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Landscape-scale positive feedbacks between fire and expansion of the large tussock grass, *Ampelodesmos mauritanica* in Catalan shrublands

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Abstract

In the northern Mediterranean Basin, agricultural land abandonment over the last century has resulted in increasing frequencies of very large, intense fires. In Catalonia (NE Spain) some fires have been locally associated with the expansion of the large, evergreen, resprouting tussock grass *Ampelodesmos mauritanica*. We tested the hypothesis of a positive feedback between the abundance of *A. mauritanica* and changing fire regimes.

We used permanent plots distributed across a natural gradient of density of *A. mauritanica* in the Garraf Natural Park near Barcelona. Total aboveground biomass nearly doubled from plots with low to high density through a combination of *A. mauritanica* replacing the biomass of other components of the community (predominantly native shrubs), and its absolute standing biomass increasing. The quantity of litter also increased. This increase in fuel load and changes in community functional composition resulted from the simultaneous decrease in shrub productivity and an increase in litter accumulation. Litter accumulation was the consequence of *A. mauritanica* litter decomposing 30% more slowly than that of shrubs. Under standardized conditions, *A. mauritanica* and its litter were considerably more flammable than any of the shrub species. This resulted in a more than 40-fold increase in calculated plot flammability from low-to-high-density plots.

Feedbacks, at the landscape scale, were then analysed using the landscape simulation platform LAMOS. Invasion success and contribution to community biomass of *A. mauritanica* increased with decreasing fire return intervals. Total area burnt in the landscape during each fire year was positively and exponentially related to the total biomass of *A. mauritanica*. Simulations showed that landscapes can abruptly switch from regimes of small localized to extensive fires as a result of the spread of *A. mauritanica*. Therefore, increases in fires under climate change represent threats not only through their direct impacts on ecosystems, but also by promoting invaders such as *A. mauritanica*, which have the potential to induce powerful feedforward processes and, thereby, fundamental changes to ecosystems.

Keywords: climate change, ecosystem function, fire, functional diversity, invasion, landscape model, land use change, Mediterranean shrubland

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Introduction

Invasions by non-native species or the expansion of indigenous ones can lead to marked changes in the composition and structure of plant communities, and potentially alter ecosystem functions such as primary production and nutrient cycling (D'Antonio & Corbin, 2002; Windham & Ehrenfeld, 2003; see also Levine *et al.*, 2003 for a synthesis). Plant invasions can also change disturbance regimes (D'Antonio, 2000) and, thereby, induce profound modifications of biodiversity and ecosystem functioning (Vitousek, 1990). Fire is a case in point. Effects of invasions on fire regimes, and their feedforward effects through modifications of entire ecosystems, have been reported and analysed extensively (see Brooks *et al.*, 2004 for an extensive review and excellent conceptual model).

Increases in fire frequency have often occurred when introduced grasses invade sites otherwise dominated by woody species because they create a more continuous, abundant and more flammable fine fuel bed. These effects result from increases in the production, a more continuous horizontal and sometimes vertical structure of biomass available to fire, in conjunction with the intrinsic fuel properties of grasses, which have a fine texture and, therefore, dry more quickly than native vegetation such as shrubs (Brooks *et al.*, 2004). Changes in fire regimes after invasion often follow on to complete alteration of the community, from woody species dominance to grassland (D'Antonio & Vitousek, 1992), although effects can be variable across invaded sites (D'Antonio *et al.*, 2000). For example, in the western USA, fire frequency has increased dramatically over the past century because of invasion of shrublands by annual grasses from the Mediterranean region (e.g. *Bromus tectorum*). This has resulted in widespread conversion of shrublands to grasslands with effects on biodiversity (e.g. Whisenant, 1989; D'Antonio & Vitousek, 1992). Likewise in Hawaii, introduced grasses have increased fire frequency more than threefold in seasonally dry shrublands and woodlands with large effects on biodiversity (Hughes *et al.*, 1991; D'Antonio & Dudley, 1994; Tunison *et al.*, 2001).

In addition to altering fire frequency, invaders can also increase fire intensity. This can in particular occur in habitats already shaped by fire (e.g. savannas and other dry woodlands), but with an invader, whether a new or already present life form, that is more productive than the native species it replaces and, thereby, increases fuel loads and packing in the ecosystem (Brooks *et al.*, 2004). These effects rely on the invader's ability to access more resources (e.g. through nitrogen fixation) and/or to turn them into more biomass and litter than the resident species (e.g. through more efficient resource economy).

In the northern Mediterranean basin agricultural land abandonment over the last century has resulted in increasing frequencies of very large, intense fires (Moreno *et al.*, 1998; Pausas, 2004). In Catalonia (NE Spain) some fires have been locally associated with the expansion of the large, evergreen, resprouting tussock grass *Ampelodesmos mauritanica* (Vilà *et al.*, 2001). *A. mauritanica* is distributed in coastal areas of the Mediterranean basin, eastwards to western Greece, but may not be native to Catalonia, where it may have been introduced from the Balearic Islands during the middle ages. Although records of this species exist from the 18th century, there is a perception by local managers and botanists that this species was becoming more abundant in the last decades of the 20th century. This grass appears to be expanding in areas with high fire frequencies (Vilà *et al.*, 2001), largely because of its reproductive pulses after fire (Vilà & Lloret, 2000a), and may produce nearly pure stands in sites previously occupied by a shrubby cover. A previous analysis using the Rothermel fire propagation model predicted increased fire risk in stands invaded by *A. mauritanica* and, thereby, potential for a fire–grass feedforward process (Vilà *et al.*, 2001).

This study further addresses the hypothesis of a positive feedback between *A. mauritanica* abundance and changing fire regimes in shrublands where this species occurs. This feedback would operate if the invasion increases the fire risk of the community where *A. mauritanica* is present, and the expansion of this grass species is also favoured by fire. A previous community modelling study suggested that life-history parameters of *A. mauritanica* and native species could be used to explain the increased occurrence of *A. mauritanica* and decreases in resprouting shrubs such as *Erica multiflora* under high fire frequencies (Lloret *et al.*, 2003).

Our general question was, therefore, broken down into four specific hypotheses.

1. Changes in the functional composition of the plant community because of *A. mauritanica* invasion increase biomass primary production and litter production.
2. Differences in litter quantity or quality affect litter decomposition rates, further increasing fuel loads.
3. These changes in community composition and litter accumulation have implications for the flammability of the plant community and may increase its fire risk.
4. Combined with the life-history characteristics of *A. mauritanica*, these changes in ecosystem properties lead to changes in fire regime and foster fundamental switches in landscape composition towards a degraded shrubland where grassy tussocks are the major component.

Hypotheses 1–3 were tested using permanent plots across a natural gradient of density of *A. mauritanica* in the Garraf Natural Park, where measurements of changes in community composition and ecosystem properties were conducted. Hypothesis 4, and hence our overall hypothesis, was tested using landscape simulations with the platform LAMOS (Lavorel *et al.*, 2000; Cousins *et al.*, 2003). Results are discussed from the perspective of fire management of Mediterranean ecosystems under global change.

Materials and methods

Study site and vegetation

During February 2000 we set up permanent plots to measure the effects of invasion by *A. mauritanica* on ecosystem properties in the Garraf Natural Park, 30 km to the south of Barcelona, Spain ('Garraf' hereafter). The dominant vegetation is a mosaic of *Pinus halepensis* forests and shrublands (*Quercus coccifera, Pistacea lentiscus, E. multiflora, Rosmarinus officinalis, Globularia alypum*). The dominant limestone substrate results in relatively high bare ground and a heterogeneous pattern of ground cover. The climate is typically Mediterranean (mean annual precipitation, 548 mm; mean annual temperature, 17 °C). The landscape is composed of a mosaic of sites that have not burnt in at least 40 years, dominated by mature *P. halepensis*, sites burnt in 1982 with regenerating *P. halepensis* amidst shrub cover with some *A. mauritanica*, and sites burnt both in 1982 and 1994, dominated by shrubs or *A. mauritanica* (see Lloret *et al.*, 2003 for a description of the abundance of the main species). The natural variation in *A. mauritanica* density at a twice burnt site was used to set up a natural gradient of *A. mauritanica* density. This site was homogeneous for soil type, slope aspect and fire history, with two large fires that swept through the entire area in 5–10 July 1982 (6945 ha) and 9–12 April 1994 (6804 ha). Since previous work at Garraf found no significant relationships between the density of *A. mauritanica* and site aspect, slope position or presence of rock outcrops (Vilà *et al.*, 2001), we assume that the variability in community structure and ecosystem function, within the study site, was largely because of the invasion by *A. mauritanica*. Furthermore, the fact that the hill slope was terraced minimized any variations in soils and other environmental parameters. Three sets of five plots, each of 36 m^2, were selected at random locations along the slope within Garraf Natural Park to replicate each of three treatment levels: (1) shrubland with no *A. mauritanica* present (none to a maximum of six individuals per plot); (2) shrubland with *A. mauritanica* present at medium density (an average of 21–29 individuals per plot); (3) shrubland with dense *A. mauritanica* cover (an average of 48–70 individuals per plot). It was assumed that this gradient of *A. mauritanica* density reflects colonization opportunity rather than an underlying gradient of site suitability for *A. mauritanica*. Evidence from the field suggests that *A. mauritanica* exhibits little site specificity within the study area (Lloret & Vilà, 2003; F. Lloret, unpublished). Rather, its abundance in sites that have been repeatedly burned has been attributed to the combination of a very strong resprouting capacity, a high seed production from resprouting individuals within 2 years after fire and large recruitment opportunities for these numerous seeds to establish on bare ground created by fire (Vilà & Lloret, 2000a).

Measurements of ecosystem properties

Standing biomass and fuel accumulation. Aboveground primary production was measured over a 1 year period, from March 2000 to March 2001, by harvesting aboveground biomass in each of the 15 plots. Each of the plots was subdivided into thirty-six $1 \times 1\,m^2$ subplots, with a central, undisturbed area left for microclimatic measurements and litter decomposition trials. Four of the 1 m^2 subplots selected at random in the plot were harvested during late winter/early spring (March 2000), four after spring growth (June 2000) and four again after one full season of growth (March 2001). The large plot size and numerous replicates were required to overcome the marked heterogeneity of the shrubby vegetation at the field sites. This level of replication appeared adequate in the view of relatively low within treatment variance in biomass estimates for each of the sampling dates (coefficient of variance less than 10%). At each harvest, the live biomass was separated into morphological groups (*A. mauritanica*, shrubs, grasses other than *A. mauritanica* and herbs) and litter, and all material was oven dried at 60°C until stable mass was reached, then weighed. The annual biomass accumulation was calculated as the difference between the final and first harvests. Patterns of annual accumulation paralleled patterns of production measured over the spring 2000, and are, therefore, the only data presented in this paper. Specific ANPP, defined as the ratio between the estimated net primary productivity and the initial standing biomass (Garnier *et al.*, 2004), was also calculated to assess the effects of *A. mauritanica* density on the per unit mass efficiency of production of native shrubs and of *A. mauritanica*.

Litter decomposition. Potential litter decomposition rates were assessed in two ways. First, we used an indicator of potential rates of litter decay in plots with different levels of invasion by determining the rate of decay of four standardized wood samples that were placed in mesh bags and fastened to the soil surface within each plot during February 2000. The weight of these samples was determined prior to being placed in the field. These were recovered in February 2001 and reweighed after cleaning and oven drying. Second, in October 2000, we placed in each of the five medium-density plots, litter bags containing dead leaves of either *A. mauritanica* or of a representative mix of the dominant shrubs of the communities (*G. alypum*, *R. officinalis*, *E. multiflora*). These were recovered after a full year of decomposition in September 2001, oven dried and weighed to determine relative mass loss. Comparison of decomposition rates across samples containing shrub or *A. mauritanica* litter was used to assess the effects of litter quality on decomposition rates.

Changes in each of these measured parameters (response variables) in response to *A. mauritanica* density were analysed with the statistical package GENSTAT 5.3 (Payne *et al*., 1993) using a one-way ANOVA with plot density treatment as an explanatory variable. All data were averaged and analysed at the plot level to ensure the independence of each replicate. Data were log + 1 transformed where required and the suitability of transformations checked by examining the residuals.

Flammability. Standardized measurements of the relative flammability of litter and live biomass of *A. mauritanica* and other common species from the communities (*E. multiflora*, *G. alypum* and *R. officinalis*) were obtained using laboratory measurements in late September 2001 at the INRA forest fire prevention facility (Ruscas, Var, France) and using the approach to flammability described by Valette (1997). For 25 replicate samples of each species, a standard mass (1 g) of structurally intact plant material (5–7 cm long leaves or branches) was placed within 24 h of harvest at 3 cm from a radiant heat source, calibrated to give out exactly 420 °C. Firstly, the period of time before the sample ignites was recorded (inflammation delay, ID). This provides a measure of the ease with which a species ignites. Secondly, the duration during which the sample burns with a flame was recorded (inflammation duration), which is a measure of how long a species will continue to burn. Thirdly, the intensity with which the sample burns, measured from the height of the flame produced on a standardized scale of 1–5, was recorded, and a measure of the amount of energy released through the combustion of a species provided. Details on the equipment and methodologies can be found in Valette (1997).

Using these measurements, we calculated the flammability of each of the communities representing the different levels of *A. mauritanica* density as the mean across species of specific flammability weighted by their relative biomass contribution in that community. Specific flammabilities were assumed to be equal to the inverse of the ID:

$$\text{Flammability (community)} = \sum_{\text{species}=1\ldots n} 1/\text{ID}\,(i).\text{Biomass}\,(i).$$

Simulating changes in fire and landscape dynamics

Fire and landscape dynamics associated with the expansion of *A. mauritanica* in the Garraf shrublands were simulated using the landscape simulation platform LAMOS (Lavorel *et al*., 2000). LAMOS was implemented with the following options.

The landscape was represented using a resolution of 20 m for a map of 50×50 pixels, representing a total area of 100 ha. For simplification, we assumed a homogeneous substrate and a flat topography. If the life histories and ecosystem effects of the different species were enough to explain the dynamics of invasion through a positive fire feedback loop, then we would expect that these processes could take place without the need to assume environmental heterogeneity.

Succession was simulated using the FATE method (Moore & Noble, 1990). FATE simulates community composition at the scale of pixels, where several plant functional types (PFT) may coexist. In essence, this method simulates fire response, recruitment and light competition among PFT as a function of a limited set of life-history parameters, or vital attributes (Noble & Gitay, 1996). Rather than modelling the dynamics of each individual plant, FATE focuses on groups of individuals with the same effective age within a PFT (cohorts). In the model, plants pass through four discrete life stages: propagules, germinants, immature plants and mature plants. Each life stage has different responses to environmental conditions and to disturbance. To account for these responses FATE is divided into three submodels: life history, competition and disturbance. A detailed description and graphical depiction of the implementation of FATE in LAMOS can be found in Cousins *et al*. (2003). Life history, disturbance response and competition parameter values were those used by Lloret *et al*. (2003) to implement a patch-scale version of FATE for the Garraf shrubland/*A. mauritanica* system.

In LAMOS succession and disturbance modules are coupled through biomass, as fires for example need fuel. Under the FATE option of LAMOS, biomass is generated by using a step function according to life stage and environmental quality. Here, the biomass of adult stands was parameterized using our field measurements for low (assumed to represent nearly pure cultures of the native shrubs) and high (assumed to represent the biomass achievable by *A. mauritanica*) invasion densities. The biomass of juveniles was then calculated as a fixed, PFT-specific proportion of adult biomass. Finally, each life stage was characterized by the allocation of its biomass across three vertical strata. The bottom stratum was also included when relevant (e.g. *A. mauritanica* litter accumulation). Flammability of each individual pixel (i.e. community) was then calculated as the sum across all life stages present and strata of the specific flammabilities of each stratum (as obtained from the standardized measurements) weighted by the biomass of the PFT present in this stratum.

Fire was simulated using a cellular automaton stochastic spreading method adapted from that used by Hargrove *et al.* (2000). At each annual time step, the occurrence of a fire year was determined using a uniform probability distribution, with a mean frequency (or fire return interval) fixed for a given simulation. Then, a fixed number of initiation points (representing a fixed proportion of the landscape) were located randomly across the landscapes. From each initiation point actual ignition was first decided depending on the flammability of the community present in that pixel, made to represent the intensity of a starting fire, as our experimental data indicated a good correlation between flammability and intensity (Lavorel *et al.*, unpublished data). Ignition and, hence, possibility of spread to neighbouring pixels, was activated if that intensity exceeded a threshold set as a model parameter. Then, spread to each of the eight neighbours was a random decision with a probability equal to the ignition intensity threshold. The same process was then repeated for each of the neighbours selected for spread, until a number of spreading steps fixed for the simulation was reached.

The second spatially explicit landscape-scale process taken into account in the model was seed dispersal away from parental sites. We used an exponential decay around cells where a PFT is present as an adult. Spatial distributions of seeds produced in a pixel were captured by two parameters: the mean dispersal distance, representing mainly short distance dispersal, and the fraction of seeds dispersed to longer distances (see Clark *et al.*, 1999). The intensity of the seed rain was determined by the fecundity of PFTs, calculated as the product between their potential fecundity and their relative abundance in the pixel. These traits were estimated from measurements in Garraf (Vilà & Lloret, 2000a) and literature data.

The parameter values used for the simulations are summarized in Table 1. These were obtained directly from our measurements, as well as from previous publications with data on the history of *A. mauritanica* collected at Garraf.

A series of simulations experiments were conducted in order to test the effects of frequency of fire ignition on the persistence and abundance of *A. mauritanica*. Simulations were started on maps representing a mixed shrubland with three functional types: seeders with resprouting capacity labelled 'Erica', obligate seeders labelled 'Rosmarinus' and obligate seeders with fire-broken dormancy labelled 'Cistus'. Within this shrubland, 25 randomly distributed pixels, representing 1% of the total area, were initiated with a low density of adult *A. mauritanica* within the shrub matrix. Simulations were then run for landscape-scale ignition frequencies ranging from annual to every 50 years. For each of these, 25 simulations were run for 100 years, and the persistence of *A. mauritanica* as well as its relative contribution to total community biomass assessed on the mean across simulations for the final 50 years. The robustness of these results against initial conditions was checked by running an additional set of simulations with a constant number of initial invasion points (1% of the map) but different degrees of spatial aggregation. Maps with invasion points aggregated into 1×2 or 5×5 clusters were generated using the program RULE (Gardner, 1999). For each of these maps, we ran simulations for three different fire return intervals (FRI) (1, 10 and 20 years). The parameters values used in the simulation experiments are presented in Table 2. Finally, to address the hypothesis of a positive feedback between *A. mauritanica* invasion and fire regimes we conducted a regression analysis of the response of total area burned per fire year to total biomass of *A. mauritanica* over the landscape.

Results

Changes in ecosystem properties along a gradient of A. mauritanica density

Community composition and fuel loadings. The presence of *A. mauritanica* significantly increased the total aboveground biomass of a site, with a near doubling in high- vs. low-density plots (Fig. 1). This increase occurred through a combination of two processes. First, *A. mauritanica* replaced the biomass of other components of the community (predominantly native shrubs, but also some grasses and herbs), as evidenced by a significantly decreasing biomass other than *A. mauritanica* ($P < 0.05$) with increasing *A. mauritanica* density. Second, the absolute standing biomass of *A. mauritanica* increased significantly. In fact, much of the increase in total biomass in high-density sites occurred

Table 1 Parameter values used for simulations under LAMOS

Functional group		Erica	Rosmarinus	Cistus	Ampelodesmos
Process	Parameter				
Life history	Life span (years)	40	25	15	25
	Maturation age (years)	7	4	3	5
	Seed bank	None	None	10 years	None
	Potential fecundity (seeds/pixel)	300	200	200	10 000 when masting
Dispersal	Fraction seeds to nearest neighbours	0.73	0.73	0.73	0.134
	Distance for 90% seeds	3	3	3	10
Light response	Germination fraction at medium light	Low	Low	None	Medium
	Germination fraction at high light	High	High	High	Very high
	Minimum light intensity for survival of immature	High	High	High	Medium
	Minimum light intensity for survival of adults	High	Medium	High	Medium
Biomass	Potential biomass ($t\,ha^{-1}$)	1.0	1.0	0.8	1.0
Fire response	Resprouting	Adults >8 years for mild or medium intensity	None	None	Adults >5 years for all intensities, immatures (2–5 years) for mild or medium intensity
	Stimulation of germination	None	None	Dormancy break: high for all intensities	Postfire masting
Flammability	Ground stratum	0.13	0.08	0.17	0.33
	Upper stratum	0.13	0.03	0.07	1.0

Parameter names and scales are as in FATE (Moore & Noble, 1990) for the succession module. Parameter values were obtained from Lloret *et al.* (2003).

Table 2 Fire and landscape map parameters used in the simulation experiments

Parameter	Values used in simulations
Fire return interval (landscape scale) (years)	1, 2, 3, 5, 10, 15, 20, 30, 40, 50
Attempted initiations per time step	100
Propagation intensity threshold	0.01
Number of propagation steps	100
Intensity thresholds	
Mild	0.1
Medium	0.5
Severe	0.75
Initial invasion density	0.01 (25 pixels)
Initial invasion pattern	Initial invaded patch size
Random	1 × 1
Aggregated	2 × 2
Single patch	5 × 5

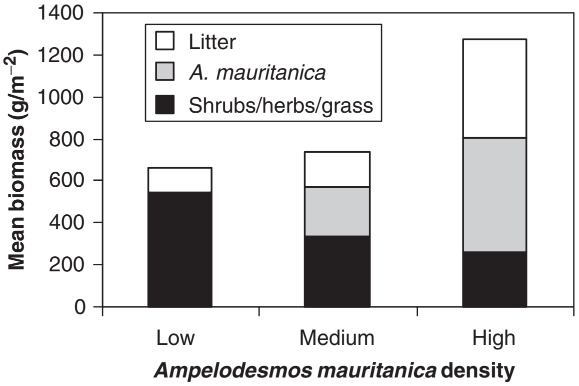

Fig. 1 The mean total biomass, the mean of biomass other than *Ampelodesmos mauritanica* (i.e. shrubs, herbs and other grasses), the mean biomass of *A. mauritanica* and the mean biomass of litter for each of the three *A. mauritanica* densities during the summer harvest. Total mean biomass was significantly higher in the high-density plots than in the medium- and low-density plots (one-way ANOVA, $P < 0.001$). Data from the winter harvest mirrored the trends identified here.

in addition to other components of the vegetation, and, hence, the morphological/functional composition of the community was considerably modified by the invasion. The quantity of litter also increased significantly with increasing *A. mauritanica* density ($P < 0.001$), leading to much higher total fuel loads in high than in low invasion plots.

Fuel accumulation. Annual shrub productivity decreased significantly with increasing *A. mauritanica* density, while litter accumulation increased significantly ($P < 0.05$) (Fig. 2). Interestingly, the productivity of *A. mauritanica* and that of the total live community peaked at medium invasion densities. Further increases in fuel accumulation occurred at high invasion density solely through the accumulation of litter, while the productivity of both *A. mauritanica* and shrubs was not detectable. Accordingly, the specific aboveground net primary productivity of all components of the community decreased significantly with increasing invasion density (data not presented).

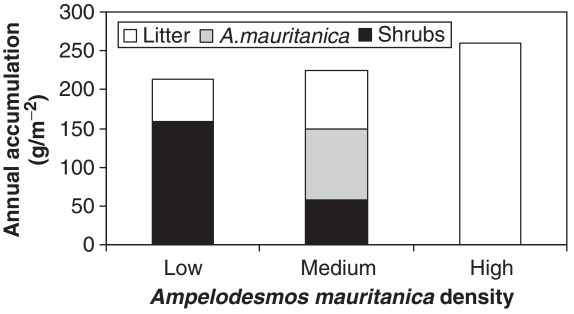

Fig. 2 The annual biomass accumulation (productivity) of *Ampelodesmos mauritanica*, shrubs and litter between the different *A. mauritanica* densities. Annual production of shrubs ($P < 0.05$) and litter ($P < 0.01$) were significantly different between the low- and high-density plots (one-way ANOVA).

Litter decomposition potential. Over 1 year the rate of decomposition of standardized wood samples reached nearly 15%. There was no significant difference in the rates of decomposition and, therefore, in the decomposition conditions between the plots with differing *A. mauritanica* densities in spite of measured differences in superficial soil moisture and temperature (K. Grigulis, unpublished data). The litter bags placed in the medium-density plots showed that litter of *A. mauritanica* decomposed at a 30% slower rate than that of the resident shrubs (23% as compared with 32% mass loss; $P > 0.05$). This dynamic, along with the considerable annual production of litter, explains the considerable litter accumulation observed with increasing density of *A. mauritanica*.

Changes in flammability. A. mauritanica ignited much more rapidly than any of the shrub species, especially its dry litter, and once burning produced a more intense flame, again especially as litter. Combined with changes in community composition (relative biomasses of different morphological groups) these changes in flammability resulted in dramatic changes in calculated plot flammability, with a more than 40-fold increase from low- to high-density plots (Fig. 3). Medium-density plots tended to only be slightly more flammable than low-density plots, a result that

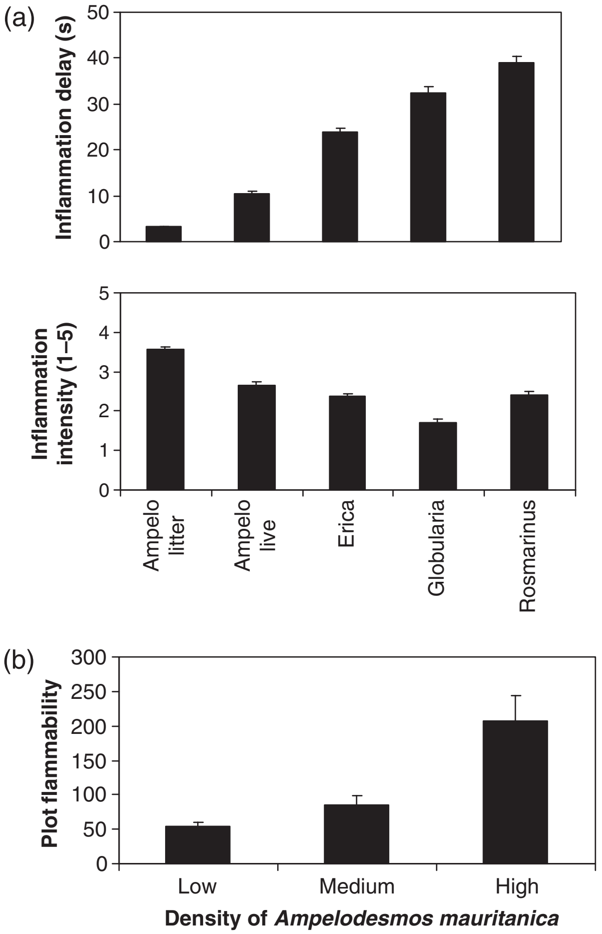

Fig. 3 Individual species flammability as measured by mean inflamation delay and inflammation intensity (a) and mean calculated plot level flammabilty (b). Plot level flammability was significantly higher in high-density *Ampelodesmos mauritanica* plots than in medium- or low-density plots (one-way ANOVA, $P<0.01$). Error bars are standard errors.

emphasizes the effect of the considerable litter accumulation in high-density plots.

Simulated dynamics of landscape patterns and fire regimes under different ignition scenarios

Invasion success, as measured by persistence and expansion of *A. mauritanica* and its equilibrium contribution to community biomass, increased with decreasing FRI (Fig. 4). Successful invasion in 100% of the runs was simulated for FRI shorter than 10 years. Invasion failure, estimated through the proportion of runs where *A. mauritanica* went extinct by the end of the simulation, increased (sigmoidally) as a function of FRI (Fig. 4a). The specific fire sequence of each simulation, however, had large stochastic effects, causing extinctions for individual simulations with intervals between fires greater than ca. 30 years. Total community biomass over the landscape peaked for 10-year FRI, as a result of the coexistence between shrubs and *A. mauritanica* (Fig. 5). Shorter FRI resulted in less total biomass because of lack of time between fires for biomass build up, although the contribution of *A. mauritanica* and 'Cistus' increased with shorter intervals (Fig. 4b). Indeed, the relative abundance of *A. mauritanica* increased markedly at the expense of native shrubs other than fire-stimulated seeders ('Cistus') when FRI were less than 10 years, making up to 50% of total community biomass (Fig. 4b). For FRI of 5 years or less, 'Cistus' contributed to over 20% of community biomass, but this contribution dropped for annual fires, where regeneration intervals were too short for this species that relies solely on seeds, while *A. mauritanica* was able to gain an even greater part of the vegetation thanks to its resprouting ability. 'Cistus' disappeared for FRI larger than 20 years. In this scenario, 'Rosmarinus' and 'Erica' accounted for the majority of total biomass, with *A. mauritanica* accounting for less than 10%. These patterns were robust to initial conditions, as invasion success was not significantly affected by initial spatial patterns of *A. mauritanica*, whatever the ignition frequency (data not shown).

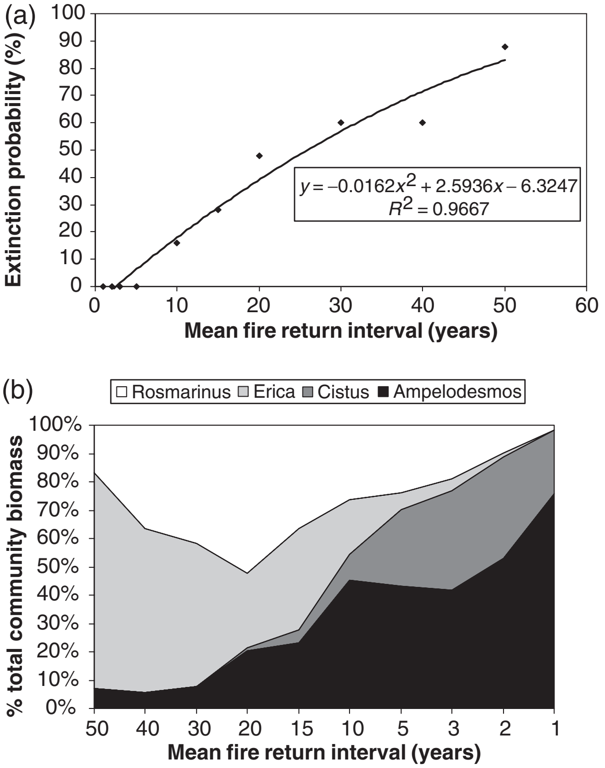

Fig. 4 Effects of fire return interval on (a) risk of extinction and (b) final abundance of *Ampelodesmos mauritanica*.

Total area burnt in the landscape during each fire year was positively and exponentially related to the

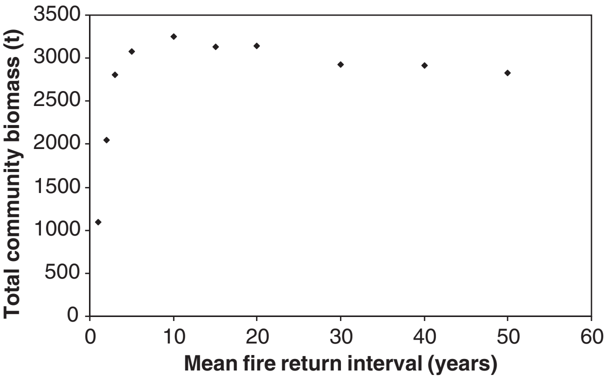

Fig. 5 Effects of fire return interval on total community biomass.

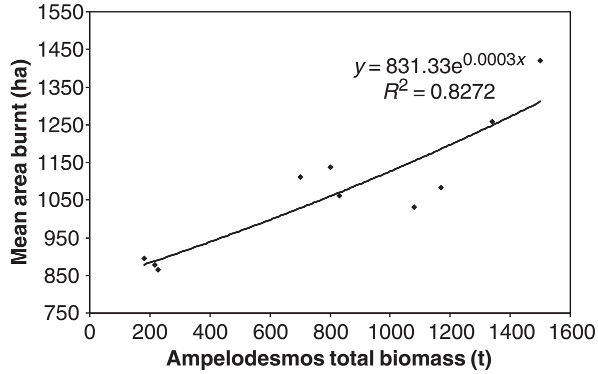

Fig. 6 Effect of total biomass of *Ampelodesmos mauritanica* on mean area burnt during fire years.

total biomass of *A. mauritanica* present in the landscape (Fig. 6). In addition, the clustering of values for total area burned indicated that landscapes can abruptly switch from regimes of small localized to medium and then landscape-wide fires as a result of the spread of *A. mauritanica* under decreasing FRI. Conversely, the total biomass of *A. mauritanica* on the landscape was a quadratic function of total area burned annually ($R^2 = 0.841$; Am biomass $= -0.0028$ area burned$^2 + 8.82$ area burned-5306). These patterns were explained by the increasing connectivity of highly flammable vegetation, as *A. mauritanica* becomes more frequent in the landscape, and the direct positive effects of fire on the demography of *A. mauritanica*.

Discussion

Effects on community composition and ecosystem properties

The invasion of shrublands by *A. mauritanica* produced a series of spectacular modifications in community structure and ecosystem properties, which translated to changes in vegetation and fire regimes at the landscape scale.

There was evidence of a significant negative association between increasing *A. mauritanica* density and biomass of other components of the community, particularly shrubs. The lower shrub biomass in invaded plots may reflect cause rather than effects of invasion, suggesting that after fire *A. mauritanica* may establish more easily in landscape patches with more bare ground (i.e. lower shrub biomass). In the short term, *A. mauritanica* may then mostly add to the existing community by filling bare ground gaps, and therefore not compete with resident species. This explanation was supported by the nonsignificant effect of *A. mauritanica* removal on the growth and water potential of native shrubs after fire (Vilà & Lloret, 2000b). As adding an invader increases community biomass it is plausible to think that the invading species can tolerate the native vegetation and that the invader is utilizing previously unused resources (Vilà & Weiner, 2004). On the other hand, once established, the much greater amount of standing biomass, and especially litter, resulting from invasion by *A. mauritanica* is likely to considerably affect the regeneration of other species through the changes in microclimatic parameters such as light levels, temperature and soil moisture. Although no significant evidence of effects of *A. mauritanica* on shrub seedling recruitment was found at the earlier stages of the succession after fire (Vila & Lloret, 2000b), more intense competitive interactions can be expected with increasing adult size and as the canopy closes. Indeed, decreases in specific ANPP with increasing density of *A. mauritanica* suggest that while standing biomass of shrubs only slightly decreased from medium to high invasion density plots, their efficiency at producing biomass decreased linearly with increasing density of *A. mauritanica*. This may suggest negative effects at the adult stage (e.g. through underground and/or light competition), which remain to be tested.

These results are overall consistent with effects observed in a range of systems invaded by grasses. In semiarid shrublands of the western USA, invasion by *B. tectorum* (Ogle *et al.*, 2001) and *Agropyron cristatum* (Smoliak & Dormaar, 1985; Redente *et al.*, 1989) resulted in significant increases in standing biomass and aboveground productivity. Likewise, invasion of South American savannas and forest edges by *Melinis minutiflora* significantly affected standing biomass and was, therefore, expected to contribute to increasing fire danger (Barger *et al.*, 2003; Hoffman *et al.*, 2004). As in these systems, we observed an increase in horizontal fuel continuity, with *A. mauritanica* initially filling bare ground rather than excluding native shrubs.

Contribution to fire risk would therefore be not only through biomass accumulation, but also by facilitating fire spead with a more continuous fuel bed.

The increased input of litter into the community because of the abundant production by *A. mauritanica*, coupled with the decreased quality of decomposing material, and, hence, the decreased rates of decomposition, resulted in a considerable accumulation of dead material in invaded ecosystems. Although several studies have reported litter accumulation as a result of grass invasion (e.g. Lenz *et al*., 2003; Hoffman *et al*., 2004), only few direct assessments of decomposition rates have been carried out (van Vuuren *et al*., 1993; Ehrenfeld *et al*., 2001; Mack *et al*., 2001; Ehrenfeld, 2003; Mack & D'Antonio, 2003). Slow rates of decomposition of invading perennial grasses are likely to have long-term ramifications for nitrogen mineralization and, hence, soil fertility (Mack *et al*., 2001; D'Antonio & Corbin, 2002).

Furthermore, we showed that *A. mauritanica* burns more easily, quickly and hotter than the native shrub species. These results are consistent with the predictions of rates of fire spread and fire intensity obtained with the Rothermel model using basic fuel properties such as fuel diameter (Vilà *et al*., 2001). Our results therefore corroborate other empirical studies of the mechanisms through which grass invaders impact ecosystem structure and function, and how these changes lead to increased flammability, and, therefore, fire frequency, as well as increases in fire spread and intensity (see reviews by D'Antonio & Vitousek, 1992; D'Antonio, 2000; Levine *et al*., 2003; Brooks *et al*., 2004).

In summary, *A. mauritanica* significantly increases the fire risk of the Garraf community through a series of effects on ecosystem properties. *A. mauritanica* produces major increases in total biomass and litter of communities. This additional litter decomposes more slowly than the original litter. Both this persistent litter and live *A. mauritanica* are significantly more flammable than the coexisting shrub species, resulting in a considerable increase in flammability of the community overall. This series of ecosystem effects may be linked with changes in plant functional traits between the native shrubs and the grass invader (Lavorel & Garnier, 2002). Indeed, *A. mauritanica* has a higher leaf dry matter content than native shrub species (Garnier, Lloret *et al*., unpublished data), which explains slower decomposition (Cornelissen *et al*., 1999; Garnier *et al*., 2004) and higher flammability (Whelan, 1995 and references therein; Lavorel *et al*., unpublished). Similar effects of invasions on disturbance regimes, with feedforward loops involving modifications of community composition and ecosystem functioning, have also been reported in the case of invasions of pastures by large unpalatable perennial tussocks. Both through the loss of ground cover by palatable species and changes in mineral resource dynamics resulting from their ecophysiology, they can change fundamental aspects of the ecosystem such as water retention, nutrient cycling and soil stability (Campbell & Vere, 1995; Moretto & Distel, 1997; Moretto & Distel, 1999; McIntyre *et al*., 2002).

Landscape-scale feedbacks

Simulations of landscape vegetation and fire dynamics based on our experimental results, as well as additional sensitivity analyses not presented here, showed that these were strongly driven not only by the life history of *A. mauritanica* previously documented at the Garraf site (Vilà *et al*., 2001), but also by fire regimes, which are the direct results of the parameters measured in this study: biomass and litter accumulation, and specific flammabilities.

The continued persistence and further invasion by *A. mauritanica* in the landscape required FRI shorter than 10 years, a value similar to that obtained by Lloret *et al*. (2003) for patch scale simulations with the FATE succession model. The patterns of community composition that we simulated by taking into account spatial processes such as seed dispersal and fire spread match generally those described by the application of FATE in the patch-scale approach. However, the landscape approach allowed for a greater contribution by the native shrubs to persist until shorter fire return intervals. This can be easily explained by the existence of fire refugia, where less flammable native shrubs may be able to persist in spite of relatively frequent ignitions in the landscape.

FRI of about 10 years are well within the range currently experienced in Garraf, confirming that recurrent fires may indeed be responsible for the recently observed expansion of *A. mauritanica* (Vilà & Lloret, 2000a; Vilà *et al*., 2001). Our simulations showed no significant effects of the initial spatial pattern of invasion suggesting that even small populations of *A. mauritanica* scattered in the landscape have a high potential to lead to rapid spread of the species with increasing frequency of ignitions. This suggests that control measures aiming at reducing large contiguous populations alone are unlikely to contain the continued invasion.

The simulations showed a nonlinear positive relationship between the total biomass of *A. mauritanica* on the landscape and fire extent. Landscapes can therefore switch from limited to extensive fires as a result of the invasion by *A. mauritanica*. Because fire in turn favours the demographic growth of *A. mauritanica* (Vilà *et al*., 2001), and the accumulation of large quantities of highly flammable fuel (this study), the landscape soon enters a positive feedback loop. Increasing density of *A. mauritanica* leads to ever greater fires, and consequently more frequent return of fire at any given point in the landscape, further enhancing local population growth and establishing an invasive plant/fire regime cycle (Brooks *et al*., 2004).

Conclusions

Overall, by combining field and simulation approaches we have demonstrated that positive feedbacks among grass invasion and fire are not only explained by local ecosystem effects enhancing flammability (e.g. D'Antonio, 2000), but can be further amplified by landscape-scale processes. To our knowledge, this is the first study that explicitly links patch scale effects of invasion on ecosystem structure and function with landscape-scale processes.

For a given climate scenario, human impacts may enhance ecosystem effects both through direct impacts on disturbance regimes (e.g. fire ignition) and indirect effects through changes in vegetation composition (i.e. promoting biological invasions; Dukes & Mooney, 1999). In Catalonia recent increases in fires, which have been related to ongoing climate change (Piñol *et al*., 1998; Pausas, 2004), represent a definite threat to Mediterranean shrublands, not only through their direct impacts on ecosystems, but also through their possible promotion of invaders such as *A. mauritanica*, which have the potential to induce powerful feedforward processes, and thereby cause fundamental changes to ecosystems (Vitousek, 1990). Such changes, involving threshold phenomena and feedback loops, require intensive management intervention to potentially reverse (Brooks *et al*., 2004), and represent considerable challenges to understanding and forecasting global change effects (Steffen *et al*., 2004).

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