal-Wallis chi-squared = 17.46, df = 2, p = 0.0002) in sites burned once than sites burned twice (Post-hoc Nemenyi test p = 0.003) and three times (Post-hoc Nemenyi test p = 0.001). The richness of native and exotic herbaceous species was significantly related to fire frequency (ANOVA F = 4.77, df = 2, p = 0.01 for native herbaceous and Kruskal-Wallis chi-squared = 6.23, df = 2, p = 0.04 for exotic herbaceous species). The richness of native herbaceous species was significantly higher in sites burned once than three times (Post-hoc pairwise test p = 0.034), and sites burned twice fell in between these two values of herbaceous species richness not differing significantly from either. The species richness of exotic herbaceous was significantly higher in sites burned once than twice (Post-hoc Nemenyi test p = 0.04). No relation was found between native and exotic herbaceous and fire frequency (Kruskal-Wallis chi-squared = 3.71, df = 2, p = 0.16 for native herbaceous and ANOVA F = 2.476, df = 2, p = 0.094 for exotic herbaceous).

The AIC in the GLM were observed to be lowest when control sites were excluded from the analysis, so we decided do not use them in this analysis. The richness and abundance of adult woody species and richness of regeneration were significantly greater in sites that had lower fire frequency (Table 4). The abundance of adult woody species was

Table 5

Significant variables for GLM analysis on herbaceous richness (number of species) and cover (absolute cover in percent) in sites burned 1 to 3 times in Central Chile.

Response variable	Model	Significant terms	AIC	D^2
Richness of native herbaceous species	b	(−0.1895) Ff	276.84	14.6
Richness of exotic herbaceous species	a	(−0.0016) E + (+0.00003) P	348.57	21.56
Native herbaceous cover	a	(+0.0012) E + (−0.0003) L + (+9.816) C(forest)	447.77	19.55
Exotic herbaceous cover	a	(−0.0012) E + (−0.0005) L + (+17.13) C(forest) + (+0.5394) C(both)	554.76	31.97

Ff: Fire frequency, E: elevation, P: proximity to populated centers, L: latitude, C: pre-fire coverage (forest, shrub or a mix of both), AIC: Akaike Information Criterion, D^2: deviance.

significantly higher in areas with pre-fire forest cover and lower in sites with pre-fire shrub cover, while it was not significant when cover was a mix of forest and shrubland. The abundance of regeneration of woody species was significantly higher close to population centers and northern latitudes and significantly lower in sites with pre-fire cover of forest, shrub and both (Table 4).

GLM analyses showed that the richness of native herbaceous species decreased with greater fire frequency. The richness of exotic herbaceous species was significantly greater at lower elevations and higher proximity to populated centers, but it was not related to fire frequency. Both native and exotic herbaceous covers were significantly greater at lower latitudes. Native herbaceous cover was significantly greater at higher elevation and in areas with pre-fire forest cover, with had no relation with fire frequency (Table 5). Exotic herbaceous cover was significantly greater at lower elevation and in areas with pre-fire cover of forest and a mix of forest and shrub.

4. Discussion

The key findings of this study are that dense vegetation cover would decrease after consecutive fires in the case of three short-interval wildfires. Besides, the percentage of dense and semi-dense vegetation cover as observed in 2015 satellite images did not differ between sites that suffered one versus two consecutive fires. Also, we found that woody species richness and abundance of individuals at the adult stage decreased after repeated fires, as seen in the case of sites with three fires compared to sites with one and two fires. Species richness of regeneration was affected negatively by repeated fires, but no the abundance of regeneration. In the case of herbaceous vegetation, native species richness, but not cover, was negatively related to fire frequency. Compared to unburned control sites, the richness and abundance of woody species was generally greater at the sites burned once than at the control sites. These patterns are consistent with the hypothesis of intermediate disturbance (Connell, 1978).

Depleted reserves in plants could represent a mechanism by which potential to recover after a third fire is reduced (Pate et al., 1991; Drewa et al., 2002; Pausas et al., 2008; Paula and Ojeda, 2009); another possible mechanism is the increased competition of woody seeds and seedlings with increased herbaceous cover. It has been showed that herbaceous cover increases over the short-interval after fire events (Gómez-González et al., 2011), remaining high even 10 years after a fire (Becerra et al., 2018).

Our findings are generally consistent with other studies conducted in the Mediterranean regions, although some differences were also detected. In the case of Chile, Becerra et al. (2018) found that 10 years after fire the vegetation of sclerophyllous forests did not regain dense cover or even semi-dense cover, which indicates that more time is necessary for these densities of vegetation cover to return (but in this study was not distinguished the number of burns occurred in the same site). In some areas of the Californian Chaparral, the ability of vegetation to recover decreased after only one fire (Keeley and Brennan, 2012; Lippitt et al., 2013). However, in other areas of Chaparral the tendency to recover after two but no three fires have been found (Storey et al. 2020a). It is interesting that Storey et al. (2020b) found that precipitation post-fire affected the vegetation recovery significatively. All the sites analyzed in our study were burned before the Mega-drought that has been occurring during the last decade in Central-Chile. Hence, we do not know what is happening with vegetation recovering after fire during this Mega-drought event.

In Chilean Mediterranean forests, woody species richness did not increase after frequent short fires as has been found in South Africa (van Wilgen, 1981). Similarly, we did not observe an increase in herbaceous cover with higher fire frequency (as has been found in almost all Mediterranean-type places studied, except some areas in Israel), at least on the timescale of our study (van Wilgen, 1981; Wittenberg et al., 2007; Vilà-Cabrera et al., 2008). In the Chilean sites studied, woody invasive species were not an important factor after fires (with the exception of *Acacia dealbata* in some mesic areas), which is a marked difference compared to the other four Mediterranean areas of the world, which are rapidly invaded after fire by woody exotic species (Vilà-Cabrera et al., 2008; Fisher et al., 2009). In our study, we found few individuals of the exotic tree species, and only in sites burned three times. Instead, in the southern part of the Chilean Mediterranean forest (our study was conducted in the northern part of this forest), *A. dealbata* and other invasives, such as *T. montpessulana*, are common after fire (Pauchard and Maheu-Giroux, 2007; García et al. 2010). Exotic herbaceous species are common across all the Mediterranean forest, as has been reported in several works (Arroyo et al., 1995). However, an increase in the abundance of different exotic herb species after fires has been reported (Contreras et al., 2011; Gómez-González et al. 2011, 2017). Our results suggest that, at least in the long term, the species richness of exotic herb species is not enhanced in areas with higher fire frequency.

It is probable that sites with greater slope and farther from populated areas are more protected from anthropogenic disturbance such as logging and cattle, which may explain the higher dense and semi-dense cover observed in these conditions. The direct relation of pre-fire conditions and actual vegetation cover, that is the return to pre-fire vegetation has been found by Hope et al. (2007) in Californian Chaparral, similar to what we found. The clearest relation showed by latitude (as a proxy of precipitation) is that at lower latitude (where there is more precipitation) there was more regeneration of woody species as expect in areas which one of the major restrictions for the vegetation recovery is the lack of precipitation. However, this regeneration increasing at lower latitude was not reflected in higher abundance of adult species. In general, the answer of regeneration was not easy to explain with the variables considered in this study, probably other variables as herbivory could be more explicative.

All species that we found in the burned areas had already been reported to sprout after fires in central Chile (Araya and Ávila, 1981; Montenegro et al., 2004; Figueroa, 2017; Droguett, 2019), except for five species that had not been documented sprouting up to date: *Chrysanthemoides monilifera*, *Echinopsis chilensis*, *Fuchsia lycioides* and two species of the genus *Lobelia*. We found that some species did not recover after fire. These were three woody species, which were found in unburned sites but not in the sites burned once, twice or three times: *Beilshmiedia miersii*, *Blepharocalyx cruschanksii* and *Berberis chilensis*. It is not clear if these species are not able to resprout after fire, or if these species were simply not present in our burned areas before the fires. Nevertheless, *B. miersii* has been observed resprouting after other disturbances such as logging and browsing (Morales et al., 2015), which

Table A1
Mean abundance (Mean $\pm$ Standard Deviation) of adults and seedlings of woody species present in sites burned once, twice, and three times between 1985 and 1995, and in control sites. Also, we include giant herbs as bamboo (Chusquea cummingii), Bromeliaceae, Cactaceae and Lobeliaceae. Species in bold are considered as threatened according to IUCN and expert opinions (authors). Scientific name of species, family and origin were assigned following Rodríguez et al. (2018). Life form was assigned following Raunkiaer (1934).

Species	Family	Life form	Origin	Adult abundance (individual number/site)				Seedlings abundance (individual number/site)			
				Fire frequency			Control	Fire frequency			Control
				1	2	3		1	2	3	
Acacia caven	Fabaceae	Tree	Native	0.13 $\pm$ 0.35	15.75 $\pm$ 17.61	8 $\pm$ 13.39	0.75 $\pm$ 0.96		0.5 $\pm$ 1	0.5 $\pm$ 1	
Acacia dealbata	Fabaceae	Tree/ Shrub	Introduced			1.25 $\pm$ 2.5					
Aristotelia chilensis	Elaeocarpaceae	Tree/ Shrub	Endemic	2.88 $\pm$ 4.67	0.5 $\pm$ 1	0.25 $\pm$ 0.5		0.25 $\pm$ 0.46			
Azara celastrina	Salicaceae	Tree/ Shrub	Endemic	5.25 $\pm$ 10.55	0.25 $\pm$ 0.5	0.5 $\pm$ 1	2 $\pm$ 2.45	0.38 $\pm$ 1.06		1.25 $\pm$ 2.5	0.25 $\pm$ 0.5
Azara dentata	Salicaceae	Shrub	Endemic			0.25 $\pm$ 0.5	0.25 $\pm$ 0.5				
Azara petiolaris	Salicaceae	Tree/ Shrub	Endemic	0.13 $\pm$ 0.35				0.13 $\pm$ 0.35			
Azara serrata	Salicaceae	Tree/ Shrub	Endemic	0.13 $\pm$ 0.35	0.75 $\pm$ 1.5				0.25 $\pm$ 0.5		
Baccharis concava	Asteraceae	Shrub	Endemic	0.13 $\pm$ 0.35							
Baccharis linearis	Asteraceae	Shrub	Native	2.75 $\pm$ 4.23	0.25 $\pm$ 0.5	3.25 $\pm$ 4.27	0.75 $\pm$ 0.5	0.25 $\pm$ 0.71			
Baccharis rhomboidalis	Asteraceae	Shrub	Endemic	0.25 $\pm$ 0.71	0.25 $\pm$ 0.5	0.25 $\pm$ 0.5	1 $\pm$ 2			0.25 $\pm$ 0.5	0.25 $\pm$ 0.5
Beilschmiedia miersii	Lauraceae	Tree	Endemic				0.75 $\pm$ 1.5				0.25 $\pm$ 0.5
Berberis chilensis	Berberidaceae	Shrub	Endemic	1.13 $\pm$ 3.18	0.25 $\pm$ 0.5		0.5 $\pm$ 1		2.5 $\pm$ 5		0.25 $\pm$ 0.5
Blepharocalyx cruckshanksii	Mirtaceae	Tree	Endemic				2.5 $\pm$ 5				
Cestrum parqui	Solanaceae	Shrub	Native	2.25 $\pm$ 6.36	2 $\pm$ 2.31	5.5 $\pm$ 8.54	0.5 $\pm$ 1	1 $\pm$ 2.83	1 $\pm$ 1.41	1.75 $\pm$ 3.5	
Chrysanthemoides monilifera	Asteraceae	Shrub	Introduced			1.5 $\pm$ 3					
Chusquea cumingii	Poaceae	Herb	Endemic	3.5 $\pm$ 3.46	1.25 $\pm$ 2.5	1.5 $\pm$ 3	2 $\pm$ 1.63				
Citronella mucronata	Cardiopteridaceae	Tree	Endemic	0.25 $\pm$ 0.71	0.25 $\pm$ 0.5		0.25 $\pm$ 0.5	0.5 $\pm$ 1.41			
Colliguaja odorifera	Euphorbiaceae	Shrub	Endemic	1.13 $\pm$ 2.8	3.25 $\pm$ 2.22	6.25 $\pm$ 8.1	6.75 $\pm$ 11.53	1 $\pm$ 2.83	0.5 $\pm$ 1	2 $\pm$ 3.37	2 $\pm$ 4
Crataegus monogyna	Rosaceae	Tree	Introduced								0.25 $\pm$ 0.5
Crinodendron patagua	Elaeocarpaceae	Tree	Endemic	0.38 $\pm$ 0.74							
Cryptocarya alba	Lauraceae	Tree	Endemic	15.75 $\pm$ 9.87	19.25 $\pm$ 13.05	1.25 $\pm$ 1.5	15 $\pm$ 15.68	25.75 $\pm$ 36.99	5.25 $\pm$ 6.7	3 $\pm$ 6	19.5 $\pm$ 32.68
Drimys winteri	Winteraceae	Tree	Endemic	1.25 $\pm$ 3.15	0.25 $\pm$ 0.5			0.38 $\pm$ 1.06			
Echinopsis chiloensis	Cactaceae	Shrub	Endemic	0.13 $\pm$ 0.35							
Escallonia pulverulenta	Escalloniaceae	Tree/ Shrub	Endemic	3.38 $\pm$ 4.41	1.25 $\pm$ 0.96		2 $\pm$ 2.83	1.63 $\pm$ 3.07			0.25 $\pm$ 0.5
Escallonia sp.	Escalloniaceae	Shrub	Native	0.25 $\pm$ 0.46			0.25 $\pm$ 0.5	0.38 $\pm$ 0.74			0.25 $\pm$ 0.5
Eucalyptus globulus	Myrtaceae	Tree	Introduced			0.75 $\pm$ 1.5					
Eupatorium salvium	Asteraceae	Shrub	Endemic	2.38 $\pm$ 2.26	0.5 $\pm$ 1	2.5 $\pm$ 5	5.5 $\pm$ 4.2	0.25 $\pm$ 0.71	0.5 $\pm$ 1	0.75 $\pm$ 1.5	
Fabiana imbricata	Solanaceae	Shrub	Native	0.5 $\pm$ 1.41							
Fuchsia lycioides	Onagraceae	Shrub	Endemic	0.25 $\pm$ 0.71							
Gochnatia foliolosa	Asteraceae	Shrub	Endemic	0.25 $\pm$ 0.71							
Haplopappus sp.	Asteraceae	Shrub	Native							0.75 $\pm$ 1.5	
Kageneckia oblonga	Rosaceae	Tree	Endemic	0.38 $\pm$ 1.06		0.5 $\pm$ 1	2.5 $\pm$ 3.79	0.38 $\pm$ 0.74			
Lithrea caustica	Anacardiaceae	Tree	Endemic	9.88 $\pm$ 5.25	7 $\pm$ 1.83		8 $\pm$ 4.55	4 $\pm$ 5.86	0.5 $\pm$ 1		1 $\pm$ 1.41
Lobelia tupa	Campanulaceae	Herb	Endemic					0.13 $\pm$ 0.35			
Lobelia sp.	Campanulaceae	Shrub	Native								

(*continued on next page*)

Table A1 (*continued*)

Species	Family	Life form	Origin	Adult abundance (individual number/site)				Seedlings abundance (individual number/site)			
				Fire frequency			Control	Fire frequency			Control
				1	2	3		1	2	3	
								0.38 ± 0.74			
Luma chequen	Myrtaceae	Tree/ Shrub	Endemic	4.25 ± 6.11	2 ± 4			5 ± 12.95	0.25 ± 0.5		
Maytenus boaria	Celastraceae	Tree	Native	0.88 ± 1.36	0.75 ± 0.96	3 ± 2.94	0.5 ± 1	14 ± 19.55	3.75 ± 3.1	17 ± 33.34	4.75 ± 9.5
Myrceugenia correifolia	Myrtaceae	Tree/ Shrub	Endemic	0.13 ± 0.35							
Myrceugenia exsucca	Myrtaceae	Tree	Native	1.88 ± 4.22			0.25 ± 0.5	1.25 ± 3.54			
Myrceugenia lanceolata	Myrtaceae	Shrub	Endemic	0.38 ± 1.06							
Otholobium glandulosum	Fabaceae	Tree/ Shrub	Native	0.13 ± 0.35							
Persea lingue	Lauraceae	Tree	Native	1.38 ± 2.88	1.25 ± 2.5		0.25 ± 0.5	1.13 ± 3.18			
Peumus boldus	Monimiaceae	Tree	Endemic	15.88 ± 10.47	9 ± 5.89	3.75 ± 5.68	13.5 ± 1.29	16.75 ± 16.51	1.25 ± 0.96	1 ± 2	25.25 ± 35.3
Podanthus mitiqui	Asteraceae	Shrub	Endemic	1.63 ± 2.07	2.5 ± 2.08	1.25 ± 2.5	2 ± 2.83	0.75 ± 1.16	1 ± 1.41		0.5 ± 1
Proustia pyrifolia	Asteraceae	Shrub	Endemic					0.25 ± 0.46			
Puya chilensis	Bromeliaceae	Herb	Endemic	0.13 ± 0.35		0.5 ± 1					
Puya sp.	Bromeliaceae	Herb	Native	0.25 ± 0.71							
Quillaja saponaria	Quillajaceae	Tree	Native	2.88 ± 2.42	2.5 ± 1.91	1 ± 2	3.75 ± 3.86	1.13 ± 2.1	7 ± 14	0.75 ± 1.5	1 ± 1.41
Retanilla ephedra	Rhamnaceae	Shrub	Endemic				0.5 ± 1				
Retanilla trinervia	Rhamnaceae	Shrub	Endemic	14.38 ± 21.09	11.5 ± 6.56	10.25 ± 12.5	5.75 ± 6.95	0.75 ± 1.16	0.75 ± 0.96	0 ± 0	0.5 ± 1
Ribes punctatum	Grossulariaceae	Shrub	Native	1 ± 2.14				0.13 ± 0.35			
Rubus ulmifolius	Rosaceae	Shrub	Introduced	0.38 ± 0.74		1.5 ± 3					
Salvia sp.	Lamiaceae	Shrub	Native					0.25 ± 0.71			0.75 ± 1.5
Schinus areira	Anacardiaceae	Tree	Native							0.25 ± 0.5	
Schinus latifolius	Anacardiaceae	Tree	Endemic	1.5 ± 2.27	3 ± 1.63	4.75 ± 4.11	0.5 ± 0.58	0.13 ± 0.35		0.25 ± 0.5	
Schinus montanus	Anacardiaceae	Shrub	Endemic	1.5 ± 2.51	2 ± 3.37	1.5 ± 3	1 ± 2				
Schinus polygamus	Anacardiaceae	Tree/ Shrub	Native	0.38 ± 1.06	0.25 ± 0.5				0.5 ± 1		
Senna candolleana	Fabaceae	Shrub	Endemic					0.13 ± 0.35			
Sophora macrocarpa	Fabaceae	Tree/ Shrub	Endemic	0.5 ± 1.41				1.38 ± 3.89			
Teline monspessulana	Fabaceae	Shrub	Introduced			3.5 ± 7				6.25 ± 12.5	
Abudance of native species				105.13 ± 41.32	88 ± 19.18	56.75 ± 15.31	79.25 ± 21.96	81.25 ± 55.15	25.5 ± 13.18	32.25 ± 53.18	60.5 ± 46.98
Abudance of introduced species				0.38 ± 0.74	0	8.5 ± 15.07	0	0	0	6.25 ± 12.5	0.25 ± 0.5

suggests that this species may indeed be able to resprout after fire. To know what happen with regeneration of the other two species require further study.

5. Conclusions

Chilean Mediterranean vegetation, including woody cover, richness and abundance of woody species in both adults and regeneration, and herbaceous species richness and cover, could recover after one and two successive fires; however, in sites that burn three times at consecutive short intervals are not likely to recover, based on the findings of this study.

CRediT authorship contribution statement

Cecilia Smith-Ramírez: Conceptualization, Methodology, Investigation, Writing - original draft, Funding acquisition, Visualization. **Jessica Castillo-Mandujano:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft. **Pablo Becerra:** Conceptualization, Methodology, Investigation, Writing - review & editing, Funding acquisition. **Nicole Sandoval:** Investigation. **Rosario Allende:** Investigation. **Rodrigo Fuentes:** Methodology, Software, Writing - review & editing.

Table B1
Cover percent per site (Mean ± Standard Deviation) of native and exotic herbaceous species present in sites burned once, twice, and three times between 1985 and 1995, and in control sites. In bold are species considered to be threatened according to IUCN and expert opinions (authors). Scientific name of species, family, life form and origin were assigned following Rodríguez et al. (2018).

Species	Family	Life form	Origin	Cover (% per site)			
				Fire frequency			Control
				1	2	3	
Adiantum chilense var. *scabrum*	Pteridaceae	Perennial herb	Native				5.08 ± 10.17
Adiantum excisum	Pteridaceae	Perennial herb	Endemic	7.75 ± 14.74			0.25 ± 0.5
Adiantum sulphureum	Pteridaceae	Perennial herb	Native	9.29 ± 19.1			
Adiantum chilense var. *chilense*	Pteridaceae	Perennial herb	Native	45.86 ± 27.49	26.33 ± 7.41	5 ± 10	16.5 ± 19.47
Adiantum chilense var. *hirsutum*	Pteridaceae	Perennial herb	Native	14.41 ± 22.01		3.81 ± 7.63	21.25 ± 18.43
Aira caryophyllea	Poaceae	Annual herb	Exotic	19.46 ± 23.01	15.38 ± 18.94	5.25 ± 9.84	5 ± 10
Alonsoa meridionalis	Scrophulariaceae	Perennial herb	Native	8.23 ± 12.43	18.92 ± 17.87	2.63 ± 5.25	8.42 ± 10.06
Alstroemeria ligtu	Alstroemeriaceae	Perennial herb	Endemic	2.67 ± 7.15			
Alstroemeria sp.	Alstroemeriaceae	Perennial herb	Native	33.48 ± 19.34	48.83 ± 10.43	13.75 ± 17.02	25.73 ± 19.78
Ambrosia artemisiifolia	Asteraceae	Annual herb	Exotic	0.13 ± 0.35			
Amsinckia calycina	Boraginaceae	Annual herb	Native	0.25 ± 0.46	5 ± 10	15 ± 19.15	
Anagallis arvensis	Primulaceae	Annual herb	Exotic	4.06 ± 7.37	21.67 ± 31.45	13.58 ± 26.5	10.13 ± 14.14
Anemone decapetala	Ranunculaceae	Perennial herb	Native				
Anthemis cotula	Asteraceae	Annual herb	Exotic		0.25 ± 0.5	5 ± 10	
Anthriscus caucalis	Apiaceae	Anual herb	Exotic	17.69 ± 23.02	38.25 ± 28.12		43.33 ± 39.44
Aristolochia chilensis	Aristolochiaceae	Perennial herb	Endemic		0.25 ± 0.5		
Avena barbata Pott ex Link	Poaceae	Annual herb	Exotic		15 ± 19.15		
Avena fatua	Poaceae	Annual herb	Exotic	10 ± 21.38	30 ± 38.3	2.63 ± 5.25	21.08 ± 24.73
Blechnum hastatum	Blechnaceae	Perennial herb	Native	8.42 ± 21	15 ± 30		0.25 ± 0.5
Bomarea salsilla	Alstroemeriaceae	Perennial herb	Native	5 ± 14.14			5 ± 10
Bowlesia incana	Apiaceae	Annual herb	Native			5 ± 10	
Bowlesia uncinata	Apiaceae	Annual herb	Endemic	6.44 ± 14.04	5 ± 10	8.42 ± 16.83	10 ± 20
Brachypodium distachyon	Poaceae	Perennial herb	Exotic		7.5 ± 15		
Briza minor	Poaceae	Annual herb	Exotic	18.1 ± 19.76	10 ± 20		0.25 ± 0.5
Bromus berteroanus	Poaceae	Annual herb	Native	2.5 ± 7.07			
Calandrinia compressa	Montiaceae	Annual herb	Native				5 ± 10
Calceolaria corymbosa	Calceolariaceae	Perennial herb	Endemic	6.88 ± 9.4	2.88 ± 5.11	5.08 ± 10.17	5 ± 10
Cardamine hirsuta	Brassicaceae	Annual herb	Exotic	12.15 ± 15.31	10.25 ± 19.84		5.25 ± 9.84
Cardionema ramosissima	Caryophyllaceae	Perennial herb	Native			5 ± 10	
Carduus pycnocephalus	Asteraceae	Annual or biennial herb	Exotic	0.13 ± 0.35	0.25 ± 0.5	10.25 ± 19.84	
Carex setifolia	Cyperaceae	Perennial herb	Native	2.5 ± 7.07			
Centunculus minimus	Primulaceae	Anual herb	Exotic	2.5 ± 7.07			0.25 ± 0.5
Cerastium glomeratum	Caryophyllaceae	Annual herb	Exotic	2.67 ± 7.15	17.75 ± 12.12	5 ± 10	7.5 ± 15
Cheilantes glauca	Pteridaceae	Perennial herb	Native	2.5 ± 7.07			0.25 ± 0.5
Chenopodium album	Chenopodiaceae	Annual herb	Exotic		0.25 ± 0.5		
Chloraea bletioides	Orchidaceae	Perennial herb	Endemic				5.13 ± 10.25
Chloraea chrysantha	Orchidaceae	Perennial herb	Endemic			0.25 ± 0.5	
Chrysanthemum coronarium	Asteraceae	Annual herb	Exotic	0.13 ± 0.35			
Chusquea quila	Poaceae	Perennial herb	Endemic	7.48 ± 8.61	0.5 ± 0.58	5 ± 10	2.63 ± 5.25
Clarkia tenella	Onagraceae	Annual herb	Native	0.25 ± 0.46		8.33 ± 16.67	0.25 ± 0.5
Convolvulus chilensis	Convolvulaceae	Perennial herb	Endemic			0.25 ± 0.5	
Crepis pulchra	Asteraceae	Annual herb	Exotic				5 ± 10
Cuscuta sp.	Convolvulaceae	Annual herb	Exotic	5 ± 9.26	0.5 ± 0.58		15 ± 19.15
Cynara cardunculus	Asteraceae	Perennial herb	Exotic		0.25 ± 0.5		
Cynodon dactylon	Poaceae	Perennial herb	Exotic	2.5 ± 7.07			
Descurainia sophia	Brassicaceae	Annual herb	Exotic	1.31 ± 3.71			
Dichondra sericea	Convolvulaceae	Perennial herb	Native	5.13 ± 14.1	12.63 ± 18.91	6.67 ± 13.33	5 ± 10
Dioscorea bryoniifolia	Dioscoreaceae	Perennial herb	Endemic	3.33 ± 9.43			
Dioscorea humifusa	Dioscoreaceae	Perennial herb	Endemic	29.65 ± 20.51	17.19 ± 13.83	10.25 ± 19.84	27.5 ± 22.17
Dioscorea parviflora	Dioscoreaceae	Perennial herb	Endemic	8.33 ± 11.68		8.81 ± 17.63	8.75 ± 17.5
Equisetum bogotense	Equisetaceae	Perennial herb	Native	7.5 ± 14.88	10 ± 11.55		
Erodium cicutarium	Geraniaceae	Annual or biennial herb	Exotic		15 ± 10	5 ± 10	
Erodium moschatum	Geraniaceae	Annual or biennial herb	Exotic				6.67 ± 13.33
Eryngium paniculatum	Apiaceae	Perennial herb	Native	5 ± 14.14			
Eschscholzia californica	Papaveraceae	Perennial herb	Exotic			7.63 ± 9.62	
Euphorbia peplus	Euphorbiaceae	Annual herb	Exotic	35.75 ± 31.15	37.88 ± 28.94	8.08 ± 11.8	44 ± 32.05
Fumaria agraria	Papaveraceae	Annual herb	Exotic	18.52 ± 24.82	52.26 ± 26.36	18.33 ± 25.17	34.17 ± 24.4
Galium aparine	Rubiaceae	Annual herb	Exotic	24.28 ± 22.78	13.72 ± 18.72	6.25 ± 12.5	13.33 ± 16.33
Galium hypocarpium	Rubiaceae	Perennial herb	Native	0.13 ± 0.35			
Gamochaeta stachydifolia	Asteraceae	Perennial herb	Native	2.69 ± 7.21		7.63 ± 9.62	
Geranium core-core	Geraniaceae	Perennial herb	Native		5.25 ± 9.84	11.75 ± 23.5	
Geranium dissectum	Geraniaceae	Annual herb	Exotic	5 ± 9.26			
Geranium robertianum	Geraniaceae	Annual herb	Exotic	25.77 ± 27.4	17.5 ± 23.63		28.75 ± 23.23
Glandularia berteroi	Verbenaceae	Perennial herb	Endemic	1.31 ± 3.71			
Hordeum murinum	Poaceae	Annual herb	Exotic		10 ± 11.55		10 ± 11.55
Hypericum perforatum	Hypericaceae	Perennial herb	Exotic	8.75 ± 12.46			0.25 ± 0.5
Hypochaeris glabra	Asteraceae	Annual herb	Exotic		10 ± 20		
Hypochaeris radicata	Asteraceae	Perennial herb	Exotic	0.13 ± 0.35	3.42 ± 6.83	5 ± 10	5 ± 10
Hypochaeris scorzonerae	Asteraceae	Perennial herb	Endemic			0.25 ± 0.5	

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Table B1 (*continued*)

Species	Family	Life form	Origin	Cover (% per site)			
				Fire frequency			Control
				1	2	3	
Juncus tenuis	Juncaceae	Perennial herb	Native	3.75 ± 10.61	5 ± 10		5 ± 10
Lactuca serriola	Asteraceae	Annual or biennial herb	Exotic		10.25 ± 19.84	1.83 ± 3.67	
Lamium amplexicaule	Lamiaceae	Perennial herb	Exotic		2.63 ± 5.25		
Lathyrus magellanicus	Fabaceae	Perennial herb	Native	0.13 ± 0.35			5 ± 10
Leontodon saxatilis	Asteraceae	Perennial herb	Exotic	2.56 ± 7.25			
Leucocoryne ixioides	Amaryllidaceae	Perennial herb	Endemic	2.5 ± 7.07			
Linum macraei var. *marticorenae*	Linaceae	Perennial herb	Endemic	0.25 ± 0.46			
Loasa tricolor	Loasaceae	Annual herb	Native	0.13 ± 0.35	0.25 ± 0.5	5 ± 10	
Loasa triloba	Loasaceae	Annual herb	Endemic	10.08 ± 10.64	19.42 ± 12.96	4.46 ± 5.31	35.25 ± 26.02
Lolium multiflorum	Poaceae	Annual or biennial herb	Exotic	6 ± 10.97	5 ± 10	19.58 ± 25.4	5 ± 10
Lolium perenne	Poaceae	Perennial herb	Exotic				7.5 ± 15
Madia sativa	Asteraceae	Annual herb	Native	5 ± 9.26			
Malva nicaeensis	Malvaceae	Perennial herb	Exotic	2.5 ± 7.07			
Marrubium vulgare	Lamiaceae	Perennial herb	Exotic		5 ± 10	5 ± 10	
Melica violacea	Poaceae	Perennial herb	Endemic			5 ± 10	
Monnina linearifolia	Polygalaceae	Perennial herb	Native	0.25 ± 0.46	2.88 ± 5.11	0.25 ± 0.5	
Nassella chilensis	Poaceae	Perennial herb	Native	6.67 ± 12.85	10 ± 11.55	2.63 ± 5.25	2.63 ± 5.25
Oenothera stricta	Onagraceae	Annual or biennial herb	Native	9.29 ± 13.42	27.5 ± 9.57	5.25 ± 9.84	
Olsynium junceum	Iridaceae	Perennial herb	Native	6.31 ± 17.85	10 ± 11.55		15 ± 19.15
Olsynium scirpoideum	Iridaceae	Perennial herb	Native				0.25 ± 0.5
Oxalis micrantha	Oxalidaceae	Annual herb	Native	5 ± 14.14			7.5 ± 15
Oxalis pes-caprae	Oxalidaceae	Perennial herb	Exotic	10.26 ± 12.04	26.25 ± 19.84	6.9 ± 9.55	20.92 ± 25.06
Oxalis rosea	Oxalidaceae	Annual herb	Endemic	2.56 ± 7.25			0.25 ± 0.5
Oziroe arida	Asparagaceae	Perennial herb	Endemic				5 ± 10
Panicum capillare	Poaceae	Annual herb	Exotic	8.75 ± 16.42	0.25 ± 0.5	15.06 ± 30.13	10 ± 11.55
Papaver somniferum	Papaveraceae	Annual herb	Exotic				0.25 ± 0.5
Pasithea caerulea	Asphodelaceae	Perennial herb	Native		5 ± 10		
Paspalum distichum	Poaceae	Perennial herb	Exotic	3.81 ± 7.5	2.58 ± 3.17	10.38 ± 20.09	10.25 ± 11.27
Pectocarya linearis	Boraginaceae	Annual herb	Exotic			5 ± 10	
Phycella cyrtanthoides	Amaryllidaceae	Perennial herb	Endemic	5.78 ± 10.5		15 ± 19.15	
Piptochaetium montevidense	Poaceae	Perennial herb	Native			5 ± 10	
Plagiobothrys myosotoides	Boraginaceae	Annual herb	Native		10 ± 20	5 ± 10	0.25 ± 0.5
Plagiobothrys procumbens	Boraginaceae	Annual herb	Native				5 ± 10
Plagiobothrys fulvus	Boraginaceae	Annual herb	Endemic	2.5 ± 7.07			
Poa annua	Poaceae	Annual herb	Exotic	4.06 ± 7.37	5.13 ± 10.25	5 ± 10	5.25 ± 9.84
Prunella vulgaris	Lamiaceae	Perennial herb	Exotic	0.13 ± 0.35			
Pseudognaphalium cabrerae	Asteraceae	Perennial herb	Native	6.63 ± 11.66	12.63 ± 15.2	12.5 ± 25	10 ± 20
Pseudognaphalium gayanum	Asteraceae	Perennial herb	Endemic	0.13 ± 0.35			
Raphanus raphanistrum	Brassicaceae	Annual or biennial herb	Exotic			5 ± 10	
Rostraria cristata	Poaceae	Annual herb	Exotic	2.5 ± 7.07			
Salvia sessilifolia	Lamiaceae	Perennial herb	Exotic		5 ± 10		
Sanicula crassicaulis	Apiaceae	Perennial herb	Native	12.29 ± 11.63	14.25 ± 9.12	3.81 ± 7.63	10 ± 20
Schismus arabicus	Poaceae	Annual herb	Exotic		7.5 ± 15		
Schizanthus pinnatus	Solanaceae	Annual herb	Endemic		0.25 ± 0.5	0.25 ± 0.5	
Senecio vulgaris	Asteraceae	Annual herb	Exotic	0.13 ± 0.35			10 ± 20
Silene gallica	Caryophyllaceae	Annual herb	Exotic		10.25 ± 19.84		
Sisymbrium officinale	Brassicaceae	Annual herb	Exotic	0.13 ± 0.35	5 ± 10		
Solanum furcatum	Solanaceae	Perennial herb	Native	2.5 ± 7.07	0.25 ± 0.5	10 ± 20	5 ± 10
Solaria miersioides	Amaryllidaceae	Perennial herb	Native	3.75 ± 10.61			
Solenomelus pedunculatus	Iridaceae	Perennial herb	Endemic	6.44 ± 9.1		10 ± 20	5 ± 10
Sonchus asper	Asteraceae	Annual or biennial herb	Exotic	1.71 ± 4.83		7.5 ± 15	
Sonchus oleraceus	Asteraceae	Annual herb	Exotic			5 ± 10	5.25 ± 9.84
Stachys albicaulis	Lamiaceae	Perennial herb	Native	0.25 ± 0.46			
Stellaria media	Caryophyllaceae	Annual herb	Exotic	13.1 ± 22.2	30.08 ± 24.63		22.69 ± 20.59
Taraxacum officinale	Asteraceae	Perennial herb	Exotic				10 ± 20
Tolpis barbata	Asteraceae	Annual herb	Exotic	2.53 ± 7.16			
Torilis nodosa	Apiaceae	Annual herb	Exotic	5 ± 14.14			0.25 ± 0.5
Trifolium dubium	Fabaceae	Annual herb	Exotic	5.13 ± 14.1	10.25 ± 19.84	10 ± 11.55	0.25 ± 0.5
Trifolium repens	Fabaceae	Perennial herb	Exotic	0.92 ± 2.59	10 ± 20		5 ± 10
Triptilion spinosum	Asteraceae	Perennial herb	Endemic	5 ± 9.26			5 ± 10
Tropaeolum brachyceras	Tropaeolaceae	Perennial herb	Endemic	0.13 ± 0.35			0.25 ± 0.5
Tropaeolum tricolor	Tropaeolaceae	Perennial herb	Endemic	4.79 ± 10.5	30 ± 20	5 ± 10	11.96 ± 10.03
Uncinia phleoides	Cyperaceae	Perennial herb	Native	5 ± 14.14			
Urtica urens	Urticaceae	Annual herb	Exotic	0.92 ± 2.59	10.13 ± 20.25		0.25 ± 0.5
Valeriana sp.	Caprifoliaceae		Native	2.5 ± 7.07	3.42 ± 6.83		
Valeriana stricta	Caprifoliaceae	Subshrub	Native	2.75 ± 6.98			
Valeriana vaga	Caprifoliaceae	Perennial herb	Endemic	2.5 ± 7.07		0.25 ± 0.5	17.63 ± 17.01
Verbascum virgatum	Scrophulariaceae	Biennial herb	Exotic		5 ± 10	0.25 ± 0.5	
Veronica persica	Plantaginaceae	Annual herb	Exotic		5 ± 10		5 ± 10
Vicia benghalensis	Fabaceae	Annual herb	Exotic	0.13 ± 0.35			
Vicia sativa	Fabaceae	Annual herb	Exotic			5 ± 10	
Viola pusilla	Violaceae	Annual herb	Endemic	0.13 ± 0.35			8.33 ± 16.67

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Table B1 (*continued*)

Species	Family	Life form	Origin	Cover (% per site)			
				Fire frequency			Control
				1	2	3	
Vulpia bromoides	Poaceae	Annual herb	Exotic	2.5 ± 7.07	10 ± 20		
Vulpia myuros	Poaceae	Annual herb	Exotic	3.81 ± 7.5		10 ± 20	
Native species cover (%)				23.74 ± 23.03	25.23 ± 21.78	22.45 ± 18.97	26.17 ± 20.21
Exotic species cover (%)				26.23 ± 24.69	30.58 ± 26.33	24.03 ± 21.27	33.94 ± 27.9

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Abundance and composition of woody species in burned and control sites

See Table A1.

Appendix B. Herbaceous cover in burned and control sites

See Table B1.

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