Modeling shrub encroachment in alpine grasslands under different enviromental and management scenarios

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Abstract

Woody plants are spreading in many alpine and subalpine ecosystems and are expected to continue increasing in response to land abandonment and global warming. This encroachment threatens species diversity, and considerable efforts have been deployed to control it. In this study, we combined a lattice model and field data to investigate the efficiency of different management strategies in controlling shrub encroachment in alpine grasslands. The model parameter values were estimated in the field based on the thorny shrub *Echinospartum horridum* (erizón) which is currently encroaching in central Spanish Pyrenees. Our study shows that encroachment could accelerate if climate warming continues. Different management scenarios consisting of a gradient of livestock pressures, fire events and mechanical removal were simulated to identify scenarios able to control the expansion of shrubs into grasslands. Our study shows that grazing alone cannot stop encroachment. Rather, a combination of grazing and shrub removal (either by fire or mechanical removal) is needed, and our model can help estimate the frequency and intensities of the shrub removal. This model can be used to investigate the consequences of different management scenarios and environmental variability which could be of practical value in the preservation of alpine grasslands.

Key-words: mountain grasslands, cellular automata, *Echinospartum horridum*, erizón, grazing, land abandonment, lattice-structured model, Pyrenees, woody encroachment.

Introduction

Woody plant encroachment refers to the expansion of grass-dominated ecosystems by indigenous woody species, most of which are unpalatable to domestic animals (Van Auken

2009). This phenomenon is widespread in arid, mesic and alpine areas (Archer 1994, Van Auken 2000, Briggs et al. 2005, Anthelme et al. 2007). Woody plant encroachment has attracted a lot of attention because it has been linked with the alteration in structure and functioning of ecosystems (Dullinger et al. 2003, Briggs et al. 2005, Eldridge et al. 2011). Moreover, it can reduce the productivity (McPherson and Wright 1990, Aguiar et al. 1996, Lett and Knapp 2003) and the diversity (Hobbs 1996, Alados et al. 2007, Price and Morgan 2008) of rangeland ecosystems, leading to land degradation and desertification in drylands (Reynolds et al. 2007).

Woody encroachment has been extensively studied in arid, semiarid and sub-humid environments of North America (Archer 1994, Van Auken 2000, Knapp et al. 2008b), Australia (Noble 1997, Brown and Carter 1998) and Africa (Tobler et al. 2003, Sankaran et al. 2005). Shrub encroachment is often associated with changes in grazing regimens (Noy-Meir 1982, Sankaran et al. 2005). Typically, increased levels of domestic grazing animals have lead to the reduction of grass biomass and more generally flammable material (McPherson et al. 1988), which causes a reduction in fire frequency (Scholes and Archer 1997, Van Auken 2009) and consequently favors shrub growth which is impeded by fire. In other words, shrub encroachment usually refers to transformations in ecosystems whose "natural", pristine state would be a grassland and where human impact has lead to (often) irreversible invasion of shrubs in the system.

Theories have been developed to attempt to better understand grass-shrub coexistence. These theories emphasize the partitioning of resource variability (Walter 1971, van Langevelde et al. 2003, Gilad et al. 2007) or the demographic dynamics caused by spatial or temporal disturbances (Jeltsch et al. 1998, Rodriguez-Iturbe et al. 1999, D'Odorico et al. 2006, Baudena et al. 2010). Although those theoretical approaches recognize the importance of fire and grazing to the coexistence of grass and shrub (Higgins et al. 2000, Sankaran et al. 2004, D'Odorico et al. 2006), the importance of environmental fluctuations, particularly annual precipitation, in the expansion of woody species remains equivocal (Sankaran et al. 2005). Additionally, high concentrations of CO_2 and N depositions (Idso 1992, Polley et al. 1992) and climate change (Knapp et al. 2008a, D' Odorico et al. 2010) can also enhance shrub encroachment.

Shrub encroachment has also been reported in European alpine grasslands, where significant socio-economic transformations over the last century have lead to widespread declines in livestock farming and agriculture (García-Ruiz et al. 1996, Krauchi et al. 2000, Bartolomé et al. 2005, Gehrig-Fasel et al. 2007, Batllori and Gutiérrez 2008). The abandonment of pastoral activities has affected plant distribution and has lead to the expansion of woody species into grasslands (Carcaillet and Brun 2000, Lasanta et al. 2005, Roura-Pascual et al. 2005, Anthelme et al. 2007). Pyrenees subalpine grasslands are secondary plant communities that have replaced the native forest and have been grazed continuously for at least the past 500 years (Montserrat and Fillat 1990). In other terms, human activities in these ecosystems have maintained a grassland state in these ecosystems for centuries, and shrub encroachment can be seen as a recovery from earlier, historical, anthropogenic disturbance.

Subalpine grasslands are highly diverse communities and, in particular, calcareous alpine grasslands are among the richest ecological communities in Europe (WallisDeVries et al. 2002). The expansion of woody species in those areas is a serious threat to biodiversity (Komac et al. 2011). Therefore, despite the fact that grasslands are not the “pristine” state of these ecosystems, management efforts have targeted the preservation of grasslands in some alpine ecosystems in order to preserve the productivity and traditional values of those man-made ecosystems. These management efforts typically involve a combination of grazing and fire, trying to keep some remains of the traditional land use of these ecosystems. Tools are required to rationalize this management.

In this paper, we focus on the Pyrenees where, the abandonment of grazing practices contributed to a 47% increase in the biomass of woody vegetation in the last 30 years (Bartolomé et al. 2005). In particular, erizón (*Echinospartum horridum*), a thorny cushion shrub, endemic of the Pyrenees that is widespread on south facing slopes (Benito Alonso 2006), is spreading rapidly in the last decades (Montserrat et al. 1984). Clonal propagation favors the persistence of the plant which forms a dense mat through successful competition with neighbors and leads to the formation of monospecific patches.

The goal of this paper was to model shrub-grass dynamic under different environmental and management scenarios and to evaluate the efficiency of different strategies to control shrub expansion in alpine and subalpine grasslands. We developed a spatially-explicit model, modeling shrub growth in a grassland. Specifically, we addressed the following questions: (i) what is the range of biological parameters that restricts erizón expansion?, (ii) what is the expansion rate under different conditions of precipitation and temperature?, (iii) can we control erizón expansion using livestock grazing only, or do we need a combination of grazing, fire and mechanical removal?

We derived real parameter values for this model based on field observations in the OMPNP, where about three fourths of the park surface is alpine grasslands (sensus (Körner 1999)). These real parameter values allow us to study the model in a realistic range of values. However the model formulation itself is general enough that it could be used to study other alpine grasslands threatened by shrub encroachment after land abandonment. A modeling approach is particularly helpful in national parks, where only traditional activities are allowed, and experiment manipulations are restricted to small areas.

Methods

Study area and biology of the system

The empirical study was conducted in the subalpine grasslands of Ordesa-Monte Perdido National Park (OMPNP), Central Pyrenees, Spain. OMPNP is a protected area (15.600 ha) since 1918. The climate is mountain continental. At the Goriz weather station (42º40'N, 00º02'E; 2.215m a.s.l.), the average annual rainfall was 1.735 mm between 1981 and 2006. Snow cover persists from early November to late May. The mean annual temperature for that period is ~ 5 ºC, but with daily temperatures between 25 ºC and –21 ºC.

More than 75% of the OMPNP is alpine and subalpine grasslands, partially threatened by the shrub colonization that takes place from ~1500 to 2000 m of altitude.

Echinospartum horridum (Vahl.) Rothm (hereafter, erizón), a strictly calcicolous chamaephyte, thorny cushion, and endemic of the central Spanish Pyrenees and the southern of France, is among the most aggressive species that are recolonizing those grasslands (Aparicio et al. 2002). It reproduces sexually and asexually. Sexual reproduction produces persistent seed banks (Aparicio and Guisande 1997). Creeping asexual reproduction is through the clonal propagation of decumbent branches, which root at nodes along the stems. Newly rooted stems can break off and become independent clonal fragments. Clonal fragments permit the plant to maintain and increase its cover, which suppresses the establishment of other species.

Shrubs thus form monospecific patches and the individuals living in the interior of these patches have a lower growth rate and a higher crown death rate than do plants at the edges of the patches (Komac 2010, Komac et al. in press). Grasses reproduce vegetatively by clonal spreading and sexually by seed dispersion throughout the lattice (Loehle 1987, Eriksson and Ehrlén 1992). Grass seedling establishment occurs within 1 m^2 of the mother plant (Komac 2010, Komac et al. in press). Shrubs are competitively superior to grasses and can displace them once established (Scholes and Archer 1997, Ball et al. 2002), and although shrub seedling establishment is lower on grass sites than it is on empty sites (personal observation) (Ball et al. 2002), grasses cannot displace the shrubs once the latter become established (personal observation).

General model structure

The model presented here is a spatially-explicit grid-based model describing the shrub-grass dynamics with the subalpine grasslands of OMPNP as an example. We focused on the demographic processes that control shrub-grass dynamics, and we evaluated how disturbances such as fire, mechanical removal and grazing affect the shrub population dynamics (Higgins et al. 2000, Sankaran and Augustine 2004, D'Odorico et al. 2006). Each cell was 1 m^2, an approximation of the average size of an adult erizón, and a time step is a year.

An ecosystem is considered to be a two-dimensional lattice of cells. At a given time step, each cell of the lattice is in one of the following three states: occupied by a shrub (S), occupied by grasses (G), or empty (E) (Fig. 1). At each time step, a cell might transition to one of the other states (e.g. a grass cell may transition to an empty or a shrub cell) based on basic processes, described by transition rates (i.e. probabilities per unit of time) expressed below. To check whether a transition occurs, the possible transition rates are first calculated, then a random number is drawn and the transition occurs if this number is inferior to the transition rate (otherwise the cell remains in the same state). The transition rates can depend on the state of nearest-neighbors (here, we used the von Neumann neighborhood, i.e. the four nearest neighbors).

Transition rates between states

We define two types of variables: global densities, ρ_σ, which describe the proportion of the lattice occupied by cells in state σ (σ can be S, G or E), and local densities, $q_{\sigma|\sigma'}$, which quantify the proportion of σ'-neighbors of a σ-cell.

Colonization of empty cell

In the model, an empty cell can be colonized by a shrub or grasses. The transition rate of an empty cell by a shrub, $w_{E,S}$, is denoted by:

$$w_{E,S} = ((1 - q_{S|E})\beta_1 + s_1)q_{S|E}\,. \qquad (3)$$

The first term in equation 3 is reproduction by seeds. β_1 is the seed establishment rate on an empty cell. Seeds can only colonize empty cells at the edge of a shrub patch (Komac 2010, Komac et al. in press); therefore, β_1 is multiplied by the probability that a cell is at the edge of a patch, 1- $q_{S|E}$. The second term of equation 3 reflects vegetative reproduction. s_1 is the expansion rate of shrub into neighboring empty cells. The two terms of the equations are multiplied by the probability that a neighboring cell is empty ($q_{S|E}$) because shrub dispersal is local.

The transition rate of an empty cell into grasses, $w_{E,G}$, is denoted by:

$$w_{E,G} = b_g q_{G|E} + \theta\rho_G\,. \qquad (4)$$

The first term of equation 4 represents clonal spreading by grass into a neighboring empty cell. b_g is the maximal expansion rate of grasses on adjacent cells, which occurs when a grass site is surrounded by empty neighbors. The second term of equation (4) reflects seed dispersal throughout the lattice (Eriksson and Ehrlén 1992). This term corresponds to the establishment rate of grass seeds on empty cells, θ, multiplied by the global density of grasses in the lattice, ρ_G.

Colonization of grasslands by shrubs

Shrubs can also colonize grasslands (Komac 2010, Komac et al. in press), and the transition rate of a grass cell into a shrub cell is expressed as:

$$w_{G,S} = ((1 - q_{S|G})\beta_2 + s_2)q_{S|G} . \quad (5)$$

Following the same reasoning as for equation 3, but replacing $q_{S|E}$ by $q_{S|G}$ since this time, we focus on the establishment in a grass cell. The parameter s_2 is the expansion rate of shrubs on grasses and β_2 is the seed establishment rate on grass-occupied cells.

Mortality

After the death of grass or erizón, the cell becomes empty. Mortality of shrubs is calculated as:

$$w_{S,E} = d_S + cq_{S|S} , \quad (7)$$

where d_s is the mortality rate of adult plants and c is the intensity of the competition among shrubs within the interior of the patch. Mortality of grasses is modeled as a density-independent rate, d_g, as follows:

$$w_{G,E} = d_g . \quad (8)$$

Inclusion of burning, mechanical removal and grazing into the model

Prescribed fires, mechanical removal and grazing were included in the model as follows. Fire is modeled in a way that mimics its use as a management tool. The shrub area to burn and the frequency of fire events are fixed beforehand. A strike is initiated at the edge of the shrub patch, which starts a fire in one shrub cell. The fire propagates to neighboring cells that contain shrubs until the area of shrub burned reaches the prescribed amount. The cells that were burned are now in a new state ’burnt’, B. After the fire has stopped, the population dynamics continue until the next fire event (determined by the frequency of fire events). Burned cells can be invaded by shrub seedlings in a way similar to that on empty cells, but at a different seedling establishment rate (Pérez-Cabello and Ibarra 2004) *β_3:*

$$w_{B,S} = ((1 - q_{S|B})\beta_3 + s_1)q_{S|B}.$$

We assumed that colonization of burned spaces by grasses is similar to colonization of empty space as follows:

$$w_{B,G} = b_g q_{G|B} + \theta\rho_G.$$

Cells that remain in state B (i.e. that are not colonized by shrub or grass) automatically return to the state empty (E) in the following year.

Mechanical removal follows the same procedure only differing in the seedling establishment rate, which is the same than the colonization on empty cells.

Livestock grazing was included in the model and, because most animals eat shrub seedlings but no adults (personal observation and information from farmers), the model assumed that livestock removes a rate of seedlings (h) from all of the shrub seedlings that become established in burned and grass cells, but not among those seedlings establishing on empty cells (the model assumes that empty cells are not visited by grazers). The two rates β_2 and β_3 are replaced by $\beta_2(1-h)$ and $\beta_3(1-h)$ where h reflects the intensity of grazing through trampling and feeding (h is between 0 and 1).

Estimation of the parameter values

The model is very general and can be used to study management strategies on alpine grasslands after grazing abandonment to prevent shrub encroachment. But here we analyzed it based on a set of parameter values observed in the field.

The parameters were estimated using data on erizón longevity, growth, demography, and seedling production collected between 2005 and 2007 in the Ordesa-Monte Perdido National Park (OMPNP), Spain (Komac 2010, Komac et al. in press). This period was representative of the general climatic situation. Meteorological data of the closet weather station (Goriz) were recorded and included minima temperature in June (the start of the erizón growing season) and total precipitation in the previous year. Seedling establishment rates of erizón β_1 (number of seedling divided by number of adult plants) differs between sites where grasses are highly competitive (low slope) and sites where they are not (high slopes) (Komac 2010, Komac et al. in press). In the field, seedlings establishment rates were 0.476 ± 0.126 and 0.275 ± 0.098 seedlings per mother plant on high (n=40 adult plants) and low slopes (n=40), respectively. We used the averaged 0.387 ± 0.082 seedlings m^{-2} yr^{-1}(n = 80). The data were collected from parcels that were visited by cattle and sheep; therefore the model assumed that the seedlings that were present reflect the livestock pressure at that time (0.34 small ruminants ha^{-1} year $^{-1}$ (Alados et al. 2007)). Thus, the parameter values are valid for a grazing pressure of 0.34 ind ha^{-1} year $^{-1}$. Seedlings establishment on empty sites (β_1) are obtained from counting number of seedlings per m^2 in empty sites in 10 plots of $1m^2$ (6.8 ± 2.32 seedlings m^{-2} yr^{-1}) (Table 1). On average, the seedling establishment rate in burned areas (β_3) was 38.8 ± 9.27 seedlings m^{-2} yr^{-1} (personal observation following a lighting event that burnt 0.5 ha in one of the sample sites). Averaged crown size (diameter) of plants > 15 years was ~ 1 m diameter (Marinas 2004, Komac 2010, Komac et al. in press) coinciding with the pixel size of our simulation.

The expansion rate of the erizón population was estimated by the difference in crown growth rate between two consecutive years (0.109 ± 0.01 and 0.061 ± 0.016 for high and low slopes, respectively; see (Komac et al. in press) (Table 1). The rates were similar to those based on the clonal expansion rate of erizón (0.125), which was estimated from the decumbent stem elongation between the main root and the first generation ramet (Komac et al. in press).

Grasses can disperse locally and globally. On average, in the study area, an empty site did not remain empty more than two years (manuscript in preparation). Local expansion of grass b_g, was the inverse of the time grasses take to colonize an empty space (i.e. $b_g=1/2=0.5$). Global dispersal, θ, was calculated as 1- (rock cover/grass cover) with erizón patches, which provided an estimate of the establishment rate of grass seeds on empty sites (Table 1).

The mortality rate of adult shrubs, d_s, is the inverse of lifespan and the average maximum age of an adult plant at the edge of a patch was 35.6 ±0.204 yr (calculated by truck ring counts from 76 plants, (Komac 2010, Komac et al. in press)); therefore, the mortality rate in the absence of competition was 1/35.6 yr^{-1} (Komac 2010, Komac et al. in press). The additional mortality caused by competition with other shrubs within the center of shrub patches, c, was estimated based on the difference between the mortality rates in the center of patches and at the edges of patches. In the centre, the average maximum age was 33.9 ±0.513 yr; therefore, the mortality rate when all the neighboring sites are occupied by shrubs was 1/33.9 yr^{-1}. So:

$$d_s + c = \frac{1}{33.9} \text{ and } c = \frac{1}{33.9} - \frac{1}{35.6} = 0.0015 \text{ yr}^{-1}.$$

The mortality rate of grasses, d_g, was 1/8= 0.125 yr^{-1} (Wildová et al. 2007).

Spatially-explicit simulations

Simulations were performed on 200 x 200 cell lattices with periodic boundary conditions and a stochastic asynchronous update (Ingerson and Buvel 1984). The simulations were run using MATLAB 7.0.

To confront the model to field data (Komac 2010, Komac et al. in press), we simulated the growth of erizón starting from the actual erizón abundance (10%) in the OMPNP within a matrix of grasses (80%) and bare soil (10%) (panel A of Fig. 2). To investigate the potential effect of environmental variability on the growth of the erizón population, we simulated variations of β and s. Seedling establishment is the parameter that is the most sensitive to environmental variation (Frazer and Davis 1988, Jeltsch et al. 1998). We simulated β values that varied between $\beta_1 = 1$ to 7 yr^{-1} and $\beta_2 = 0$ to 0.6 yr^{-1} and s values between $s_1 = 0.05$ to 0.16 yr^{-1} and $s_2 = s_1 - 0.05$ yr^{-1}. Those values were based on the values observed in field between 2005 and 2011. The model simulated a 20-yr period.

Results

In our spatially explicit, grid-based model, starting with a single erizón covering 10% in the middle of a matrix of randomly distributed grass and empty cells (Fig. 2 panel A), the shrub growth rate is similar to the observed in the field (0.008 ± 0.001, Komac et al in press) (Fig. 2 B). Starting from an initial condition in which patches of erizón covered 10% of the lattice (Fig. 2 D), after about 20 yr, the erizón duplicate its surface to 20% of the lattice (Fig 2 E). It takes 170 yr for the shrubs to replacing completely the grasslands. During the erizón invasion, the local densities of shrubs in the neighborhood of empty cells increased ($q_{S|E}$, Fig. 2G); meanwhile, local densities of grasses in the neighborhood of empty cells declined ($q_{G|E}$, Fig. 2G). The local densities of shrubs in the neighborhood of shrubs ($q_{S|S}$) increased gradually in parallel with the decline of grass cells in the neighborhood of shrubs ($q_{G|S}$, Fig. 2 G).

Effect of the environmental conditions on erizón expansion

Seedling establishment is one of the crucial stages underlying the population dynamics of erizón, which, like the vegetation expansion of erizón, can be strongly influenced by environmental conditions. β_1 and β_2 as well as s_1 and s_2 are expected to increase when rainfall and temperature are favorable and to decrease when they are not. The minimum temperature in June (2005–2011) and s_1 were positively correlated ($R^2 = 0.56$, $n = 5$, slope = 0.014, P = 0.15), which reflects the inhibitory effect of low temperatures on shoot growth. Annual precipitation in the previous year and vegetative reproduction rate s_1 were not related ($R^2 = 0.09$ $n = 6$, NS).

We investigated how changes in the environment (in parallel with changes in the capacity to establish and vegetative expansion) affected the population dynamics of erizón by modeling shrub expansion using different combinations of β_1 and s_1 (Fig. 3), which simulated a change in the environment from unfavorable to favorable. The difference in erizón density between consecutive years indicates whether erizón invaded the system or not. When the slope of this change is positive, erizón populations continue to expand and, when the slope is negative, erizón populations shrink. In addition, the higher the slope, the faster invasion of erizón in the system. At the end of the 20-yr simulation, the erizón growth rate was positive when $\beta_1 > 2.1$ yr^{-1} and $s_1 > 0.10$ yr^{-1}. Furthermore, the higher the values of β_1 and s_1 (i.e. the more favorable the environment), the faster the invasion rate of erizón.

Effect of burning, mechanical removal and grazing on erizón expansion

To identify the conditions that might hamper the spread of erizón in grasslands, the model simulated prescribed fire at regular intervals and with variable proportion of area covered by erizón burned, which mimicked strategies that can be performed in the field and, traditionally, have been used to manage and protect grasslands threatened by shrub encroachment. Changes in erizón density between consecutive fire events indicate whether erizón expansion has been controlled by the fire regime. Fig. 4A shows the slope of the difference in erizón density between consecutive years, representing the outcome of the erizón expansion as a function of fire frequency and burning rate in 20-yr simulations. In the simulation, burning rate was varied, incrementally, by 0.1 from 0.1 to 1, and at a range of burning frequencies (every 1, 2, 4, 6, 8 or 10 yr from the starting condition) (panel δ of Fig 2). The simulations indicated that, when fire alone is used to control the erizón population, a burning rate of 20 % every year or 80 % every 2 years was needed to ensure the control of erizón population.

Burning can have negative effects on soil conservation, by reducing microbial activity, increasing run-off, erosion and nutrients loss after the first rainfall, and triggering the germination of erizón seeds. For those reasons, fire events should be minimized to the most feasible extent. Mechanical removal of erizón is an alternative practice, which although more expensive, does not alter so drastically soil structure and presents a seedling establishment rate 6 times lower than burning treatment. The simulation showed that 20% of removal every 2 years was enough to control erizón expansion (Fig 4B).

In the simulations, grazing alone cannot control the expansion of the shrub population (not shown). We simulated the effect of shrub removal, by burning or mechanical removal, and grazing simultaneously. Shrubs are most sensitive to grazing when they are seedling; therefore, we simulated livestock activity acting on seedling survival (h=1 when all seeds are destroyed by cattle, and h=0 when none was destroyed by cattle). In the simulation, removal was increased, incrementally, by 0.05 from 0.1 to 0.5, with a frequency of one fire every 5 years, or one mechanical removal every 3 years. Furthermore, for a given area of shrub removed there is a threshold grazing pressure below which the shrub growth rate increases to a level whereby shrubs invade the entire lattice. When shrubs were burnt, a burning intensity of 50 % every 5 years and a grazing pressure above 60% of seedling removed ($h = 6\ \mathrm{yr}^{-1}$) were necessary to control shrub population (Fig 5A). When shrubs were mechanically removed, a small increment of shrub removal extent to 0.2 (20% of shrub area removed every 3 years) can control the shrub expansion even under low grazing pressure (rate of seedlings removed $h = 0.08\ \mathrm{yr}^{-1}$), indicating the better ability of mechanical removal to control shrub expansion compared to fire.

Discussion

We developed a spatially-explicit model for shrub-grass dynamic for which parameter values were derived using data collected in OMPNP and in the scientific literature.

Our model was able to reproduce a rate of erizón invasion into grassland similar to the rate observed in the field (Komac 2010, Komac et al. in press). Given a starting occupancy of 10% (the actual occupancy area at OMPNP is 2.5%, Komac, 2010), our model predicts a complete invasion of the potential area of occupancy (25% of OMPNP, Komac, 2010) under the current growing conditions in 170 yr.

Environmental fluctuations such as annual rainfall influence the competitiveness and colonization abilities of species during the growing season and, more particularly, influence species abundance in water-limited ecosystems (Fernández-Illescas and Rodríguez-Iturbe 2003). Environmental change acting on seedlings recruitment, which is a key factor in shrub-grass coexistence (Jeltsch et al. 1998, van Wijk and Rodriguez-Iturbe 2002) will lead to an erizón expansion, unless seedling establishment rate on empty sites remains $< 2.1\ \mathrm{m}^{-2}\ \mathrm{yr}^{-1}$ and the vegetative expansion (crown growth rate) remains $< 0.10\ \mathrm{yr}^{-1}$. In the field, between 2005 and 2011, 67% of the crown growth rates were $< 0.10\ \mathrm{yr}^{-1}$. In the region, the expansion of erizón populations is favored by long-term increases in temperature resulting from global climate change, which will enhance the conditions for regeneration or establishment at elevations that are higher than the current distributional limit (Benito Alonso 2006). In warm years, seed establishment rates are likely to be higher at the tree line (Millar and Cummins 1982, Barclay and Crawford 1984). Conversely, the inhibitory effect of low temperatures on shoot growth (Palacio 2006) was reflected in our study by the positive correlation between the minimum temperature in June (2005–2011) and vegetative reproduction rate on empty sites (s_1). As in other temperate mountain ecosystems (Grabherr et al. 1994, Theurillat and Guisan 2001), global warming might have a significant effects on the successional processes, ecosystem functioning, and landscape structure in the alpine grasslands of the Pyrenees. However, annual precipitation in the previous year and vegetative reproduction rate s_1 were not related, which reflected that water availability is not a limiting factor in shrub encroachment in alpine grasslands. In areas where mean annual precipitation is > 650 mm, human disturbances such as livestock and fire are required to maintain grasslands (Sankaran et al. 2005). In the Pyrenean alpine grasslands, the average annual precipitation is > 1500 mm and naturally tends to woody canopy closure; consequently, to control shrub expansion, disturbances (fire, herbivory) are required. It appears that periodic or stochastic disturbances can prevent shrublands from dominating the system (see also (Baudena et al. 2010)). Disturbances such as fire and grazing can limit the germination and establishment of tree seedling (Scholes and Archer 1997, Higgins et al. 2000, van Langevelde et al. 2003), particularly in areas that experience high annual precipitation (Sankaran et al. 2005). Our model showed that the encroachment efficiency depended on both the frequency and intensity of shrub removal, mechanical removal being much more effective than fire. When mechanical removal was simulated at a frequency of ~ 20% every two years it was possible to control the shrub expansion. However, when fire events were simulated at a frequency lower than once every year and with an intensity of ~ 20% of the shrub burned, the model forecasted a recovery of shrub within 20 yr. To control shrub, the smaller the area burned the higher the frequency of fire events required, which was expected because shrub erizón rapidly re-colonizes after fire events (Pérez-Cabello and Ibarra 2004). In mesic grasslands in North America, once shrubs are established, fire can accelerate the expansion of woody species

(Briggs et al. 2005), which can lead to a reduction in the productivity of extensive grazing systems (Molinillo et al. 1997, Marinas 2004) and increase the spread of accidental fire events (Vázquez and Moreno 1998). To combat the expansion of shrublands and to recover grazing areas, some local governments have performed clearance treatment, which have increased productivity and reduced fire events in some areas of Spain (Lasanta et al. 2009).

The colonization of grasslands by shrub is strongly affected by competition with vigorous grass and herb layers as has been reported for several woody species (Richardson and Bond 1991, Magee and Antos 1992). In addition, grasses are well adapted to being grazed, and grazing even favors grasses performance as previously reported (McNaughton 1984). Consequently, a reduction in grazing pressure can favor an increase in the encroachment by erizón in lightly grazed sites (Montserrat et al. 1984), and conversely, grazing can help the control of expansion of erizón populations. In the subalpine grasslands of the Pyrenees, high livestock grazing pressure is the main factor in the control of woody encroachment (Lasanta et al. 2005), being fire and grazing always associated, well to increase grasslands productivity, or just to provide fuel for heating and cooking. It is necessary to take into account the fact that current grazing pressure is ten times less than the one observed in the early twentieth century, and trampling effect is only important around shelter and water points (Komac 2010). When grazing was included in our model, the control of the erizón expansion depended on the combination of grazing intensity and mechanical or fire removal rate. Even under high grazing pressure (h=1 yr^{-1}, i.e., 100% seedlings are removed by grazing), vegetative expansion by erizón can continue to invade unless at least 6 % of the shrub area is mechanically removed every 3 yr or 10 % of shrub is burnt every 5 years. Grazing alone was not able to control erizón expansion in our study. Heavy grazing after fire, is the traditional means of reducing woody plants (Ellenberg 1988) but it might be the best practice to use mechanical removal for maintaining pastures and preventing plant succession in alpine ecosystems, although mechanical removal is a more costly measure in terms of man power. Using this model we have examined how different managements (mechanical removal, prescribed fire and grazing) can influence the dynamics of grass-shrub and ultimately the grassland colonization. This model allows us to investigate the consequences of different management scenarios and environmental variability which could be of practical relevance for the preservation of alpine grasslands. In our model, a combination of grazing and mechanical removal was able to control shrub encroachment, and grasses and shrubs coexisted when there was a combination of mechanical removal and grazing. The model could be used in more general situations than the specific case we have applied.

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Table 1. Parameter values used in the model.

Symbol	Interpretation	Estimation from field data	Value	*Source*
β_1	establishment rate of erizón seedlings on empty sites	seedlings/m^2 on empty	6.8 ± 2.323 seedlings m^{-2} yr^{-1}	Field data observation
β_2	establishment rate of erizón seedlings on grass sites	seedlings/ m^2 on grass	0.387 ± 0.082 seedlings m^{-2} yr^{-1}	Field data observation
β_3	establishment rate of erizón seedlings on burnt sites	seedlings/number of adult erizón on burnt sites	38.8 ± 9.768 seedlings m^{-2} yr^{-1}	Field data observation
s_1	vegetative reproduction rate of erizón on empty sites	(D2-D1)/D1 with D1 and D2 the crown diameters of erizón in two consecutive years; calculated in high slope	0.109 ± 0.01 yr^{-1}	*Komac et al* (in press)
s_2	vegetative reproduction rate of erizón on grass sites	(D2-D1)/D1 with D1 and D2 the crown diameters of erizón in two consecutive years; calculated in low slope	0.061 ± 0.016 yr^{-1}	*Komac et al* (in press)
b_g	clonal reproduction rate of grasses on empty sites	1/time to colonize an empty site	½= 0.5 yr^{-1}	Personal observation
c	competition among erizón plants in the patch centre	Erizón mortality rate in the centre of a patch – erizón mortality rate at the edge of a patch	0.0015 ± 0.001 yr^{-1}	*Komac et al* (in press)
d_s	mortality rate of erizón	1/(life span)	0.028 ± 0.0005 yr^{-1}	*Komac et al* (in press)
d_g	mortality rate of grasses	1/(life span)	1/8 = 0.125 yr^{-1}	*Wildová et al. 2007*
θ	establishment rate of grass seeds on empty sites	1-(rock/grass) inside erizón patches	0.8 yr^{-1}	Field data observation

Legends

Figure 1. Conceptual graph showing the transitions between the different possible states of the model: occupied by a shrub (S); occupied by grasses (G) or empty (E). $W_{\sigma\sigma'}$ are the rates of the transitions between the states. Their mathematical expressions are given in the text.

Figure 2. Propagation of Erizón in a grassland. The initial condition corresponds to patches of shrubs (covering 10% of the matrix) in a matrix of grasses (80%) and empty cells (10%) (panel A single central shrub, panel D a group of shrubs). The lattices A, C, D, E are snapshots of the system at times t=0 and t=20. Dark green: shrub, light green: grass, white: empty. B) The growth of the shrub patch is followed through time [growth = log(shrub(i)/shrub(i-10))]. F) Global densities of shrub patches (panel D) (black) and grass (gray) cells through time. G) Local densities through time.

Figure 3. Effect of directional environmental change (via changes in the establishment parameters, β and s) on the shrub expansion. On the y-axis, β_1 varies from 7 until 1 and β_2 from 0.6 to 0, following values observed in the field. On the x-axis, s_1 varies from 0.05 until 0.16 and $s_2 = s_1 - 0.05$, following values observed in the field. For each combination of parameter values, the simulations started from an initial condition corresponding to panel δ of figure 2 and ran for 20 years. The slope of the increase was calculated on the second half of the time-series (i.e. the last 10 years of the simulation). In black: the population of erizón does not invade the system. In Green: the shrub population invades the system and the speed of the increase is faster when the color is greener.

Figure 4. Effect of frequency of shrub removal (by fire A, or mechanically B) and percentage of shrub area removed on the growth rate of the shrub population. Columns: frequency of removal (from every year at the bottom to every 10 years at the top of the diagram). Rows: percentage of shrub area removed, from 1% on the left to 100% on the right of the diagram. For each combination of frequency of shrub clearance and percentage of clearance area, the simulation was run for 20 year and the slope of the growth rate of the shrub population was recorded. Initial conditions corresponded to panel δ of figure 2. If the slope is positive, the shrub population increases despite management (in green); if the slope is null or negative, the shrub population is controlled and the management is successful (in black).

Figure 5. Combined effects of grazing and removal (by fire A, or mechanically B) on the growth rate of the erizón population. Columns: grazing pressure (from $h = 0.1$, 10% of the seedlings destroyed per year at the bottom to $h = 1$, 100 % of the seedlings destroyed per year at the top of the diagram). Rows: percentage of shrub area removed by fire every 5 years or mechanically every 3 years, from 0.05 (5%) on the left to 0.5 (50%) on the right of the diagram. For each combination of grazing pressure and percentage of area removed, the simulation was run for 20 year and the slope of the growth rate of the shrub population was recorded. Initial conditions corresponded to panel δ of figure 2. If the slope is positive, the shrub population increases despite management (in green); if the slope is null or negative, the shrub population is controlled and the management is successful (in black).

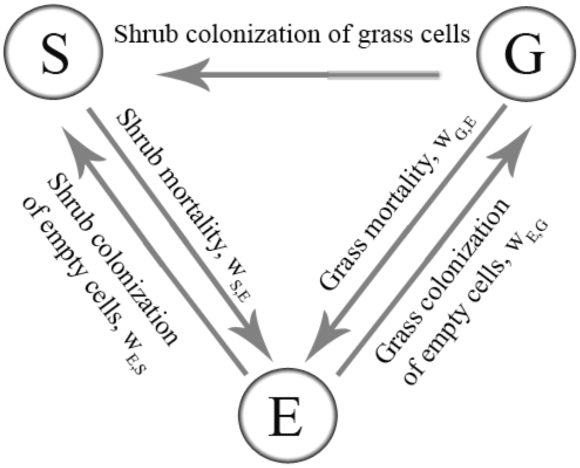
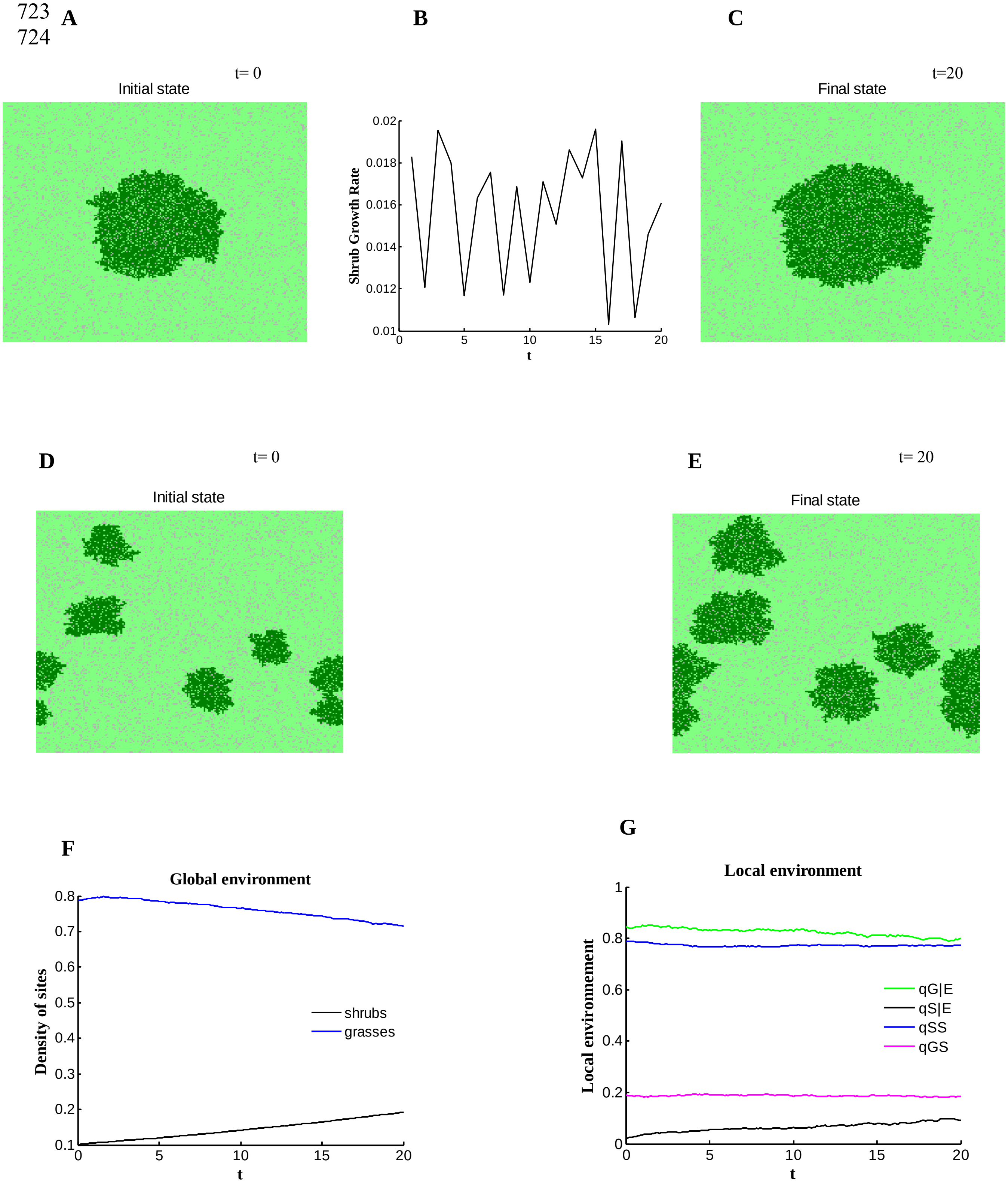

S
G
E
Shrub colonization of grass cells
Shrub mortality, $w_{S,E}$
Shrub colonization of empty cells, $w_{E,S}$
Grass mortality, $w_{G,E}$
Grass colonization of empty cells, $w_{E,G}$

Figure 1


A
B
C
t= 0
Initial state
0.02
0.018
0.016
0.014
0.012
0.01
0
5
10
15
20
Shrub Growth Rate
t
t=20
Final state
D
t= 0
Initial state
E
t= 20
Final state
F
Global environment
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
Density of sites
shrubs
grasses
0
5
10
15
20
t
G
Local environment
1
0.8
0.6
0.4
0.2
0
Local environmement
qG|E
qS|E
qSS
qGS
0
5
10
15
20
t

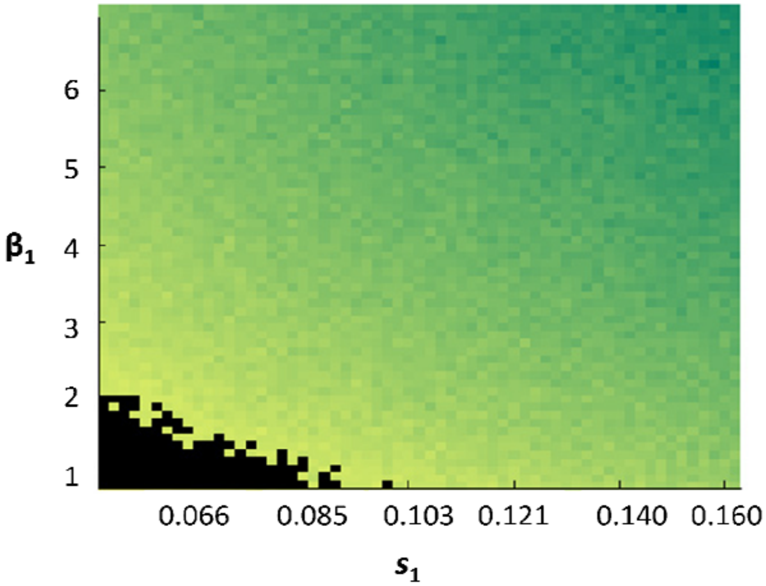


Figure 3

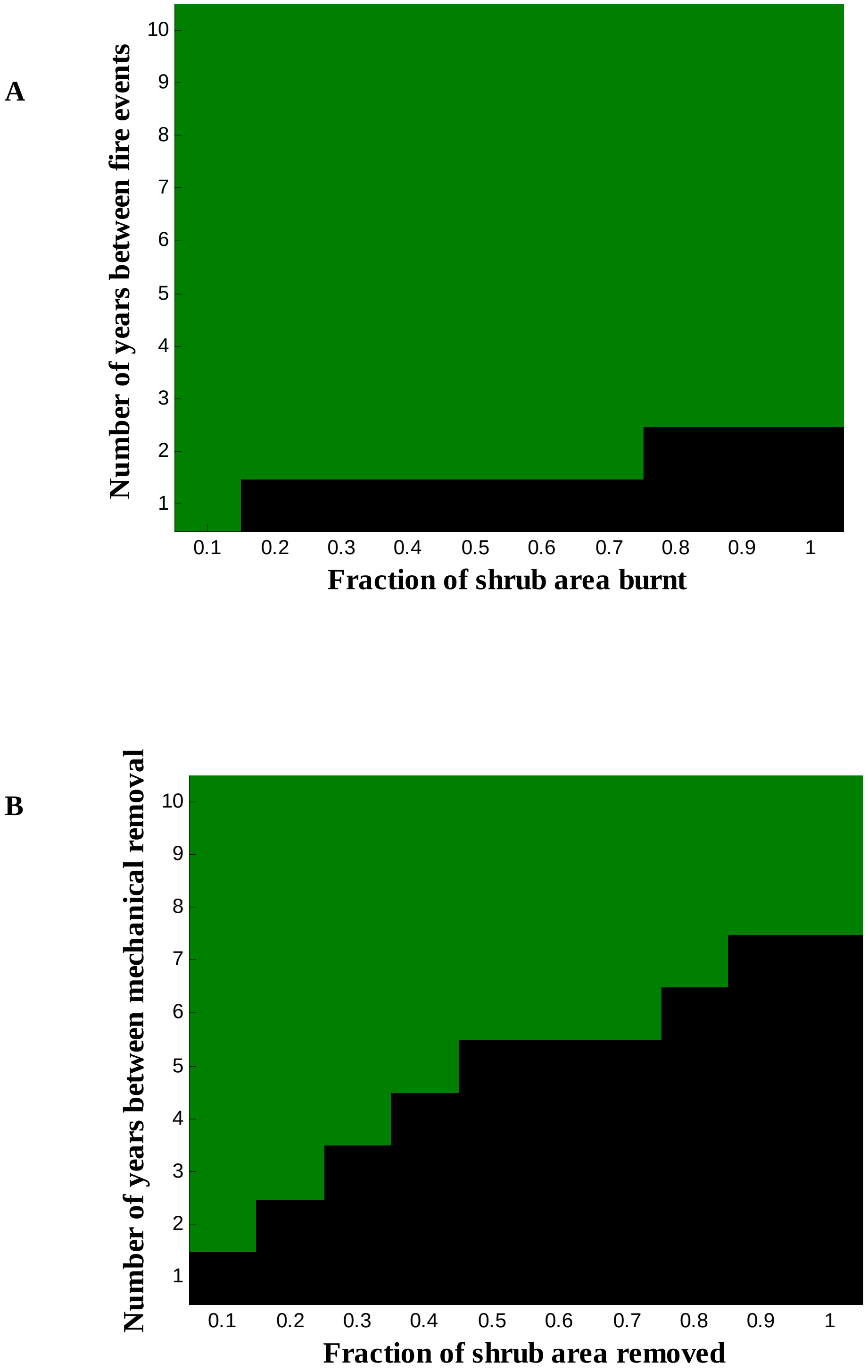

A
Number of years between fire events
10
9
8
7
6
5
4
3
2
1
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Fraction of shrub area burnt
B
Number of years between mechanical removal
10
9
8
7
6
5
4
3
2
1
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Fraction of shrub area removed

Figure 4

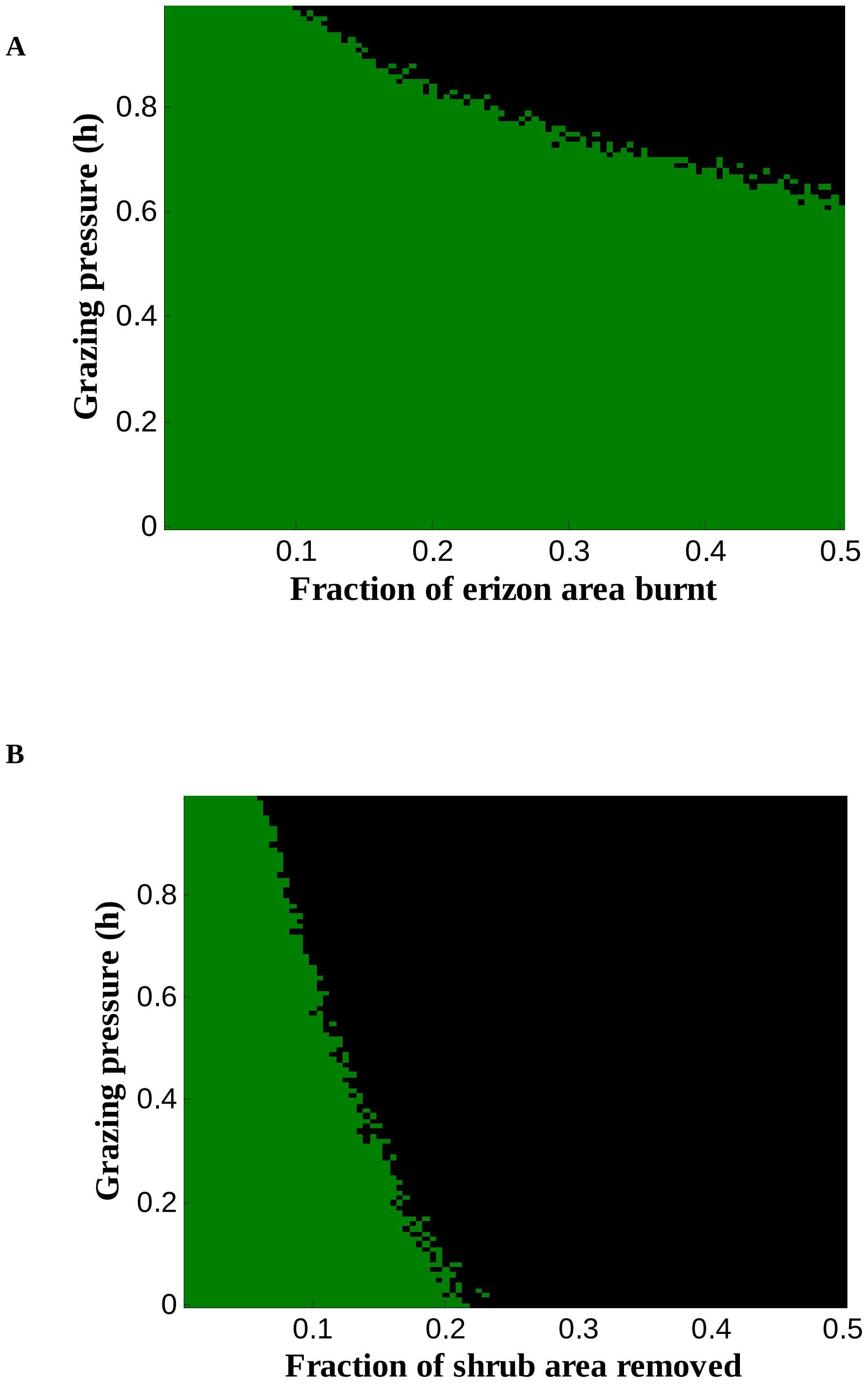

A
Grazing pressure (h)
0.8
0.6
0.4
0.2
0
0.1
0.2
0.3
0.4
0.5
Fraction of erizon area burnt
B
Grazing pressure (h)
0.8
0.6
0.4
0.2
0
0.1
0.2
0.3
0.4
0.5
Fraction of shrub area removed

Figure 5