Diversity and Distributions, (Diversity Distrib.) (2007) **13**, 799–807

BIODIVERSITY
RESEARCH

Fagus sylvatica L. recruitment across a fragmented Mediterranean Landscape, importance of long distance effective dispersal, abiotic conditions and biotic interactions

Georges Kunstler[1,2]*, Wilfried Thuiller[3], Thomas Curt[1], Monique Bouchaud[1], René Jouvie[1], Florian Deruette[2] and Jacques Lepart[2]

[1]*Cemagref, Equipe Ecologie appliquée des écosystèmes boisés, 24 Avenue des Landais, BP 50085, 63172 Aubière Cedex, France,* [2]*CNRS, Centre d'Ecologie Fonctionnelle et Evolutive, 1919 Route de Mende, 34293 Montpellier Cedex 05, France,* [3]*Laboratoire d'Ecologie Alpine, UMR-CNRS 5553, Université Joseph Fourier, BP 53, 38041 Grenoble Cedex 9, France*

*Correspondence: Georges Kunstler, Cemagref – Unité de Recherche Ecosystèmes Montagnards, 2, rue de la Papeterie, BP 76, 38402 St-Martin-D'Heres Cedex, France.
E-mail: georges.kunstler@grenoble.cemagref.fr

ABSTRACT

Native tree populations have been fragmented by anthropogenic disturbance worldwide, leaving them at risk from extinction. The possibility of sizable recovery of fragmented populations is a function of their dispersal, the abiotic conditions, and the biotic interactions. The relative importance of these three drivers for the recruitment rate of a fragmented population of the late-successional *Fagus sylvatica* L. was analysed at the landscape scale in Causse du Larzac, southern margins of the Massif Central, in the South of France. We used regression models on observational data to analyse the response of *Fagus* recruitment rate to the distance to the nearest mature population, to climatic and geological variables, and to variables describing biotic interactions (pine vs. grassland, light, shrub cover). Distance to the nearest *F. sylvatica* adult population was the most important explanatory variable. Recruitment rate was also influenced by facilitative biotic interactions with shrubs, and by the climatic conditions of the plot. Recruitment occurred at a greater distance from the nearest mature population of *Fagus* in pine forests than in grassland. Dispersal was the major limitation to recruitment of *F. sylvatica* in this landscape. The recruitment rate was then modulated by the climate and positive biotic interactions. The activity of the European jay could be of great importance for such fragmented populations, because it can lead to long-distance dispersal events and may result in a preferential dispersal towards pine forests.

Keywords

Climate, dispersal, facilitation, *Fagus sylvatica*, fragmentation, recruitment.

INTRODUCTION

Anthropogenic disturbances have fragmented native forests worldwide (Riitters *et al.*, 2000; Wade *et al.*, 2003). In fragmented areas, remaining tree populations are usually of small size and scattered through the landscape, questioning the possibility of the maintenance or of the development of these populations (Hanski, 1998; Bruna, 1999; Vellend, 2004). The establishment of new individuals for these species in isolated populations is a function of the presence of potential sites for germination and growth, and also of their ability to disperse seeds into these potential sites (Hanski, 1998; Clark *et al.*, 1999; Trakhtenbrot *et al.*, 2005). In a fragmented landscape, long-distance dispersal is extremely important (Verheyen & Hermy, 2001; Bohrer *et al.*, 2005) because potential sites may be far from mature individuals. The suitability of a potential site is determined by abiotic conditions, such as soil nutrients, water availability, and climatic conditions. The composition and the structure of the local vegetation then influence the potential site through biotic interactions such as competition (Connell, 1983), facilitation (Bruno *et al.*, 2003), or herbivory (Fine *et al.*, 2004). Very few studies have analysed the role of long-distance dispersal in combination with abiotic factors and biotic interactions in the dynamics of plant species at the landscape scale (but see Hewitt & Kellman, 2002; Turner *et al.*, 2003; Dullinger *et al.*, 2005; Soons & Ozinga, 2005). This lack of studies could result from the methodological difficulties of studying seed dispersal over long distances – the rarity of observation of such events precludes any statistical analysis (Silvertown, 1991). A solution is to analyse not the seed dispersal *per se*, but the effective dispersal through

DOI: 10.1111/j.1472-4642.2007.00404.x
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indirect indicators such as the distance of the plot to the nearest mature individuals (e.g. Turner *et al.*, 2003; Dullinger *et al.*, 2005), and to include variables describing biotic interactions and abiotic factors. This would allow us to account for the local-scale effect of biotic interactions jointly with the landscape-scale effects of long-distance dispersal and climatic conditions.

In the mountains surrounding the Mediterranean basin, the landscape has been profoundly modified and fragmented by human activity since the Neolithic (Vernet, 1990; Rackham & Grove, 2001; Quézel & Medail, 2003). In these areas, late successional tree species are usually only present as isolated patches of forest. Since the middle of the 19th century, the abandonment of farmland (Lepart & Debussche, 1992; Marty *et al.*, 2003) has led to considerable forest expansion (Marty *et al.*, 2003). However, although land abandonment provides a window of opportunity for forest expansion, late successional species such as *Fagus sylvatica* have strikingly slower colonization dynamics than pioneer species such as *Pinus sylvestris* (Debain *et al.*, 2003; Kunstler *et al.*, 2006). The slow recovery of the fragmented population of *Fagus* could result primarily from its short mean dispersal distance. Indeed, long-distance dispersal events of *Fagus* seeds are extremely rare. The seed hoarding activity of the European jay (*Garrulus glandarius*) might lead to rare events of long-distance dispersal (Bossema, 1979; Nilsson, 1985) and also preferential dispersal towards pine forests (as shown for *Quercus ilex*'s acorns by Gomez, 2003). The slow recovery of *Fagus* could also result from biotic interactions. For instance, previous studies (Kunstler *et al.*, 2006; Kunstler *et al.*, 2007) have shown that establishment of *Fagus* in grasslands is low, with recruitment being limited to the immediate vicinity of shrubs because of their protective effect against sheep grazing and limitation of competition from herbaceous species (Kunstler *et al.*, 2006). In contrast, its establishment rate is high in the understorey of pine forest, due to its high shade tolerance (Kunstler *et al.*, 2005). The Mediterranean mountains are at the extreme southern limit of the natural range of most late successional temperate tree species such as *F. sylvatica* or *Abies alba* (Quézel & Medail, 2003), and climatic conditions could determine establishment even at the landscape scale. There is also large variability in bedrock type in Mediterranean landscapes, with different degrees of bedrock fragmentation allowing different degrees of root penetration and thus modulating drought effects (Quézel & Medail, 2003).

In this study, we analysed the interplay of dispersal, biotic interaction, and abiotic factors in the recovery dynamics of a fragmented population of *F. sylvatica* in Causse du Larzac in the south of France. Based on the above considerations we tested five hypotheses. (1) Recruitment is mainly determined by the distance to the nearest adult *Fagus* population. (2) Recruitment is a function of the composition and the structure of the local vegetation (related to biotic interactions) represented in this study by the type of habitat (pine forest vs. grassland), the light transmission, and the cover of unpalatable shrub species. (3) Recruitment is affected by abiotic factors, i.e. it is higher on fragmented bedrock and in areas with a wetter climate. (4) The effect of cover of unpalatable shrubs is only positive in grasslands. (5) If there is preferential dispersal towards pine forests because of the activity of the European jay, the effects of the variable 'distance to the nearest *Fagus* adult population' will differ between pine forests and grassland. We tested these hypotheses by analysing tree recruitment data from 264 sampling plots in pine forests and in grassland, under different climatic and geological conditions and at different distances from mature stands of *Fagus*.

METHODS

Study area

The Causse du Larzac is a 1000 km^2 limestone plateau on the southern margins of the Massif Central, France. The three dominant bedrocks in this area are crystalline dolomite (which is a heavily weathered and fragmented bedrock allowing a deep root penetration), the marls (with superficial rooting due to the high bulk density of this rock with high percentage of clay and a high water capacity) and compact limestone or dolomite (with a low level of root penetration due to compact bedrock). These three bedrocks differ also in their chemical composition. The altitude of the plateau varies from 560 to 920 m a.s.l., the plateau is lined with deep gorges. This area is under different climatic influences; the Mediterranean climate is increasingly important heading from north to south, whereas the Atlantic climate is increasingly influential heading from west to east. The mean annual rainfall over the period 1969–99 varies spatially from 800 to 1470 mm in the area, with the maximum rainfall in the south-west of the plateau. Maximal rainfall occurs in autumn (300–500 mm from September to November) and winter (300–500 mm from December to February), whereas summer is very dry (< 200 mm from June to August) (Benichou & Le Breton, 1987; Meteo France AURHELY). Mean annual minimum temperatures range from 4 °C to 8 °C and maximum from 13 °C to 18 °C. The number of days with frost varies from 47 to 83 days per year (Benichou & Le Breton, 1987; Meteo France AURHELY).

The landscape of the Causse du Larzac results from the long and complex influences of human activity. Forest started to be cleared during the Neolithic, about 7000 BP (Vernet, 1972), with the development of pre-agricultural society. Historical changes in human activities, principally abandoning sheep grazing, shifting cultivation, and exploiting woodland (Marty *et al.*, 2003), have been postulated as having a major impact on woodlands and vegetation dynamics over the past decades (Lepart & Debussche, 1992). At present the landscape consists of a mosaic of croplands, open and encroached grasslands, and *Pinus* (plantations of *Pinus nigra* L. and natural forests of *P. sylvestris* L.) and *Quercus pubescens* L. woods. Isolated *F. sylvatica* L. (European beech) forests are mostly located on the border of the plateau. *Fagus* is a late successional, long-lived, and large deciduous tree with maximum heights of 35 m. *Fagus* is a shade-tolerant species of cool climates that can tolerate shallow soils but is more frequent on moist sites (Ellenberg, 1988). The Causse du Larzac is located at the southern margin of the natural range of *Fagus*. Plant nomenclature is taken from Tutin *et al.* (1964–1993).

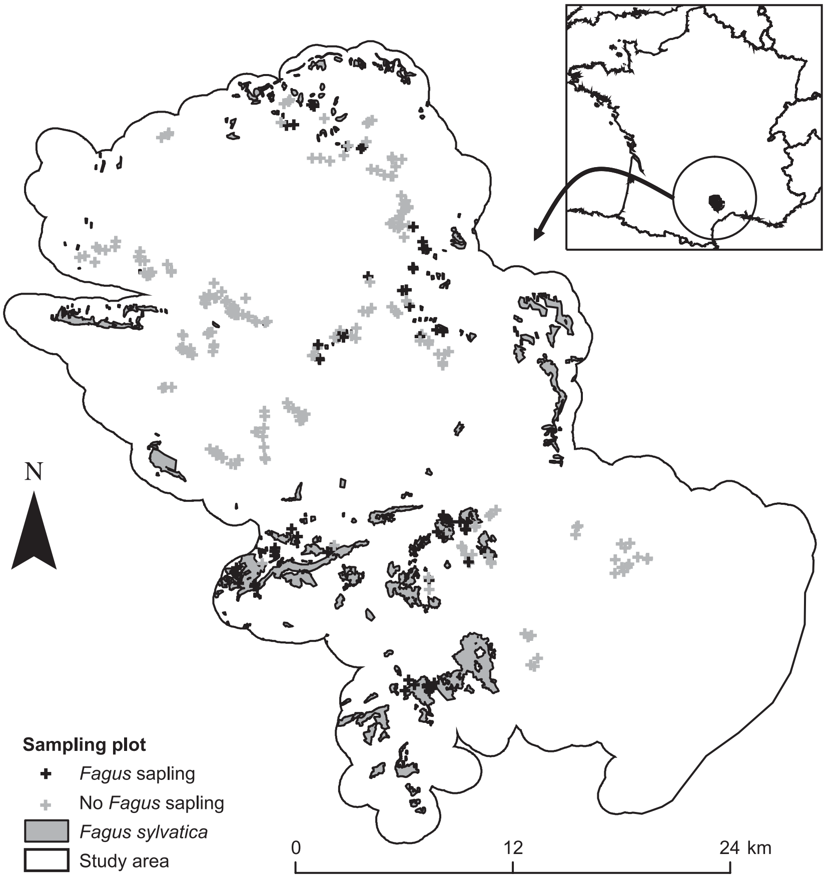

Figure 1 Spatial distribution of beech *Fagus sylvatica* populations in the Larzac limestone plateau (South France) and location of the sampling plots (with presence or absence of *F. sylvatica* sapling). Map projection UTM 31 N, datum WGS84.

Environmental data

The distribution of pine forest, and grassland vegetation type was based on a map produced by the National Forest Inventory in 2001 (1 : 25,000 scale) digitized in a geographical information system (Arc View 3.2, Environmental Systems Research Institute, Inc., Redlands, CA, USA). It was critical to have an accurate map of *Fagus* populations, including very small populations corresponding to a few trees, in order to estimate the distance to the nearest adult. As stated in the introduction, *Fagus* is rare in the Larzac area. The Regional Park of the Grand Causses have recently produced a revised map by merging several earlier maps (the National Forest Inventory, the vegetation map of France Dupias, 1966; a map of the distribution of dominant tree species produced by the Conservatory of Natural Area of Languedoc-Roussillon), and also from very precise fieldwork to locate populations of *Fagus* in the landscape (Steinmetz, 2003). This work thus provides an opportunity to have very detailed information about the location of adult trees in the landscape (Fig. 1).

Climatic data were produced by Meteo France with a kriging method named AURELHY (Benichou & Le Breton, 1987), predicting the mean for different climatic variables over the period 1969 and 1999. These variables are the average temperature of the hottest month (T_X in °C), the average temperature of the coldest month (T_N in °C), the number of frosty days (Nb_F), and the average precipitation for each month. These variables were calculated by the model for a grid of 1 km mesh. We used the Emberger's pluviothermic index (Emberger, 1930), defined by the following equation, to summarize the climate variables.

$$Q_2 = \frac{1000 \times P_{annu}}{\left(273 + \dfrac{T_X + T_N}{2}\right) \times (T_X - T_N)}$$

where P_{annu} is the mean annual precipitation, and the addition of 273 converts temperature in °C to Kelvin. This index is commonly used in Mediterranean climates (De Philippis, 1951; M'Hirit, 1999). Climate is more arid when the index is smaller. We also used the number of days below freezing line (frosty days), because this variable expresses the degree and the duration of the critical frost period. Climatic layers were imported into GIS as 1 × 1 km grid cell.

Bedrock data were taken from a geological map (BRGM, 1980–1990) of the area (according to the coordinates of the points) or from a digitized pedological map with the reference to the bedrock (Cadillon, 1970). The bedrock was classified in three categories: (1) crystalline dolomite, (2) marls, and (3) compact limestone or dolomite.

Field sampling

In July and August 2004, we established 264 20 × 20 m plots to record *Fagus* sapling abundance. The position of these plots was selected by means of a stratified random sampling design equally balanced between the three habitat types (pine, edge of pine forest, and grassland), to span a range of distances to the nearest population of mature *Fagus* trees. We first selected a pine forest to localize a plot in pine forest, then the nearest grassland was selected for a plot in grassland, and then the edge of the pine forest to the grassland was selected for a plot at the edge. For the purpose of stratification, the distance of each pine forest to the nearest population of *Fagus* was estimated using GIS and then transformed to a discrete class. An attempt was made to randomly select 10 pine forests in each of the 10 distance classes and select 10 grasslands and 10 edges between pine forest and grassland close to these pine forests. Based on the GIS analysis, we selected 92 plots for the grassland, 92 plots for the pine forest, and 92 plots for the edge of the pine forest. However, during the fieldwork, only 80 grasslands were sampled because 12 GIS polygons of grassland appeared to have been converted to crop fields. All the recorded plots were located in the field with a GPS receiver (see Fig. 1 for the location of the plots). The centre of the plot at the edge of pine forest was located 10 m from the edge of the boundary, within the pine forest.

We established the 20 × 20 m sampling plots with a tape measure, and marked them temporarily with coloured ropes. The number of *Fagus* saplings (defined here as having a height between 0 m and 6 m, so including seedlings *sensu stricto*) was recorded for each plot. We estimated the percentage cover of shrubs (*Juniperus communis* L. and *Buxus sempervirens* L.) for each plot. We then estimated the percentage light transmission under the forest canopy using a class-class system, each class being a 25% increment of light transmission. The grassland plots were always recorded as the maximum light class, 75–100%.

Statistical analysis

We examined the effect of the distance to the nearest *Fagus* population, the type of vegetation, the percentage of light transmission, shrub cover, the type of bedrock, and the meteorological variables (pluviothermic index and number of frosty days) on the number of saplings with a Generalized Linear Model (GLM) with a Poisson distribution and a log link function.

We used a stepwise procedure to select the most significant variables using the Akaike Information Criteria (AIC) (stepAIC library MASS in R, Venable & Ripley, 2002). The continuous variables were included as a linear, a second-, and a third-order polynomial term, to select the best transformation of the explicative variables to account for non-linearity (Austin, 2002). Then the interaction between vegetation type and the distance to the nearest *Fagus* population, and the interaction between the vegetation type and the shrub cover, were included in the selected model to test the hypotheses 4 and 5 of the introduction, i.e. that the effect of the variable 'distance to the nearest *Fagus* population' is different between pine stands and open areas because of the behaviour of the jay, and that the effect of shrub cover is positive in open areas and negative in pine forests. The response curves for the explanatory variables were computed with the values of the other variables fixed at the mean (except when other values are given in the caption of figures). All statistical analyses were performed with R 2.2.1 (Ihaca & Gentleman, 1996).

RESULTS

Overall we collected data on 264 plots with a total of 650 *Fagus* saplings. The distance of the plot to the nearest beech stand ranged from 10 m to 7000 m. In general, the recruitment rate was very low in the studied plots. The mean density of saplings in the plots was 6.1 10^{-3} individuals m^{-2}, quartiles at 2.5 and 97.5% are 0–0.067 individuals m^{-2}, with a large variability of this density between habitat type (grassland density = 3.9 10^{-3} individuals m^{-2} quartiles at 2.5 and 97.5% are 0–0.023 individuals m^{-2}; pine forest density = 5.2 10^{-3} individuals m^{-2} quartiles at 2.5 and 97.5% are 0–0.042 individuals m^{-2}; edge of pine forest density = 8.9 10^{-3} individuals m^{-2} quartiles at 2.5 and 97.5% are 0–0.093 individuals m^{-2}).

Model selection

The distance to the nearest beech population explained the most variance (Table 1). The automatic selection procedure gives rise to a model including six explanatory variables, all highly significant according to a χ^2 test (Table 1). The bedrock variable was not selected by the stepwise procedure; and the inclusion of this variable in the selected model was marginally non-significant (d.f. = 3, deviance = 7.5, $P = 0.06$). For all the continuous variables a polynomial transformation of order 3 was selected, except for the number of frosty days which was included in the model as polynomial of order 2, indicating that non-linearity was present in the response curve for all these variables. The deviance explained by the polynomial transformation of order 3 of the distance to the nearest beech population was 12 times larger than the deviance explained by the remaining biotic or abiotic variables (Table 1). The light, the pluviothermic index, the type of habitat, the number of frosty days, and the shrub cover explained only a small part of the total deviance.

We then tested the interaction of the type of habitat with the distance to the nearest *Fagus* population (as polynomial of order 3) and the interaction between the type of habitat and the shrub cover (as polynomial of order 3) in the model selected by the stepwise procedure, to test the hypotheses 4 and 5 of the introduction. According to χ^2 test, both interactions were highly significant and explained a large part of the deviance (interaction habitat × dist *Fagus poly*(*3*): d.f. = 6, deviance = 114.4, $P < 0.0001$; interaction habitat × shrub cover *poly*(*3*): d.f. = 6, deviance = 68.1, $P < 0.0001$). The final model including these two interactions had a R^2 of 0.757, and the plot (not shown) of the prediction vs. observation indicated a good fit of the data with little bias.

Response curves

According to the estimated model, recruitment was higher in pine forests and at the edge of pine forests than in grassland. The predicted number of saplings per plot at 100 m from a *Fagus*

Table 1 Best model (Generalized Linear Model with a log link and a Poisson distribution) of *Fagus* sapling recruitment estimate by a stepwise procedure (stepAIC from the library MASS in R software). The selected transformation (*poly*(*2*) and *poly*(*3*)) is, respectively, polynomial transformation of order 2 or (3), degree of freedom (d.f.), residual degree of freedom (Resid. d.f.), residual deviance (Resid. Dev), and probabilities of χ^2 tests of the effect of the variable are given. The abbreviations of the explicative variables are: Dist *Fagus*: distance to the nearest *Fagus* population; Light: percentage of light transmission (four classes); Q2: Emberger's pluviothermic index; Habitat: type of vegetation (grassland, pine forest, and the edge of pine forest); Frosty days: number of frost days per year; and Shrub cover: cover of unpalatable shrub species (*Juniperus communis* and *Buxus sempervirens*) in percentage.

	d.f.	Deviance	Resid. d.f.	Resid. Dev	P (χ^2 test)	AIC
Null			263	2818.32		
Dist *Fagus poly*(*3*)	3	1390.75	260	1427.57	< 0.0001	1640
Light *poly*(*3*)	3	115.15	257	1312.43	< 0.0001	1531
Q2 poly(*3*)	3	98.22	254	1214.20	< 0.0001	1439
Habitat	2	86.27	252	1127.94	< 0.0001	1356
Frosty days *poly*(*2*)	2	59.44	250	1068.50	< 0.0001	1301
Shrub cover *poly*(*3*)	3	54.21	247	1014.29	< 0.0001	1104

AIC, Akaike Information Criteria.

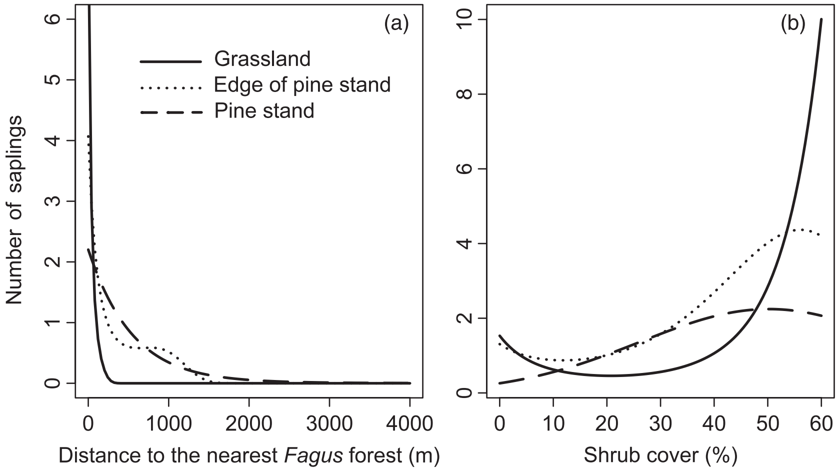

Figure 2 (a) Effect of the distance to the nearest *Fagus* population on the predicted number of *Fagus* sapling recruited for the three types of habitat. (b) Effect of shrub cover on the predicted number of *Fagus* saplings recruited for the three types of habitat according to estimated model. The response curves were computed with all the other variables fixed at the mean of the observation, excepted, in the panel b, the distance to the nearest *Fagus* population was fixed to 100 m.

population, for a light level between 75% and 100% and with all the other variables fixed at the mean of the observed data, was 0.48 in grassland, but 0.87 in pine forest and 0.93 at the edge of pine forest. The response curves of the effect of the distance to the nearest *Fagus* population were also strikingly different between grassland and pine forests or the edge of pine forest (Fig. 2a), and this effect was significant as reported by the test of the interaction (see Model selection). The predicted number of saplings was greater than zero up to 2000 m from a *Fagus* population in pine forest and at the edge of pine forests, whereas in grassland the number of saplings was close to zero at 300 m (Fig. 2a). In the observed data, there was sapling establishment at the edge of pine forests up to 1400 m from a *Fagus* stand, and up to 3000 m away in pine forests, whereas establishment was limited to less than 200 m in grassland. Similarly, the response curves for the effect of shrub cover was different between grassland and pine forests or the edge of pine forest (Fig. 2b), and this effect was significant as reported by the test of the interaction (see Model selection). For the three habitat types the number of saplings recruited increased with shrub cover, but this increase was strongest for the grassland (Fig. 2b).

For the remaining three variables no interaction term was included. The effect of light was globally negative, with higher recruitment in the shade (Fig. 3a). The number of saplings recruited increased with an increase in the pluviothermic index (corresponding to less water stress) (Fig. 3b). Finally, the number of saplings recruited was maximal for the plot with the lowest frequency of frost (Fig. 3c). There was a weak increase for a number of days with frost greater than 80 days per year, but there are relatively little observations for this part of the curve (10% of the observations are greater than 80 days with frost).

DISCUSSION

Distance to the nearest *Fagus sylvatica* population

Our study suggests that three processes are important for the dynamics of *F. sylvatica* in this landscape: biotic interactions,

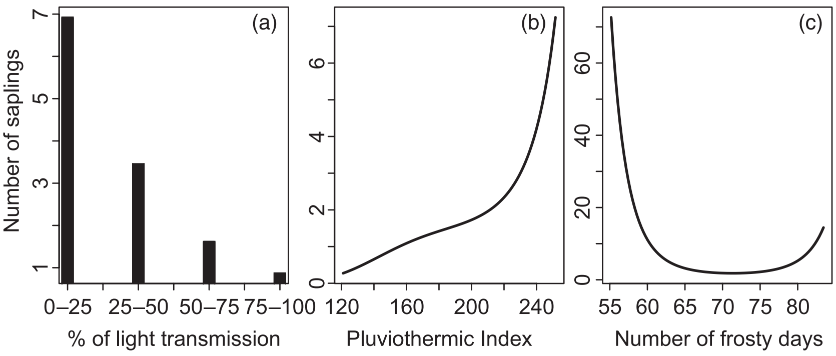

Figure 3 Response of the predicted number of *Fagus* saplings recruited to (a) the percentage of light transmission on the number of *Fagus* saplings recruited, (b) the pluviothermic index (Emberger's index including annual precipitation, average minimum temperature, and average maximum temperature, see equation 1 and the Environmental data section), and (c) the number of frosty days. The response curves were computed, with the estimated model, for a pine forest at a distance of 100 m of the nearest *Fagus* population, and all the other variables are fixed at the mean of the observation.

abiotic factors, and dispersal limitation. However, according to our results for this late successional species restricted to rare and isolated populations, dispersal limitation is clearly the major determinant of recruitment rate. This result corroborates other studies (Turner *et al.*, 2003; Dullinger *et al.*, 2005) showing that the recruitment of tree species at the landscape scale is largely explained by the distance to the nearest population of mature trees. This is in line with studies of forest herbs (Verheyen & Hermy, 2001; Flinn & Vellend, 2005; Matlack, 2005), showing that the re-establishment of these herbaceous species in recent forests developed on abandoned agricultural lands is limited by their dispersal ability.

The number of saplings recruited decreases quickly with increasing distance to the nearest *Fagus* population. The interpretation of the ecological meaning of this result requires caution. First, the variable 'distance to the nearest *Fagus* population' estimates effective dispersal (seedling dispersal in opposition to seed dispersal, according to Nathan *et al.*, 2003), which includes the effect of germination and seedling survival. Second, we consider the distance to the nearest sexually mature population as the effective dispersal distance, whereas the parent tree may be more distant. The use of the distance to the nearest tree as an estimation of the dispersal distance is a biased estimator, providing underestimations of the dispersal distance (Nathan & Muller-Landau, 2000). Nevertheless, our study reports some events of effective dispersal up to 3000 m from the nearest *Fagus* population. Such events of long-distance dispersal are rare in the landscape, and were not visible in a previous study at the community scale in grassland of the same area, in which the predicted mean distance of dispersal was 49 m (Kunstler *et al.*, 2007). These events of long-distance effective dispersal likely result from the activity of European jay (*G. glandarius*), as other animal vectors of dispersal (mainly rodents) have a very short-dispersal distance [less than 100 m (Bossema, 1979; Nilsson, 1985; Gomez, 2003)]. Indeed, jay species are known to lead to extremely long-distance dispersal events, for instance Gomez (2003) reports dispersal events of *Quercus ilex* acorns by the European jay up to 1000 m from the parent tree, and Johnson & Adkisson (1985) report dispersal events of *Fagus grandifolia* nuts by the blue jay (*Cyanocitta cristata* L.) up to 4000 m from the parent tree. In addition, jays bury seed at 1–3 cm depth and this thus enhances seed germination and seedling establishment (Bossema, 1979). This is why jays are considered the main explanation of the fast migration of fagaceous trees during Holocene (Johnson & Thompson, 1989).

Because of strong dispersal limitation in the recruitment process, the position of remnant *Fagus* populations is one of the major drivers of the re-colonization of this landscape. The location of these relict populations is mainly determined by the previous human activity in the landscape. Areas subject to a lower pressure of human wood exploitation have a higher density of mature *Fagus*. The legacy of human activity on the landscape is thus a determinant of current vegetation dynamics. For instance, in the south-west of the Larzac (the Guilhaumard area) there is a high density of remnant patches. This part of the landscape was completely forested until the French revolution (according to the map of Cassini 1780). During the French revolution, the abrupt decreases of the policy applied to forest protection led to a partial deforestation of this area by the local population for fuel wood.

Effect of the composition and structure of the local vegetation

The importance of the composition and the structure of the local vegetation in determining recruitment of *F. sylvatica* concurs with previous studies based on field experiments (Kunstler *et al.*, 2005; Kunstler *et al.*, 2006). Recruitment is higher in plots in shade than in plots in full light and higher in pine forest than in grassland in agreement with the high shade tolerance (in terms of growth and survival) of *F. sylvatica* (Kunstler *et al.*, 2005) and its low tolerance to competition by herbaceous species (Coll *et al.*, 2004) and grazing. Growth and survival of *Fagus* have been reported to increase with light availability in pine forests, but they reach an asymptote at 5–10% of light (Kunstler *et al.*, 2005), which is included in the first class of light (0–25%) of this study. Decrease in recruitment at higher light levels can be related to either an increase in the abundance of herbs correlated to light levels at the plot scale and thus higher herbaceous competition (Kunstler *et al.*, 2006), or to light inhibition (Valladares *et al.*, 2002). Similarly, shrub cover has a positive effect on recruitment and this effect is particularly important in grassland, in agreement with previous studies (Rousset & Lepart, 2000; Kunstler *et al*., 2006) that have shown shrub facilitation on recruitment of trees in grassland because of protection against herbivores and indirect facilitation through a limitation of herb competition. The recruitment of *Fagus* in the Larzac landscape occurs mainly in pine forests (with a slightly higher recruitment at the edge of pine forest that could be related either to a favourable conditions for sapling establishment or to a higher input of seed), with the rare events of regeneration in grassland promoted by shrub facilitation. The existence of new potential habitat for *Fagus* is thus related to the dynamics of *Pinus*. The area cover by *Pinus* forests has increased quickly in the last 50 years because of the natural expansion of native *P. sylvestris* (Caplat *et al*. 2006) and the plantation of *P. sylvestris* or *P. nigra*. The potential suitable habitat for *Fagus* regeneration is thus expanding in this region.

Abiotic factors

One striking result of this study is that even at the landscape scale (the Larzac area includes in 40 × 40 km^2) there is a strong climatic effect on tree dynamics. Usually the effect of climate is considered important for the distribution of a species over larger areas such as the regional (Thuiller *et al*., 2003; Dullinger *et al*., 2005) or the continental scales (Pearson & Dawson, 2004; Guisan & Thuiller, 2005; Thuiller *et al*., 2005). Two points can be put forward to explain this result. First, a number of different climatic influences are present in the Larzac area (Mediterranean, Oceanic, and Continental climates), and the climate may be extremely different from one point to another. For instance, precipitation is higher on the western part of the plateau because of oceanic influences. Second, the study area is located at the southern limit of the distribution of *Fagus* (Quézel & Medail, 2003), the climate is stressful (low rainfall) for this temperate species, and recruitment is likely to be limited by climate. Indeed, recruitment increases with an increasing pluviothermic index, being itself positively related to the annual rainfall and negatively correlated to temperature. *Fagus* recruitment is thus negatively affected by drought. This is in agreement with previous studies that have shown that *Fagus* is associated with high rainfall in Mediterranean areas (Thuiller *et al*., 2003) and across Europe (Sykes *et al*., 1996), that the radial growth of *Fagus* is negatively correlated to summer drought (Dittmar *et al*., 2003; Lebourgeois *et al*., 2005), and that *Fagus* has high seedling mortality and is vulnerable to air embolism in drought conditions (Cochard *et al*., 1999; Coll *et al*., 2004; Kunstler *et al*., 2006). The number of days with frost also negatively affects recruitment, with a strong decrease in the number of saplings with increasing frost days. Previous studies (Piutti & Cescatti, 1997; Lebourgeois *et al*., 2005) have shown that freezing temperatures can limit the growth of *Fagus*, as well as tree survival because of freezing-induced embolism (Lemoine *et al*., 1999).

Our expectation was that recruitment rates would be higher on the more fragmented bedrock (crystalline dolomite) than on the other bedrocks due to higher root penetration allowing easier access to soil water during summer drought. The effect of the bedrock type is not significant in our study. However, because the *P*-value of the test of this variable is marginally insignificant, thus its impact on recruitment cannot be completely excluded. A similar study (Dullinger *et al*., 2005) reports no effect of bedrock or soil type on the recruitment of tree species across an alpine landscape. According to this study, the effect of soil type was important only for the growth of the species.

Directed dispersal towards pine

The interpretation of the interaction between habitat (grassland or pine forest) and the distance to the nearest *Fagus* population is complex. Nevertheless, the interaction could be the result of a long-distance dispersal by jay preferentially orientated towards pine forests in comparison to grassland, in agreement with the study of Gomez (2003). In grassland, dispersal is likely to result principally from rodent activity, explaining the shorter dispersal distance. Direct dispersal towards pine forests resulting from the activity of the jay is likely, but a more detailed study of bird behaviour in this landscape is required to understand the impact of jays in this pattern. The existence of directed dispersal by jays towards pine forests, the habitat type with highest survival and growth (Kunstler *et al*., 2005; Kunstler *et al*., 2006), may be of great importance for the dynamics of colonization of this fragmented landscape by a late successional tree limited to few relict populations. This study emphasizes the need to study jointly dispersal, abiotic factors, and biotic interactions to understand the landscape dynamic of tree species.

ACKNOWLEDGEMENTS

We thank Rob Brooker, Marc Fuhr, Stephanie Gaucherand, and Patrick Saccone for helpful comments on an earlier version of the manuscript. We thank the Regional Park of the Grand Causse and J-P. Ansonnaud (ONF) for providing the map of the *Fagus* population. This work was completed as part of a research project of the French Ministry of Agriculture, FNADT, Convention no. 0413-2002 'Gestion durable des boisements naturels feuillus en moyenne montagne: comprendre et favouriser le retour du chêne et du hêtre'. WT was partly funded by the EU FP6 MACIS specific targeted project (Minimization of and adaptation to climate change: impacts on biodiversity No.044399) and EU FP6 ECOCHANGE integrated project (Challenges in assessing and forecasting biodiversity and ecosystem changes in Europe).

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