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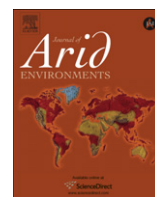
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Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Are *Fabiana imbricata* shrublands advancing over northwestern Patagonian grasslands? A population dynamics study involving fire and precipitation

M.I. de Torres Curth*, L. Ghermandi, C. Biscayart

Laboratorio Ecotono – Departamento de Matemática, INIBIOMA – Universidad Nacional del Comahue, Quintral 1250, 8400 San Carlos de Bariloche, Rio Negro, Argentina

ARTICLE INFO

Article history:

Received 18 December 2009
 Received in revised form
 25 November 2011
 Accepted 14 March 2012
 Available online xxx

Keywords:

Elasticities
 Patagonian steppe
 Shrub encroachment
 Stochastic models

ABSTRACT

Shrub encroachment is the advance of woody plants over grasslands. For some shrub species this process is favoured by fire and high precipitation. In northwestern Patagonia spring precipitation is related with the El Niño Southern Oscillation (ENSO). Over the past years, ENSO has shown an increase in both amplitude and frequency. Our study focuses on the population dynamics of the shrub *Fabiana imbricata* Ruiz & Pav. (Solanaceae) using stochastic models which involve different fire frequencies and variations in spring precipitation. Our results indicate that *F. imbricata*'s population grows at a wide range of fire frequencies, reaching its maximum every 6–10 years. The elasticity analysis show that, as fire frequency diminishes, population growth rate depends almost exclusively on adult survival, recruitment events are rare and the presence of seedlings or juveniles is seldom observed. In this case, the landscape would be formed by mature *F. imbricata* shrublands, and population persistence would depend on adult survival, seed production and their accumulation in the soil bank. However, in the case of very high fire frequencies, more recurrent recruitment pulses would be observed, with a landscape dominated by young shrublands composed of individuals of different ages and reproductive status.

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1. Introduction

Both fire and climate are key drivers of community composition, and can function independently, or synergistically. Fire represents a great environmental impact that causes strong changes in community structure, and plays a crucial role in ecosystem distribution, organization and evolution (Bond and van Wilgen, 1996). This disturbance, together with inter-annual climate variations, provokes changes in environmental characteristics. Due to human intervention, fire frequency can increase or diminish up to total suppression. On the other hand, climatic variations can be associated with the El Niño Southern Oscillation (ENSO) (Villalba and Veblen, 1998). During an El Niño episode rainfall can increase dramatically in certain regions of the world, up to four times more deposition than average, whereas in other regions severe droughts are registered. The following phase, known as La Niña, produces opposite climate patterns (Holmgren et al., 2001). In northwestern Patagonia, during El Niño, very rainy winters and springs are registered, while dry and warm summers are observed during La Niña (Daniels and Veblen, 2000; Veblen and Kitzberger, 2002). Abundant spring rainfall allows for great biomass accumulation,

which becomes available fuel for fires during dry and warm summers. In this region, in the last 100 years, the fire regime has been affected both by climatic variation and anthropogenic activity (Kitzberger et al., 2005; Veblen et al., 1999). These variations in the environment (natural or anthropogenic), form a set of possible scenarios in which plant communities can develop. Plants show variable responses to these variations which regulate their population dynamics. Many species are stimulated by fire, which increases their germination and seedling recruitment (Bond and van Wilgen, 1996; Franzese et al., 2009; Ghermandi et al., 2004, 2010; Pausas et al., 1999) to the point that, for some species, reproduction has a forced dependence on fire and they can be driven to extinction by fire suppression (Bond and van Wilgen, 1996).

In steppe environments attention has been drawn to shrub encroachment; over the last century it has increased in several parts of the world (Polley et al., 1996). Long-term climate changes associated with ENSO seem to promote the establishment of shrub seedlings and, consistently, their advance over grasslands (Drewa et al., 2001). Moreover, changes in fire frequency are one of the most often mentioned reasons for this phenomenon (Van Auken, 2000). Though some authors report a positive link between fire and shrub invasion (Ghermandi et al., 2010; Van Auken, 2000) others show opposite results (Guevara et al., 1999; Heisler et al.,

* Corresponding author. Tel.: +54 294 4428505.

E-mail address: mdetorrescurth@gmail.com (M.I. de Torres Curth).

2004; Roques et al., 2001). These contrasting results may be due to multiple factors such as species characteristics, fire frequency and intensity, as well as environmental conditions (Bond and van Wilgen, 1996). For example, in the southeast savannas of South Africa frequent fires prevent shrub encroachment and, when coupled with droughts, might reduce shrub density (Roques et al., 2001).

Several studies discuss the relationship between post-disturbance recruitment strategies and disturbance frequency. Heisler et al. (2004) found an increase in shrub abundance due to fire suppression in eastern USA mesic grasslands, and that the reestablishment of the fire regime might prevent the conversion of grasslands to shrublands. A general model suggests that plants that recruit post-fire only by seeds (non-resprouter shrubs and annual plants) would increase their populations at low and very high fire frequencies (Bellingham and Sparrow, 2000). Nevertheless, shrubs that recruit exclusively by seed can be abundant in the community if they reach reproductive maturity within two consecutive fires (Pausas, 2001). Though post-fire seedling density can be high (Ferrandis et al., 1999), in general, very few survive summer stress conditions (Seligman and Zalmen, 2000). For several shrub species that grow in grasslands, there is a critical fire frequency which allows their persistence (Stokes et al., 2004). If species in the community are capable of persisting only under a narrow range of fire frequencies, important changes in species composition should be expected in response to changes in fire frequency (Hoffman, 1999). In Argentina, in Monte Phytogeographic Province, it has been shown that fire contributes to the conversion of shrublands in communities with a more favourable balance for herbaceous species (Guevara et al., 1999).

Northwestern grasslands are economically important because they are used for cattle grazing. In this environment, spatial heterogeneity and fire regime create a vegetation mosaic formed by grasses and *Fabiana imbricata* Ruiz & Pav. (Solanaceae) shrublands (Ghermandi et al., 2004). Given that *F. imbricata* is unpalatable, environmental value as a production unit might diminish because of its advance. Several previous studies suggest that fire can promote shrub invasion in the Patagonian steppe (Franzese et al., 2009; Ghermandi et al., 2004, 2010; Gonzalez et al., 2010). In early post-fire succession, new encroachment foci of *F. imbricata* were observed (Ghermandi et al., 2004). Usually, in mature *F. imbricata* shrublands, seedling recruitment is extremely low. Nevertheless, in the spring following the extensive wildfire during January 1999 (which was an especially rainy month), a high germination rate was detected. These new shrub encroachment foci were monitored over nine years and no further recruitment was observed two years after the fire. This may support the hypothesis that *F. imbricata* needs fire cues to germinate (Gonzalez et al., 2010). Furthermore, these foci were found both in the proximity of unburned shrublands and away from them, the latter possibly favoured by the slope that led to seed dispersal by runoff. These findings suggest that *F. imbricata* successfully competes during early post-fire with resprouting tussock grasses, which constitute the grassland matrix (Ghermandi et al., 2010).

Global climate change models predict for northwestern Patagonia an increased frequency of very humid springs with abundant accumulation of biomass, followed by dry and warm summers. Together with possible variations in grassland management policies that might enhance or diminish the impact of fire on these environments, it is relevant to question in which way the different fire frequencies when combined with climatic variations would influence the advance or setback of this shrub population. The use of mathematical models offers the possibility of studying different hypothetical scenarios involving variations in climate and fire frequency, and then we may be able to suggest an answer.

In a previous study, (Ghermandi et al., 2010) *F. imbricata* population dynamics were studied by means of a megamatrix model that incorporated environmental variability and species response to several habitat conditions. The model assumes that the environment is divided in patches that change their condition over time and are affected in different ways by the aforementioned variations. As a result, their characteristics influence species' demography at the landscape scale. The dominant eigenvalue of the megamatrix is a measure of the species' performance in a patchy variable environment. For different scenarios, characterized by three fire frequencies and a fixed frequency of humid springs, results suggest that the *F. imbricata* population will grow no matter the circumstances (Ghermandi et al., 2010).

Matrix models are probably the most commonly used in structured population dynamics studies (Caswell, 2001). They have been widely used in threatened or invading species study, and in management plan design (Golubov et al., 1999; Menges et al., 2006; Satterthwaite et al., 2002). Moreover, they are relatively simple to construct and analyze. Matrix models are based on two kinds of discretization. On one hand, a population is subdivided into discrete categories, and on the other hand, its dynamics are described in terms of discrete-time, projecting the population condition from time t to a time $t + 1$. The latter has an advantage, due to the fact that field data necessarily comes from a discrete observation set and it can be fitted without having to solve the inverse problem of inferring unmeasured continuous-time parameters from discrete-time observations (Ellner and Rees, 2007). Population parameters can change by influencing several factors such as fire and precipitation (Pickett and White, 1985). Thus, the model can be formulated as $n(t + 1) = A(t) \bullet n(t)$, where $\{A(t), t = 1, 2, \dots\}$ is a stochastic sequence of non-negative matrices chosen from a finite set of projection matrices. These stochastic models have been largely used in demographic studies in temporally variable environments (see Fieberg and Ellner, 2001; or Nakaoka, 1996; for a review). Population projection using simulation provides a method to estimate the rate of population growth.

In the present work, we evaluate by means of stochastic matrix models the demographic dynamics of *F. imbricata*, and thenceforth the possible advance of these shrubs on the northwestern Patagonia steppe grasslands. Our analysis integrates the influence of fire and abundant spring rainfalls on demographic dynamics. To do so, we calculated the stochastic population growth rate λ_S (Caswell, 2001) for different fire frequencies going from one fire per year to total fire exclusion, incorporating the climatic variability associated with current El Niño frequency. In order to analyze which vital parameters have a major influence on the population growth rate we also carried out an elasticity analysis.

2. Materials and methods

2.1. Study area

The data used in the present study were collected at the San Ramon Ranch (41° 03' S; 71° 02' W) and Pichileufu Ranch (41° 10' S; 70° 41' W), 30 and 60 km east of San Carlos de Bariloche, respectively (Fig. 1). The climate is Mediterranean with an average annual rainfall of 580 mm (60% of which falls within May and August), and a moderate water deficit in summer (Anchorena and Cingolani, 2002). The vegetation is dominated by the tussock grasses *Pappostipa speciosa* (Trin & Rupr.) Romasch., *Festuca pallescens* (St.-Yves) Parodi and *Poa* spp., shrubs including *Acaena splendens* Hook. & Arn., *Mulinum spinosum* (Cav.) Pers. and *Senecio bracteolatus* Hook. & Arn. dispersed in the grassland, and *Discaria articulata* (Phil.) Miers and *F. imbricata* forming shrublands.

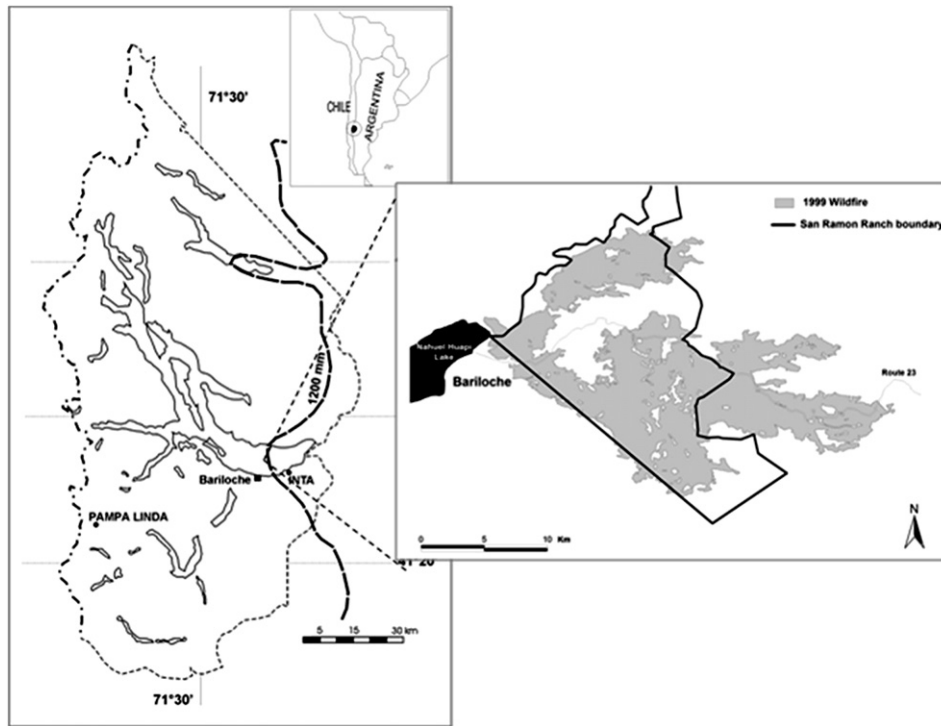


Fig. 1. Study area. The enlarged region shows the area of Estancia San Ramon. The grey area represents the area burned by fire in January 1999. Modified from Oddi et al. (2010).

2.2. *Fabiana imbricata*

F. imbricata is a non-resprouting long-lived woody shrub that reaches sexual maturity in approximately six years. The flowering period extends from September to January. Seed production was estimated at 200 000 seeds per adult (Ruete, 2006), forming persistent banks (Gonzalez and Ghermandi, 2008). Very long-lived individuals were found up to 140 years old (Oddi et al., 2010). This shrub has a broad distribution, extending from the south of Mendoza to Chubut in Argentina, and from Atacama up to Valdivia in Chile (Correa, 1999). In northwestern Patagonia, it inhabits the steppe, forming monospecific shrublands (Anchorena and Cingolani, 2002) and covering areas of variable extension (100 m² – few hectares).

2.3. Environmental dynamics

Environmental dynamics were modelled as a linear Markov process, described by an environmental state transition matrix, *C*. Each entry *c_{ij}* in *C* is the conditional probability for the environment to have the characteristics of the *j*-th state in time *t* + 1, given the characteristics of the state *i* in time *t*. The parameters used to calculate the entries in *C* are the probabilities of having fire in summer, and a wet spring following it. The four environmental states in each time period (one year) are: 1) fire and wet spring (Burned Wet, BW); 2) fire and normal spring (Burned Normal, BN); 3) no fire and wet spring (Unburned Wet, UW); 4) no fire and normal spring (Unburned Normal, UN).

We considered 23 different environmental scenarios, varying the fire frequencies from one fire per year up to total exclusion of fire (Annual, 3 times every 4 years, 2 times every 3 years, 1 time every 2, 3, 4, 5, 6, 7, 8, 9, 10, 20, 30, 40, 50, 75, 80, 90, 100, 130 and 150 years, and Fire Exclusion). Fire frequencies were combined with wet spring probability occurrence according to El Niño Southern Oscillation records for the last 20 years (National Weather Service, 2008).

2.4. Population dynamics within each environmental state

Population dynamics of *F. imbricata* were analyzed using a Lefkovich stage-classified matrix model (Caswell, 2001), and a combination of age and reproductive status criteria. Adults were separated into three classes according to their vulnerability to environmental conditions: First year seedlings (*S1*), Second year seedlings (*S2*), Juveniles (*J*) (3–5 years), and Adults (*A*) (reproductive 6–100 year old plants). We did not consider a “Seed class” in the model because seeds do not represent a limiting condition for recruitment. We also assumed that no plants survive on average more than 100 years. The life cycle diagram shows the possible transitions among classes from one year to the next (Fig. 2).

For each environmental-specific state, population dynamics were described by a 4 × 4 time invariant projection matrix *L* where each entry, *l_{ij}*, represents the contribution of individuals in the *j*-th class at time *t* to the *i*-th class at time *t* + 1. For each set of environmental conditions, fertility rate (*κ*), growth (*α*) and stasis

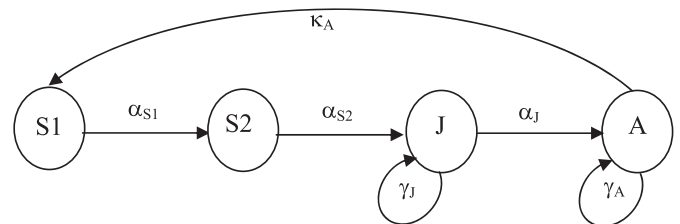


Fig. 2. Conceptual life cycle model for *F. imbricata*. Each circle represents a specific class, *P1*: seedlings of the present year, *P2*: seedlings of the second year, *J*: juveniles, *A*: Adults. Arrows represent the contributions from one class to the next from *t* to *t* + 1. *α_i*: transition probability from one class to the next, *γ_i*: stasis within the class and *κ_A*: reproduction (seedlings quantity produced per adult in time *t* which survive from *t* to *t* + 1) (from Ghermandi et al., 2010).

(γ) probabilities (Fig. 2) for each individual in every single category were calculated from field monitoring and greenhouse experiments (Ruete, 2006), and incorporated into the relevant matrix entries. Annual seedling emergence was estimated by the percentage of germination under greenhouse conditions using two different watering levels: high (wet spring) and low (normal spring) (Ruete, 2006). From these data we calculated the number of new seedlings per adult. Given that in environments with no fire, first year seedlings are seldom observed, we established very low fertility values only to guarantee projection matrix primitivity. For normal springs, annual transition probabilities from S1 to S2 and from S2 to J were calculated by post-fire monitoring (Ghermandi et al., 2010). In the case of wet springs these transitions were obtained from Ruete (2006). Without fire, survival probability of juveniles and adults equalled unity. If this matrix entry is given a value of one, it would effectively imply that shrubs are immortal, which is certainly not the case. Thus, we assumed (following Jiménez-Lobato and Valverde, 2006) that in unburned environments survival probability was 0.99 for juveniles, and 0.98 for adults. This assumption appears to be reasonable for a steppe shrub such as *F. imbricata*. The 1999 wildfire that affected the study area burned 70% of the San Ramon ranch. Then, we assumed that fire affects all individuals equally, killing 70% of the population. We considered that, although this assumption is arbitrary, it would not affect our results because we would use this model for comparative purposes. Starting on this information we generated four population projection matrices, one for each possible environmental state (Table 1). We used a December–December census interval (Fig. 3).

2.5. Population growth under environmental variability

We calculated the stochastic growth rate λ_S that represents a measure of population growth under environmental variability (Kaye et al., 2001; Tuljapurkar, 1990). The model assumes that environment changes from one year to the next, and that the particular characteristics of the environment affect the population. Rate λ_S is defined as:

$$\ln \lambda_S = \lim_{t \rightarrow \infty} (1/t) \cdot \ln [P(t)/P(0)] \tag{1}$$

where $P(t)$ is the total population at time t , and $P(0)$ is the initial population. Given that the analytic calculation of λ_S (Eq. (1)) is not possible, it can be obtained by numerical simulation (Tuljapurkar et al., 2003). For each environmental scenario (with a different fire frequency) we generated a sequence of T environmental states using the corresponding state transition matrix C (e.g. UN-UN-BN-UN-UN-UN-UW-UN-BW-...). For each sequence, the longitude T was set between 5000 and 40 000 for convergence guaranty. Once the sequence was set, we assigned to each environmental state the corresponding projection matrix. Through this sequence of matrices we projected an arbitrary initial population.

The stochastic growth rate was estimated as:

$$\hat{\ln \lambda_S} = (1/T) \cdot [\ln (P(T)) - \ln P(0)] \tag{2}$$

If $\hat{\ln \lambda_S} > 0$ the population has a growing asymptotic dynamic, when $\hat{\ln \lambda_S} < 0$, it will be diminishing; and if $\hat{\ln \lambda_S} = 0$ no variations in population numbers would be expected (or, λ_S major, minor or equal to 1). We also calculated 95% confidence intervals for the estimator as follows:

$$\hat{\ln \lambda_S} \pm 1.96 \cdot \sqrt{[V(r(t))/T]} \tag{3}$$

where $V(r(t))$ is the variance of $r(t) = \ln P(t + 1) - \ln P(t)$, for $t = 1 \dots T$ (Caswell, 2001). Numerical simulations were performed with MATLAB (2001)

Given that simulation introduces stochasticity into the environmental state sequence sorting, for each environmental scenario we replicated the procedure 100 times, calculating the mean of the λ_S estimations and a 95% confidence interval. We tested mean differences by means of a Kruskal–Wallis test with a 5% significance level.

For each environmental scenario we performed an elasticity analysis. Elasticities represent the proportional changes in finite rates resulting from proportional changes in matrix elements and permit evaluations of the relative contributions of different matrix entries to population growth rate. Due to elasticities summing to one, they can be added in subsets according to environmental states, classes, environmental state transitions or class transitions, to provide a proportional measure of the importance of each class for population growth (Tuljapurkar and Caswell, 1997). We use elasticity analysis to evaluate which demographic processes are most relevant to growth rate changes. Definition and calculation procedures can be found in Caswell (2001).

3. Results

Table 2 shows the estimated values of $\ln \lambda_S$ and the 95% confidence intervals for the 100 replicates of the estimation for each environmental state. The last two columns show the 95% confidence intervals for the mean estimator (Eq. (2)). It must be noted that these last confidence intervals were not calculated based on simulation replicates, but on the variance of annual variation rates along the environmental states sequence within each simulation. For fire frequencies between Annual up to once every 2 years $\ln \lambda_S < 0$, as well as for frequencies lower than once every 150 years and fire Exclusion. For fire frequencies from once every 3 years up to once every 130 years, the estimation of $\ln \lambda_S$ predicts a growing population with a population growth rate that increases up to a frequency of once every 7 years, gradually diminishing afterwards. In all cases, except once every 150 years, the estimation of $\ln \lambda_S$ is significantly different from 0. The confidence intervals for the estimator (Eq. (3)) showed higher variability. In the cases where 0 was not included in the confidence interval, the population keeps an increasing or diminishing trend, according to whether $\ln \lambda_S$ is

Table 1

Projection matrices for each environmental state. Parameters in italics were not calculated directly from empirical data. P1: current year seedlings, P2: last year seedlings, J: juveniles, A: Adults; BW: fire and wet spring; BN: fire and normal spring; UW: no fire and wet spring; UN: no fire and normal spring.

Environmental state Classes	BH				UH				BN				UN			
	P1	P2	J	A	P1	P2	J	A	P1	P2	J	A	P1	P2	J	A
P1	0	0	0	408	0	0	0	0.01	0	0	0	50	0	0	0	0.001
P2	0.37	0	0	0	0.94	0	0	0	0.002	0	0	0	0.005	0	0	0
J	0	0.32	0.26	0	0	0.8	0.66	0	0	0.04	0.26	0	0	0.11	0.66	0
A	0	0	0.13	0.39	0	0	0.33	0.98	0	0	0.13	0.39	0	0	0.33	0.98

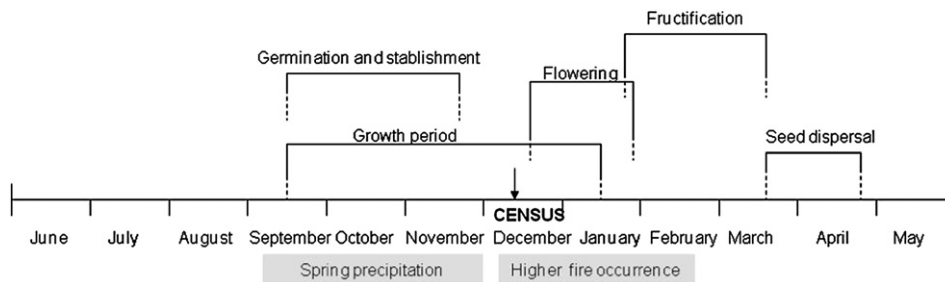


Fig. 3. Environmental dynamics scheme, census location and phenology for *F. imbricata* during the year (Ruete, 2006).

higher or lower than 0, respectively. In the remaining cases (once every 3 years and every 80, 90, 100, 130 and 150 years) the confidence interval of the estimator includes 0.

The estimators of $\ln \lambda_S$ for all fire frequencies showed significant differences as shown in Table 3 (K–W, $p < 0.05$). The population growth rate reaches its maximum when there is a fire frequency of once every 7 years (Fig. 4). Since non-significant differences were found among frequencies once every 6 years to once every 10 years, we could say that with a fire once every 6–10 years the population stochastic growth rate will reach a maximum between 6.1% and 6.6% per year. In scenarios in which the population diminishes, the decrease goes from 2.5% per year, for once every 4 years in fire frequency, up to 21.6% for annual fire frequency, reaching a 4.2% decrease with fire exclusion.

For each fire frequency the elasticity analysis showed that the contribution to λ_S of the growth process is the same for all classes (i.e., the transitions of S_1 to S_2 , S_2 to J and J to A), as well as the recruitment of new individuals. The elasticities of these processes diminish as fire frequency diminishes, whereas the elasticities of stasis processes increase (Fig. 5a). In particular, the elasticity increase of stasis processes (taken together) is due to Adult class

elasticity, given that Juvenile stasis elasticities show the same pattern as recruitment process elasticities (Fig. 5b). For fire exclusion, elasticities were closely similar to those obtained from Annual fire frequency (Fig. 5). All demographic parameter elasticities diminish with fire frequency, except that Adult stasis grows. This pattern is valid except for fire exclusion (Fig. 5).

4. Discussion

Woody encroachment in arid and semiarid environments is a frequently irreversible non-linear phenomenon accentuated by climatic events such as drought or above-normal rainfall, and by topographic and edaphic factors (Archer, 1996). Explanations for this increase in woody plant abundance are centred on changes in climate and fire regimes (Archer, 1996). The model developed in the present study focuses on the demographic consequences of fire frequency and spring rainfall variations on the native shrub *F. imbricata* in the northwestern Patagonian steppe. It allowed us to analyze hypothetical scenarios that contemplate a gradual decrease of fire frequency, from one fire per year up to total fire exclusion. The central assumption of the model, based on experimental studies (Ghermandi et al., 2004, 2010; Gonzalez and Ghermandi, 2008; Ruete, 2006;), is that the combination of fire in summer with abundant rainfall the following spring, is the most favourable environmental condition for recruitment of this species. Juvenile and adult mortality due to other reasons than fire is very low for this species, which is very long-lived. Under these assumptions, our model predicts that the *F. imbricata* population will increase under a wide range of fire frequencies, from one fire every 4 years up to one every 100 years, reaching a maximum population growth rate at one fire every 6–10 years. This result is consistent with other studies on the influence of fire on the grassland encroachment process in semiarid steppes and savannas (Pausas, 2001; Stokes et al., 2004).

Ghermandi et al. (2010) developed a megamatrix model to evaluate the advance of *F. imbricata* shrublands over grasslands. They analyzed three fire frequencies, combined with an El Niño frequency, assuming that all environmental states are present at the same time as a patchy environment. Under all these assumptions, their model results suggest that *F. imbricata* is in expansion. Certainly, one can find, at the same time, burned and unburned patches, although springs are wet or dry in all patches simultaneously. Nevertheless, results are accurate if considered at the landscape scale. Tuljapurkar et al. (2003) suggest that the population growth rate given by the megamatrix model is also the growth rate of the expected population in one patch, but it is always greater than the stochastic growth rate λ_S that estimates the population growth in a single patch with environmental conditions changing from one year to the next. In this sense, our work improves the long-term population growth estimate for this species, and exhaustively explores fire frequencies ranging from one fire per year to total fire exclusion, allowing us to determine

Table 2

Estimated values of $\ln \lambda_S$ and confidence intervals for the 100 replicates of the estimation for each environmental state. *Indicates significantly different from 0 ($p < 0.05$). The last two columns show the confidence intervals for the mean estimator for each fire frequency (Eq. (2)). Italics show the highest fire frequencies, without significant differences (K–W, $p < 0.05$). Bold values show non-significant differences among higher $\ln \lambda_S$ means (K–W, $p > 0.05$).

Fire interval return (years)	$\ln \lambda_S$	Confidence intervals			
		For the mean of all simulations		For the estimator	
Annual	-0.2436*	-0.24535	-0.24188	-0.3705	-0.1167
1.3	-0.1305*	-0.13180	-0.12924	-0.2042	-0.0568
1.5	-0.0888*	-0.09034	-0.08741	-0.1666	-0.0111
2	-0.0250*	-0.02611	-0.02398	-0.0828	0.0327
3	0.02881*	0.02814	0.02949	-0.0117	0.0694
4	0.05046*	0.04971	0.05121	0.0344	0.0664
5	0.05280*	0.05177	0.05383	0.0081	0.0975
6	0.06157*	0.06081	0.06233	0.0101	0.1130
7	0.06393*	0.06331	0.06455	0.0143	0.1134
8	0.06377*	0.06308	0.06446	0.0159	0.1115
9	0.06156*	0.06005	0.06307	0.0164	0.1066
10	0.05909*	0.05828	0.05990	0.0156	0.1025
20	0.04244*	0.04172	0.04315	0.0109	0.0739
30	0.03052*	0.03007	0.03098	0.0095	0.0515
40	0.02239*	0.02194	0.02284	0.0041	0.0406
50	0.01771*	0.01725	0.01816	0.0007	0.0346
75	0.00921*	0.00889	0.00954	-0.004	0.0229
80	0.00579*	0.00557	0.00602	-0.003	0.0146
90	0.00440*	0.00420	0.00461	-0.004	0.0128
100	0.00355*	0.00338	0.00371	-0.005	0.0117
130	0.00154*	0.00137	0.00172	-0.006	0.009
150	-0.0001	-0.00024	0.00003	-0.006	0.0061
Exclusion	-0.04298*	-0.04365	-0.04231	-0.051	-0.0341

Table 3

Differences in averages of the estimators $\ln \lambda_5$ for 100 simulations (Kruskal–Wallis Test) ($p < 0.05$). Coloured cells show the frequencies for which no significant differences were found.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
1- Annual																								
2- 3 each 4																								
3- 2 each 3																								
4- 1 each 2																								
5- 1 each 3																								
6- 1 each 4																								
7- 1 each 5																								
8- 1 each 6																								
9- 1 each 7																								
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15- 1 each 40																								
16- 1 each 50																								
17- 1 each 75																								
18- 1 each 80																								
19- 1 each 90																								
20- 1 each 100																								
21- 1 each 130																								
22- 1 each 150																								
23- Exclusion																								

a fire frequency interval for which the population growth rate under fire and climate influence is a maximum.

A change in fire regime provoked by human activities (Papanastasis, 1992) could break the natural balance between herbs and woody plants (Guevara et al., 1999) promoting increased shrub cover, even at high fire frequencies (Heisler et al., 2004). In our study, for several of the analyzed fire frequencies, results indicate that even if the trend of population variation is towards growth, long simulation population decrease periods are registered between growth periods. At low fire frequencies, decreasing periods would be related to the absence of fire, and those of growing periods might be related to (rare) fire events connected to humid springs and, therefore, with recruitment periods. Our model suggests that when fire frequency is very low, recruitment events are rare and consistently so are seedlings. In these scenarios, the landscape would be composed of mature *F. imbricata*, and the persistence of the population would depend on their survival, and seed production and accumulation in the soil bank. At high fire frequencies, decreasing periods are possibly related to the destructive effect of fire, because even if it stimulates recruitment, it also eliminates a large proportion of the

population. That is, in this case the variability in the annual population growth rates would be related to high mortality rates as well as to the recruitment rates of new individuals, because of the most frequent recruitment pulses. At high fire frequencies the landscape would be dominated by younger shrublands composed of individuals having different ages and reproductive conditions.

Our model also analyzes the case of fire exclusion predicting a slow decline in shrubs, in which *F. imbricata* individuals would age up to dying. This might turn out to be a benefit from the viewpoint of shrub expansion control in areas dominated by grasslands, but would counter with dominant grass dry biomass accumulation plus an increase in fuel continuity that might lead to a large scale fire with severe consequences.

The ENSO forecast predicts for this region an increase in El Niño event frequency. This phenomenon produces particularly wet springs in northwestern Patagonia; while the following phase, La Niña, presents dry and warm summers with an increase in lightning storms (Veblen and Kitzberger, 2002). Within this frame, the coincidence of summer fire and a later abundant rainfall in spring would be more probable, which constitute the set of ideal environmental conditions for the population growth of *F. imbricata*. These environmental characteristics form a set of complex scenarios that produce different responses in the vegetation, in its richness and diversity as well as in its spatial and temporal distribution; also producing changes in the type of relations that are established among the various functional groups, thus determining community dynamics. An interesting addition to the model proposed here could be the incorporation of the dynamics of other dominant species of the steppe community and the integration of the spatial component of their distribution.

Among the possible effects of recurrent fires in grasslands, those related to diversity are important. Shrubs can be considered landscape modulators through the resource distribution changes that influence the abundance of species and organisms and, hence, biodiversity (Shachack et al., 2008). On the other hand, unpalatable shrubs could protect palatable species through the nurse effect, thus contributing to the maintenance of biodiversity (Oesterheld and Oyarzabal, 2004). Nevertheless, shrub advance could replace the grasslands completely (Sala et al., 2000; Van Auken, 2000), having in this case a negative effect related to diversity and productivity. This

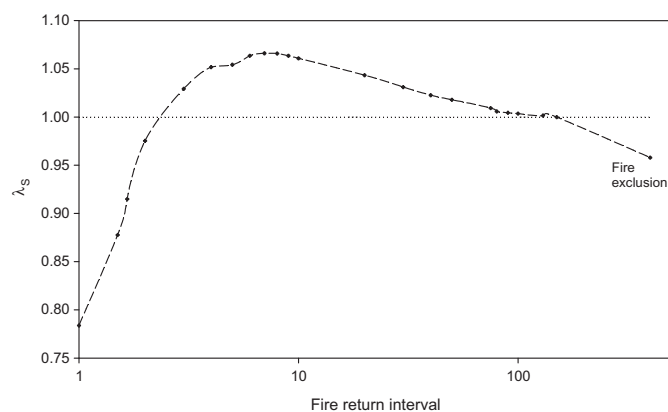


Fig. 4. λ_5 according to the return of fire interval, from one annual fire to total exclusion. Fire frequency is shown in a logarithmic scale to facilitate graphic interpretation. Horizontal line stands for the equilibrium $\lambda_5 = 1$. The last point to the right stands for Fire Exclusion.

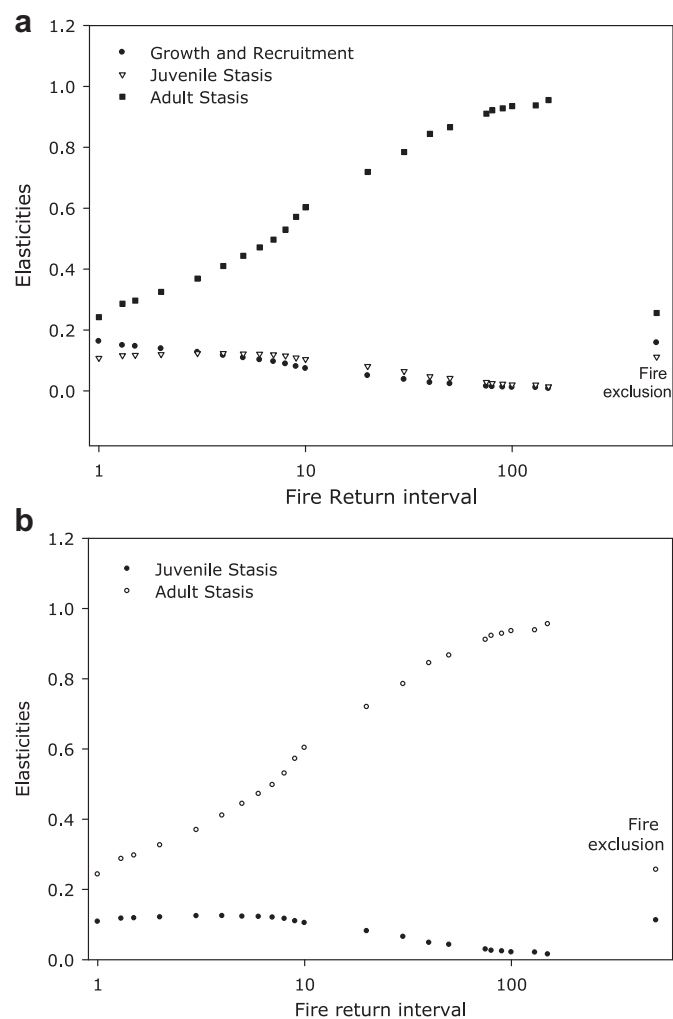


Fig. 5. a) Elasticities for demographic processes: Growth (transitions P_1 to P_2 , P_2 to J and J to A), recruitment and stasis of new individuals. The return interval axis is presented on a logarithmic scale to facilitate graphic interpretation. b) Process elasticities for stasis, Juveniles and Adults. The elasticity for Fire Exclusion is shown on the right.

happens because shrub advance usually induces drastic changes in a landscape stemming from the increase of unpalatable woody species at the expense of palatable grass species, thus reducing the carrying capacity of rangelands (Cabral et al., 2003). However, biodiversity changes are relative to the analysis of spatial scale. We are currently conducting studies to evaluate grassland and *F. imbricata* shrubland richness in northwestern Patagonia (unpublished data). This information will be useful to assess if *F. imbricata* shrubland advance diminishes biodiversity on the northwest Patagonian grasslands.

F. imbricata competes successfully with dominant tussock grasses after fire because of its fast growth. This characteristic involves support costs with which the species partially compensates by using a low and efficient investment in leaf area (very small perennial leaves with structures that avoid water loss via transpiration). This is an evolutionarily stable strategy that influences competitive asymmetry via shading between shrubs and grasses (*sensu* Falster and Westoby, 2003). Consequently, the *F. imbricata* post-fire encroachment in northwestern Patagonia grasslands is the result of a balance between the different mechanisms that this species and the dominant species possess.

Our model describes the high potentiality of *F. imbricata* shrublands to advance in northwestern Patagonian grasslands.

However, a better approximation to the real dynamic between environmental variability and the advance or retraction of shrubland areas would be known more accurately after a detailed comparison of the space occupied by *F. imbricata* patches in the past and present utilizing aerial photos and satellite images covering an extensive time window.

Acknowledgements

We acknowledge constructive comments on an earlier version of anonymous referees and Editor. We also thank to one of the anonymous referees the English corrections and comments on the manuscript. This research was supported by Agencia Nacional de Promoción Científica y Tecnológica (project PICTO 36894), CONICET, and Universidad Nacional del Comahue.

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