

Seed supply, drought, and grazing determine spatio-temporal patterns of recruitment for native and introduced invasive pines in grasslands

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ABSTRACT

Aim The rate of grassland invasion by trees depends on the ability of the species to invade, i.e. their invasiveness, and on the susceptibility of the environments to invasion, i.e. their invasibility. Knowledge of the invasiveness of native and introduced tree species and of the environmental factors that contribute to invasibility is necessary to understand landscape evolution and assess required management measures. Our main aim was to explore this by estimating the separate effects of propagule pressure and environmental factors on the spatio-temporal patterns of sapling recruitment, a key stage in the tree life cycle.

Location Causse Mejean calcareous plateau (southern France).

Methods The effects of seed supply and environmental variables (grazing, geological substrate, and duration or intensity of drought) on the spatio-temporal patterns of sapling recruitment were assessed for the native Scots pine (*Pinus sylvestris* L.) and the introduced black pine (*Pinus nigra* Arn. ssp. *nigra*). Estimates were derived by inverse modelling with data of locations and ages of 4- to 20-year-old saplings and seed-bearing trees in 32 sites. Yearly indices of drought were derived from a soil–water content model.

Results For both species, seed supply was as important as the whole set of environmental factors in explaining sapling recruitment rates. Grazing and the duration of drought from July to August decreased sapling recruitment rates, which were also lower on hard limestone than on dolomite. Dispersal distances and effective fecundities were higher for the introduced *P. nigra*, which was less susceptible to drought but more affected by grazing than the native *P. sylvestris*. In grazed grasslands, shrubs facilitated sapling establishment of both species.

Main conclusions This study shows how seed supply and environmental factors shape spatio-temporal patterns of sapling recruitment for trees invading grasslands. Implications for landscape evolution and management, of the difference in invasiveness of the two pine species and of the hierarchy of environmental factors in determining invasibility, are discussed.

Keywords

drought, grazing, invasion, inverse modelling, *Pinus nigra*, *Pinus sylvestris*

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INTRODUCTION

Invasion of grasslands and savannas by native and alien woody species is an increasingly global ecological phenomenon (Scholes & Archer, 1997; Richardson & Higgins, 1998; Van Auken, 2000; Richardson, 2006). It happens mostly because of the introduction of exotic trees by humans and the release of ecological constraints owing to changes in climate, grazing pressure, fire

regime, and/or cultivation practices (Richardson & Bond, 1991; Richardson *et al.*, 2000; Van Auken, 2000; Roques *et al.*, 2001; Wilmhurst *et al.*, 2004).

Rates of invasion depend on the ability of the species to invade, i.e. their invasiveness, and on the susceptibility of the environments to invasion, i.e. their invasibility (Richardson & Pyšek, 2006). Variation in invasiveness results from several key traits. For instance, in *Pinus*, one of the most invasive tree genera

(Richardson *et al.*, 1994; Richardson, 2006), a short juvenile period, a high relative growth rate, and a low seed mass are good predictors of invasiveness (Grotkopp *et al.*, 2002; Richardson & Rejmánek, 2004). Variation in environment invasibility results mainly from abiotic factors, like climate, and from natural or human disturbance (Roques *et al.*, 2001; Rouget *et al.*, 2001; Thuiller *et al.*, 2006). Native and exotic species can differ in their invasiveness and in their response to environmental conditions, which can translate in dramatically different invasion rates (Siemann & Rogers, 2003). Notably, changes in climate or disturbance regime are generally expected to benefit the pioneer introduced species, whereas natives species may be less adapted to the modification of local conditions, especially when they are located at the limits of their distribution ranges (Dukes & Mooney, 1999; Gaston, 2003). Better knowledge of the invasiveness of native and introduced tree species and the factors contributing to environment invasibility would help our understanding of landscape evolution and the assessment of required management measures.

One way to address these two issues, tree invasiveness and environment invasibility, is to analyse the spatio-temporal patterns of sapling recruitment, i.e. the production of new saplings in the population, which is usually the major demographic filter for woody species (Grubb, 1977; Richardson & Bond, 1991; Sankaran *et al.*, 2004). Spatio-temporal patterns of recruitment result from the spatial and temporal variability in both propagule pressure and environmental factors (Davis *et al.*, 2000; Rouget & Richardson, 2003; Dovčiak *et al.*, 2005, 2008), but few studies have attempted to identify the effects of these two components in determining the invasion rate of expanding populations (Richardson & Pyšek, 2006).

In Mediterranean grasslands, grazing by domestic livestock and water shortage are the major environmental constraints in tree seedling establishment (Rousset & Lepart, 2000; Castro *et al.*, 2004a, 2005), although unpalatable shrubs can facilitate seedling recruitment in grazed or dry conditions (Rousset & Lepart, 2000; Gómez-Aparicio *et al.*, 2004; Kunstler *et al.*, 2006). In this study, we aimed at quantifying the effects and importance of main environmental factors (sheep grazing, drought duration or intensity, and geological substrate) and of seed supply in shaping the spatio-temporal patterns of recruitment for two congeneric invasive trees, the native Scots pine (*P. sylvestris* L.) and the introduced black pine (*Pinus nigra* Arn. ssp. *nigra*), on the Causse Mejean, southern France. We inferred recruitment parameters from data on locations and ages of saplings and seed-bearing trees by inverse modelling, which allows seed supply to be explicitly taking into account (Canham & Uriarte, 2006). We addressed the following questions:

- (1) What is the relative importance of seed supply and environmental factors in shaping the spatio-temporal patterns of pine sapling recruitment?
- (2) How do the different environmental factors contribute to invasibility?
- (3) Do sapling recruitment of the introduced species and the native species respond differently to environmental conditions?
- (4) What can be inferred for landscape evolution and management?

METHODS

Study site and species

The Causse Mejean is a 350-km² limestone plateau in southern France, 800–1250 m a.s.l., part of which occurs in the protected area of the Cévennes National Park. Climate is characterized by Mediterranean, oceanic, and continental influences, with long, cold winters and hot summers (mean temperature of 0.8 °C and 17.5 °C in January and July, respectively, Météo France, Hures-Drigas, 44°15'00" N and 3°24'12" E, 1040 m, 1986–2005). Mean annual rainfall is of 920 mm, spring and summer rainfall being quite low and highly variable between years, with 95 mm (range: 32–173 mm) in May, 81 mm (23–238) in June, 51 mm (8–121) in July, and 60 mm (18–117) in August. Soil texture differs between the two main geological substrate types, with sands on dolomitic bedrocks and sandy clay loams on hard limestone (USDA soil classification) (Cadillon, 1970).

Since the beginning of the 20th century, the native *Pinus sylvestris* has progressed into grasslands because of the abandonment of the traditional cultivation-fallow cycle (Caplat *et al.*, 2006). Invasion rates have been higher in the western and mostly dolomitic part of the plateau than in the eastern part, which is dominated by hard limestone. This is because of the differences in soil fertility between the two geological substrates, which imply that fallow duration, i.e. the time before fields were cleared for the new culture, was longer on dolomite than on hard limestone. This has allowed longer durations of pine seed-bearing tree presence on dolomite than on hard limestone, and hence higher invasion rates (Caplat *et al.*, 2006). *Pinus nigra* Arn. ssp. *nigra* was planted from the end of the 19th century until the 1980s, but its spread into grasslands is still relatively slow because it is only a short time since plantations began to produce abundant seed crops. Nowadays, the western part of the plateau is dominated by spontaneous *P. sylvestris* woodlands, whereas the eastern part is characterized by open grasslands, small woods of *P. sylvestris*, *P. nigra* plantations, and scattered individuals of the two pines.

Seeds of these two pioneer and invasive trees (Richardson *et al.*, 1994) are dispersed by wind between January and April and germinate soon afterwards. *P. sylvestris* is present in Eurasia and in the Mediterranean basin (Barbéro *et al.*, 1998; Willis *et al.*, 1998), whereas the natural distribution of *P. nigra* is restricted to the Mediterranean Basin, the subspecies *nigra* being native to the Balkans (Barbéro *et al.*, 1998). Higher adult tree survival after severe droughts indicates that *P. nigra* is more resistant to drought than *P. sylvestris* (Martinez-Vilalta & Piñol, 2002). Previous studies also showed higher sapling production and higher effective seed dispersal for *P. nigra* than for *P. sylvestris* (Debain *et al.*, 2007).

Sampling and field data

In the eastern part of the Causse Mejean, in winter 2006, 32 belt transects, 10 m wide and 50 or 100 m long, composed of a series of five to 10 square plots of 100 m², were established in different

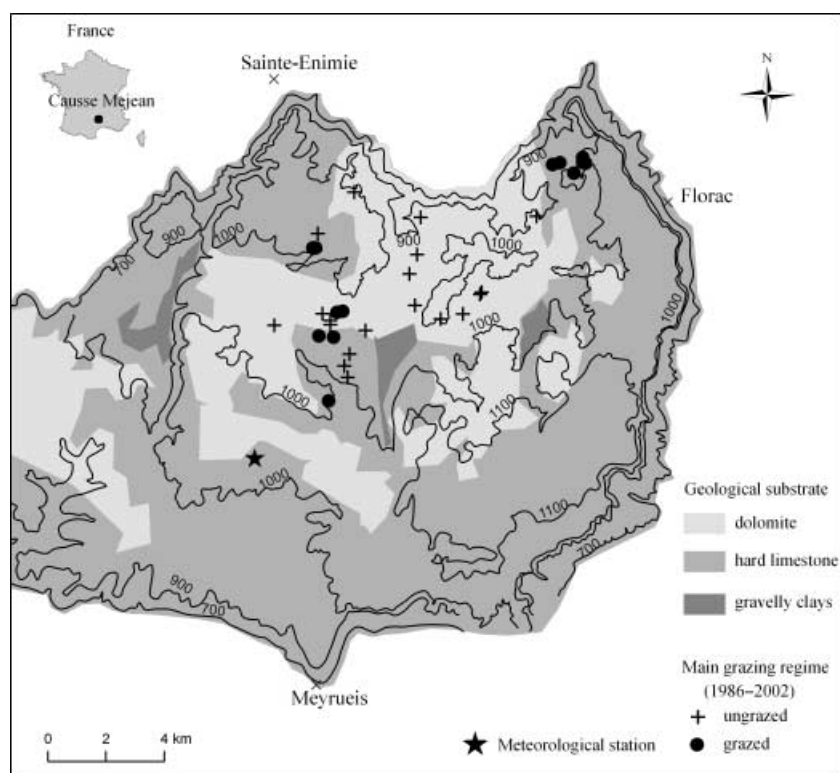


Figure 1 Location of the transects and meteorological station in the eastern part of the Causse Mejean, southern France. Geological substrate map was simplified from BRGM (2003).

Table 1 Summary of the number of transects and corresponding mean altitudes and slopes for each grazing history (for the period 1986–2002) and geological substrate in the Causse Mejean, southern France.

Grazing history (1986–2002)	Geological substrate	Number of transects	Mean altitude (m a.s.l.)	Mean slope (°)
Never grazed	Hard limestone	6	968	4.2
	Dolomite	9	952	6.5
Grazed from 2000 to 2002	Dolomite	4	988	3.9
Grazed from 1993 to 2002	Dolomite	2	1020	5.8
Grazed from 1986 to 2001	Hard limestone	2	973	3.0
Always grazed	Hard limestone	7	996	5.3
	Dolomite	2	938	2.0
Total/Mean		32	976	4.9

conditions of grazing and geology (Table 1, Fig. 1). Areas were first located on aerial photographs, based on the presence of isolated trees in grasslands. Then, as pine species could not be identified on aerial photographs, transects were set up when seed-bearing trees of the two pine species were present. Dominant grassland vegetation included *Bromus erectus*, *Stipa pennata*, *Festuca ovina*, *Carex humilis*, and the shrubs *Buxus sempervirens*, *Juniperus communis*, and *Lavandula angustifolia*. Yearly stocking rates of the past 20 years (number of sheep grazing days/hectare/year) were assessed by interviews of farmers. In each 100 m² plot located inside each transect, shrub cover was visually estimated, and the species, age (whorl number), and location (in grassland or next to shrub, i.e. less than 30 cm away from shrub canopy) of each pine sapling of

4–20 years old were recorded. Because of the strong summer drought that occurred all over Europe in 2003 (Rebetez *et al.*, 2006), some saplings were dead; their species and approximate age were also recorded. Age at sexual maturity is about 12 years (Debain *et al.*, 2007) so that 4-year-old saplings can be produced by trees aged of at least 16. In a buffer zone consisting of a 50-m-wide strip centred on the transect, the species, position, and age (whorl number) of every tree older than 16 years (thereafter ‘seed-bearing tree’) were therefore recorded.

Estimations of drought indices

Soil water content of the top 0- to 20-cm soil layer was estimated at a daily time step with a bucket-type model (see Appendix S1 in

Supplementary Material). The validity of this model was verified, thanks to field measurements of soil water content with at least 10 pairs of time domain reflectometry (TDR) probes permanently installed in each of four grasslands located on a neighbouring plateau. Soil water content was then estimated at a daily time step from 1986 to 2002 for the Causse Mejean by use of data from the nearest meteorological station (Meteo France, Hures-Drigas, 44°15'00" N and 3°24'12" E, 1040 m) (Fig. 1). On the basis of these values, several indices of drought were derived (DI_{d25MJ} , DI_{d25JA} , DI_{d30MJ} , DI_{d30JA} , DI_{i25MJ} , DI_{i25JA} , DI_{i30MJ} , DI_{i30JA}) through definition of the duration (d) or intensity (i) of drought, corresponding to a soil water content beneath 25 mm ($_{25}$) or 30 mm ($_{30}$), for May–June ($_{MJ}$) or July–August ($_{JA}$). These indices were assumed to reflect the regional trend of drought intensity and duration.

Recruitment model

We used maximum likelihood methods (Canham & Uriarte, 2006) to predict sapling recruitment in each year t and in each 100 m² plot i_n of transect n , as a function of six components: (1) the number of saplings produced by a local parent tree as a function of its age (effective fecundity); (2) the dispersal kernel; (3) a background sapling recruitment, i.e. the contribution to recruitment of long-distance dispersal events from outside the buffer areas (Uriarte *et al.*, 2005) and the proportional decrease or increase in sapling recruitment (4) in grazed areas compared with ungrazed ones, and (5) on dolomite compared with hard limestone; and (6) the effect of drought on sapling recruitment. The first three components, linked to seed supply, determined the number of 1-year-old saplings recruited based on the number, age, and distribution of seed-bearing trees and background sapling recruitment, while the other three components, the environmental conditions, acted to influence sapling establishment. The model did not include mortality rates for saplings of more than 4 years old, which are usually very low (Debain *et al.*, 2005). Mortality owing to the strong summer drought of 2003 is analysed and discussed later.

The effective fecundity of a tree m at year t (i.e. the annual number of saplings produced by a tree) was assumed to be the product of the probability for the tree m to be sexually mature times the number of saplings produced, which is proportional to tree age (Debain *et al.*, 2007):

$$\lambda(m, t) = \frac{e^{(-f_1 + f_2 \times A(m, t))}}{1 + e^{(-f_1 + f_2 \times A(m, t))}} f_3 \times A(m, t) \quad (1)$$

with $A(m, t)$ the age of a tree m in year t , and f_1, f_2, f_3 the effective fecundity parameters to be estimated, respectively, related to the age at first reproduction, the increase in probability of becoming sexually mature with ageing, and the proportional increase of sapling production with the age of the tree. The probability that a sapling produced by a seed-bearing tree m disperse to a location j , at a radial distance r_{mj} , was given by the dispersal kernel $k(r_{mj})$, which is best described by an exponential function for short distance dispersal (Debain *et al.*, 2007):

$$k(r_{mj}) = \frac{e^{(-r_{mj}/a)}}{2\pi a^2} \quad (2)$$

with a the parameter to estimate.

$E(j, t)$, the effect of environmental conditions on pine recruitment at location j in year t , was modelled as follow:

$$E(j, t) = (1 + p \times gr(j, t))(1 + g \times geol(j)) \times WS(t) \quad (3)$$

where $gr(j, t)$ was 0 when location j in year t was grazed, and 1 if not, and $geol(j)$ was 0 for hard limestone and 1 for dolomite in location j . p and g , respectively, describing the effect of grazing and geology on sapling establishment, were parameters to estimate. $WS(t)$, the effect of drought intensity or duration on sapling establishment, was modelled by a logistic function:

$$WS(t) = e^{(-w_1 \times DI_t + w_2)} / (1 + e^{(-w_1 \times DI_t + w_2)}) \quad (4)$$

with DI_t an index of drought at year t , and w_1, w_2 the parameters to estimate.

The mean expected number of saplings in a plot was then assumed to be the product of basic effective fecundity, linked to seed supply (fecundity and dispersal of all seed-bearing trees plus background sapling recruitment ϵ), by the effects of environmental conditions, and parameter estimates were computed by maximizing the likelihood of observing the data (see Appendix S2 in Supplementary Material).

Comparison of candidate models

The null model assumed a uniform distribution of saplings across the plots. Twelve candidate models were then tested for each species by adding successively seed supply, grazing, geological substrate, and drought indices. They were compared with Akaike's Information Criteria (AIC), defined as $AIC = -2 \log(\text{maximized likelihood}) + 2 \times K$, with K the number of parameters (Burnham & Anderson, 2002). Δ_i , calculated as the difference in AIC between the model i and the best model, was also reported. Models with Δ_i between four and seven have a great probability of being worse than the best model, and those with Δ_i higher than 10 fail to explain some substantial variation in the data (Burnham & Anderson, 2002). Model goodness of fit was assessed by the deviance-based R^2 (R_p^2) (Cameron & Windmeijer, 1996).

Statistical analysis of sapling mortality

The effects of pine species, sapling age in 2003, geology and grazing on the probability of sapling mortality owing to the strong summer drought of 2003 were tested with a generalized linear mixed model, with a binomial distribution for mortality occurrence, a logit link, and transect as a random factor.

Statistical analysis of sapling location

The effect of drought and grazing on pine sapling location (grassland or next to shrubs) was tested by a log linear analysis.

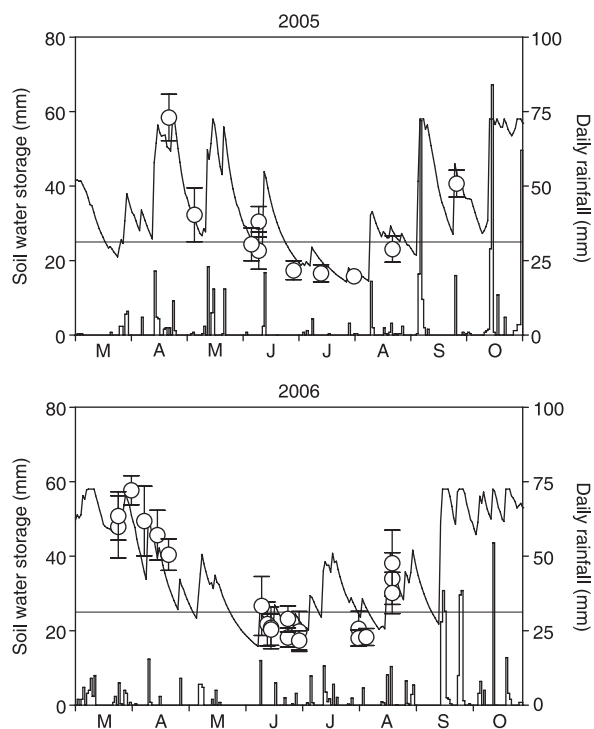


Figure 2 Predicted soil water content in the upper 20 cm (plain line) and observed data (dots with bars showing standard deviation) from March to October in 2005 and 2006. Observed measurements include data from at least 10 pairs of time domain reflectometry (TDR) probes installed in each of four grasslands. Daily rainfall is shown at the bottom. The thin horizontal line corresponds to the 25 mm threshold.

Years were classified into two groups (dry or wet) according to their DI_{d25JA} (see Results). Because sapling location strongly depends on the availability of each microhabitat, data were divided into two classes of shrub cover: 0–10% and 10–20%. Plots where shrub cover exceeded 20% were not analysed because of the low number of such plots sampled in ungrazed conditions. We thus produced a five-way contingency table classified by species (*P. nigra* and *P. sylvestris*), location (shrub or grassland), grazing occurrence (grazed or not), drought (dry or wet), and shrub cover (0–10 or 10–20%). The model was simplified by backward elimination of non-significant effects based on likelihood ratio tests. Significance of the effects remaining in the most parsimonious model was determined by Wald tests.

RESULTS

Population age structures and environmental factors

A total of 266 and 206 seed-bearing trees were sampled for *P. sylvestris* and *P. nigra*, respectively. Mean ages were similar for the two species (t -test, $P > 0.05$): mean (\pm SE) values were 28.3 (\pm 0.54) years for *P. sylvestris* and 28.8 (\pm 0.50) years for *P. nigra*, with ranges of 16–56 and 16–52 years, respectively. A total of 1035 and 1903 saplings were sampled for *P. sylvestris* and *P. nigra*,

respectively. Stocking rate of grazed grasslands, with a mean value of 162 sheep grazing days $ha^{-1} year^{-1}$, ranged from 56 to 315 sheep grazing days $ha^{-1} year^{-1}$ and was independent of geological substrate ($P > 0.1$). The model of soil water content was strongly supported by field measurements, as daily predicted soil water storages were well correlated with field data for both years ($r^2 = 0.89$ in 2005 and $r^2 = 0.82$ in 2006, with $P < 0.001$ for both years) (Fig. 2).

Comparison of candidate recruitment models

The best fitting recruitment model was the same for the two pine species and included seed supply, grazing, geology, and DI_{d25JA} . It explained 48% and 24% of the total deviance for *P. nigra* and *P. sylvestris*, respectively (Table 2). It was largely supported by the data, as shown by the high values of the Δ_i of the remaining models, always higher than 6.5 (Table 2), indicating that the uncertainty in the selection of the best model was very low. Although some observed data fell outside the 95% confidence intervals, the predicted number of saplings per year per plot were overall very consistent with observed data (Fig. 3).

Relative importance of seed supply and environmental factors

Seed supply, including the number and age of seed-bearing trees, seed dispersal, and background recruitment, was about as important as the whole set of environmental variables in explaining data (Table 2). For *P. sylvestris*, 11.7% of the total deviance was explained by seed supply and 12.5% by the environmental variables, these values being, respectively, of 26.3% and 21.4% for *P. nigra* (Table 2).

Effect of grazing, geology, drought, and shrubs

Recruitment rates were twice as low on hard limestone as on dolomite, and two to four times lower in grazed than ungrazed conditions, the negative effect of grazing being more pronounced on dolomite than on hard limestone (Fig. 4, Table 3). Sapling recruitment was further reduced by the increase in DI_{d25JA} , which better explained recruitment patterns than any other drought indices (Table 2). The proportion of saplings established next to shrubs was not influenced by drought conditions (location*drought interaction: $P > 0.05$), but was higher in grazed than ungrazed conditions (location*grazing interaction: $P < 0.001$), indicating a protective effect of shrubs in grazed areas, which was similar for both pine species (location*grazing*species interaction: $P > 0.05$). For shrub cover lower than 10%, 15.3% of saplings were situated next to shrubs in grazed conditions, compared with 8.1% in ungrazed conditions. For shrub cover between 10% and 20%, these values reached 29.1% and 7.1%, respectively.

Comparison between the two species

The two pine species had contrasting age-specific reproduction curves. The f_1 parameter, which is linked to the age at first

Table 2 Comparison of the candidate models for sapling recruitment of (a) *Pinus sylvestris* and (b) *Pinus nigra*, including seed supply, grazing, geology, and indices of drought (DI: index of drought; i : intensity or d : duration; $_{25}$ or $_{30}$: soil water content threshold value (mm); $_{MJ}$ and $_{JA}$: May–June or July–August) (see Material and Method for details). LL is the negative logarithm of the likelihood, K the number of parameters, AIC the Akaike's Information Criterion (smaller is better), Δ_i the difference between the AIC of the each model and the AIC of the best model among all candidate models (in bold), and R_D^2 the deviance base R^2 , which can be interpreted as the fraction of the total deviance explained.

(a)

Model	LL	K	AIC	Δ_i	R_D^2
Null (constant recruitment)	2992.0	1	7645.6		
Seed supply	2714.9	5	7099.4	640.1	0.117
Seed supply and grazing	2519.3	6	6710.2	250.9	
Seed supply and geology	2517.3	6	6706.5	247.2	0.191
Seed supply, grazing, and geology	2450.9	7	6575.4	116.1	0.218
Seed supply, grazing, geology, and DI _{25MJ}	2449.7	9	6577.0	117.7	
Seed supply, grazing, geology, and DI _{25MJ}	2450.0	9	6577.6	118.3	
Seed supply, grazing, geology, and DI _{30MJ}	2447.7	9	6573.0	113.7	
Seed supply, grazing, geology, and DI _{30MJ}	2445.4	9	6568.3	103.0	
Seed supply, grazing, geology, and DI _{25JA}	2420.9	9	6519.4	30.1	
Seed supply, grazing, geology, and DI_{25JA}	2390.9	9	6459.3	0.0	0.242
Seed supply, grazing, geology, and DI _{30JA}	2435.2	9	6548.0	88.6	
Seed supply, grazing, geology, and DI _{30JA}	2428.6	9	6534.7	75.4	

(b)

Model	LL	K	AIC	Δ_i	R_D^2
Null (constant recruitment)	4858.3	1	9718.5		
Seed supply	3875.3	5	7760.7	1606.6	0.263
Seed supply and grazing	3310.1	6	6632.3	478.3	0.414
Seed supply and geology	3375.3	6	6762.7	608.6	
Seed supply, grazing, and geology	3147.6	7	6243.3	89.2	0.467
Seed supply, grazing, geology, and DI _{25MJ}	3111.9	9	6241.9	87.9	
Seed supply, grazing, geology, and DI _{25MJ}	3095.1	9	6208.2	54.2	
Seed supply, grazing, geology, and DI _{30MJ}	3108.4	9	6234.9	80.9	
Seed supply, grazing, geology and DI _{30MJ}	3094.9	9	6208.0	53.9	
Seed supply, grazing, geology and DI _{25JA}	3071.5	9	6161.0	6.9	
Seed supply, grazing, geology, and DI_{25JA}	3068.0	9	6154.1	0.0	0.477
Seed supply, grazing, geology, and DI _{30JA}	3077.4	9	6172.8	18.7	
Seed supply, grazing, geology, and DI _{30JA}	3094.2	9	6206.5	52.5	

reproduction, was lower for *P. sylvestris* than for *P. nigra*, and the f_2 parameter, which is linked to the increase in probability of being sexually mature with age, was higher for *P. nigra* than *P. sylvestris* (Table 3). The median ages at reproduction (f_1/f_2) were 13.7 and 21.8 years for *P. sylvestris* and *P. nigra*, respectively. The f_3 parameter, linked to the production of saplings as a function of tree age once maturity is reached, was higher for *P. nigra* than for *P. sylvestris* (Table 3): once maturity is reached, effective fecundity is higher for *P. nigra* than for *P. sylvestris* in all environmental conditions (Fig. 4). The higher value of a for *P. nigra* (Table 3) indicates that it disperses seeds further than *P. sylvestris* (mean dispersal distances of 40.0 and 18.8 m, respectively). The estimated background sapling recruitment was about 10 times higher for *P. sylvestris* than for *P. nigra*, but remained very low for both species, with values of 0.020 and 0.0019 saplings per plot per year, respectively (Table 3), and

contributed to a maximum of 20% of the observed saplings per plot per year in every environmental condition.

Relative weights and effects of environmental variables differ between the two species. For *P. sylvestris*, geological substrate accounted for 7.4% of the deviance, while grazing and DI_{25JA} only explained 2.7% and 2.4% of the deviance, respectively (Table 2). In contrast, grazing appeared to be by far the most important environmental variable for *P. nigra*, explaining 15.1% of the deviance, whereas geological substrate and DI_{25JA} only accounted for 5.3% and 1% of the total deviance, respectively (Table 2). Recruitment rates of *P. nigra* were more affected by grazing but less reduced by DI_{25JA} than those of *P. sylvestris*. Grazing reduced the recruitment rates of *P. nigra* and *P. sylvestris* by 80 and 60%, respectively, and a DI_{25JA} of 20 days reduced sapling recruitment by 10 and 50%, respectively (Table 3, Fig. 4).

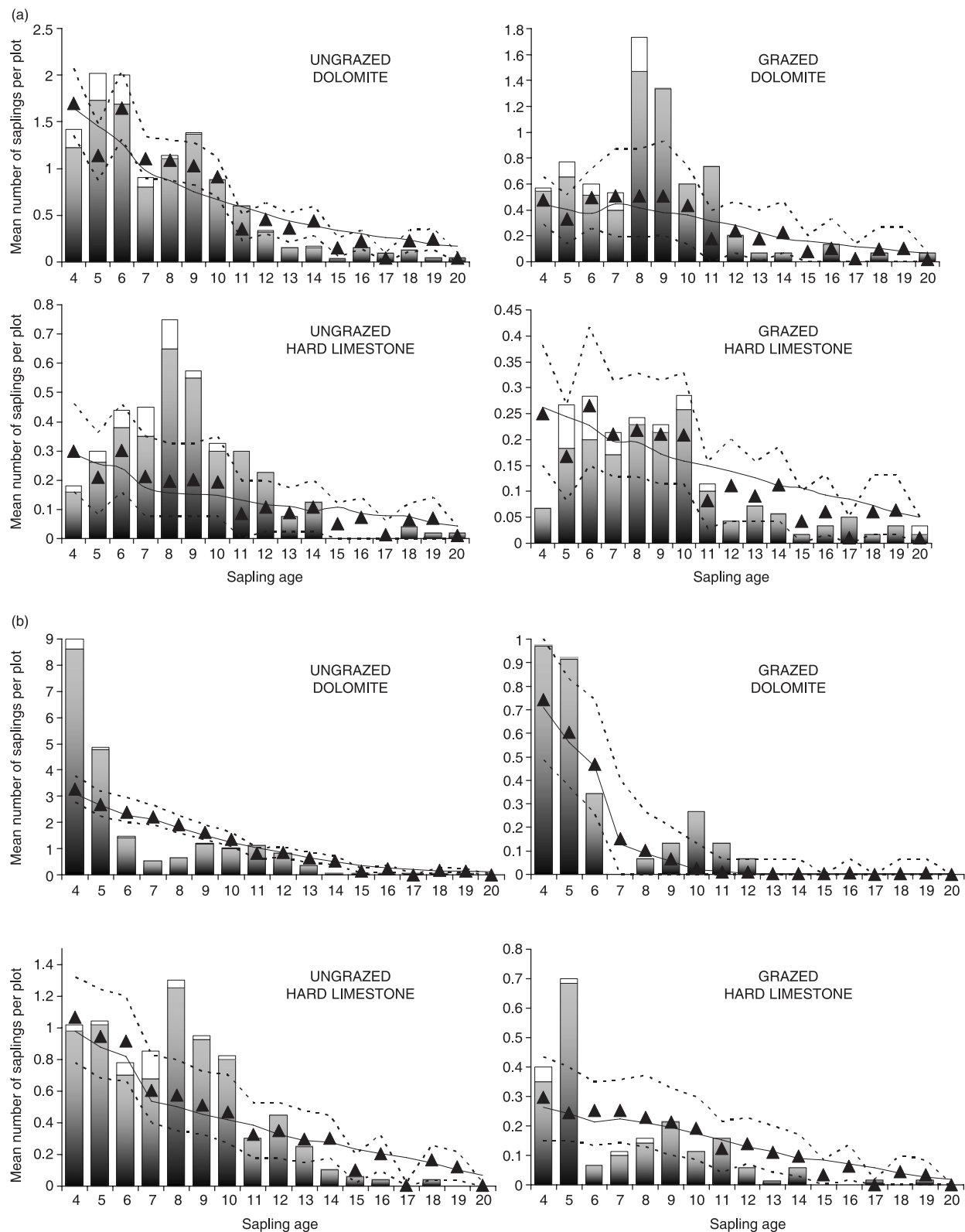


Figure 3 Observed and predicted number of 4- to 20-year-old saplings per plot (100 m²) in grazed and ungrazed grasslands, on dolomite and hard limestone, for (a) *Pinus sylvestris* and (b) *Pinus nigra*. Grey bars show observed numbers of living saplings, and white bars observed numbers of dead saplings. The plain line show mean predicted values with the best model that does not include DI_{d25JA} , black triangles show the predicted values with the best model including DI_{d25JA} , and dotted lines show 95% confidence intervals after 200 simulations for predicted values under the best model including the drought index. Note that Y-scales differ between graphs.

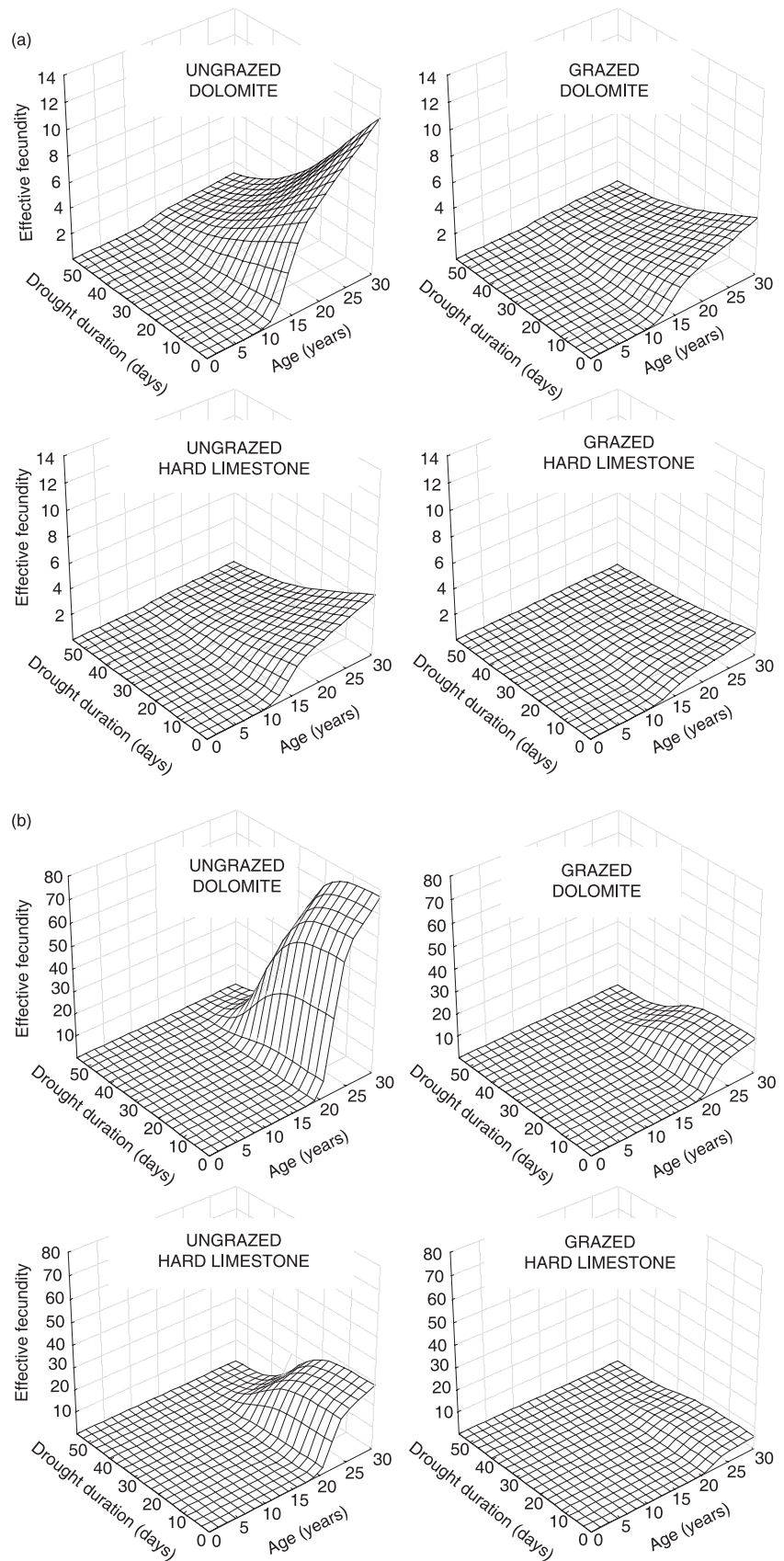


Figure 4 Effective fecundity (number of saplings produced per tree per year) in grazed or ungrazed conditions, on dolomite or hard limestone, as a function of tree age and the duration of drought from July to August based on the 25 mm threshold value (DI_{25JA}) for (a) *Pinus sylvestris* and (b) *Pinus nigra*.

Table 3 Estimation and confidence limits of the best model parameters for *Pinus sylvestris* and *Pinus nigra*.

Biological process	Species	Parameter	Estimation (95% confidence limits)	
Fecundity	<i>P. sylvestris</i>	f_1	12.2	(11.7; 12.9)
		f_2	0.889	(0.842; 0.930)
		f_3	0.0894	(0.0846; 0.0975)
	<i>P. nigra</i>	f_1	29.9	(29.7; 30.3)
		f_2	1.37	(1.35; 1.38)
		f_3	0.197	(0.185; 0.205)
Dispersal	<i>P. sylvestris</i>	a	9.40	(8.35; 10.16)
	<i>P. nigra</i>	a	20.0	(19.1; 21.0)
Background sapling recruitment	<i>P. sylvestris</i>	ϵ	0.0203	(0.00895; 0.0311)
	<i>P. nigra</i>	ϵ	0.00191	(0.000912; 0.00360)
Grazing	<i>P. sylvestris</i>	p	1.53	(1.34; 1.70)
	<i>P. nigra</i>	p	3.91	(3.62; 4.14)
Geological substrate	<i>P. sylvestris</i>	g	1.68	(1.46; 1.85)
	<i>P. nigra</i>	g	1.67	(1.49; 1.81)
Drought duration (DI_{d25JA})	<i>P. sylvestris</i>	w_1	0.0632	(0.0552; 0.0712)
		w_2	0.646	(0.523; 0.775)
	<i>P. nigra</i>	w_1	0.201	(0.184; 0.221)
		w_2	6.13	(5.69; 6.67)

f_1 , f_2 , and f_3 , are parameters of the logistic effective fecundity curve (Equation 1), a the parameter of the negative exponential dispersal curve (Equation 2), ϵ the background sapling recruitment (Equation S2a), p the increase in effective fecundity in ungrazed compared with grazed areas (Equation 3), g the increase in effective fecundity on dolomite compared with hard limestone (Equation 3), and w_1 and w_2 the parameters of the logistic curve describing the effect of drought duration or intensity on sapling recruitment (Equation 4).

Sapling mortality owing to the 2003 summer drought

Mortality rates due to the 2003 summer drought decreased with sapling age ($P < 0.001$), the low number of 4-year-old saplings which died probably being underestimated because of sapling decomposition and breakage (Fig. 3). Mortality rates were independent of grazing or transect ($P > 0.05$). They were higher for *P. sylvestris* than for *P. nigra* ($P < 0.001$) and for hard limestone than for dolomite ($P < 0.001$), with mean values for *P. nigra* of 6.8% and 3.7%, and for *P. sylvestris* of 11.5% and 6.7%, on hard limestone and dolomite, respectively.

DISCUSSION

Recruitment model quality and limitations

This study shows that inverse modelling is a powerful tool to assess the effects and relative importance of propagule supply and environmental variables in shaping spatio-temporal recruitment patterns of trees invading grasslands. Our ability to explain recruitment variability was comparable to the other studies that used this method to understand spatial patterns of sapling recruitment in forests (Ribbens *et al.*, 1994; LePage *et al.*, 2000; Uriarte *et al.*, 2005).

It should be stressed here that our model was based on several assumptions. First, owing to the lack of data, interannual variation in seed production and predation was neglected. This

could account for part of the unexplained temporal variability in recruitment rates (Fig. 3). Second, mortality rates after 4 years were neglected. This assumption is supported by experimental results showing that mortality rates decrease with time, the highest mortality rate occurring during the first growing season (Castro *et al.*, 2004b; Debain *et al.*, 2005). The mortality induced by the strong summer drought of 2003, however, implied that the number of established saplings and thus the net fecundities were slightly underestimated (Fig. 3). It remained, however, rather low in the study area, compared with the mortality observed in a more southern limestone plateau, where mortality rates reached, for *P. sylvestris*, 13% for 12- to 15-year-old saplings, 19% for 9- to 11-year-old saplings, and 35% for 5- to 8-year-old saplings, whereas almost all younger saplings died (N. Boulant & J. Lepart, unpublished data).

Relative importance of seed supply and environmental factors

Although fine-scale recruitment patterns can be mostly determined by the availability of favourable microsites (Dovčiak *et al.*, 2008), many invasive populations of shrub and tree species have been found to be seed limited on local (Mazia *et al.*, 2001; Siemann & Rogers, 2003; Manning *et al.*, 2004) and regional (Rouget & Richardson, 2003; Foxcroft *et al.*, 2004) scales. The spread of *Pinus* is a stratified process, characterized by the establishment of trees isolated from the main invasion front by

rare events of long-distance seed dispersal, which create new invasion foci (Higgins & Richardson, 1999; Lepart *et al.*, 2001; Camarero *et al.*, 2005; Debain *et al.*, 2007). The reproduction rates of those isolated trees mostly determine colonization rates (Neubert & Caswell, 2000). We worked on such low-density populations, where the small initial number of seeds is a limiting factor. It was therefore not surprising that the variation of seed supply in time, linked to the ageing of seed-bearing trees, and in space, related to the number and location of seed-bearing trees, was as important as the combined set of environmental factors in determining recruitment patterns for both species.

Environmental factors contributing to invasibility

A major factor limiting pine sapling recruitment was sheep-grazing. Grazing reduced sapling recruitment more than double, even if this effect was buffered by the presence of unpalatable shrubs, which protected tree saplings established in their vicinity by deterring herbivores (Callaway, 1992; Rousset & Lepart, 2000; Bakker *et al.*, 2004). On the contrary, in some regions, the introduction of grazing at moderate to heavy intensities was found to coincide with the initiation of invasions, because it reduced the competitive effect of grasses on tree seedlings (Richardson & Bond, 1991; Brown & Archer, 1999). In our study, the direct negative effects of herbivory and trampling were more important than any possible indirect positive effect (Fig. 4). This is probably because of the long history of grazing in the study area and the high grazing pressure imposed by domestic livestock.

Our results further indicate that the difference in pine invasion rate between the two geological substrates did not result only from past human activities, i.e. longer fallow duration on dolomite than on hard limestone (Caplat *et al.*, 2006), but also from the direct effects of geological substrate on sapling recruitment and mortality. Those direct effects may mostly be the result of differences in water availability. For a given soil water content, absolute values of soil water potential are indeed higher on sandy clay loams that overlay hard limestone than on sands that characterize dolomitic substrates (Clapp & Hornberger, 1978). Thus, for a given drought index value, the water available to pine saplings is probably lower on hard limestone than on dolomite, a feature that may explain at least partly the lower sapling recruitment rates and the higher sapling mortality on hard limestone after the 2003 drought.

The temporal variability in sapling recruitment owing to the duration of summer drought was not as important as in more arid areas, where *Pinus* recruitment only occurred in fewer than 10 years of a 4-year period (League & Veblen, 2006). Surprisingly, despite the fact that young pine saplings are highly susceptible to water stress soon after emergence (Castro, 2006), drought indices calculated for May–June did not have much effect on pine sapling establishment. This was probably because of the relatively low intensities and durations of spring drought for the period 1986–2002. We found no indication that shrubs buffer recruitment rates against dry conditions, although facilitation of tree sapling survival by shrubs has been found to increase with water stress in the Mediterranean area (Gómez-Aparicio *et al.*, 2004).

Differences in invasiveness between *P. nigra* and *P. sylvestris*

Despite their high phylogenetic relatedness and ecological similarity (Richardson, 1998), the native and the introduced congener species differ in many traits. *Pinus nigra* begins reproduction later than *P. sylvestris* and once mature produces markedly more saplings in all studied environmental conditions, as reported for a single site by Debain *et al.* (2007). The difference in effective fecundities between the two species, however, was more pronounced in our study, partly because of the higher sapling mortality of *P. sylvestris* than of *P. nigra* after the 2003 drought, which increased the difference in the number of observed saplings between the two species. At a given age, the higher effective fecundity of *P. nigra* than of *P. sylvestris* may result from a higher seed production; to our knowledge, however, no study has compared the seed production of the two species. It could also be because of its higher seed and sapling mass, which may convey better resistance to herb competition (Debain *et al.*, 2003, 2005). Mean seed dispersal distances of 40 m and 19 m for *P. nigra* and *P. sylvestris* are also very consistent with those found in the work of Debain *et al.* (2007) and confirm that *P. nigra* should spread more rapidly than *P. sylvestris*.

Drought and grazing differentially affect recruitment of *P. nigra* and *P. sylvestris*

The environmental factors driving invasion rates can differ between tree species (Rouget & Richardson, 2003). In our study, the introduced *P. nigra* was more resistant to drought but less resistant to grazing than the native *P. sylvestris*. The high resistance to water stress of saplings of *P. nigra* is in accordance with its Mediterranean distribution and the high drought tolerance of adults (Martinez-Vilalta & Piñol, 2002). The native *P. sylvestris* is at the southern limit of its natural distribution range, and thus particularly exposed to climate changes (Gaston, 2003; Lavergne *et al.*, 2006). *Pinus* species present a drought-avoiding strategy, with an early stomatal closure as soil water potential decline (Picon-Cochard *et al.*, 2006). In the absence of data available to compare the two species, we suppose that the difference in drought tolerance between them could be linked to the differential depletion of carbon reserve when stomata are closed (Guehl *et al.*, 1993).

The higher decrease in recruitment rates for *P. nigra* than for *P. sylvestris* in grazed conditions can be explained by both direct and indirect effects. Experiments conducted in Spain showed higher herbivory on *P. nigra* than on *P. sylvestris* (Castro *et al.*, 2004b), which could be because of the greater height of *P. nigra* saplings, increasing their chance to be grazed in the herb cover, or because of differences in leaf traits between the two species. Furthermore, *P. nigra* saplings are also more resistant to herb competition, especially for light, than those of *P. sylvestris* (Debain *et al.*, 2005). Thus, in the absence of grazing, the dense herb cover strongly limits the establishment of *P. sylvestris* saplings, whereas it has lesser effects on the establishment of *P. nigra* saplings.

Implication for landscape evolution and management

Because of the time lag between introduction and invasion (Richardson & Pyšek, 2006), the spread of *P. nigra* remains limited. Despite its delayed maturity and heavier seeds (Debain *et al.*, 2003), usually related to a low invasiveness (Grotkopp *et al.*, 2002; Richardson & Rejmánek, 2004), the introduced *P. nigra* should, however, ultimately be more invasive than the native *P. sylvestris* because of its higher effective seed dispersal distances, competitive ability, and effective fecundity in all environmental conditions. Plantations of *P. nigra* in the eastern part of the plateau, by introducing a strongly invasive species and by adding seed sources in an area where native pine woods were rather scarce, will therefore speed up the conversion of grasslands to pine woodlands.

A pine forest could thus become established on the Causse Mejean during this century, implying a return to the vegetation present after the end of the last glaciations (Quilès *et al.*, 2002). This initial pine forest had been cleared after the first human settlements and maintained through farming (Marty *et al.*, 2003). The reforestation would have major impacts on biodiversity as most of the endangered species on the Causse Mejean depend on the persistence of open habitats. Managers should thus anticipate pine invasion before it gets out of control and threatens the typical natural and cultural landscapes of the area (Lepart *et al.*, 2000; Etienne, 2001).

The fairly recent increase in grazing pressure in the study area (Quétier *et al.*, 2005) will efficiently limit the progression of pines, especially of *P. nigra*, but will remain insufficient to contain tree invasion entirely, as saplings keep becoming established (Caplat *et al.*, 2006). Other more efficient methods are necessary to maintain grasslands, like mechanical clearing, which is increasingly used by farmers and promoted by the Cévennes National Park (Etienne, 2001). The intensification of spring and summer drought in Europe (Beniston *et al.*, 2007) will further strongly decrease the invasion speed of both pine species by killing saplings and preventing first-year seedling establishment. This impact is likely to be stronger on the native and Euro-Siberian *P. sylvestris* than on the introduced and Mediterranean *P. nigra*.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Determination of drought indices.

Appendix S2 Recruitment model and likelihood computation.

This material is available as part of the online article from:
<http://www.blackwell-synergy.com/doi/abs/10.1111/j.1472-4642.2008.00494.x>
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