Non-linear ecological processes, fires, environmental heterogeneity and shrub invasion in northwestern Patagonia

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ABSTRACT

The emergent behaviors of nature are not only the sum of interactions among ecosystem parts but also depend on the organization of these interactions. Fire, climate and vegetation patterns produce non-linear fire propagation across the landscape. Environmental heterogeneity, like outcrop presence and hare density, increases landscape patchiness and makes possible the occupation of fire refuges by plants, like *Fabiana imbricata* shrubs. We monitored shrub recruitment and cover during nine postfire years in northwestern Patagonia grasslands and we studied the long-term population dynamics under different environmental conditions through a matrix model, exploring different fire frequencies and spring precipitation regimes. Both, the field monitoring and the model seem to confirm the relationships between shrub invasion and fire. The climate change forecast predicts an increase in the frequency of El Niño Southern Oscillation phenomena that could causes more coupled fires—rainy springs in northwestern Patagonia, and consequently, more recruitment windows for shrubs, like *F. imbricata*. The matrix model also indicates that this scenario would be the most favourable for shrub invasion. Our results contribute to the knowledge of the ecosystem properties and processes, providing useful information to improve the grasslands sustainable use.

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1. Introduction

An increasing number of climate impact studies provide evidence that climate change is affecting the species distribution, and the composition and structure of communities and ecosystems (Walther et al., 2005). Assessing impacts of climatic variability is complicated by the difficulties related to translating models across spatial and temporal scales because of the self-organized structure of ecosystems (Peterson, 2000). Particularly, it is difficult to downscale global models to local sites. For example, the consequences of El Niño Southern Oscillation are very different depending on the region of the word where they happen.

Local non-linearity combined with spatial heterogeneity makes difficult to predict local processes (Peterson, 2000). For instance, fire, climate and vegetation patterns produce non-linear fire propagation across the landscape. Environmental heterogeneity (e.g. outcrops) favours landscape patchiness that generates different fire frequencies and make possible the occupation of fire refuges by shrubs.

For the last three decades scientists have studied the relationships between fire occurrence and shrub abundance in fire-prone Mediterranean communities (Keeley and Zedler, 1978; Lloret et al., 1999; Bond and Midgley, 2003; Franzese et al., 2009). Bellingham and Sparrow (2000) suggest that the seeders (plants that recruit postfire only by seeds) would increase with low and very high fire frequency although seeder shrubs can only persist in the community if they reach the sexual maturity before plants are killed by fire (Bond and Midgley, 2003).

After fire, seedling density of seeder shrubs may be high (Iglesia et al., 1998; Ferrandis et al., 1999) but very few seedlings survive to dry and hot postfire summers (Seligman and Zalmer, 2000). Long-term climate changes, like precipitation increase related to El Niño Southern Oscillation (ENSO), favour shrub seedling establishment and then, their invasion (Drewa et al., 2001). Besides climate conditions, rabbit and hare browsing is another factor that has a significant effect on shrub seedling survival and morphology (Cohn and Bradstock, 2000; Drewa et al., 2001).

In northwestern Patagonia landscape, environmental heterogeneity and fire regime create a vegetation mosaic of grasslands and *Fabiana imbricata* shrublands (Ghermandi et al., 2004). These environments are economically important because they are used for stockbreeding and forestry. Due to the fact *F. imbricata* is an unpalatable shrub, their invasion could decrease grassland productivity.

In the frame of global climate change, the study of shrubland dynamics could be useful to evaluate the impact of shrubland invasion in grasslands. For this purpose the use of matrix models constitute a valuable tool that allows simulating different scenarios,

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assessing population trends, and evaluating management options (Burgman and Lamont, 1992).

In the classical discrete-time theory, population is described at each time t by a projection matrix; and the long run population dynamics is absolutely determined by this matrix if the environmental conditions remain constant. However, populations experience temporal variation in their demography because of both intrinsic species dynamics and environmental changes. Particularly, strong changes in demography can occur due to large-scale disturbances like fire (Pickett and White, 1985). Moreover, the knowledge about the interactions between fire and weather conditions is crucial for the understanding of population dynamics (Li et al., 1999).

The effects of fire regime on population dynamics have been studied through various modeling approaches (e.g. Silva et al., 1991; Canales et al., 1994; Kaye et al., 2001; Menges and Quintana-Ascencio, 2004; Stokes et al., 2004).

The theory of stochastic demography has been largely developed in the last three decades, and it has made possible to examine the effects of stochastic variation in environments on the population dynamics (Tuljapurkar, 1990; Tuljapurkar and Caswell, 1997; Caswell, 2001; Tuljapurkar et al., 2003). Environmental stochasticity can be incorporated in the model in several ways. Silva et al. (1991) studied the population responses to fire of *Andropogon semiberbis* by a matrix model. They examined the effect of fire in two opposite situations: annual fire frequency and fire exclusion. Their results reveal that the burnt population increases rapidly, whereas the unburned population is unable to persist. They conclude that there is a critical fire frequency below which this species was unable to maintain itself. Pascarella and Horvitz (1998) constructed a model (the megamatrix) to study the population dynamics of a tropical shrub affected by hurricanes. The megamatrix is a large matrix that uses two nested projection matrix models and includes two dynamics processes: the stochastic dynamics of the environment and the dynamics of the plant within each environmental state. We are not aware of other studies in which the effect of environmental variation on population dynamics has been assessed using megamatrix analysis.

For 9 years we monitored new potentially invasive foci of *F. imbricata* shrub in northwestern Patagonia grasslands, and we studied the landscape distribution of this species in relation to the spatial heterogeneity represented by outcrops presence and hare abundance. Also, we modeled the influence of different fire frequencies and abundant spring precipitations on the long-term demography of this shrub, using a megamatrix approach.

The aim of this work was to evaluate the influence of fire, climate and spatial heterogeneity on the potential invasion of *F. imbricata* shrubs.

2. Methods

2.1. Study site

The study was carried out in San Ramón ranch (41°03′S – 71°01′W) and Pichileufu ranch (41°10′S – 70°41′W) in NW Patagonia, Argentina. Precipitation regime is Mediterranean (60% falls in autumn and winter). In San Ramón ranch the mean annual temperature is 9 °C and the mean annual rainfall is 582 mm, whereas in Pichileufu ranch the mean annual temperature is 8 °C and the mean annual rainfall is 308 mm (Bustos and Rocchi, 1993). The study area is dominated by *Stipa speciosa* and *Festuca pallescens* grasslands with *F. imbricata* shrublands (Ghermandi et al., 2004).

These grasslands are fire-prone and in January 1999 a severe and very extensive wildfire affected the study area. In burned grassland we detected three incipient foci of *F. imbricata* invasion: (1) Near to unburned shrubland in San Ramón site (Near SR), (2) Far (250 m) from the same unburned shrubland (Far SR), and (3) Far (200 m) from unburned shrubland in Pichileufu site (Far P).

2.2. Study species

F. imbricata is a long-lived shrub (more of 100 years), of 1.5–3 m height that reaches the sexual maturity approximately at 6 years. Their seeds are very small (0.1-mg) and form persistent seed bank (Gonzalez and Ghermandi, 2008), two typical characteristics of a potential postfire invader.

Shrublands are distributed along the forest – steppe ecotone (Dimitri, 1972) covering variable extensions (100 m² to several hectares) and frequently are located in the middle slope (Anchorena and Cingolani, 2002). *F. imbricata* shrubs do not resprout, and it recruits in spring almost exclusively after fire.

2.3. Experimental design

2.3.1. Postfire shrub establishment

In November 1999 (first postfire spring), we recorded the seedling recruitment and survival in eight plots (0.25 m² each one) on the burned edge of unburned shrubland in Near SR. The following year (2000) we added one plot ($n = 9$). From November 1999 to January 2005 we yearly counted the seedlings and, in the following 3 years (2006–2008), we estimated the plant cover because the lateral growth made it impossible to distinguish the individuals. Monitoring lasted 9 years (1999–2008) and we calculated seedling survival.

In January 2002 we detected a second invasion focus (Far SR) in another sector of burned grassland, located 250 m down hill from the Near SR. There, we monitored the seedling size (height and two radii) and survival in eight circular plots (3.14 m² each one) for 7 years (2002–2008).

We detected a third invasion focus in other burned grassland, situated in Pichileufu ranch, far from unburned shrubland (Far P). The same fire that in January 1999 affected the San Ramón ranch also burned the Pichileufu site. In the Far P site we estimated plant density and height in March 2006.

2.4. Data analysis

We tested data for normality; data were then log-transformed as needed, prior to analysis. If no transformation yielded normal data, we used non-parametric tests. Plant density and cover were analyzed by one-way repeated-measures ANOVA and post hoc Tukey test. We used non-parametric Mann–Whitney test to compare plant height.

2.5. The model

We choose a matrix model because several reasons. On one hand, matrix models are easy to construct, and relatively easy to analyze, parameters are easy to estimate and, under certain conditions, results are strong. On the other hand, they allow including the differences that individuals have along their development process and the environmental variability.

The general formulation for a matrix projection model invariant in time takes the form:

$$n(t + 1) = \mathbf{A}.n(t) \tag{1}$$

where $\mathbf{A}$ is the population projection model (Caswell, 2001) incorporating data as survival, birth and growth rates for each population stage, and $n(t)$ is a vector with the abundance of individuals in each life cycle stage at time t. In environments characterized by vari-

Table 1

Environmental transition matrices for each fire frequency. Each entry $c_{\alpha\beta}$ in C is the conditional probability for the environment to get the characteristics of the β-state in time $t+1$, given the characteristics of the state α in time t. BW: fire and wet spring, BN: fire and normal spring, UW: no fire and wet spring, and UN: no fire and normal spring.

Fire frequency	Low				Current				High			
	BW	UW	BN	UN	BW	UW	BN	UN	BW	UW	BN	UN
BW	2.6×10^{-5}	2.6×10^{-3}	1.14×10^{-4}	1.14×10^{-2}	4×10^{-3}	1.3×10^{-2}	1.7×10^{-3}	5.7×10^{-3}	3.9×10^{-3}	4.16×10^{-2}	1.71×10^{-2}	0.1824
UW	0.1299	0.1274	0.5699	0.5586	0.1296	0.117	0.5682	0.513	0.1261	0.0884	0.5529	0.3876
BN	1.74×10^{-4}	1.74×10^{-2}	8.6×10^{-5}	8.6×10^{-3}	2.61×10^{-3}	8.7×10^{-2}	1.3×10^{-3}	4.3×10^{-2}	0.0261	0.2784	0.0129	0.1276
UN	0.8698	0.8526	0.4299	0.4214	0.8674	0.783	0.4288	0.387	0.8439	0.5916	0.4171	0.2924

ations that modify demographic parameters, **A** can change over time.

We construct a model to describe environmental dynamics, and another model to describe population dynamics within each environmental-specific state, and then we join these models into a megamatrix (Pascarella and Horvitz, 1998).

2.5.1. The environmental dynamics

The environmental dynamics was modeled as a linear Markov process, described by an environmental state transition matrix, say C. Each entry $c_{\alpha\beta}$ in C is the conditional probability for the environment to get the characteristics of the β-state in time $t+1$, given the characteristics of the state α in time t. The parameters used to calculate the entries of C, are the probabilities of fire and wet spring occurrence.

The four environment states in each time period (1 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 three fire frequency which represent different environmental scenarios. The first, modeled the *current fire frequency*. The entries of its matrix were calculated from NW Patagonia data on historical fires (Ghermandi, unpublished) and El Niño Southern Oscillation records for the last 20 years (National Weather Service, Climate Prediction Centre, 2008). We chose other two scenarios by setting two different fire frequencies: *high fire frequency* (once each 6 years, allowing plant reproduction), and *low fire frequency* (once each 100 years, at least once in the plant life), and maintaining the same wet spring occurrence probability. Thus, we obtained three *environmental state transition matrices*, one for each environmental scenario (Table 1).

To determine the predicted distribution of environmental states at landscape level we found the column eigenvector f* associated with the dominant eigenvalue of environmental state transition matrices.

2.5.2. Population dynamics within each environmental state

Population dynamics of *F. imbricata* was analyzed by using a Lefkovitch stage-classified matrix model (Caswell, 2001) (Eq. (1)), using a combination of age and reproductive status criteria. Adults were the reproductive plants. The pre-reproductive individuals were separated in three classes, according to their vulnerability to environmental conditions. In semiarid regions, first year seedlings have high mortality rates (Tiver and Andrew, 1997), while second year seedlings and juveniles, have higher survival probability (but differential) to summer stress (Jiménez-Lobato and Valverde, 2006).

The four classes where: *first year seedlings* (S_1), *second year seedlings* (S_2), *juveniles* (J) (3–5 years) and *adults* (A) (reproductive 6–100 years old plants). We did not consider a "seed class" in the model because seeds do not represent a limiting condition for recruitment (seed production was estimated in 200 000 seeds per adult, Ruete, 2006). By counting growth rings, we determined *F. imbricata* longevity in 100 years approximately (Ghermandi, unpublished). We assume that no plants survive after 100 years.

For each environmental-specific state, population dynamics was described by a 4×4 time invariant projection matrix L, where each entry, say l_{ij}, represents the contribution of individuals in the jth class at time t to the ith class at time $t+1$. The life cycle diagram (Fig. 1) shows the possible transitions among classes from a year to the next.

2.5.3. Parameter estimation

For each set of environmental conditions, fecundity (κ_A), stasis (γ_i) and growth (α_i) probabilities for individuals in each category were calculated from field monitoring and greenhouse experi-

Table 2
Population projection matrices by environmental state. Parameter values in italics were not derived directly from empirical data. S_1: first year seedlings, S_2: second year seedlings, J: juveniles, A: adults; BW: fire and wet spring, BN: fire and normal spring, UW: no fire and wet spring, and UN: no fire and normal spring.

Environmental state	BW				UW				BN				UN			
Classes	S_1	S_2	J	A	S_1	S_2	J	A	S_1	S_2	J	A	S_1	S_2	J	A
S_1	0	0	0	408	0	0	0	*0.01*	0	0	0	50	0	0	0	*0.001*
S_2	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

ments (Ruete, 2006) and were incorporated in the relevant matrix entries.

Annual seedling emergence was estimated by the percentage of germination in greenhouse conditions under two different watering levels: high (wet spring) and low (normal spring, Ruete, 2006). From this data we calculated the number of new seedlings per adult. Due to the fact that in environments without fire, first year seedlings are seldom observed we established very low fecundity values only to guarantee primitivity of the projection matrices.

Annual transition probabilities from S_1 to S_2 and from S_2 to J were calculated from postfire monitoring (see Section 3.1). For wet springs these transitions were obtained from Ruete (2006). We used December–December census interval.

The observed survival probability of juveniles and adults equaled 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 to Jiménez-Lobato and Valverde, 2006) that, in unburned environments the survival probability of juveniles was 0.99, and the survival probability of adults was 0.98. This assumption appears reasonable for a steppe shrub such as *F. imbricata*.

The later wildfire that affected the study area burned 70% of the San Ramon ranch. Then, we assumed that the fire affects all individuals with the same probability, killing the 70% of the whole population. We consider that although this assumption is arbitrary, it will not affect our results given that we use this model for comparative purposes. Then, we generated four population projection matrices, one for each possible environmental state (Table 2), named environmental state-specific population projection matrix.

We calculated the dominant eigenvalue λ_L of each environmental state-specific matrix, which is an estimate of the asymptotic population growth under fixed environmental conditions. It is a measure of the fitness of individuals in a given environment.

The associated right column eigenvector $\mathbf{w}_L$ and left row eigenvector $\mathbf{v}_L$, that gives the stable stage distribution and the stage specific reproductive value respectively, were also calculated (Caswell, 2001).

2.5.4. The population growth under environmental variability: the megamatrix analysis

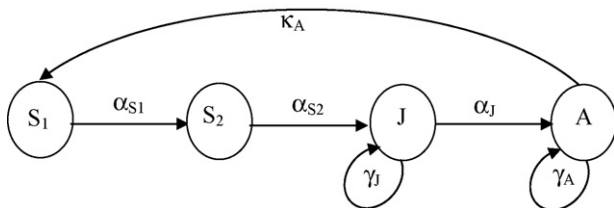As a measure of population growth under environmental variability we calculated the growth rate of average population λ_M,

which is the dominant eigenvalue of the megamatrix. The megamatrix M is organized in 4×4 blocks, which are arranged in 4 rows and 4 columns corresponding to the transition between the four environmental states. Each entry of the megamatrix ($m_{ij\alpha\beta}$) refers to the transition probability from stage j in the environmental state β to stage i in environmental state α (Pascarella and Horvitz, 1998).

We obtained three megamatrices, one for each environmental scenario defined by different fire frequencies.

The dominant eigenvalue of the megamatrix λ_M is an estimate of the asymptotic overall population growth in the dynamic system including fire and spring precipitations. The associated right eigenvector $\mathbf{w}_M$ is proportional to the stable stage by environmental state distribution. The reproductive value vector $\mathbf{v}_M$ is given by the left eigenvector of the megamatrix corresponding to λ_M. The elements of $\mathbf{v}_M$ give the relative value to long-term population growth of each class and environmental state (Caswell, 2001). The reproductive value was calculated by multiplying the left eigenvector of the megamatrix $\mathbf{v}_M$ (summed by class or summed by environmental state) by f*, which weights the reproductive value by the stable environmental state frequency (Pascarella and Horvitz, 1998).

For each environmental scenario, we built elasticity matrices of the megamatrix as:

$$e_{ij\alpha\beta} = \frac{\partial(\log \lambda)}{\partial(\log m_{ij\alpha\beta})} = \frac{m_{ij\alpha\beta}}{\lambda} \frac{\partial \lambda}{\partial m_{ij\alpha\beta}}$$

where $m_{ij\alpha\beta}$ corresponds to each element of the megamatrix (Caswell, 2001).

Elasticity represents the proportional changes in finite rates resulting from proportional changes in matrix elements and permits to evaluate the relative contribution of different matrix entries to population growth rate. Because elasticities sum to one, they can be summed in subsets with respect to environmental states, classes, environmental states 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 important to changes in growth rate caused by fire and spring precipitations.

To evaluate the relative contribution to population growth of proportional perturbations in life-stage transitions summed within environmental state, as well as summed by class, both within and across environmental states, we calculated three types of summed elasticities (Pascarella and Horvitz, 1998):

1) *Environmental state elasticity*, which was calculated with the following equation:

$$\sum_{ij\alpha} e_{ij\alpha\beta} = E_\beta \qquad (2)$$

This yields a 1×4 vector (one sum for each environmental state) that gives the importance of life history events within one environmental state compared overall to life history events in another environmental state.
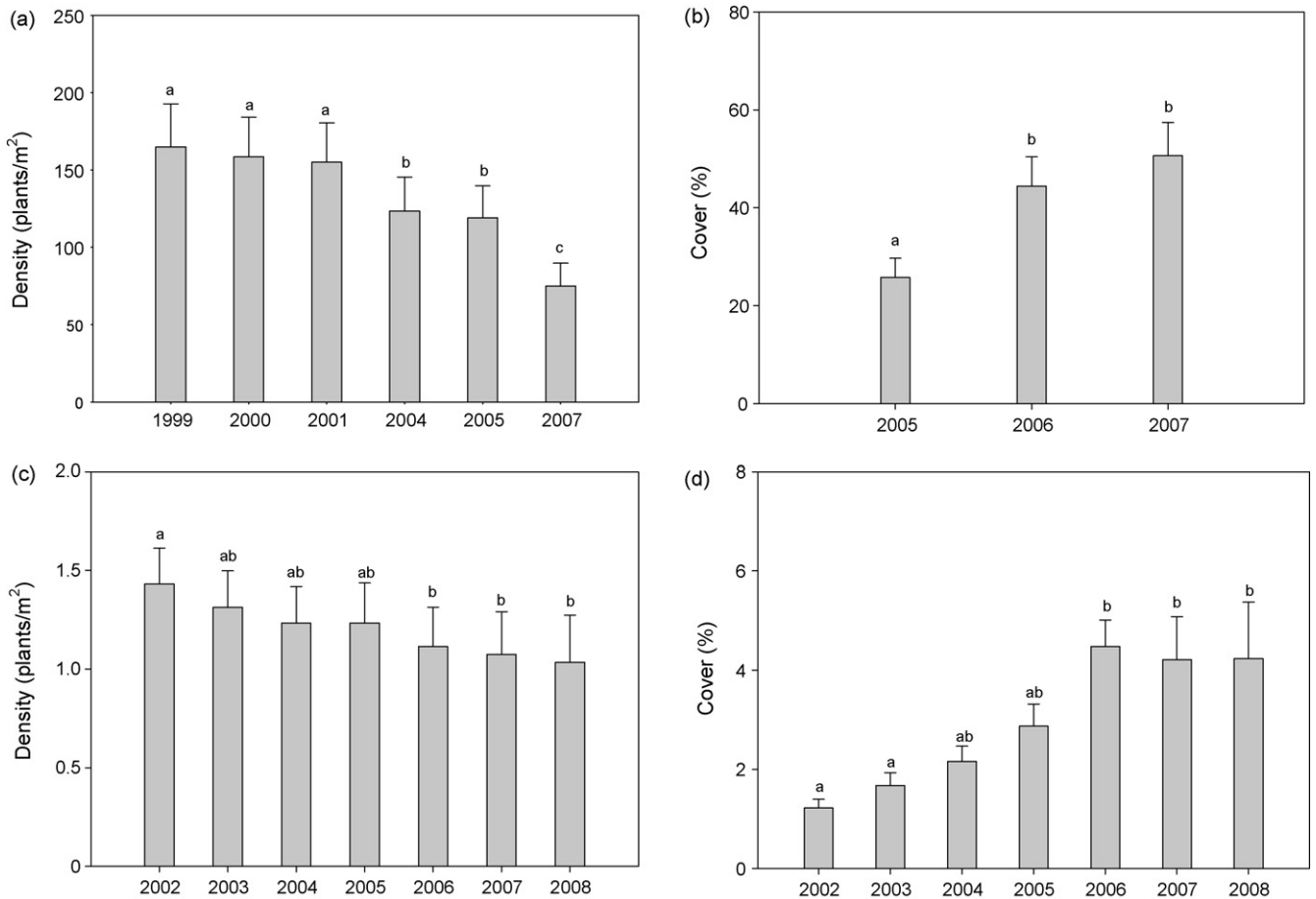

Fig. 1. Conceptual model of the life cycle of *F. imbricata*. S_1: first year seedlings, S_2: second year seedlings, J: juveniles, A: adults. Arrows represent the transition from one stage class to another (α_{S_1}, α_{S_2}, α_J: growth probability), permanence within a class (γ_J, γ_A: stasis) and reproduction (κ_A: fecundity).

Fig. 2. Postfire plant density (mean ± SE): (a) near and (c) far to the unburned shrubland; and postfire plant cover (mean ± SE); (b) near and (d) far to the unburned shrubland. Lower case letters indicate significant differences among years.

2) *Class elasticity by environmental state* defined for a given state β and a given class j summed over all i and α:

$$\sum_{i\alpha} e_{ij\alpha\beta} = E_{j\beta} \tag{3}$$

This yields a 1×16 vector of class elasticity by initial environmental state. It gives the magnitude of the impact on λ produced by a proportional perturbation to the elements of the megamatrix that involve a particular class within a particular environmental state, relative to other (or the same) class in other environmental states.

3) *Summed class elasticity*: for a given class, summed over α, β and i:

$$\sum_{i\alpha\beta} e_{ij\alpha\beta} = E_j \tag{4}$$

This yields a 1×4 vector (one sum for each class) that gives the importance of life history events involving a particular class compared overall to other life history stages.

Eigenvalues, scaled eigenvectors, and elasticity matrices were calculated using PopTools version 2.7.1 (Hood, 2005).

3. Results

3.1. Postfire shrub establishment

Ten months after fire, in Near SR invasive focus, seedling density was 165 plants/m^2 ($\pm$28). Seedling density decreased significantly

($p < 0.05$) since 2004 year, reaching the lowest density in 2007 (75 plants/m^2 $\pm$ 14.6, 55% survival) (Fig. 2a). Cover increased significantly since 2005, achieving 60% ($p < 0.05$, Fig. 2b).

In 2002 monitoring in Far SR site seedling density was 1.4 plants/m^2 ($\pm$0.18), significantly higher than 2006–2008 density (1 plants/m^2 $\pm$ 0.2, 71% survival, $p < 0.05$) (Fig. 2c). Maximum cover was reached in 2006–2008 years ($\approx$4.2%) and it was significantly higher than the first 2 years ($p < 0.05$) (Fig. 2d).

Eight years after fire, in Far P site, plant density was 0.18 plants/m^2 ($\pm$0.1). Plant high in this site (61 $\pm$ 9 cm), was significantly different ($p < 0.05$) from that found in Far SR site (16 $\pm$ 0.9 cm).

3.2. The environmental dynamics

The environmental state transition matrices for each environmental scenario are shown in Table 1. For all fire frequencies the stable environmental state distribution (f*) predicts that UN environments will be the most common (45.5, 55.0, and 59.3% for high, current, and low fire frequency, respectively). The UW environments will have an intermediate frequency (29.8, 36.0 and 38.9%), and the BN and BW environments will have the lowest frequency (14.9, 5.4 and 1.1%; and 9.8, 3.5 and 0.7%, respectively) (Fig. 3).

3.3. Population growth rates

Several demographic parameters varied from one environmental state to another (Table 2). Recruitment was enhanced with fire, especially when it was followed by a wet spring. Survival was obvi-
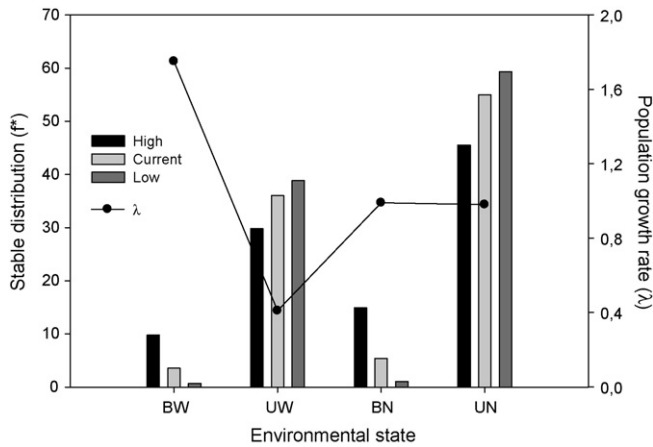
Fig. 3. Stable distribution (f*) of environmental states for high, current and low fire frequency (bars) and population growth rates (λ) of environmental state-specific matrices (line). BW: fire and wet spring, UW: no fire and wet spring, BN: fire and normal spring and UN: no fire and normal spring.

ously affected by fire. The transition from S_1 to S_2 was close to 0 in UN (0.5%) and BN (0.2%) due to S_1 response to water stress, and close to 1 in UW (98%). In BW environment, this transition was 37% because of the effect of fire. Juvenile survival and transition to adult class were only affected by fire.

Population growth rates for specific environmental state matrices (λ_L) ranged from 0.411 within BN to 1.755 within BW; and they were intermediate and closely similar for UW ($\lambda = 0.988$) and UN ($\lambda = 0.980$) (Fig. 3). The stable stage distribution showed that for burned environments, the highest proportion of individuals was concentrated in S_1, while in unburned environments it was concentrated in adult class. Juvenile proportion was always less than 4%. S_2 represented the 16.8% of the stable distribution for BW, and was less than 1% in the other environmental states (Fig. 4a).

In BW reproductive values were concentrated in adult class. In BN and UN reproductive values for juvenile and adult classes were closely similar (44.3 and 51.3% in BN, and 46.6 and 48% in UN) and higher than S_1 and S_2 reproductive values. In UW, all reproductive values were similar, ranging from 21.5 to 28%, being Juvenile class the highest (Fig. 4b).

3.4. Megamatrix analysis

Asymptotic overall population growth rate (λ_M) for the megamatrices were 1.06 for low, 1.19 for current, and 1.24 for high fire frequency.

All matrices were tested to be primitive, and irreducible and by the strong ergodic theorem (Caswell, 2001), the long-term dynamics is described by the population growth rate and the stable population structure, independently of the initial conditions. Thus, under our modeling assumptions the results are robust.

Summing across all classes by environmental state, the stable distribution had higher plant frequency in environments without fire (Fig. 5a). Summing by classes across all environmental states, the stable stage was characterized by high frequency of S_1 (Fig. 5b). It was followed by S_2, juveniles and adults, except for low fire frequency, where adults are present in higher proportion than S_2 and juveniles.

Summing across classes, the highest reproductive values were concentrated in unburned environments for all fire frequencies. In burned sites reproductive values increase as fire frequency increases. In unburned environments, the lower the fire frequency, the higher the reproductive value (Fig. 5c). Summing across environmental state, reproductive values were concentrated in adult
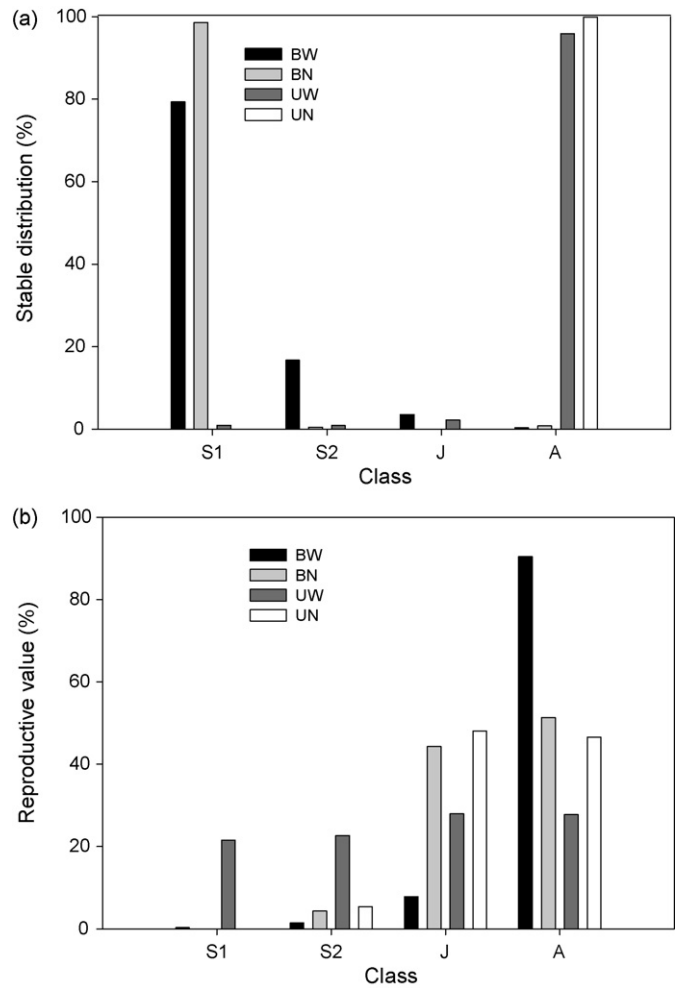

Fig. 4. (a) Stable distribution (%) and (b) reproductive values (%) by environmental state-specific matrix for each class. S_1: first year seedlings, S_2: second year seedlings, J: juveniles, A: adults; BW: fire and wet spring, BN: fire and normal spring, UW: no fire and wet spring, and UN: no fire and normal spring.

class for all fire frequencies. S_1 reproductive values summed always less than 1.2% (Fig. 5d).

3.5. Elasticity analysis

Elasticities of population projection matrices for each environmental state are shown in Fig. 6. In UW and UN, all the elasticity was contained in adults class (95 and 99%, respectively), while it was lower in BW and BN (6.4 and 76.7%, respectively). In BW, higher elasticities corresponded to fecundity, and growth to a larger class (22% approximately). Stasis in juveniles and adult classes elasticities were both lower than 7%.

Summing across environmental states, UN elasticity increased as fire frequency decreased. For low and current fire frequency, UN elasticity was the highest (52.1 and 44.2%, respectively), and for high fire frequency, UW elasticity was lightly higher (38.4%), followed by UN elasticity (36.4%). For all fire frequencies, BW and BN contributed always less than 13%, which were the most uncommon (Fig. 7).

Megamatrix elasticities of each class within an environmental state are shown in Fig. 8, organized by class (Fig. 8a) and by environmental state (Fig. 8b).

For S_1, elasticity was higher in UW environment for all fire frequencies. BN, BW and UN environments had close to 0 S_1-elasticities. For S_2 and J, unburned environments had higher
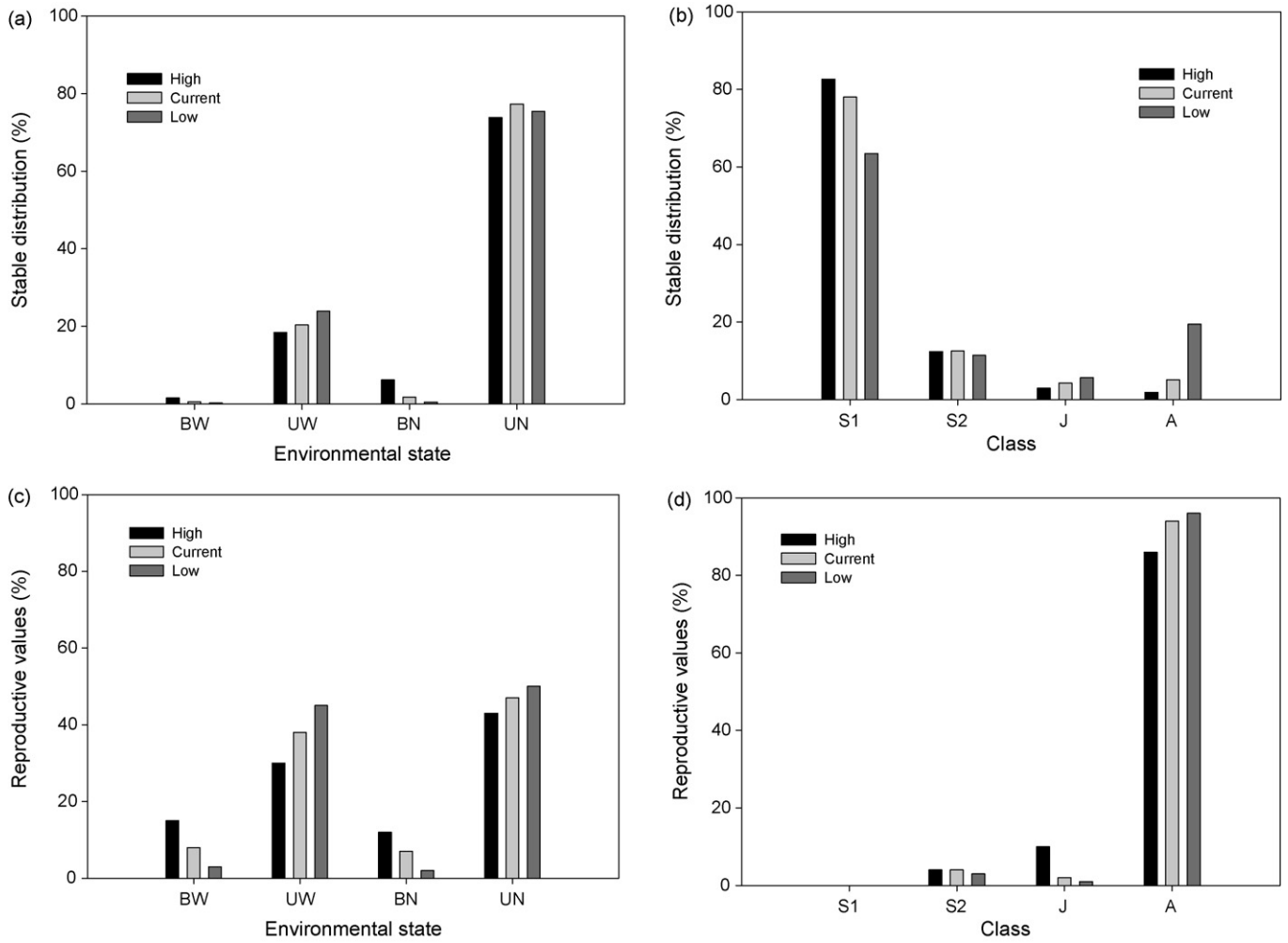
Fig. 5. Megamatrix analysis for high, current and low fire frequency. Stable distribution (%) summed (a) by classes for each environmental state and (b) by environmental state for each class. Weighted reproductive values (%) summed (a) by classes for each environmental state and (d) by environmental state for each class. S_1: first year seedlings, S_2: second year seedlings, J: juveniles, A: adults; BW: fire and wet spring, UW: no fire and wet spring, BN: fire and normal spring, and UN: no fire and normal spring.

elasticities than burned environments. For both classes, the highest elasticities occurred in high and current fire frequencies. For adults, unburned environments had the highest elasticities, and they were higher in the low fire frequency (Fig. 8a).

Class elasticity by environmental state shows that the lowest elasticities were in the burned environments. Adults showed higher elasticities than the other classes within each environmental state (Fig. 8b).
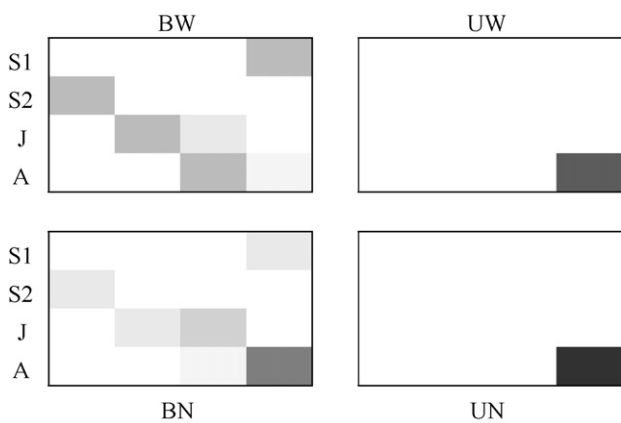

Fig. 6. Elasticity of population projection matrices for each environmental state. Darker cells represent higher elasticity values. BW: fire and wet spring, UW: no fire and a wet spring, BN: fire and normal spring, and UN: no fire and normal spring.
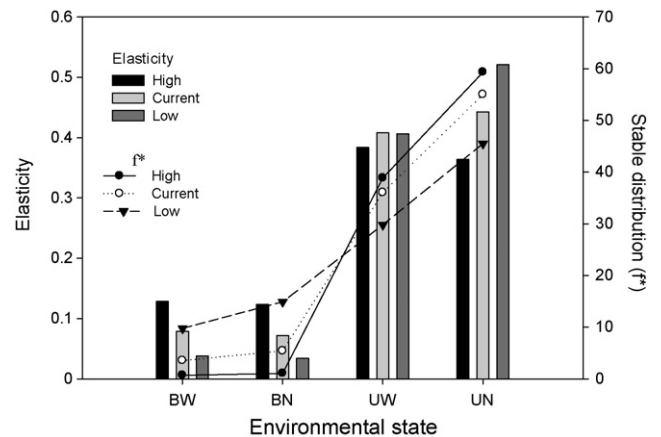

Fig. 7. Environmental states elasticity (bars) and the stable distribution of environmental states (f*) (lines) for high, current and low fire frequency. BW: fire and wet spring, BN: fire and normal spring, UW: no fire and wet spring, and UN: no fire and normal spring.
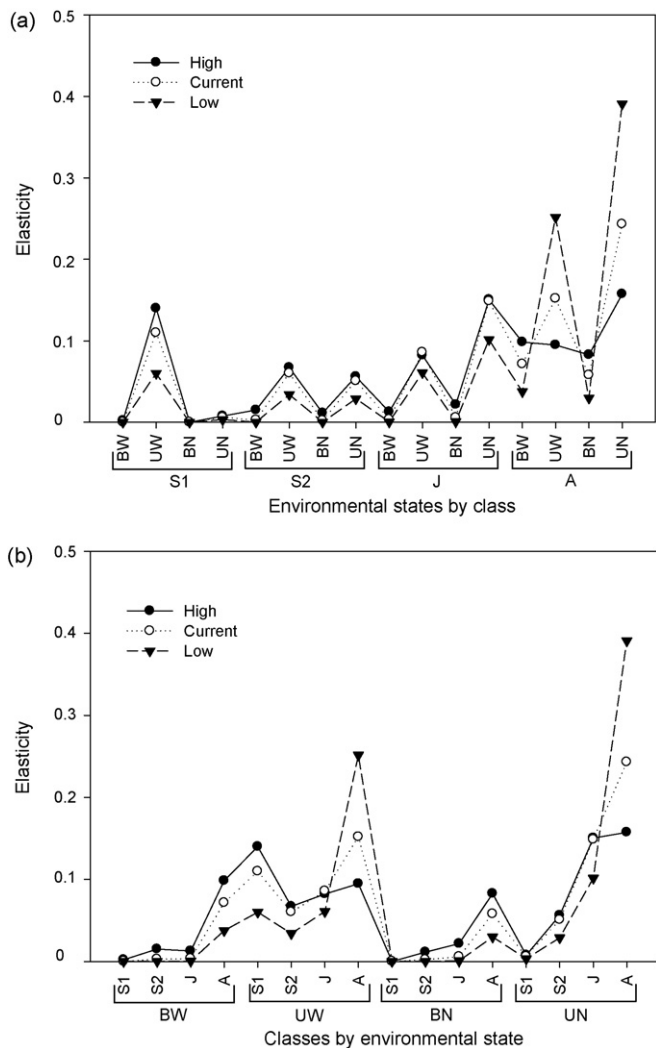
Fig. 8. Class elasticity by environmental state for high, current and low fire frequency, organized by (a) environmental states and (b) classes.

4. Discussion

The scientific opinions about the role of fire in shrub encroachment are divided. Some authors report negative relationships between fire and shrub invasion (Lloret and Zedler, 1991; Drewa et al., 2001), while other authors show the opposite (Heisler et al., 2004; Pugnaire and Lozano, 1997). The general conclusion of the model suggests that *F. imbricata* shrublands are currently growing and they will continue growing even if they are affected by the other analyzed fire frequencies. The postfire 1999 encroachment foci in San Ramón and Pichileufu sites seem to validate the model results. In the hypothetical situation of fire exclusion *F. imbricata* shrublands would no advance in the grassland because of the low recruitment and adult mortality. However, the worst situation for these shrublands it will be when the environment will be subjected to annual fires followed by normal or dry springs because the massive mortality that provokes a very fast shrublands disappearance. On other hand, the best situation for the shrublands it will be fire followed by wet springs, but this is the less frequent condition.

During El Niño years the high precipitations increase the biomass growth of fine fuel that dries off during La Niña summers and then it turn prone to be burned. In fact, since 1972–1999 three El Niño events followed by strong La Niña were coupled with extensive fires in northwestern Patagonia (National Weather Service,

Climate Prediction Centre, 2008; Ghermandi, unpublished). Global climate change models suggest an increase of frequency and amplitude of ENSO phenomena and, considering that *F. imbricata* recruitment is strongly favoured by fire and wet springs, it could be also expected more recruitment windows of this species.

In our model, we had considered wet spring probability related to current ENSO frequency. It would be interesting to explore the shrublands performance related to higher frequencies of wet or dry growth seasons. In Northwestern Patagonia the dry springs and the hot summers during La Niña events (Daniels and Veblen, 2000) could be harmful to seedling germination and establishment, which are the most vulnerable stages for population growth.

In mature *F. imbricata* shrublands, we observed an extremely low recruitment, whereas high germination was detected immediately after the first postfire spring that had been very rainy. Two years after fire we also observed that in the new invasion foci the recruitment stopped and all this patterns could support the hypothesis that *F. imbricata* seeds need fire cues (e.g. heat and smoke) or the release of some resources to germinate. For example, the establishment of shrub *Sarcopterium spinosum* is inhibited early, after fire, by the changes in the light spectral composition caused by the canopy close (Seligman and Zalmer, 2000).

In semiarid environments, shrub recruitment depends on favourable climate in growth season. In the case of *F. imbricata* the recruitment after fire, near the unburned shrubland (1 650 000 seedlings/ha) was stimulated by abundant spring rains and was closely similar to those recorded in other Mediterranean species, as *Erica australis* (1 150 000/ha; Iglesia et al., 1998) and *Cistus* sp. (1 070 000/ha; Ferrandis et al., 1999).

The new focus of invasion established far from the seed source derived from seeds that were transported at long distances by runoff mechanism favoured by the gentle soil inclination. Seed source was the unburned shrubland distant 250 m up hill, and seedling density in the far focus was lower than in near focus (14 000 seedlings/ha vs 1 650 000 seedlings/ha). Seedling survival was different between both foci (45% in near vs 71% in far), probably due to the self-thinning mechanism occurred in near focus where the seedling density was very high.

Shrublands distribution at landscape scale is associated with heterogeneity, especially with the outcrops presence (Anchorena and Cingolani, 2002). In the study area there is a fire risk gradient related to the fuel biomass. The extreme values of this gradient correspond to the grassland and the outcrops, and shrublands have an intermediate value. Outcrops can be considered fire refuges because of the low fuel continuity, as a result of their low cover. The mature shrublands are located close to outcrops and have lower herbaceous cover than grasslands. On the contrary, all the new shrublands are located in the foothill and they are completely surrounded by grassland matrix with high fine fuel biomass that notably increases the fire risk. Probably, during fires, all the shrubs in this new shrublands will die. Instead of that, if the new shrublands are not affected by fire during a long time, their persistence will depend on the ability of plants to achieve sexual maturity and to accumulate soil seed bank. However, we have observed that 9 years old plants cannot reach the reproductive maturity when they were severely browsed by hares. Similarly, rabbit grazing was a significant factor in decreasing the survival of *Acacia* (Cohn and Bradstock, 2000), and in Chihuahuan desert, *Lepus californicus* comprises *Prosopis glandulosa* in its diet (Drewa et al., 2001). In San Ramon postfire focus hare browsing reduced the plant growth, prevented plants to achieve sexual maturity and, consequently, decreased the potential invasiveness of *F. imbricata*. In fact, in Pichileufu site, where we observed lower hare density, plants were higher than in San Ramón site, and produced seeds 6 years after fire. Though, in San Ramón site the annual precipitation is higher than in Pichileufu site (582 mm vs 308 mm, respectively), this favourable

climatic condition was not enough to compensate the severe hare browsing damage. Then, at fine scale, high hare density constitutes a filter to the shrubland invasion. Like outcrops, the variation in hare density is another component of landscape heterogeneity.

The model predicted the potential invasion of *F. imbricata* at all the fire frequencies analyzed but did not consider the spatial distribution of shrublands and the landscape heterogeneity. Shrublands dynamics strongly depend on the landscape heterogeneity, that could change at local scale and then the resultant pattern at regional scale is not easy to predict.

Acknowledgments

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