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Original article

# Dendroecological potential of shrubs for reconstructing fire history at landscape scale in Mediterranean-type climate grasslands: The case of *Fabiana imbricata*



Facundo José Oddi\*, Luciana Ghermandi

Laboratorio Ecotono, Universidad Nacional del Comahue – Consejo Nacional de Investigaciones Científicas y Tecnológicas, Instituto de Investigaciones en Biodiversidad y Medioambiente, Quintral 1250, 8400 Bariloche, Argentina

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## ABSTRACT

Fire recurrently affects Mediterranean-type climate (MTC) regions causing major implications on the structure and dynamics of vegetation. In these regions, it is important to know the fire regime for which reliable fire records are needed. Dendroecology offers the possibility of obtaining fire occurrence data from woody species and has been widely used in forest ecosystems for fire research. Grasslands are regions with no trees where shrubs can provide dendroecological evidence for reconstructing fire history at landscape scale. We studied the dendroecological potential of the shrub *Fabiana imbricata* to reconstruct fire history at landscape scale in MTC grasslands of northwestern Patagonia. In order to accomplish this, we combined spatio-temporal information of recorded fires from the study area with the age structure of *F. imbricata* shrublands obtained from dendroecological methods. Shrubland age structure correctly described how often fires occurred in the past. In rocky outcrops, where fires cannot reach, individuals are long-lived and heterogeneous in age; while downhill, individuals are young and shrublands are even-aged. Five pulses of massive recruitment were found: three of these coincided with three known fires; the remaining two had not been recorded before. A bi-variated analysis showed that *F. imbricata* recruited mainly during two years after fire, and the spatial distribution of pulses coincided with the fire map. Information derived from shrubland age structure could be used to estimate fire regime parameters such as fire return interval at landscape or community scale. For instance, we estimated a fire return interval of nine years at landscape scale and ranging from 11 to 24 years at community scale (shrubland). Our results in northwestern Patagonia grasslands showed that the *F. imbricata* chronology can be used to complement other information sources such as remote sensing and operational databases improving the knowledge about fire regime. The present study demonstrates that is possible to utilize shrubs as a dendroecological data source to study fire history in regions where tree cover is absent.

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## Introduction

Fire is one of the most relevant disturbances in ecosystems of Mediterranean-type climate (MTC) regions (Keeley et al., 2012). The marked climatic seasonality determines that these regions are prone to fire occurrence (Lloret, 2004): water stress in summer dries the vegetation which becomes fuel for fires. In MTC, vegetation is recurrently affected by fire (Montenegro et al., 2004) and has evolved in the presence of this disturbance (Pausas and

Schwilk, 2012). Consequently, fire has modified the performance of plant species (Naveh, 1975; Keeley et al., 2011) and influenced both assembly and dynamic of plant communities (Lloret, 2004; de Luis et al., 2006; Verdú and Pausas, 2007) as a key component of these ecosystems (Keeley et al., 2012).

To understand the role fire plays on the dynamic of fire-prone ecosystems it is important to not only view fire as a single event but also consider its regime (Lloret, 2004; Keeley et al., 2011). Fire frequency is one of the most relevant parameters used to characterize fire regimes (Krebs et al., 2010) because species that recruit only in post-fire will not thrive with fire recurrence periods longer than their life cycle (Zedler, 1995; Pausas and Vallejo, 1999). These species could have a lack of seeds in the respective seed banks due to fire intervals shorter than the reproductive age which could lead

\* Corresponding author. Tel.: +54 294 442505; fax: +54 294 4422111.

E-mail addresses: [foddi@comahue-conicet.gob.ar](mailto:foddi@comahue-conicet.gob.ar), [facundo.oddid@hotmail.com](mailto:facundo.oddid@hotmail.com) (F.J. Oddi).

to local extinction (Lloret, 2004). Consequently, post-fire recovery of plant species is an ecological process dependent on the interval between fires (Bond and van Wilgen, 1996) and this interval affects landscape configuration in fire-prone ecosystems (Brown et al., 1999).

Information about fire occurrence can be obtained from several tools and records such as: satellite images, operational databases, and growth ring analysis in woody species (Agee, 1993; Morgan et al., 2001; Fulé et al., 2003) – the latter generically called “dendrochronology” and “dendroecology” when growth rings are utilized to address ecological questions (Fritts and Swetnam, 1989). However, depending on the study area, there are limitations for obtaining information about fires. For example, in some regions it is difficult to acquire a continuous temporal series of satellite images prior to 2000, the time in which many sensors that are currently widely used in fire studies (e.g., MODIS) were put into operation. In other regions, organization of fire records by government agencies is relatively recent and this complicates the access to historical information. These difficulties make dendroecology a valuable tool for dating the occurrence of fire (Fritts and Swetnam, 1989) and reconstructing fire history in an ecosystem (Medina, 2003). There are two types of woody species for reconstructing fire history by dendroecology: species where time of fire is inferred from wood fire scars; and species where time of fire is derived from population age structure (Johnson and Gutsell, 1994; O'Donnell et al., 2010). Although dendroecology is widely used in forest regions (Fritts and Swetnam, 1989), in parts of the world lacking forests, shrubs can be an important alternative for dendroecological studies (Liang and Eckstein, 2009; Myers-Smith et al., 2011) such as in fire regime research.

In northwestern extra-Andean Patagonia, a region characterized by a Mediterranean climate, fire is a key component in the structure and functioning of plant communities (Ghermandi et al., 2004). However, despite its ecological relevance, fire regime in this region has been scarcely studied (Oddi, 2013) and specific information is still needed about its frequency which is more difficult to obtain the longer the study period. In northwestern Patagonia, where a strong west–east precipitation gradient determines the vegetation type (forest-ecotone-steppe), the study of fire occurrence using growth rings has been implemented within forest ecosystems (e.g., Kitzberger et al., 1997; Veblen et al., 1999). These authors have worked up to the forest-steppe ecotone analyzing *Austrocedrus chilensis* (ciprés de la cordillera) samples. *A. chilensis* is a valuable source for dating fires although its usefulness decreases in the steppe where trees begin to cluster in groups, becoming highly isolated or absent further toward the east (Pastorino and Gallo, 2004).

As in forests, the age structure of shrublands can be determined through growth ring analysis (Keeley, 1993; Schweingruber and Poschlod, 2005). Therefore, long-lived seeder shrubs could be used to estimate time elapsed since the last fire in grasslands where tree cover is absent. *Fabiana imbricata* Ruiz & Pav. (palo picho) is a characteristic shrub of northwestern Patagonia and its spatial dynamic is associated with fires (Ghermandi et al., 2004; Oddi et al., 2010). This species is an “obligate seeder” (Pausas and Schwillk, 2012) that is killed by fire and recruits seedlings almost exclusively in post-fire conditions establishing even-aged patches (Ghermandi et al., 2013). In successive fires, shrublands are subject to advance-retreat pulses depending on the balance between recruitment and mature shrubs eliminated by fire (Ghermandi et al., 2004, 2010). Overall, shrublands are associated with rocky outcrops located in the highest areas where older plants remain sheltered from fire (Oddi et al., 2010). From these areas, shrublands advance over hillsides creating a mosaic of even-age patches corresponding to different fires. *F. imbricata* is a 1–4 m tall long-lived shrub ( $\approx 150$  years; Oddi et al.,

2010) which has identifiable annual growth rings. Shrublands from this species are extensive and form part of the landscape mosaic in the northwestern Patagonian steppe (Anchorena and Cingolani, 2002). Thus, in contrast to the grassland matrix, the age structure of *F. imbricata* shrublands could be useful in reconstructing fire histories at landscape scale by improving the information acquired from operational databases and remote sensing.

The aim of this work was to assess the potential of *F. imbricata* for reconstructing fire histories at landscape scale. Thus, given the features mentioned above, if *F. imbricata* were a species useful for dating fires, shrubland age structure should show how fires occurred in the past. The reconstruction of fire history from *F. imbricata* dendroecology could be a starting point for other future fire regime studies in grasslands with long-lived seeder shrubs.

## Materials and methods

### Study area descriptions

Sampling sites were located in an area of 2500 ha in San Ramón ranch, 30 km east of Bariloche, Argentina (latitude  $-41^{\circ}04'$ ; longitude  $-70^{\circ}51'$ ) (Fig. 1). The landscape has a relief with smooth plains and sierras (Anchorena and Cingolani, 2002) where numerous rocky outcrops can be observed. Soils are classified as Haploxeroles, moderately developed, of sandy-loam texture with a superficial horizon containing moderate organic matter (Gaitán et al., 2004). The climate is temperate with a mean annual temperature of  $8.6^{\circ}\text{C}$  and 586 mm of rainfall showing a Mediterranean regime (60% of precipitation occurring between May and August) (Meteorological Station, San Ramón ranch). Phytogeographically, the study area is within the sub-Andean district (Cabrera, 1971) and vegetation is characterized by the tussock grasses *Pappostipa speciosa* and *Festuca pallescens* accompanied by scattered shrubs of *Senecio bracteolatus* and *Mulinum spinosum* (Ghermandi et al., 2004), leaving some areas covered by native shrublands of *F. imbricata* and *Discaria articulata* (Anchorena and Cingolani, 2002). In particular, *F. imbricata* shrublands are commonly located along hillsides with decreasing shrub density toward rocky outcrops.

### Methods: Sampling and element analysis

In order to study the potential of *F. imbricata* for reconstructing fire history at landscape scale, we combined spatio-temporal information of recorded fires in the study area with dendroecological information.

For fire information, we worked on three fires recorded in cartography and bibliography sources (Fig. 2). Two of them (January of 1989, 760 ha and January of 1999, 21,000 ha) have been mapped from Landsat images (Lanorte, non-published data; Oddi et al., 2010). The remaining fire occurred in San Ramón in 1981 and was located near La Fragua village (de Caso, 1984, 160 ha).

For dendroecological analysis, nine sampling sites were established in different shrublands of *F. imbricata*. Five of these were placed in burned sectors of the 1981, 1989, and 1999 fires, and the other four sites were placed in areas with no records of previous fires (Fig. 2). Since the location of *F. imbricata* is near hilltops, all the sites were characterized by moderate slopes except site 1 which was flat (Table 1).

To determine the relationship between fires and shrublands age structure (i.e. to identify post-fire recruitments), each site was divided into sampling strips ( $30 \times 100$  m) perpendicular to the terrain slope. Sampling design depended on density, size, and morphology of plants in shrublands, which are variables strongly related to topography (Ruete, 2006; Ghermandi et al., 2010). Plants

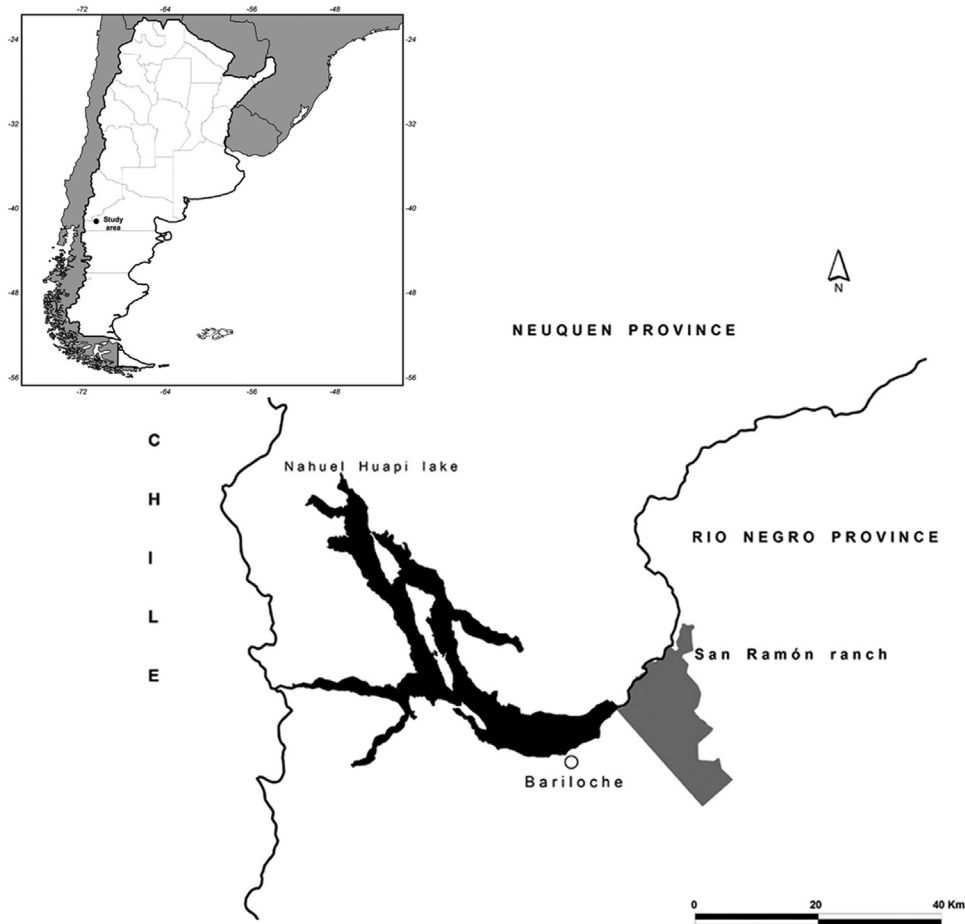


Fig. 1. Location of study area.

growing near rocky outcrops are sparse, with thick trunks, and tall although sometimes could be prostrate. Plants downhill form continuous shrublands and strips formed by plants of different sizes (taller plants nearest to rocky outcrops) can be distinguished. This repeated shrubland distribution suggests cohorts related to different *F. imbricata* pulses of recruitment. We placed one sampling strip near rocky outcrops and one or two strips farther away depending on the homogeneity of individuals (Fig. 3). In site 1, we used a simple random sampling because topography was flat and the size of all plants was similar. In site 7 (burned in the 1999 fire), a nearby non-burned patch was also sampled (Table 1). In each sampling strip, we randomly selected different numbers of individuals according to shrubland plant density. The number of individuals sampled near rocky outcrops was lower (but >5) than in strips placed farther

away, sampling a total of 337 plants. Individuals were cut to soil level using a power saw to extract a stem disk (or stump). These samples were sanded up allowing growth rings to be read. Then, stumps were read in the laboratory using a magnifying glass and plant age was determined by a simple ring count.

To study the spatio-temporal fit between shrubland age structure and fire, we depicted frequency histograms from the establishment year per strips and sites. We visually inspected whether the establishment frequency pattern of the entire study area corresponded chronologically to the time of fires. Finally, to statistically assess the association between fire occurrences and establishment of individuals, a bi-variated event analysis was used. Bi-variated event analysis is utilized to examine temporal relationships between climatic and/or disturbance events with

**Table 1**  
Sampling sites where *F. imbricata* stumps were cut. We defined flat as slope <5%, and moderate as 5% < slope <25%.

Site	Topography		Type of sampling	Strip number	n	Fire
	Slope	Aspect				
1	Flat	–	Random	–	50	Unknown
2	Moderate	East	Strips	3	145	1999
3	Moderate	East	Strips	2	19	1999
4	Moderate	South	Strips	2	22	1989
5	Moderate	North	Strips	2	16	Unknown
6	Moderate	North	Strips	2	15	Unknown
7	Moderate	North	Strips	3 <sup>a</sup>	25	1999
8	Moderate	South	Strips	2	15	Unknown
9	Moderate	West	Strips	2	30	1981/1999

<sup>a</sup> One of three strips corresponds to the nearby non-burned patch.

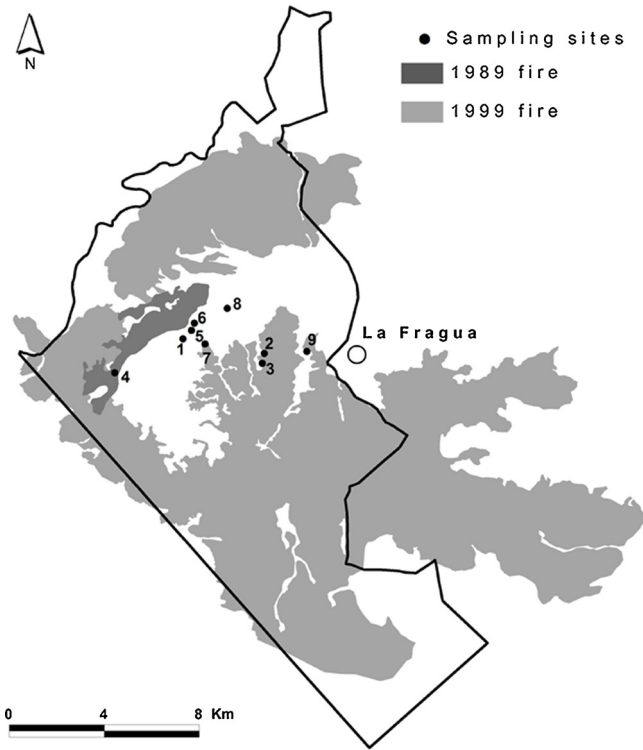


Fig. 2. Map of recorded fires in the study area and location of sampling sites.

demographic patterns (Suarez and Kitzberger, 2010). This is a temporal modification to Ripley’s K function used for point pattern analysis in space (Bigler et al., 2007). We used KD1 software (Gavin, 2007) because it enables testing dependence between two event types ordered in one direction. Since we assessed a one-directional process in time (fire occurrence followed by establishment events), forward selection was used (Bigler et al., 2007). KD1 estimates  $L$  function from  $K$  function as  $L_{RF}(t) = K_{RF}(t)/2 - t$  being  $R$  an event co-occurring with or followed by an  $F$  event (recruitment and fire) (Gavin, 2007). Confidence envelopes (95%) were estimated by Monte Carlo simulations with 1000 replicates randomizing fire time by a process without replacement. In the same way as point pattern analysis, values above the upper confidence limit indicate synchrony between the two evaluated events, and values below the lower confidence limit indicate asynchrony (Gavin, 2007). We considered the years 1981, 1989, and 1999 as fire events. Since the first recorded fire occurred in 1981, *F. imbricata* establishments in the temporal window 1981–2011 were used as recruitment events.

Fire information derived from age structure was used to estimate fire intervals at landscape and community scales. At landscape scale (2500 ha in our target landscape), fire interval is estimated as  $(f - 1)/d$ , where “ $f$ ” is the number of fires occurred in the entire landscape, therefore “ $f - 1$ ” represents the quantity of fire intervals and “ $d$ ” is the elapsed time between the first fire and the last one (Arno and Petersen, 1983). At community scale, fire interval can only be estimated from sites where more than one fire has occurred (Arno and Petersen, 1983). At this scale, the interval is also estimated as  $(f - 1)/d$ , but in this case “ $f$ ” represents the quantity of fires occurred in a same community (a same site in our study) and “ $d$ ” is the time elapsed between the first fire and the last one occurring in the assessed community.

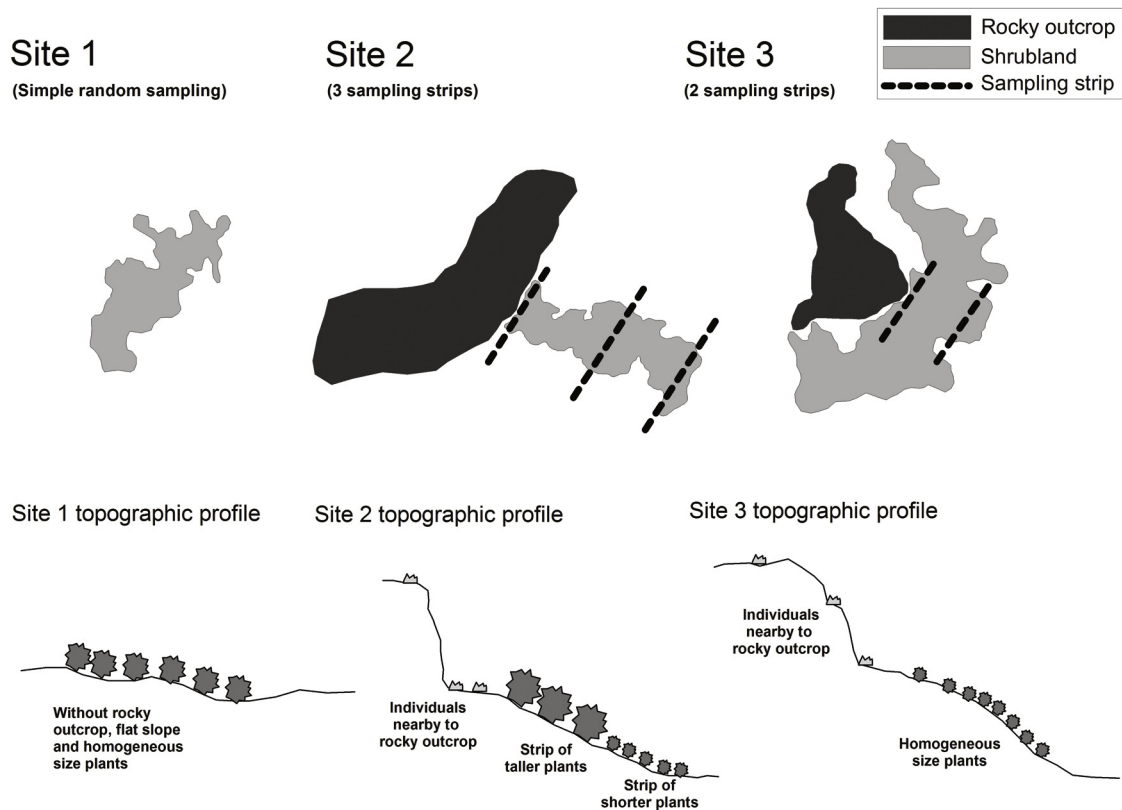
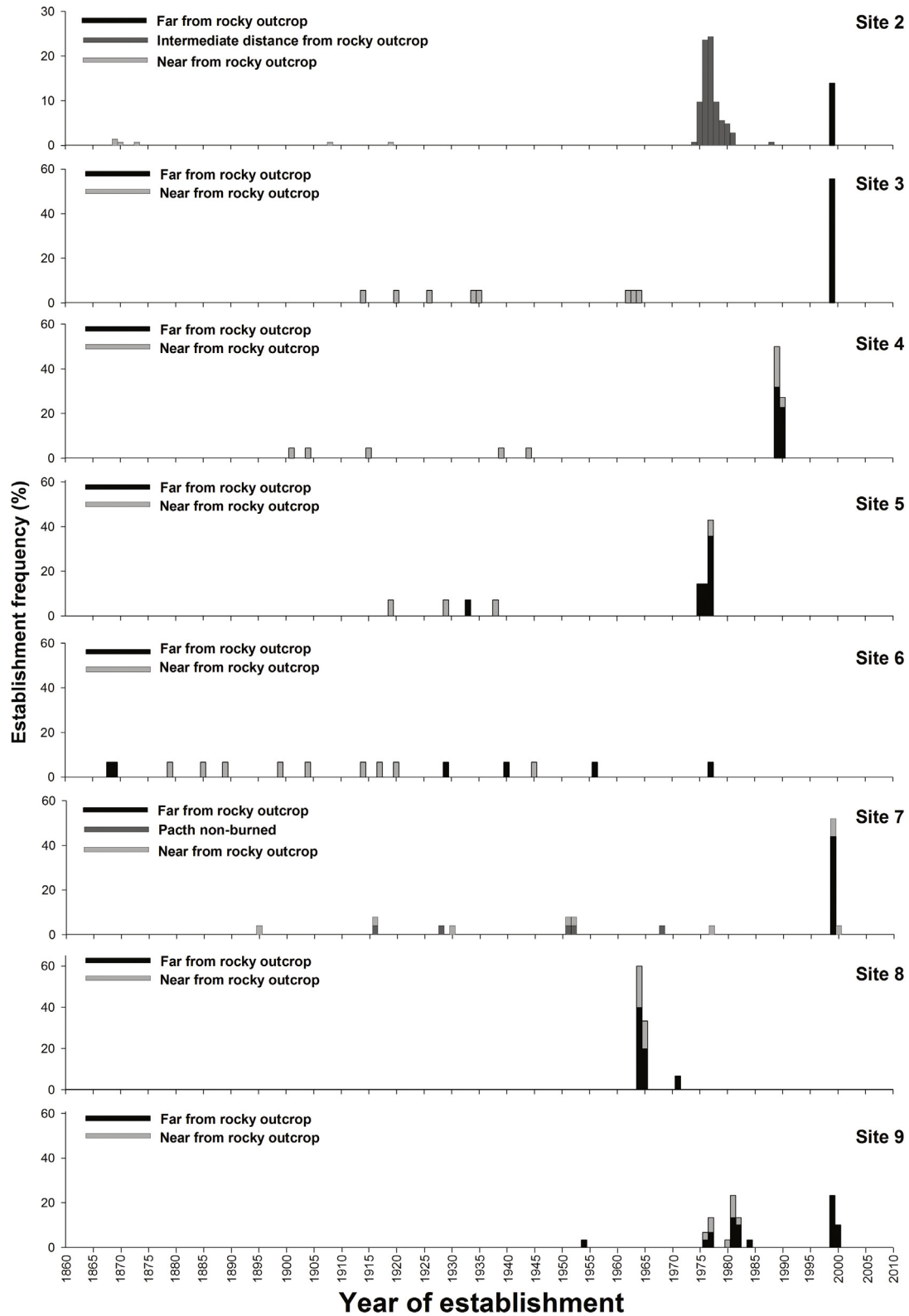


Fig. 3. Sampling designs used in three sampled sites (upper), and site features by which those designs were employed (lower). Site 1 was characterized by a gentle slope and individuals similar in size, and therefore simple random sampling was used. In Site 2 (moderate slope), three sampling strips were used since we found two plant size classes far from rocky outcrops. In site 3 (moderate slope), because there was a single plant size class downhill, two sampling strips were used.



**Fig. 4.** Age structure of *F. imbricata* shrublands found in each sampling site. In site 1 we used a simple random sampling design and therefore this site is not included here.

**Table 2**

Year of establishment of *F. imbricata* individuals and fires identified from cohorts observed. Establishment years and number of recruitments (in parentheses) are showed according to sampling design of each site.

Site	Year of establishment					Cohorts	Fires <sup>a</sup>
	Without rocky outcrop		With rocky outcrop				
	Simple random sampling	Near rock	Intermediate distance	Far rock	Unburned patch		
1	1975 (7); 1976 (8); 1977 (22); 1978 (7); 1979 (6)	–	–	–	–	1	1999
2	–	1862 (2); 1870 (1); 1873 (1); 1909 (1); 1919 (1)	1974 (1); 1975 (14); 1976 (34); 1977 (35); 1978 (14); 1979 (8); 1980 (7); 1981 (4); 1988 (1)	1999 (20)	–	2	1975–1978; 1999
3	–	1914 (1); 1920 (1); 1926 (1); 1934 (1); 1935 (1); 1962 (1); 1963 (1); 1964 (1)	–	1999 (12)	–	1	1999
4	–	1989 (4); 1990 (1)	–	1901 (1); 1904 (1); 1915 (1); 1939 (1); 1944 (1); 1989 (7); 1990 (5)	–	1	1989
5	–	1918 (1); 1929 (1); 1938 (1); 1977 (1)	–	1933 (1); 1975 (2); 1976 (2); 1977 (5)	–	1	1975–1978
6	–	Specimens with pith rotten but all establishments before to 1945 (6)	–	1977 (1); Remaining with pith rotten, but all establishments before to 1956 (9)	–	0	None
7	–	1895 (1); 1916 (1); 1930 (1); 1951 (1); 1952 (1); 1977 (1); 1999 (2); 2000 (1)	–	1999 (11)	1916 (1); 1928 (1); 1951 (1); 1952 (1); 1968 (1)	1	1999
8	–	1963 (3); 1964 (2)	–	1963 (6); 1964 (3); 1971 (1)	–	1	1963–1964
9	–	1976 (1); 1977 (2); 1980 (1); 1981 (3); 1982 (1)	–	1954 (1); 1976 (1); 1977 (2); 1984 (1); 1981 (4); 1982 (3); 1999 (7); 2000 (3)	–	3	1975–1978; 1981; 1999

<sup>a</sup> Fires dates that were known before to this study are showed in bold.

## Results

The age structure of *F. imbricata* shrublands is described by site in Table 2 and Fig. 4.

### Site 1

In this site there were no rocky outcrops nearby and we used a simple random sampling design (therefore site 1 is not included in Fig. 4). Plants were grouped in one age class ranging from 33 to 36 years.

### Site 2

At this site, three strips were placed. We observed old plants in the strip near rocky outcrops, and two cohorts of younger ages in the two downhill strips. In the higher sector, long-lived individuals varied in age. At intermediate distance from rocky outcrops most individuals ranged from 32 to 35 years, while in the farthest strip the age of all individuals was just 12 years.

### Site 3

Individuals distant from rocky outcrops formed one even-aged group (12 years old). Near the rocky outcrops individuals were long-lived and varied in age.

### Site 4

The age structure was formed by one group of individuals homogeneous in age, and several individuals without a clearly defined pattern. The even-age group (ages 21–22) corresponded to individuals sampled far from rocky outcrops. Of the individuals sampled near rocky outcrops, half were also ages 21–22 and the remaining were long-lived plants.

### Site 5

Age pattern was similar to site 3. Most individuals sampled distant from the rocky outcrops formed an even-age group (ranging from 34 to 36 years), while individuals near rocky outcrops were long-lived and heterogeneous in age.

### Site 6

In this site it was very difficult to identify the age of most individuals cut since in general the piths were rotten. Nevertheless, when reading growth rings from the outermost ring toward the core, we found specimens over age 55 and several individuals with ages >100 years in both near and far strips.

### Site 7

Plants from the 1999 unburned patch had various ages but all were older than 43 years. In the burned patch, the age pattern was similar to site 4. Individuals located far from rocky outcrops were

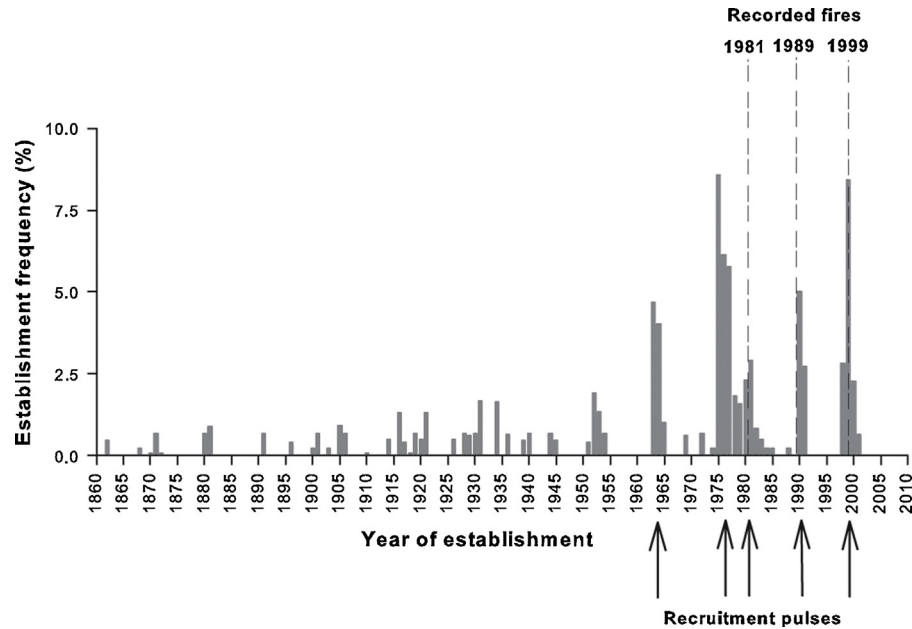


Fig. 5. Age structure of *F. imbricata* shrublands found in entire sampling.

even-aged (12 years). Near rocky outcrops, a few plants were 12 years old while most plants were older and varied in age.

#### Site 8

In both strips, we found even-aged individuals ranging from 47 to 48 years.

#### Site 9

We found three age groups (11–12, 29–31, and 34–35 years) in the two strips sampled. These three groups were present in the strip far from rocky outcrops. However, in the strip near rocky outcrops only the groups aged 29–31 and 34–35 were present.

Fig. 5 shows the age structure of all sampled shrublands where five massive pulses of recruitments can be observed. Three of these recruitment pulses are related to the 1981, 1989, and 1999 recorded fires. The remaining recruitments occurred in 1963–1964 and 1975–1978 and are probably related to two unknown fires. Visual observation is supported by the bi-variated event analysis which showed  $L_{RF}$  values above the upper confidence level in the two years after fire (Fig. 6). This analysis shows that *F. imbricata* recruitment of individuals during the two years after fire is greater than that expected by chance and therefore fire and recruitment are temporally related events.

Five identified recruitment pulses (Fig. 5) indicate the occurrence of five fires on the studied landscape. Since the oldest fire corresponded to 1963–1964 and the most recent occurred in 1999, the interval between fires estimated at landscape scale was of approximately nine years. Fire interval at community scale was estimated only from sites 2 and 9 (burned more than once and without stand-replacing fires). Site 2 was burned twice (1975–1978 and 1999 fires) and the fire interval was 21–24 years. Site 9 was affected by three fires (1975–1978, 1981, and 1999) and the fire interval was 10.5–12 years.

## Discussion

Forest age structures derived from dendrochronology have been widely used for reconstructing past ecological events (Veblen,

1986; Williams and Johnson, 1990; Wells et al., 2001; Taylor, 2010; Poulos et al., 2013), such as fire occurrences (Van Wagner, 1978; Bergeron et al., 2004; Silver et al., 2013). Although shrubs are potentially useful for ecological reconstructions (Schweingruber and Poschlod, 2005), only a few have been performed with these plant species (Rayback and Henry, 2006; Schmidt et al., 2006; Danby and Hik, 2007; Lantz et al., 2010; Buras et al., 2012) and none in fire regimes. For example, in a recent review Lu and Liang (2013) showed that thus far dendrochronologists have worked only with 30 shrub species worldwide and no studies infer fire occurrence. However, shrubs provide the opportunity to obtain

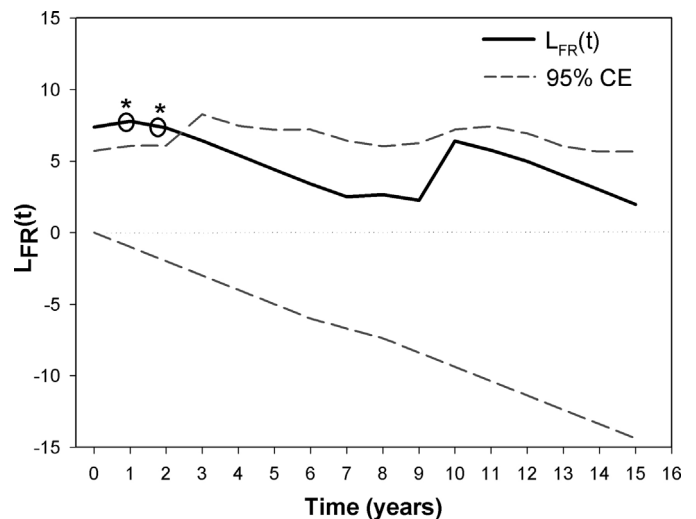


Fig. 6. Bi-variated event analysis for fire occurrence and individual establishment.  $L_{RF}$  function (black line) shows  $L_{RF}$  values for fire occurrence ( $F$ ) followed by establishment events ( $R$ ) observed during an interval of 15 years after fire.  $L_{RF}$  is a temporal modification to Ripley's  $K$  function that enables testing dependence between two event types ordered in one direction (fire and recruitment in this case). Confidence envelopes (dashed lines) are based on 1000 Monte-Carlo simulations and show the 2.5 and 97.5 percentiles of the distribution of  $L_{RF}$  values simulated under a null model of independence between events. \* indicates years with  $L_{RF}$  values above the upper confidence envelopes ( $p < 0.05$ ).

dendroecological information where tree cover is reduced such as in tundra ecosystems or in arid/semiarid regions (Eckstein and Schweingruber, 2009; Copenheaver et al., 2010; Hallinger et al., 2010). *F. imbricata* is a long-lived shrub with legible growth rings which recruits individuals in post-fire. These characteristics make it potentially suitable for dendroecological studies associated with fire regime. In the present study, we showed that age structure of *F. imbricata* shrublands was associated with fire occurrence and descriptive of the landscape fire history.

At site level, shrubland age structure showed a clear pattern related to fire. Long-lived individuals not reached by fire are located in rocky outcrops, while younger and even-age populations are found downhill (Fig. 4). This pattern describes how the structure of *F. imbricata* populations is shaped by fire which is important for understanding shrubland spatial dynamics (Oddi et al., 2010). Fires advance from the grass matrix and burn *F. imbricata* plants located in the lowest sectors adjacent to the grassland. Due to the decrease of fuel continuity, fires lose their capability of spreading when reaching rocky outcrops (Swanson et al., 1988; Turner et al., 2001), lowering the chance of plants being killed by fire.

At landscape scale, we observed synchrony between the recruitment of *F. imbricata* and fire occurrence. Shrublands of this species are established during two years post-fire as the bi-variated event analysis indicated. In MTC ecosystems, germination of seeder shrubs is commonly enhanced by direct fire effects such as heat or smoke (Keeley and Fotheringham, 2000). According to recent *F. imbricata* studies (Ghermandi et al., 2013; Dudinszky and Ghermandi, 2013), seedling establishment was linked to direct (heat and smoke) but also indirect (seeds exposure on soil surface by erosion and elimination of allelopathic substances) fire effects. As well, the shrubland age structure described fire activity in space. Sites burned in 1981, 1989, and 1999 showed post-fire recruitments, while in non-burned sites during these years, the recruitment pulses showed no correspondence to the known fires. This was important since we could determine occurrence of two fires not previously recorded. One of these fires was identified from the recruitment pulses between 1975 and 1978 that along with corresponding shrub ages of 32–35 years suggest that sites 1, 2, 5, and 9 were affected by the same fire. The remaining fire was identified in site 8 where an even-age pattern as the result of a massive establishment during 1963–1964 was observed.

At landscape scale, we estimated a fire return interval of nine years, leading us to expect that on average, a fire will occur “at any place of the landscape” every nine years. In order to better understand the effects of fires, it is also necessary to know the length of time between fires within a same community (Morrison et al., 1995). At sites burned more than once, *F. imbricata* allowed us to identify previous fires showing that this species could be potentially useful in estimating the fire interval at community scale. In fact, at site level the estimated return interval ranged between 11 and 24 years. Unlike with the fire return interval estimated at landscape scale (Arno and Petersen, 1983), we expect that on average, a fire will affect “a same community” every 11–24 years. It is important to highlight the constraint imposed by the longevity of individuals (analysis could not be extended beyond 150 years). Furthermore, recent high-severity fires (stand-replacing) could erase the imprint that old fires leave on age structure making more than one fire in the same shrubland difficult to identify from dendroecological analysis.

To fully understand relationships between fire and vegetation dynamic in MTC ecosystems, it is necessary to have accurate fire occurrence records (Mouillot et al., 2003). However, information about fire regime in the southern hemisphere is limited (O'Donnell et al., 2010). In open shrub-grassland complexes, this lack of information is partly due to the absence of trees. However, in these

ecosystems, shrubby species are a potential source of information for obtaining fire records at landscape scale. We found that age structures of *F. imbricata* shrublands contain information related to fire occurrence which could be utilized complementary with other sources such as satellite images and operational databases to improve our knowledge about fire regime. In addition, climate influences fire regimes by affecting productivity and vegetation moisture (Pausas and Paula, 2012; Pausas and Ribeiro, 2013). In this regard, it is important to highlight the importance of old shrubs near rocky outcrops. Ring-width series of long-lived specimens of *F. imbricata* could be used to show aboveground biomass dynamic from the linkage between these series and remote sensed NDVI. These long-lived individuals could also allow us to reconstruct past climate and therefore infer when fire-conducive weather conditions occurred (i.e., dry conditions).

## Conclusion

Grasslands are regions with no trees where shrubs can provide dendroecological evidence for reconstructing fire history at landscape scale. Recruitment pulses of *F. imbricata* were associated with fire in time and space causing the shrubland age structure to correctly describe how fires occurred in the past. Recruitment took place during the two years after fire and spatial distribution of recruitment pulses coincided with the fire map. Fire information derived from shrublands age structure could be used to estimate fire frequency at landscape or community scale in northwestern Patagonian MTC grasslands. As we showed in this study, shrubs are an alternative for improving knowledge on fire regime in other regions of the world where forests are absent.

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## References

- Agee, J.K., 1993. *Fire Ecology of Pacific Northwest forests*. Island, Washington, DC.
- Anchorena, J., Cingolani, A., 2002. Identifying habitat types in a disturbed area of the forest-steppe ecotone of Patagonia. *Plant Ecol.* 15, 97–112.
- Arno, S.F., Petersen, T.D., 1983. Variation in estimates of fire intervals: a closer look at fire history on the Bitterroot National Forest. In: Research Paper INT-301. US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, 8 pp.
- Bergeron, Y., Gauthier, S., Flannigan, M., Kafka, V., 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. *Ecology* 85 (7), 1916–1932.
- Bigler, C., Gavin, D.G., Gunning, C., Veblen, T.T., 2007. Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. *Oikos* 116, 1983–1994.
- Bond, W.J., van Wilgen, B.W., 1996. Fire and plants. In: *Population and Community Biology*. Series 14, Chapman & Hall, London.
- Brown, P.M., Kaufmann, M.R., Shepperd, W.D., 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. *Landscape Ecol.* 14, 513–532.
- Buras, A., Hallinger, M., Wilmking, M., 2012. Can shrubs help to reconstruct historical glacier retreats? *Environ. Res. Lett.* 7, 1–8.
- Cabrera, A.L., 1971. Regiones fitogeográficas Argentinas. Acme, Buenos Aires.
- Copenheaver, C.A., Gärtner, H., Schäfer, I., Vaccari, F.P., Cherubini, P., 2010. Drought-triggered false ring formation in a Mediterranean shrub. *Botany* 88, 545–555.
- Danby, R.K., Hik, D.S., 2007. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *J. Ecol.* 95, 352–363.
- Dudinszky, N., Ghermandi, L., 2013. Fire as a stimulant of shrub recruitment in northwestern Patagonian (Argentina) grasslands. *Ecol. Res.* 28 (6), 981–990.



- de Caso, M.I., 1984. Efecto del fuego en los pastizales naturales patagónicos. Universidad Nacional del Comahue, San Carlos de Bariloche, Argentina, Tesis (in Spanish).
- de Luis, M., Raventós, J., González-Hidalgo, J.C., 2006. Post-fire vegetation succession in Mediterranean gorse shrublands. *Acta Oecol.* 30, 54–61.
- Eckstein, D., Schweingruber, F., 2009. Dendrochronologia – a mirror for 25 years of tree-ring research and a sensor for promising topics. *Dendrochronologia* 27, 7–13.
- Fritts, H.C., Swetnam, T.W., 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. *Adv. Ecol. Res.* 19, 111–189.
- Fulé, P.Z., Crouse, J.E., Heinlein, T.A., Moore, M.M., Covington, W.W., Verkamp, G., 2003. Mixed-severity fire regime in a high-elevation forest of Grand Canyon, Arizona, USA. *Landscape Ecol.* 18, 465–486.
- Gaitán, J., López, C., Ayesa, J., Bran, D., Umaña, F., 2004. Características y distribución espacial de los paisajes y los suelos del área Bariloche-Comallo. Área Recursos Naturales. In: Informe Técnico. INTA, Bariloche, 44 pp.
- Gavin, D.G., 2007. K1D: Multivariate Ripley's K-function for One-dimensional Data. Department of Geography, University of Oregon, Eugene.
- Ghermandi, L., Guthmann, N., Bran, D., 2004. Early post-fire succession in northwestern Patagonia grasslands. *J. Veg. Sci.* 15, 67–76.
- Ghermandi, L., de Torres Curth, M.I., Franzese, J., Gonzalez, S., 2010. Non-linear ecological processes, fires, environmental heterogeneity and shrub invasion in Northwestern Patagonia. *Ecol. Model.* 221, 113–121.
- Ghermandi, L., Franzese, J., Gonzalez, S.L., de Torres Curth, M., Ruete, A., 2013. Disentangling *Fabiana imbricata* (Solanaceae) regeneration: the importance of disturbance and rainfall. *J. Arid Environ.* 97, 9–13.
- Hallinger, M., Manthey, M., Wilmking, M., 2010. Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytol.* 186, 890–899.
- Johnson, E.A., Gutsell, S.L., 1994. Fire frequency models. Methods and interpretations. *Adv. Ecol. Res.* 25, 239–287.
- Keeley, J.E., 1993. Utility of growth rings in the age determination of chaparral shrubs. *Madrono* 40 (1), 1–14.
- Keeley, J.E., Fotheringham, C.J., 2000. Role of fire in regeneration from seed. In: Fenner, M. (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities*. vol. 13., second ed. CAB International, Oxon, pp. 311–330.
- Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J., Bradstock, R.A., 2011. Fire as an evolutionary pressure shaping plant traits. *Trends Plant Sci.* 16 (8), 406–411.
- Keeley, J.E., Bond, W.J., Bradstock, R.A., Pausas, J.G., Rundel, P.W., 2012. *Fire in Mediterranean Ecosystems: Ecology, Evolution and Management*. Cambridge University Press, Cambridge.
- Kitzberger, T., Veblen, T.T., Villalba, R., 1997. Climatic influences of fire regimes along a rain forest-to-xeric woodland gradient in northern Patagonia, Argentina. *J. Biogeogr.* 24, 35–47.
- Krebs, P., Pezatti, G.B., Mazzoleni, S., Talbot, L.M., Conedera, M., 2010. Fire regime: history and definition of a key concept in disturbance ecology. *Theory Biosci.* 129, 53–69.
- Lantz, T.C., Gergel, S.E., Henry, G.H.R., 2010. Response of green alder (*Alnus viridis* subsp. *fruticosa*) patch dynamics and plant community composition to fire and regional temperature in north-western Canada. *J. Biogeogr.* 37, 1597–1610.
- Liang, E., Eckstein, D., 2009. Dendrochronological potential of the alpine shrub *Rhododendron nivale* on the south-eastern Tibetan Plateau. *Ann. Bot.* 104, 665–670.
- Lloret, F., 2004. Régimen de incendios y regeneración. In: Valladares, F. (Ed.), *Ecología del bosque mediterráneo en un mundo cambiante*. Ministerio de Medio Ambiente, Madrid, pp. 101–126.
- Lu, X., Liang, E., 2013. Progresses in dendrochronology of shrubs. *Acta Ecol. Sin.* Vol. 33 (5), 1367–1374.
- Medina, A., 2003. Reconstrucción de historias de fuego en bosques mediante técnicas dendrocronológicas. In: Kunst, C., Bravo, S., Panigatti, J.L. (Eds.), *Fuego en los ecosistemas argentinos*. INTA, Buenos Aires, pp. 133–144.
- Montenegro, G., Ginocchio, R., Segura, A., Keeley, J., Gomez, M., 2004. Fire regimes and vegetation responses in two Mediterranean-climate regions. *Rev. Chil. Hist. Nat.* 77, 455–464.
- Morgan, P., Hardy, C.C., Swetnam, T.W., Rollins, M.G., Long, D.G., 2001. Mapping fire regimes across time and space: understanding coarse and fine-scale fire patterns. *Int. J. Wildland Fire* 10, 329–342.
- Morrison, D.A., Cary, G.J., Pengelly, S.M., Ross, D.G., Mullins, B.J., Thomas, C.R., Anderson, T.S., 1995. Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: inter-fire interval and timesince-fire. *Aust. J. Ecol.* 20, 239–247.
- Mouillot, F., Ratte, J.P., Joffre, R., Moreno, J.M., Rambal, S., 2003. Some determinants of the spatio-temporal fire cycle in a Mediterranean landscape (Corsica, France). *Landscape Ecol.* 18, 665–674.
- Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., Macias-Fauria, M., Sass-Klaassen, U., Levesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, S.A., Schmidt, N.M., Schaepman-Strub, G., Wipf, S., Rixen, C., Menard, C.B., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H.E., Hik, D.S., 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environ. Res. Lett.* 6, 1–15.
- Naveh, Z., 1975. The evolutionary significance of fire in the Mediterranean region. *Vegetatio* 29, 199–208.
- Oddi, F., Dudinszky, N., Ghermandi, L., 2010. Spatial dynamics of *Fabiana imbricata* shrublands in northwestern Patagonia in relation to natural fires. *Nat. Hazard. Syst. Sci.* 10, 957–966.
- Oddi, F., 2013. Los incendios y la dinámica de *Fabiana imbricata* en el noroeste de la Patagonia a escala de paisaje. Su relación con factores ambientales y el uso del suelo. Universidad Nacional del Comahue, San Carlos de Bariloche (Tesis Doctoral (in Spanish, with English abstract)).
- O'Donnell, A.J., Cullen, L.E., McCaw, W.L., Boer, M.M., Grierson, P.F., 2010. Dendroecological potential of *Callitris preissii* for dating historical fires in semi-arid shrublands of southern Western Australia. *Dendrochronologia* 28, 37–48.
- Pastorino, M.J., Gallo, L., 2004. Los cipreses de Pilcaniyeu. El extremo más árido de la distribución natural del ciprés de la cordillera. *Presencia* 16, 17–19.
- Pausas, J.G., Paula, S., 2012. Fuel shapes the fire-climate relationship: evidence from Mediterranean ecosystems. *Global Ecol. Biogeogr.* 21 (11), 1074–1082.
- Pausas, J.G., Ribeiro, E., 2013. The global fire-productivity relationship. *Global Ecol. Biogeogr.* 22, 728–736.
- Pausas, J.G., Schwilk, D.W., 2012. Fire and plant evolution. *New Phytol.* 193, 301–303.
- Pausas, J.G., Vallejo, V.R., 1999. The role of fire in European Mediterranean ecosystems. In: Chuvieco, E. (Ed.), *Remote Sensing of Large Wildfires in the European Mediterranean Basin*. Springer, Berlin, pp. 3–16.
- Poulos, H.M., Villanueva Díaz, J., Cerano Paredes, J., Camp, A.E., Gatewood, R.G., 2013. Human influences on fire regimes and forest structure in the Chihuahuan Desert Borderlands. *For. Ecol. Manage.* 298, 1–11.
- Rayback, S.A., Henry, G.H.R., 2006. Reconstruction of summer temperature for a Canadian High Arctic site from retrospective analysis of the dwarf shrub, *Cassiope tetragona*. *Arct. Antarct. Alpine Res.* 38, 228–238.
- Ruete, A., 2006. Efectos de disturbios en la dinámica de los matorrales de *Fabiana imbricata* en la noroeste de la Patagonia. ¿Arbustización en la estepa? Universidad Nacional del Comahue, San Carlos de Bariloche (Tesis (in Spanish, with English abstract)).
- Schmidt, N.M., Baittinger, C., Forchhammer, M.C., 2006. Reconstructing century-long snow regimes using estimates of high arctic *Salix arctica* radial growth. *Arct. Antarct. Alpine Res.* 38, 257–262.
- Suarez, M.L., Kitzberger, T., 2010. Differential effects of climate variability on forest dynamics along a precipitation gradient in northern Patagonia. *J. Ecol.* 98, 1023–1034.
- Schweingruber, F.H., Poschold, P., 2005. Growth Rings in Herbs and Shrubs: life span, age determination and stem anatomy. *For. Snow Landscape Res.* 79 (3), 195–415.
- Silver, E.J., Speer, J.H., Kaye, M., Reo, N.J., Howard, L.F., Anning, A.K., Wood, S.W., Wilbur, H.M., 2013. Fire history and age structure of an Oakpine Forest on Price Mountain, Virginia, USA. *Nat. Areas J.* 33 (4), 440–446.
- Swanson, F.J., Kratz, T.K., Caine, N., Woodmansee, R.G., 1988. Landform effects on ecosystem patterns and processes. *BioScience* 38 (2), 92–98.
- Taylor, A.H., 2010. Fire disturbance and forest structure in an old-growth *Pinus ponderosa* forest, southern Cascades, USA. *J. Veg. Sci.* 21 (3), 561–572.
- Turner, M.G., Gardner, R.H., O'Neill, R.V., 2001. *Landscape Ecology in Theory and Practice*. Springer, New York, NY.
- Van Wagner, C.E., 1978. Age-class distribution and the forest fire cycle. *Can. J. For. Res.* 8, 220–227.
- Veblen, T.T., 1986. Age and size structure of subalpine forests in the Colorado Front Range. *Bull. Torrey Bot. Club* 113 (3), 225–240.
- Veblen, T.T., Kitzberger, T., Villalba, R., Donnegan, J., 1999. Fire history in northern Patagonian: the roles of humans and climatic variation. *Ecol. Monogr.* 69 (1), 47–67.
- Verdú, M., Pausas, J.G., 2007. Fire drives phylogenetic clustering in Mediterranean Basin woody plant communities. *J. Ecol.* 95, 1316–1323.
- Wells, A., Duncan, R.P., Stewart, G.H., 2001. Forest dynamics in Westland, New Zealand: the importance of large, infrequent earthquake induced disturbance. *J. Ecol.* 89 (6), 1006–1018.
- Williams, C.E., Johnson, W.C., 1990. Age Structure and the Maintenance of *Pinus pungens* in Pine-oak Forests of Southwestern Virginia. *Am. Midland Nat.* 124 (1), 130–141.
- Zedler, P.H., 1995. Fire frequency in southern California shrublands: biological effects and management options. In: Keeley, J.E., Scott, T. (Eds.), *Brushfires in California: Ecology and Resource Management*. International Association of Wildland Fire, Fairfield, WA, pp. 101–112.