



# Temporal shifts in the interaction between woody resprouters and an obligate seeder tree during a post-fire succession in Patagonia

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## Keywords

*Austrocedrus chilensis*; Competition; Facilitation; Long term; Radial growth; Shrubs; Temporal changes; Tree rings

## Abbreviations

BAI = Basal area increment; RII = Relative interaction index.

## Nomenclature

Correa (1969–1997)

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## Abstract

**Question:** The study of temporal variation of plant–plant interactions has received little attention despite its importance in community dynamics. Successional processes triggered by disturbances such as fire may be determined by changes in key interactions between dominant woody plants. Taking advantage of a 95-yr-old post-fire natural experiment we assessed temporal shifts in post-fire interactions between woody resprouters and the obligate seeder tree *Austrocedrus chilensis*. We hypothesized that during the initial post-fire period, resprouters may facilitate *A. chilensis* trees' growth, while at advanced time since fire the interaction between *A. chilensis* trees and resprouters may turn to competition.

**Location:** Northwestern Río Negro province, Patagonia, Argentina.

**Methods:** We selected pairs of *A. chilensis* trees and woody resprouters growing 80 cm apart (growing in association) and both *A. chilensis* trees and resprouters growing at more than 3 m apart from any individual (controls). We cored all individuals, measured ring widths and calculated basal area increment (BAI) and the relative interaction index (RII).

**Results:** During mid-early stages of post-fire succession, *A. chilensis* trees' BAI was suppressed for at least 15 yr when growing in association with resprouters, and accordingly displayed a negative RII. Strikingly, during the same period, resprouters associated with *A. chilensis* trees showed higher BAI than control resprouters, and a positive RII. At advanced time since fire, RII showed a neutral interaction, and according to model estimations, the BAI of *A. chilensis* trees in association may eventually exceed control BAI whereas resprouters' BAI in association may decline earlier than that of the controls. Interestingly, *A. chilensis* trees and resprouters' growth was less correlated with climate when growing in association than when growing in isolation.

**Conclusions:** Competition of resprouters over *A. chilensis* trees' growth during intermediate post-fire stages may be slowing the successional process. However, the association appears to be at the same time mutually beneficial as it buffers against adverse climatic conditions. Studying how plant growth varies along the succession is essential to understand community functioning and to predict possible alterations associated with changes in disturbance regimes due to climate change.

## Introduction

Understanding shifts in plant–plant interactions through time becomes especially important when considering the post-disturbance successional sorting of foundation species

with different life-history traits (Stultz et al. 2007). Fire, a particularly important global ecological process, has the capacity to favour some life history traits, such as resprouting. Furthermore, in the absence of successional replacements, resprouting vegetation can feed back into fire

regimes and thus maintain flammable fire-resilient plant communities in the landscape (Paritsis et al. 2015; Pausas 2015). These ‘fire-trapped’ states (Lindenmayer et al. 2011) can only revert to an alternative state, of fire-sensitive and less flammable species, if fire-free periods are long enough to allow successional replacement. Assessing temporal changes in interactions between foundation species after fire becomes crucial to understand processes that govern successional replacement rates that may push the system beyond thresholds of flammability and fire resistance (Pausas 2015).

Plant species interactions involve a complex balance of competition and facilitation, which determine community structure (Callaway & Walker 1997). While the spatial aspects of these interactions has received much recent attention (e.g. stress gradients, Bertness & Callaway 1994; Maestre et al. 2005; Sthultz et al. 2007; Fajardo & McIntire 2011), the temporal variation of the relative importance of competition vs facilitation has received less empirical support, despite having been a central point since the early development of ecological theory of succession (Clements 1916; Tansley 1920; Connell & Slatyer 1977). Growing empirical evidence suggests that the temporal sequences in species interactions are both dependent on changes in stress conditions along spatial gradients as well as temporal changes in stress levels (Sthultz et al. 2007; Kunstler et al. 2011). In general, it is predicted that shifts from net competitive to net facilitative effects would be expected in more stressful environments, whereas competition would increasingly dominate throughout succession in more productive environments (Grime 1977; Chapin et al. 1994; Callaway 2007). However, independent of stress amelioration, facilitation may be, by itself, a key mechanism driving long-term processes such as succession and community structuring (McIntire & Fajardo 2014). Temporal changes in species interactions can be even more complex in the form of transient events associated with climatic variability (Greenlee & Callaway 1996; Kitzberger et al. 2000; Tielbörger & Kadmon 2000). Furthermore, it has been proposed that the outcome of plant–plant interactions would change with ontogeny, i.e. across the life stages of the interacting plants (Pugnaire et al. 1996; Callaway & Walker 1997; Rousset & Lepart 2000; Miriti 2006; Schiffers & Tielbörger 2006; Soliveres et al. 2010).

The study of temporal variation in species interactions is challenging because monitoring communities for long periods of time can be impractical, particularly for long-lived plant communities such as forests. Most studies developed short-term manipulative experiments on vegetation communities of short-lived species (Tielbörger & Kadmon 2000; Brooker et al. 2008; Soliveres et al. 2010) or on the early establishment of long-lived communities (Franco & Nobel 1988; Raffaele & Veblen 1998; Kitzberger

et al. 2000). Therefore, the study of interactions between long-lived species during long-term periods of time has received less attention (Callaway 1998; Sthultz et al. 2007; Brooker et al. 2008; Cavard et al. 2011; Lebourgeois et al. 2013). Retrospective techniques, such as the use of tree rings, could be very useful for unravelling these long-term interaction patterns, especially in sites under relatively stable conditions (e.g. in the absence of forest management). To our knowledge, tree rings have sporadically been used to detect competitive and facilitative effects in growth rates between long-lived species (Burns 1993; Cavard et al. 2011; Kunstler et al. 2011; von Oheimb et al. 2011; Lebourgeois et al. 2013; Pretzsch et al. 2013; Río et al. 2014). More importantly, this technique could also be useful to study temporal variations in species interactions and temporal changes in climatic responses driven by specific species associations (Lebourgeois et al. 2013; Pretzsch et al. 2013), which could eventually shed light on the mechanisms that drive forest dynamics.

In northern Patagonia, fires have long modulated the structure and composition of vegetation, and particularly of *Austrocedrus chilensis* forests and shrublands (Veblen et al. 2003). The relatively long-lived woody species of the shrubland, such as *Maytenus boaria*, *Diostea juncea*, *Nothofagus antarctica* and *Lomatia hirsuta*, are able to resprout after fire and usually display fast initial growth (Raffaele & Veblen 1998; Veblen et al. 2003). *A. chilensis*, on the other hand, are long-lived, relatively slow-growing, non-resprouting and obligate-seeder trees (Veblen et al. 2003). These contrasting life-history traits allow for a successional cycle along time since fire, in which shrubland species rapidly regrow and usually dominate the site after fire, while *A. chilensis* seedlings frequently depend on shrub facilitation mechanisms to successfully establish (Gobbi & Schilchter 1998; Raffaele & Veblen 1998; Kitzberger et al. 2000; Letourneau et al. 2004; Nuñez et al. 2009). Indeed, *A. chilensis* trees have been found to grow more frequently spatially associated with shrubs than in open areas (Kitzberger et al. 2000; Nuñez et al. 2009). However, after establishment *A. chilensis* saplings may start to compete with their protective shrub (Veblen et al. 1992; Kitzberger et al. 2000; Letourneau et al. 2004), ultimately determining that, in the absence of another fire event, the shrubland may be replaced by an *A. chilensis* forest or a mixed forest–shrubland stand (Veblen & Lorenz 1987, 1988). In the region, a reduction in live resprouters’ canopy and an increase in dead resprouters beneath dense *A. chilensis* stands is frequently observed (Veblen & Lorenz 1987, 1988; Nuñez et al. 2009). Most studies have focused on the initial stages of *A. chilensis* life cycle and developed manipulative short-term experiments. Yet, no studies have tested if there is actually a temporal variation in the interaction between these

foundational species along time since fire, nor have they evaluated their growth responses as a result of their interaction. Furthermore, it is not known how long these interaction processes last.

In this work we took advantage of a 95-yr-old post-fire natural experiment to study the long-term dynamics of the interaction between resprouting woody species (hereafter, resprouters) and *A. chilensis* trees (also referred to as obligate seeder tree) along time since fire through the analysis of their radial growth patterns. Our hypothesis was that resprouters facilitate *A. chilensis* seedlings growth during the initial post-fire stage, through protection from adverse conditions, such as direct sunlight and soil desiccation. However, the interaction turns into competition when *A. chilensis* trees are already established, because light becomes a limiting factor. We also hypothesized that, eventually, *A. chilensis* trees may overtop resprouters' canopy and thus suppress their growth due to shading. To test our hypothesis we performed a retrospective study in which we cored pairs of obligate seeder trees growing in close association with resprouters and obligate seeder trees and resprouters growing in isolation to compare their radial growth along time since fire. Based on field observations and previous studies (Veblen & Lorenz 1987, 1988; Veblen et al. 1992; Kitzberger et al. 2000; Letourneau et al. 2004; Nuñez et al. 2009) we predicted that during early post-fire stages (i.e. during the first decade of growth, after shrub resprouting and during *A. chilensis* establishment and initial growth), *A. chilensis* seedlings established beneath resprouters would grow faster than seedlings growing in isolated microsites. During intermediate stages, approximately in the second and third decade of growth (i.e. when *A. chilensis* saplings are already established and are still beneath the resprouters' canopy), we predicted that *A. chilensis* saplings growing in association with resprouters would grow slower than saplings growing in the open. Conversely, during this stage resprouters should grow equally, irrespectively of whether they are growing in association with an *A. chilensis* tree sapling or alone. Finally, during advanced stages of succession, after the fourth decade of growth onwards (i.e. when *A. chilensis* trees have already overtopped the resprouter' canopy), we predicted that resprouters in association with *A. chilensis* trees would have lower growth rates than resprouters in isolated microsites; and that *A. chilensis* trees in association would not differ in growth from *A. chilensis* trees in isolated microsites.

## Methods

The study was performed in an area burned 95 yr ago within the vicinity of Cerro Tronador (41°15' S, 71°39' W) in Nahuel Huapi National Park. This area is characterized

by 1355 mm mean annual precipitation, 7.9 °C mean annual temperature, and is at 870 m a.s.l. The site is composed of resprouting species with emergent *A. chilensis* individuals (Cupressaceae). The more abundant resprouting woody species were *Maytenus boaria* (Celastraceae), *Diostea juncea* (Verbenaceae), *Nothofagus antarctica* (Nothofagaceae) and *Lomatia hirsuta* (Proteaceae). *A. chilensis* trees were, on average, 10.5 ± 0.6 m in height and 20.4 ± 1.1 cm in DBH. Resprouting woody species were on average 9.62 ± 0.57-m high and 23.2 ± 1.1 cm DBH. Within the study site we selected 25 pairs of *A. chilensis* trees and any resprouting woody species growing on average 80 cm away from each other (hereafter referred to as growing in association), assuming that at this distance their growth would be affected by each other's presence because the canopy and their root systems are partly superimposed. The identity of the resprouting species was not very important in this case because we were interested in looking for differences between resprouters in general and *A. chilensis* trees. Furthermore, it is considered that the association between *A. chilensis* and resprouters is not species-specific (Kitzberger et al. 2000; Nuñez et al. 2009). We worked with the first three resprouting species named above because their growth rings are easier to determine from core samples. Another condition for selecting pairs of resprouters and obligate seeder trees was that the resprouter had to be older than the obligate seeder tree because we were trying to detect if resprouter facilitation over *A. chilensis* growth occurred during the initial post-fire stage. To achieve these criteria in the field, we selected pairs in which resprouters had larger diameter trunks than obligate seeder trees and we subsequently verified resprouter and obligate seeder tree age in the laboratory. Furthermore, *A. chilensis* individuals had to be taller than resprouters because we wanted to detect if suppression of obligate seeder trees over resprouters' growth occurred at advanced time since fire.

In the same study site, we also selected 21 *A. chilensis* trees and 22 resprouters that fulfilled the same criteria as the pairs, except that these individuals had to be growing at more than 3 m apart from any other tree, resprouter or stump. In this way, we assumed that in the immediate microsite no woody species would be affecting their growth. Also, to reduce the variation that could exist in soil conditions and that could influence growth, each control corresponded to the nearer pair (respecting the criterion of >3 m distance). These individuals functioned as a control to compare their growth with that of the individuals growing in association and to discard any growth changes not associated with an interaction mechanism. Therefore, one important condition was that obligate seeder trees and resprouters growing in association must have similar ages as their controls to assure that they were in the same

growth stage. Accordingly, we expected control obligate seeder trees to present a similar growth pattern but different from obligate seeder trees growing in association with resprouters, and anticipated the same for control resprouters and those in association with obligate seeder trees.

We measured the diameter at coring height, DBH and the height of every resprouter and obligate seeder tree. Furthermore, we extracted a core sample at 40 cm above ground from every resprouter and obligate seeder tree, mainly because old resprouting woody shrubs are usually putrefactive at lower height and therefore it is not possible to extract a complete core sample. We mounted and sanded all cores with successively finer grades of sandpaper and studied the growth rings under a stereomicroscope. We performed visual cross-dating with signature years and measured tree ring width on all cores. This procedure was conducted with a computer compatible increment tree ring measurer (0.01 mm resolution) and a stereomicroscope. All ring-width series were statistically verified using an existing master chronology for *A. chilensis* (R. Villalba: Pampa del Toro; ITRDB, NOAA, Boulder, CO, US, US,ftp://ftp.ncdc.noaa.gov/pub/data/paleo/treering/measurements/southamerica/arge080.rwl) and the program COFECHA (Holmes 1983). We assessed both obligate seeder tree and resprouter age, assigning the date of an annual ring to the calendar year when growth began (Schulman 1956). For the samples that did not reach the pith, we estimated age using a geometric technique (Duncan 1989). Ages were considered as age at coring height. After carefully studying all cores samples, we finally selected 14 obligate seeder tree–resprouter pairs that presented clearly visible rings, no decayed section and accomplished with the condition of the resprouter being older than the obligate seeder tree (resprouter at least >3 yr older than the obligate seeder tree). Accordingly, we selected the 14 control resprouters and 14 control *A. chilensis* trees that corresponded to each pair.

## Data analysis

We performed paired *t*-tests to determine if obligate seeder trees and resprouters growing in association ( $n = 14$ , respectively) had similar age to their controls ( $n = 14$ , respectively). Furthermore, we fitted a LME model to compare annual growth between: resprouters and obligate seeder trees growing in association ( $n = 14$  pairs), between control resprouters ( $n = 14$ ) and control obligate seeder trees ( $n = 14$ ), control resprouters and resprouters growing in association and control obligate seeder trees and obligate seeder trees in association. We used basal area increment (BAI) as response variable, because it allows to compare growth between individuals of different age, given that it standardizes growth in relation to tree diameter (Biondi

1999). In this way, the potential discrepancy between different species' growth is minimized. Furthermore, obligate seeder tree and resprouter age was included in the model to control for ontogeny-related effects. We calculated BAI from the ring widths and the diameter at coring height as:

$$BAI_t = \pi R_t^2 - \pi R_{t-1}^2$$

where  $R_t$  is the radius of the stem at year  $t$  and  $R_{t-1}$  is the radius of the stem at year  $t-1$  (Biondi & Qeadan 2008). BAI was log-transformed to accomplish normality. The model was integrated by the fixed effects life-history trait (resprouter or obligate seeder tree; hereafter, Lht), growing condition (in association or control; hereafter, Gcd), time since fire (hereafter, Tsf), time since fire squared (given that we expected *A. chilensis* trees and resprouters to display a decreased growth pattern with increasing time), obligate seeder tree and resprouter age (hereafter, Age). In addition, we included the following interactions: Lht  $\times$  Gcd to test if there were differences in BAI between resprouters and the obligate seeder tree depending on their growing condition; Lht  $\times$  Tsf to determine if BAI of resprouters and the obligate seeder tree differ along time since fire (independently of their growing condition); Gcd  $\times$  Tsf to assess if BAI of individuals growing in association and control differ along time since fire (independent of their life-history trait); and Lht  $\times$  Gcd  $\times$  Tsf to test if there are differences in BAI between resprouters and the obligate seeder tree depending on their growing condition along time since fire. The random effects of the model were the individual pairs and the plant species to take into account the paired structure of the sample design and the growth variability that may exist between species. We modelled temporal autocorrelation with a corARMA structure because the data consisted of repeated measurements of annual tree ring growth. Moreover, we model variance heterogeneity between species with a varIdent structure (Zuur et al. 2009). We performed the analysis with the lme function of the nlme package in the R software v 3.0.2 (R Foundation for Statistical Computing, Vienna, AT).

To quantify the effect of resprouters on obligate seeder trees' growth and *vice versa*, we used the relative interaction index (RII; Armas et al. 2004), which allowed us to quantitatively assess the nature of the interaction and reveal temporal shifts. RII values range between  $-1$  and  $1$ , where  $RII > 0$  indicates an increase in plant biomass produced by facilitation and  $RII < 0$  indicates a reduction in biomass caused by competition. RII was calculated as:

$$RII = (BAI_a - BAI_c) / (BAI_a + BAI_c)$$

where  $BAI_a$  is the BAI of the individual growing in association and  $BAI_c$  is the BAI of the control individual. RII was calculated annually for both the resprouters and the obligate seeder tree. To determine if RII overlaps 0 (i.e. neutral

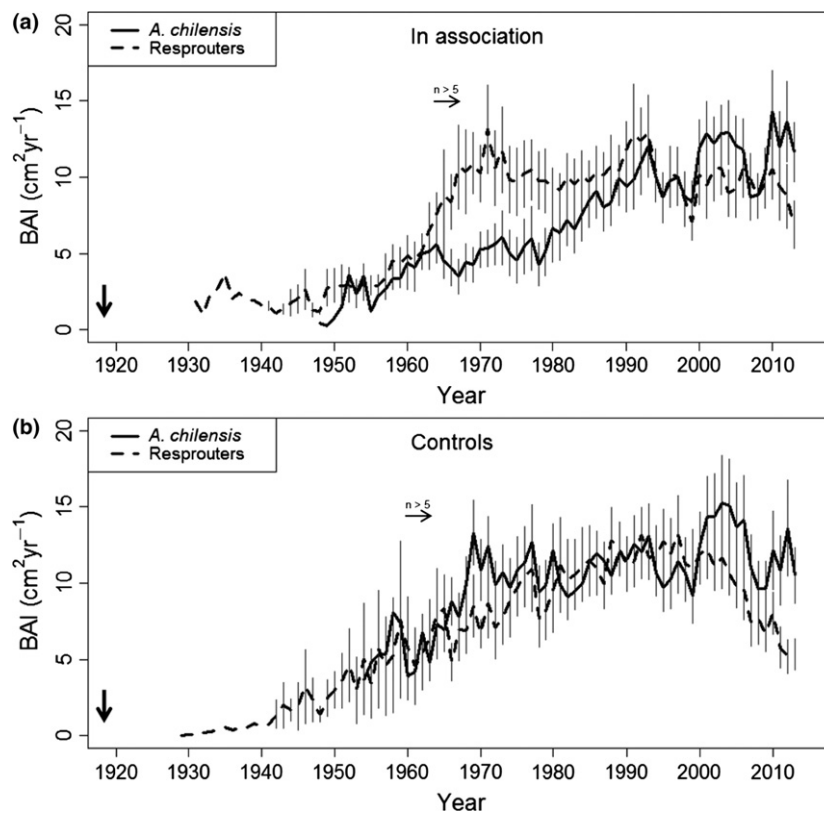
interaction), we calculated 95% percentile intervals from the distribution of the RII values obtained with 10 000 bootstrap samples.

Given that our study was retrospective, we performed correlation function analyses to assess whether obligate seeder trees and resprouters growing in association differed in their response to climate from the controls. For this, tree ring series were detrended with the dplR package of the R software (Bunn 2008) using a cubic smoothing spline. Subsequently, a residual chronology was developed for the individuals growing in association and another for the controls for both life-history traits (Cook & Kairiukstis 1990). Correlation function analyses included monthly temperature and precipitation from Oct of the previous year of growth to May of the current growth year, as it is known that climatic conditions of the previous year also influence the current year tree growth (Fritts 1976). Climatic data was obtained from the meteorological station that was closest to the study area and which had the longest time period available (1931–2013). The meteorological station is located at Bariloche Airport, 77 km from the study site (41°09' S, 71°10' W; 845 m a.s.l.). The analysis was performed with the bootRes package of the R software (Zang

& Biondi 2013). Furthermore, with the dplR package (Bunn 2008), we calculated the mean sensitivity, SD and first-order autocorrelation on the detrended ring width series to assess the sensitivity of growth to climate (i.e. year-to-year variability; Bunn et al. 2013). Mean sensitivity was calculated as the absolute difference between adjacent indices divided by the mean of the two indices (Fritts 1976).

## Results

The age of obligate seeder trees growing in association was not different from that of the obligate seeders control ( $t = -0.476$ ,  $df = 13$ ,  $P = 0.641$ ). Likewise, resprouter age in association did not differ from that of their control ( $t = 0.952$ ,  $df = 13$ ,  $P = 0.358$ ). Describing growth patterns, resprouters and *A. chilensis* trees growing in association displayed similar BAI during the initial post-fire stage (Fig. 1a). However, 50 yr after fire, and for at least 15 yr, when growing in association resprouters had two- to three-fold higher BAI compared to that of *A. chilensis* trees. At long Tsf, BAI of resprouters and obligate seeder trees became very similar. In contrast, control *A. chilensis* trees'



**Fig. 1.** Basal area increment along time since fire (calendar years) for: (a) resprouters and *A. chilensis* in association and (b) resprouter and *A. chilensis* control. Vertical black arrows indicate year of the fire (1919) and horizontal arrows indicate the first year at which the number of samples is >5. Vertical grey lines indicate  $\pm$ SE.

BAI was similar to that of resprouters except at about 50 yr after fire, when *A. chilensis* trees displayed superior BAI to resprouters and at long Tsf when resprouters' BAI declines (Fig. 1b).

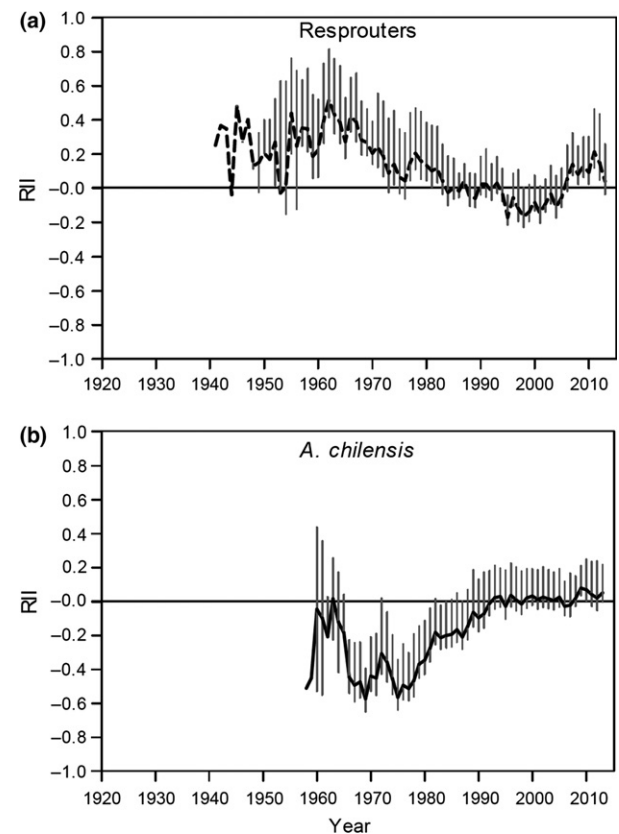
The LME model found significant effects in the variables Lht, Gcd, Tsf, Tsf<sup>2</sup>, Age and the interactions Lht × Gcd, Lht × Tsf, Gcd × Tsf and Lht × Gcd × Tsf (Table 1). Our model predicted that 50 yr after fire, resprouters (with age 39 yr) had increased 9.55 cm<sup>2</sup>·yr<sup>-1</sup> in BAI, while *A. chilensis* trees (aged 22 yr) grew at rates of only 3.69 cm<sup>2</sup>·yr<sup>-1</sup> when growing in association (Appendix S1). However, given that the intercept of the model represents resprouters' growth when associated with *A. chilensis* trees, Lht represents only the obligate seeder growth. Therefore, a significant positive interaction between Lht and Tsf (Table 1) meant that, when growing in association, the slope of the BAI of the obligate seeder tree was higher than that of resprouters, suggesting that obligate seeder tree BAI would eventually exceed that of resprouters. In contrast, when growing as control, at Tsf = 0 the slope of *A. chilensis* trees' BAI was higher than that of resprouters, but both showed a similar slope along Tsf (Appendix S1). Moreover, our model predicted that 50 yr after fire, control *A. chilensis* trees with an age of 22 yr, increased 7.77 cm<sup>2</sup>·yr<sup>-1</sup> in BAI (positive Lht × Gcd interaction), whereas obligate seeder trees in association with resprouters increased BAI by 3.69 cm<sup>2</sup> (Appendix S1). Nevertheless, the negative triple interaction between Lht × Gcd × Tsf indicated that the slope of the BAI of *A. chilensis* trees was significantly lower when growing in isolated microsites than when

growing in association with resprouters, thus suggesting that BAI of *A. chilensis* growing in association would eventually exceed that of the control. Strikingly, in the case of resprouters, 50 yr after fire, our model predicted 2.36 cm<sup>2</sup>·yr<sup>-1</sup> higher BAI when growing in association with *A. chilensis* trees than controls (Appendix S1). However, the positive interaction between Gcd × Tsf indicated that the slope of control resprouters' BAI was greater than when growing associated with obligate seeder trees, thus suggesting that BAI tends to decline earlier for resprouters growing in association with *A. chilensis* trees than for control resprouters (Appendix S1). Finally, the model found a drop in growth rate for all individuals at advanced Tsf (Tsf<sup>2</sup>) and Age had a positive effect on BAI (Table 1).

The RII displayed a neutral effect of *A. chilensis* trees on resprouters' growth during the initial post-fire stage and, in accordance with the LME model, it then shifted to positive for a period of almost 30 yr (Fig. 2a). Then, at advanced Tsf the interaction mostly reverted to neutral. Conversely, the effect of resprouters on *A. chilensis* trees' growth was also initially neutral but rapidly shifted to

**Table 1.** Parameter estimates of the linear mixed effects model to compare basal area increment (BAI) between resprouters and *A. chilensis* trees growing in association and control along time since fire. The independent variables included in the analysis were life-history trait (Lht; resprouter or obligate seeder tree), growing condition (Gcd; in association or control), time since fire (Tsf), time since fire squared (Tsf<sup>2</sup>), age and the following interactions: Lht × Gcd, Lht × Tsf, Gcd × Tsf and Lht × Gcd × Tsf. The intercept represents resprouters' growth when associated with *A. chilensis* (Lht = resprouter; Gcd = in association), thus in this summary obtained from the model, Lht represents only obligate seeder tree growth and Gcd represents the control. Coefficients (logarithmic scale), SE (logarithmic scale), *df*, *t*- and *P*-values are shown.

	Coefficient	SE	<i>df</i>	<i>t</i> -Value	<i>P</i> -Value
Intercept	-0.252	0.386	2637	-0.653	0.513
Lht	-2.616	0.471	2637	-5.553	0.000
Gcd	-0.975	0.440	2637	-2.214	0.026
Tsf	3.947	0.557	2637	7.083	0.000
Tsf <sup>2</sup>	-1.863	0.236	2637	-7.872	0.000
Age	0.286	0.085	2637	3.340	0.000
Lht × Gcd	2.913	0.656	2637	4.438	0.000
Lht × Tsf	2.103	0.340	2637	6.174	0.000
Gcd × Tsf	0.778	0.351	2637	2.213	0.027
Lht × Gcd × Tsf	-2.119	0.495	2637	-4.279	0.000



**Fig. 2.** Mean of the relative interaction index (RII) along time since fire (calendar years) for: (a) resprouters and (b) *A. chilensis* trees. Vertical grey lines indicate 95% percentile intervals from the distribution of the RII values obtained with 10 000 bootstrap samples.

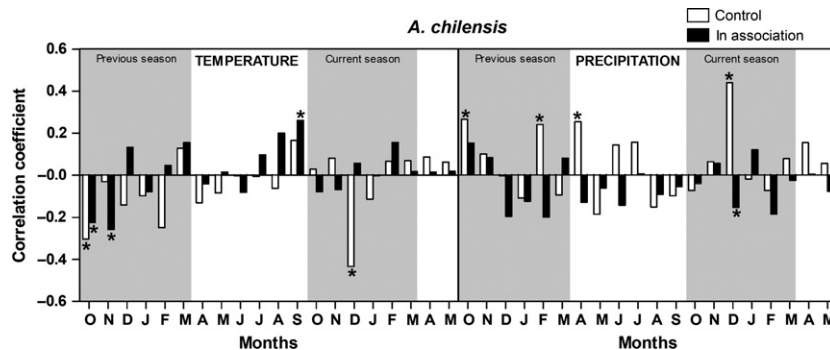
negative for a period of at least 15 yr (Fig. 2b), as also estimated from the model. Afterwards, the effect of resprouters on *A. chilensis* trees' growth turned to neutral again and finally became slightly positive.

The correlation function analyses displayed a markedly lower climatic response for both obligate seeder trees and resprouters in association than for the controls. In the case of obligate seeder trees, the controls showed higher correlation with Oct temperature of the previous season than those growing in association (Fig. 3). During the current season, Dec temperature was extremely negatively correlated with control *A. chilensis* trees' growth, whereas *A. chilensis* trees in association showed no significant correlation. Regarding precipitation, correlations with growth were positive and significant only for control *A. chilensis* trees in Oct and Feb of the previous season and in Dec of the current season. In the case of resprouters, correlations were higher between control growth and temperature, particularly during the previous season when growth was significantly and negatively correlated with Dec temperature, and also highly correlated during Nov, Jan and Feb

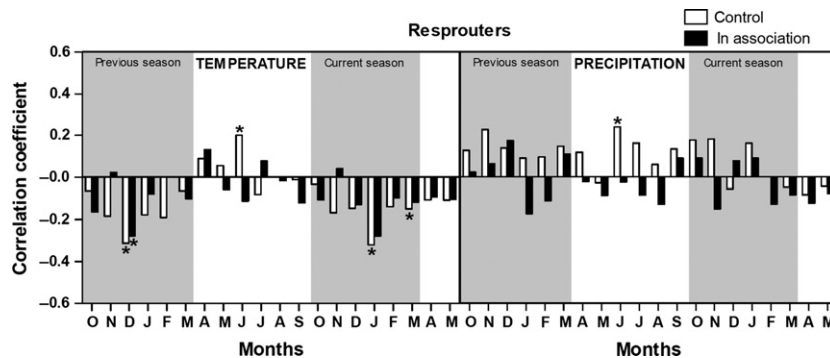
(Fig. 4). During the current season, correlations with temperature were also superior for control resprouters, showing a negative and significant correlation with Jan and Mar temperature. Regarding precipitation, correlations were predominantly higher and positive with control resprouters' growth, although the only significant correlation was during Jun. Regarding descriptive statistics, higher SD and usually higher values of mean sensitivity would indicate more climatically responsive chronologies (Bunn et al. 2013). According to these, and unlike the correlation functions, the response to climate was not different for the obligate seeder trees, but was slightly lower for resprouters in association than for the controls (Table 2).

### Discussion

In this study we found that the interaction between resprouters and the obligate seeder *A. chilensis* tree shifted from neutral to a complex interaction at intermediate post-fire stages in which resprouters suppressed *A. chilensis* trees' growth at the same time that the latter exerted a



**Fig. 3.** Correlation functions between annual *A. chilensis* radial growth and monthly temperature (left) and precipitation (right) for *A. chilensis* trees growing in association with resprouters and control. Months are shown in the x-axis, where the first Oct–May period corresponds to the year prior to growth (previous season) and the second Oct–May period corresponds to the growth year (current season). Significant correlations are indicated with asterisks.



**Fig. 4.** Correlation functions between annual radial growth and monthly temperature (left) and precipitation (right) for resprouters growing in association with *A. chilensis* trees and control. Months are shown in the x-axis, where the first Oct–May period corresponds to the year prior to growth (previous season) and the second Oct–May period corresponds to the growth year (current season). Significant correlations are indicated with asterisks.

**Table 2.** Descriptive statistics for the obligate seeder tree and resprouters' tree-ring chronologies per growing condition (Gcd). Number of series (N series) used to build up the chronologies and time span are shown. We report the mean sensitivity (Ms  $\pm$  SE), standard deviation (SD  $\pm$  SE) and the first-order autocorrelation (Ar1  $\pm$  SE) of all detrended ring width series.

Life-History Trait	Gcd	N Series	Time Span	Ms	SD	Ar1
Obligate Seeder Tree	Pair	19	1947–2013	0.22 $\pm$ 0.007	0.32 $\pm$ 0.06	0.35 $\pm$ 0.04
Obligate Seeder Tree	Control	20	1950–2013	0.22 $\pm$ 0.009	0.24 $\pm$ 0.01	0.31 $\pm$ 0.04
Resprouters	Pair	18	1936–2013	0.34 $\pm$ 0.01	0.61 $\pm$ 0.17	0.24 $\pm$ 0.05
Resprouters	Control	19	1923–2013	0.37 $\pm$ 0.01	0.51 $\pm$ 0.05	0.31 $\pm$ 0.06

positive effect on resprouters' growth. Subsequently, at advanced time since fire, the interaction reverted mostly to neutral, although there also appears to be a slight suppression effect of *A. chilensis* trees over resprouters' growth at this stage. Strikingly, we also found that the association between *A. chilensis* trees and resprouters may have a mutually beneficial effect against climatic variability, given that both were less responsive to climate than when growing in isolation. Our work highlights the importance of studying plant interactions of long-lived plant communities along successional processes, because it may not only shed light on how a community structures through time, but may also contribute to understand the associated changes in community functioning, such as the disruption of fire–vegetation feedbacks due to changes in community flammability.

The classic post-fire successional pattern of replacement based on early facilitation from resprouters on seed-dispersed trees, followed by a competitive displacement when the tree overtops the resprouters' canopy (Veblen et al. 1992; [Kitzberger et al. 2000](#)), does not completely fit our data. First, no evidence was found of early facilitation, at least using growth as response variable. Accordingly, the RII displayed a neutral interaction during this stage. However, considering that coring height was at 40 cm, it is possible that core samples may not have included all *A. chilensis* tree rings associated with the initial growth stage. Thus, the occurrence of early facilitation from resprouters on obligate seeder tree growth cannot be discarded, especially considering the abundant literature that indicate facilitation at least as an important mechanism of *A. chilensis* establishment ([Gobbi & Schilchter 1998](#); [Rafaele & Veblen 1998](#); [Kitzberger et al. 2000](#); [Letourneau et al. 2004](#); [Nuñez et al. 2009](#)). Alternatively, in our study, harshness of site may not have been strong enough to induce early facilitation of resprouters over obligate seeder tree growth. Furthermore, lower sample size during this stage may be another factor that hampered the detection of a clear interaction effect.

During the intermediate post-fire stage, resprouters strongly suppressed growth of obligate seeder trees for at least 15 yr, probably due to shading, at the same time that these exerted a positive effect on resprouters' growth. This

agrees with previous studies that documented a negative effect of resprouters over *A. chilensis* trees' growth after their establishment ([Kitzberger et al. 2000](#); [Letourneau et al. 2004](#); [Nuñez et al. 2009](#)); however, our work now sheds light on the extension of the competition period and underlines the importance of shrublands in determining the post-fire succession rate. Unexpectedly, resprouters in association with *A. chilensis* trees had higher growth rates than control resprouters. This may suggest that *A. chilensis* trees growing still beneath resprouters could be somehow facilitating resprouters' growth through an improvement in local conditions. It has been documented that the litter of *A. chilensis* trees is rich in Ca and, accordingly, soils beneath this species have higher pH values and increased cation concentrations ([Satti et al. 2007](#)). Another explanation may be the occurrence of hydraulic lift, i.e. the movement of water via the root system from deeper and moister soil layers to shallower and more xeric ones, thus increasing available water and nutrients in surface layers ([Dawson 1993](#)). This mechanism may be a possible explanation since *A. chilensis* trees attain more profound rooting depth than resprouters and thus access deeper water sources (Veblen et al. 1996). However, facilitative interactions of understorey to overstorey plants, in this and other plant communities, are still not well understood and thus our inferences deserve further experimental exploration.

At advanced time since fire, possibly when obligate seeder trees begin overtopping and shading resprouters, both showed mostly a neutral interaction. However, resprouters' RII also displayed a negative tendency during this stage, suggesting suppression of *A. chilensis* trees on resprouters' growth. This agrees with the lower slope of BAI of resprouters in association, which implies an earlier decline in growth than control resprouters. Nevertheless, differences appear to rapidly blur out as control resprouters' growth also started to decline, probably due to ageing ([Veblen & Lorenz 1987, 1988](#)). The suppression of obligate seeder trees over resprouters was moderate compared to the competition effect that resprouters exerted on *A. chilensis* trees in the intermediate stage, possibly because obligate seeder trees were still slightly taller than resprouters. Conversely, we would expect stronger suppression of obligate seeder trees on resprouters' growth at longer time



since fire, when obligate seeder trees had totally overtopped the resprouters' canopy, as broadly documented in post-fire stands (Veblen & Lorenz 1987, 1988). Furthermore, moderate suppression of obligate seeder trees on resprouters' growth may only occur in successional situations in which the obligate seeder tree enters the shrubland at low density, because resprouters' mortality beneath dense *A. chilensis* stands has been extensively documented (Veblen & Lorenz 1987, 1988; Nuñez et al. 2009). Accordingly, further effort should focus on studying the relative importance of *A. chilensis* suppression and ageing in the reduction of resprouters' growth rate. In the case of *A. chilensis* trees, the slope of BAI was higher when growing in association with resprouters, suggesting that their growth will decline later in time compared to control *A. chilensis*. This may be explained by an important growth release of *A. chilensis* growing in association, after years of growth suppression and competition for light until they finally overtopped resprouters' canopy.

Strikingly, we found that there might also be a mutually positive interaction between *A. chilensis* trees and resprouters growing in association, since correlation functions showed that both were less responsive to climate than when growing alone. *A. chilensis* trees, on one hand, displayed unusual low correlations between growth and climatic variables when growing in association with resprouters, thus suggesting that such an association made *A. chilensis* less responsive to climatic variability; whereas the higher response of control *A. chilensis* trees agrees with what is usually found for this species (Villalba & Veblen 1997). In particular, *A. chilensis* trees growing in isolation were favoured with above average precipitation but not with above-average temperatures (during Dec of the current season and Oct and Feb of the previous season). Even though there were some discrepancies, isolated resprouters' growth was also high and positively correlated with precipitation and negatively with temperature during spring–summer months. Although the lower response of plants growing in isolation may be an expected result for the dendrochronologist, here we consider the response to climate in terms of species interactions; i.e. how growing within plant complexes may allow individuals to be climate-independent. It is possible that resprouters may be moderating environmental conditions and indirectly allowing *A. chilensis* trees' growth to be less influenced by climate. This agrees with previous works, which found that solar radiation and temperature are reduced beneath shrubs and humidity is increased (Gobbi & Schilchter 1998; Raffaele & Veblen 1998; Kitzberger et al. 2000). In the case of resprouters, we suggest that the beneficial effect of *A. chilensis* trees on resprouters' responses to climate may be explained by hydraulic lift, as discussed for the facilitation effect, and as already suggested for other long-

lived woody species (Lebourgeois et al. 2013; Pretzsch et al. 2013). However, we did not find important differences in sensitivity of the chronologies. Accordingly, more effort should be focused on the study of how responses to climate vary according to plant–plant interactions and also how the sign of the interactions may change in relation to climatic variability.

Temporal shifts in plant–plant interactions shape community structure along post-fire succession, which at the same time influences community flammability and may determine how plants respond to climate. In this study we found that although resprouters may be essential for the establishment of obligate seeder trees, they subsequently inhibit their growth for a long period of time, actually slowing down post-fire succession. This may have implications for fire–vegetation feedbacks, because community structure remains more flammable for a longer period of time. That is, the community dominated by resprouting shrubs displays multiple strata (with trees in the understory and resprouters in the overstorey), which provides vertical continuity of fuels, thus increasing fire ignition probability and fire spread (Blackhall et al. 2015; Paritsis et al. 2015). Considering the expected increase in fire frequency due to global change, this may cause a reduction in fire-free periods, trapping the community in a more flammable state and promoting positive fire–vegetation feedbacks (Paritsis et al. 2015). In this way, the course of post-fire succession may shift to an alternative state with lower obligate seeder trees' abundance (Pausas 2015).

We also show that some plant–plant associations might explain how they respond to climate. This is particularly important for demographic processes, as being near other plants may make the difference to individuals' survival during climatically unfavourable years. Complementary to previous results, which found that shrubs may be buffering moderate droughts and promoting tree establishment during climatically suboptimal years (Kitzberger et al. 2000), here we show that this idea could be extended to growth: neighbouring plants may be buffering climatic variability so that growth in closely associated plant complexes is less sensitive to climatic extremes. In this work, we highlight the importance of facilitation in terms of providing buffering against climatic fluctuations during long-term successional periods and in long-lived plant communities. Studying how plant growth varies throughout the succession is essential to understand community functioning and to predict possible alterations associated with changes in disturbance regimes due to climate change.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Figures of basal area increment (BAI) along time since fire, estimated with a linear mixed effects model to compare growth of resprouters and *A. chilensis* trees growing in association and control.