Neighbourhood interactions and environmental factors influencing old-pasture succession in the Central Pyrenees

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Abstract. The shrub *Buxus sempervirens* and the trees *Abies alba* and *Fagus sylvatica* have recently recolonized old-pastures in the Central Pyrenees. We mapped all live and dead individuals (> 1.3 m tall) in a large forest plot in Ordesa Valley to examine the importance of density-dependent processes during recolonization. Biotic interactions were inferred from changes in horizontal structure and the influences of neighbours on tree survival. *Buxus* differentially influenced establishment and survival of tree species, thereby controlling future canopy composition and spatial structure. The rapidly invading *Abies* formed denser patches on elevated sites less occupied by *Buxus*, whereas *Fagus* preferentially established within shrubs. *Abies* reached densities which led to intense intraspecific competition and high mortality rates among saplings. Self-thinning in *Abies* led to smaller numbers of regularly spaced survivors, and greater relative dominance of *Fagus*. Disregarding intraspecific effects and abiotic environment, *Abies* survival was significantly lower under *Buxus* shrubs, which suggests that the spatial location and abundance of *Abies* was constrained by the location of *Buxus*. *Fagus* survival was not related to *Buxus* density, but remained significantly lower in denser *Abies* patches. The higher mortality of *Fagus* in denser *Abies* patches, and the resulting spatial segregation of the species, reflects asymmetric interspecific competition. Inhibition from *Buxus* shrubs and intraspecific competition prevent invading *Abies* from dominating and may therefore help in maintaining a mixed *Abies-Fagus* stand.

Keywords: Competition; Density-dependent mortality; Facilitation; Interference; Logistic regression; Population dynamics; Ripley's *K*-function; Spain; Species segregation.

Introduction

Density-dependent interactions among forest trees and their effects on individual performance such as growth and survival have been studied mostly in relatively crowded monospecific stands where competition was the most common interaction (e.g. Hara 1985; Peet & Christensen 1987; Kenkel et al. 1997). These studies have demonstrated that local crowding (associated with intense competition for light and soil resources) reduces growth,

reproductive output, and tree survival. Density-dependent interactions in mixed stands have been little studied (e.g. Condit et al. 1994; Hara et al. 1995) and their role in early forest succession is hardly known. We examine the importance of competitive and facilitative interactions among the shrub *Buxus sempervirens* and the trees *Abies alba* and *Fagus sylvatica* during an old-pasture succession.

The spatial arrangement of plants within the community is of fundamental importance for plant species interactions. In forest communities, most species are not randomly distributed but often aggregated at one or more spatial scales. Limited seed dispersal, patchy environment, and competition with neighbouring plants often create aggregations of conspecifics. Such local clustering may increase the proportion of interactions that are intraspecific, thereby reducing interspecific interactions. This can slow down the exclusion of weaker competitors and thus promotes coexistence among species (Pacala 1997). Many studies revealed that shrubs and trees that initially colonize large forest disturbances prevent later successional species from being recruited to the canopy by reducing their growth and survivorship in the understorey (Nakashizuka 1987). However, intense intraspecific competition after canopy closure usually results in self-thinning. The mortality in early-successional species progressively creates canopy gaps, which can promote the recruitment of late-successional species (Faliński 1988). Indeed, density-dependent mortality have been shown to play a role in promoting succession or maintaining mixed stands by reducing the population size of species that would otherwise have the potential to dominate the forest community and drive other species to local extinction (Lookingbill & Zavala 2000).

Most generalizations about effects of density-dependent interactions on forest development have been based on observations, since experiments are not easy to perform in tree populations of large and long-lived individuals. Density-dependent interactions in forest communities are either inferred from spatial arrangement of individuals in a stand (Kenkel 1988; Peterson & Squiers 1995), or

from correlations between tree performance and influence of neighbours (Hara et al. 1995; Vacek & Lepš 1996). We combined these two approaches. The study site has been densely invaded by *Abies alba*, and to a lesser extent by *Fagus sylvatica* after the cessation of intense grazing. Many trees died during the first decades of stand development. Because of the slow decomposition rate of dead trees we could reconstruct the initial distribution of individuals and test if tree death occurred at random, independently of stem location. Since the study area showed some variation in elevation, topography and surface rock cover, we also examined effects of these factors on tree establishment and survival.

Material and Methods

Study site

The study site was a north-facing slope in the Ordesa Valley on the left bank of the River Arazas ca. 6 km NE of the town of Torla, Spain (42° 39'N, 00° 01'E). Mean annual precipitation is 1600 mm (range 900 - 2000 mm) (Camarero & Gutiérrez 1999). Mean annual temperature is ca. 5 °C; mean temperature for February is –1 °C, for July 12 °C. Ordesa Valley is a E-W oriented glacial cirque with the bottom at 1050-1350 m a.s.l. and the crest at 2000-2200 m. Brown forest soil developed from weathered limestone and sandstone bedrock and accumulated material. Total N = 13-16 g.kg^{-1} dry soil weight; organic C = 34-46%; C/N ratio = 25-35; pH - (KCl) 5.5-6.6.

Pasturing in the area largely ceased after World War II. Some low-intensity livestock grazing is still practised now and the forest vegetation is moderately grazed by native herbivores. Reforestation was mostly with *Pinus*, particularly on the southern slopes where timber harvest and grazing were intense. On northern slopes, above ca. 1400 m, where the study site is located, low accessibility prevented clear-cutting, and an adverse microclimate made the site less attractive for grazing. Between 1300 and 1700 m slopes are now covered with mixed forest of *Fagus sylvatica*, *Abies alba* and subordinate *Pinus sylvestris*, *Sorbus aucuparia* and *Acer opalus*. The understorey is poor in herbs, but has a shrub layer of *Buxus sempervirens*.

Data collection

In 1998, we established a 70 m × 70 m (0.49-ha) plot in a mixed forest that had regenerated after land abandonment 50 - 60 yr ago. Before abandonment, some old *Pinus* and *Fagus* trees formed an open-canopy forest, interspersed with *Buxus*. The plot was located at a mean elevation of 1365 m (range 24 m) on a foothill of a north-facing slope with a mean inclination of 10.6°. The site was selected to avoid the presence of avalanche gullies and corridors, to minimize confounding effects of local abiotic factors. We mapped the locations of all live and dead trees (> 1.3 m tall) and shrubs using a grid of 49 10 m × 10 m squares, and recorded DBH, total height, crown height, health state (living tree, standing dead stem, and fallen log) and number of stems per clump in shrubs. Trees were divided into:

Saplings	< 6 cm DBH	ca. 1.3 - 6 m high
Subcanopy trees	6 - 20 cm	ca. 6 - 19 m
Canopy trees	> 20 cm	ca. 19-32 m

To characterize site conditions, elevation, % rock cover (*RC*) and slope inclination were recorded in every square. Mean *RC* was 15.9% (range 2 - 60%), slope ranged from 4 to 16°. Slope and *RC* increased with elevation (r = 0.43 and 0.45, P < 0.01); slope and *RC* were not correlated.

Data analysis

Tree density (live, dead, pooled) was correlated with elevation, slope inclination and *RC* for 49 squares. Because the variables were not spatially independent, the significance of association between tree density and abiotic factors was tested by randomization. Density values were randomly assigned to values of environmental factors and a Pearson correlation determined. This was repeated 400 × using torodial shifts, to create a null distribution of correlation coefficients. If the observed correlation fell in either of the 2.5% tails of the null distribution, the relationship was assumed significant.

Spatial distributions of trees and shrubs were examined by the univariate $K(r)$ function (Ripley 1977), with the edge correction by Diggle (1983). To compare an observed pattern to a random model, we used the L function, a transformation of the K function (Ripley 1977). On a graph of $L(r)$ versus r, positive, negative, and zero values of $L(r)$ indicate a clumped, regular and random pattern at a scale of r, respectively. To show a change in the pattern after mortality, we plotted the initial distribution (live plus dead trees) together with that for live trees only. The significance of departure from randomness was determined by Monte Carlo simulations. We constructed approximate 99% confidence envelopes from high and low values of $L(r)$ obtained from 99 randomly simulated point patterns.

To further test if tree mortality was spatially nonrandom, the observed pattern for live trees was compared with that expected if tree death occurred at random (Kenkel 1988). Random mortality was simulated by selecting and removing trees at random from the combined (live plus dead trees) data set, i.e. the same number of individuals as there were dead trees, and determining values of $L(r)$ for the remaining individuals.

Spatial associations between two species were examined by the $L_{12}(r)$ function (Lotwick & Silverman

1982). L_{12} (r) has zero values in case of spatial independence, while negative and positive values indicate spatial segregation and aggregation between two species, respectively. Approximate 99% confidence envelopes from the maximum and minimum values of function L_{12} (r) were generated from 99 torodial shifts of one species with respect to the other (Diggle 1983). To test for changes in the pattern of associations, L_{12} (r) values were first calculated between species pairs of *Buxus*, *Abies* and *Fagus* for combined live and dead individuals and then for live individuals only.

To check the influence of neighbours on tree survival the state of a tree (alive or dead) was correlated with interference indices calculated on the basis of the number, size and distance of live neighbours and modified to account for both intra- and interspecific effects. Since the relationship between plant survival and neighbourhood effects can be confounded with local variation in abiotic factors, we first tested whether or not there is a significant relationship between tree survival and elevation, slope, and rock cover. We used a stepwise selection with AIC (Akaike Information Criterion; Chambers & Hastie 1992) statistics with all of these variables for each tree species and given radius. There were no significant effects on tree survival.

We then tested for a significant relationship between tree survival and interference indices of each species added to a univariate logistic regression. A tree in denser patches, or with taller neighbours, may have a lower probability of survival than a tree in less dense patches, or with an equivalent number of smaller neighbours. Hence, three neighbourhood definitions were used to test for both density and size effects: (1) total number of live neighbours of each species within the radius of each live and dead target tree; (2) as (1) but only neighbours taller than the target tree included; (3) as (1) but only neighbours smaller than the target tree included. Radii of the neighbourhood area were 4 and 8 m. Edge effects were avoided by including only subject trees from the inner square within r m of the plot border. Logistic regression and analysis of deviance (Chambers & Hastie 1992) were used to test for relationships between tree survival and local interference. The statistical significance of this relationship was tested by randomization since our observations were not independent (individuals were analysed

both as target trees and as neighbours of other individuals). Tree values (alive or dead) were randomly assigned to values of neighbourhood density, and the regression coefficient determined. This was repeated 1000 × to create a null distribution of 1000 coefficients. The observed coefficient was then compared with this null distribution. Finally, series of analyses were conducted where a model that included the density of neighbouring conspecifics for a given radius was compared with a model where the density of other species was added as a predictor of tree survival.

Results

Composition and size structure

In total 715 individual trees were recorded (74% alive) and 306 shrubs (93% alive) (Table 1). *Buxus* had a mean height of 2.9 m, with some individuals 6 m tall. *Abies* was the most abundant colonizer, with 71.3% of all trees. *Fagus* with old, scattered trees remaining from the grazing period, was less abundant but almost equally dominant in terms of basal area. Apparently, these trees experienced little competition prior to the establishment of new cohorts. *Abies* had a positively skewed stem diameter distribution (App. 1), suggesting that most trees have established recently. Saplings and subcanopy trees (< 20 cm DBH) formed 82% of the *Abies* population, but only 37% of the *Fagus* population. The diameter distribution of *Fagus* was bimodal, indicating that cohorts have established at different periods of stand development.

Abies had many more dead trees than *Fagus*, and overall accounted for 79% of stand mortality. As a result, relative abundance and dominance (based on basal area) decreased for *Abies* and increased for *Fagus*. *Abies* had the highest mortality in small trees (height class 2 - 6 m; diameter class 5-10 cm); 91% dead *Abies* trees were left with bark and branches intact. In both tree populations, mean stem size increased, whereas size inequality, as measured by the coefficient of variation, decreased with removal of smaller trees. Post-mortality *Abies* maintained dominance in the lower canopy, and was almost equally abundant in the upper canopy as *Fagus*.

Table 1. Tree species composition, number of individuals, and their total basal area in m^2/ha (BA).

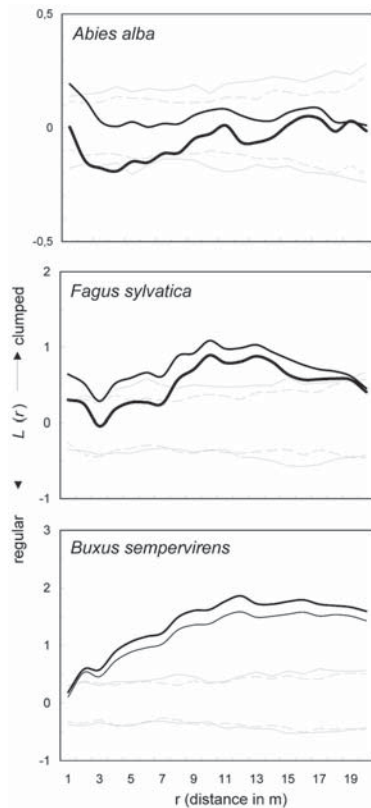| Species	Live + dead				Live				Dead	
	Count	%	BA	%	Count	%	BA	%	Standing	Log
Abies alba	510	71.3	26.4	45.1	363	68.6	25.1	45.4	135	12
Fagus sylvatica	182	25.5	26.2	44.7	151	28.5	25.5	46.1	24	7
Pinus sylvestris	17	2.4	5.8	9.9	11	2.1	4.6	8.3	4	2
Sorbus aucuparia	3	0.4	0.1	0.2	1	0.2	0.0	0.0	0	2
Acer opalus	3	0.4	0.1	0.2	3	0.6	0.1	0.1	0	0
Total	715	100	58.7	100	529	100	55.3	100	163	23

Fig. 1. *L(r)* showing the spatial dispersion of both live + dead (solid thin lines) and live individuals (solid thick lines) over 20 m distances. 99 % confidence envelopes constructed from 99 random point patterns are shown for both live + dead (dotted lines) and live trees (dashed lines).

Spatial patterns

Mean density of all trees (living + dead) was 0.15 ind.m^{-2}, of live trees only 0.11 ind.m^{-2}. Mean number of conspecific neighbours within a circle of 5-m radius around target *Abies* trees was 8.9 ind. for both live and dead trees and 6.2 ind. for live trees only. Mean conspecific density around *Fagus* decreased from 3.4 to 2.6 individuals at neighbourhood 0 - 5 m. Combined live and dead *Abies* trees were significantly clumped at short distances of 3 m (Fig. 1), whereas live trees were regularly spaced at those scales (App. 2). *Abies* mortality was spatially non-random. Dead *Abies* trees were significantly clumped at distances of 1 - 3 m (Fig. 2). The spatial distribution of surviving *Abies* became regular at scales of 1 - 4 m. Mortality also changed the spatial pattern of *Fagus* distribution. Its combined live and dead trees were clumped at all distances up to 20 m, whereas live trees were randomly dispersed to a distance of 7 m, and remained significantly clumped at distances > 7 m (Fig. 1). *Buxus* shrubs were also significantly aggregated at all distances up to 20 m, but unlike
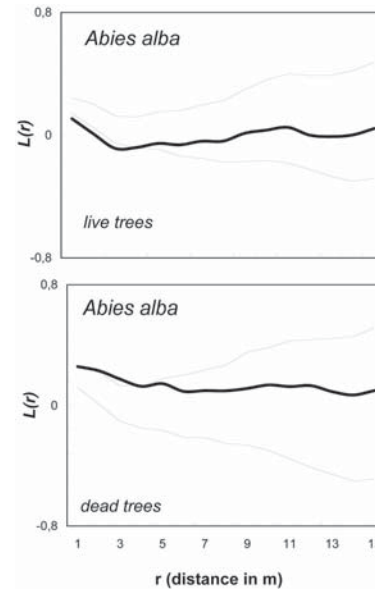

Fig. 2. Random mortality test. Spatial distribution pattern of live and dead trees of *Abies alba*.

Fagus or *Abies* in which the spatial pattern shifted toward regularity, the distribution of *Buxus* became more clumped after some, usually the oldest, individuals died.

Mortality also changed interspecifc associations. *Abies* saplings and *Buxus* shrubs were initially negatively associated, but significantly only at a scale of 3 m, whereas surviving *Abies* saplings were strongly repulsed from shrub patches at short distances (Fig. 3). Smaller *Abies* trees and *Buxus* shrubs showed a strong repulsive pattern at almost all scales, and the intensity of negative association between them increased after mortality. In contrast, taller *Abies* trees and *Buxus* shrubs were positively associated at short distances (<4 m), and also taller *Fagus* trees and *Buxus* showed significant attraction at smaller scales (<2 m). Unlike *Abies*, *Fagus* saplings and subcanopy trees were positively associated with *Buxus* at short distances. *Abies* and *Fagus* initially were positively associated at smaller scales (< 2 m), but were negatively associated at larger scales of 5 - 10 m, and 15 - 20 m (Fig. 4). Mortality resulted in significant negative association (segregation) between the surviving individuals of these two species at short distances of 2 - 5 m.

Site heterogeneity

Local variation in site conditions significantly influenced the spatial pattern of colonization. *Buxus* density increased with decreasing elevation ($r = -0.55, P < 0.01$) and slope ($r = -0.46, P < 0.01$). In contrast, *Abies* stem density (living plus dead trees) increased significantly with slope and marginally with elevation (Table 2). This pattern changed because of higher rates of mortality of
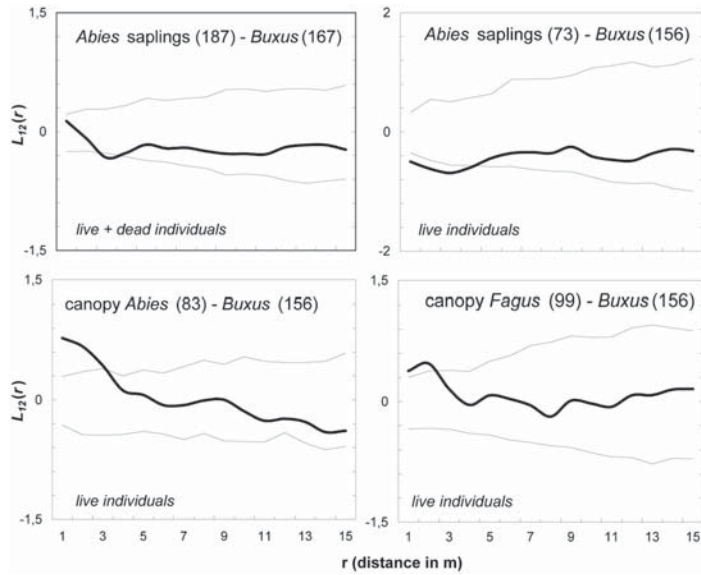
Fig. 3. $L_{12}(r)$ showing spatial associations among tree species and *Buxus sempervirens* shrubs. Thin lines gives ca. 99 % confidence limits for independent distributions of two point patterns.

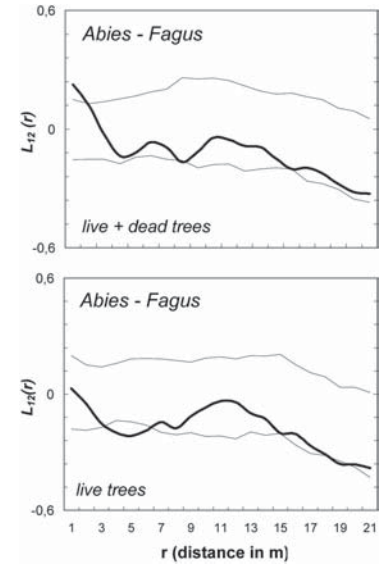**Fig. 4.** $L_{12}(r)$ showing spatial associations between *Abies* and *Fagus*. Thin lines gives the 99 % confidence limits.

small stems in denser patches of conspecifics on steeper sites so that the density of surviving *Abies* was no longer correlated with slope, but remained slightly higher at higher elevation. The density of dead *Abies* increased somewhat with slope, $r = 0.24$, $P = 0.069$. *Abies* was initially unrelated to rock cover, but there was a slight decrease in the density of smaller (< 20 m height) live trees with increasing *RC* ($r = -0.26$, $P = 0.059$). This would suggest that the *Abies* mortality was higher where the amount of rocks increased, however there was no significant relationship between the number of dead *Abies* trees and variation in *RC*. *Fagus* tree density was unrelated to any measured abiotic factors. The density of smaller live *Fagus* trees was positively correlated with *Buxus* shrub density at the 10 m × 10 m scale.

Table 2. Pearson correlation coefficients between tree density (in 49 10 m × 10 m subplots) and elevation, slope inclination, percentage rock cover, and shrub density.

Species / state	Elev	Slope	Rock	Shrub
Abies				
live + dead	0.27	0.28 *	−0.06	− 0.29 *
live	0.33 *	0.22	− 0.18	− 0.42 **
live (≤ 20 cm DBH)	0.41 **	0.25	− 0.26	− 0.52 ***
live (> 20 cm DBH)	− 0.15	− 0.03	0.19	0.05
dead	0.05	0.24	0.11	− 0.11
Fagus				
live + dead	− 0.16	0.02	− 0.13	0.01
live	− 0.12	0.13	− 0.17	0.02
live (≤ 20 cm DBH)	− 0.17	0.15	− 0.14	0.27 *
live (> 20 cm DBH)	− 0.09	0.07	− 0.03	− 0.11
dead	0.03	0.00	− 0.01	− 0.03

* < 0.05; ** < 0.01; *** < 0.001.

Neighbourhood effects on tree survival

Abies survival was negatively influenced by the number and size of conspecific neighbours. Compared to live *Abies*, dead *Abies* had significantly higher density of live conspecifics at 0 - 4 m. However, when live *Abies* taller and smaller than the target tree were tested separately as predictors of *Abies* survival, only taller neighbours showed a significant negative effect on survival, whereas smaller neighbours showed a positive relationship (Table 3). The probability of *Abies* survival decreased most strongly with the density of taller

Table 3. Values of the *F*-statistic and significance levels of a univariate logistic regression of target tree state (alive or dead, the response variables, corresponding to table columns) vs. number of live neighbours (A = all neighbours; L = larger than target tree; M = smaller than target tree) of each species, at two neighbourhood radii. Negative signs indicate that trees with more neighbours had lower probability of survival (higher mortality). df2 = residual df for each response variable.

	Abies 4 m		*Abies* 8 m		*Fagus* 4 m		*Fagus* 8 m	
Abies A	5.65*	–	n.s. (2.0)		n.s. (0.2)		n.s. (1.2)	
Abies L	78.8***	–	108.0***	–	15.7***	–	37.7***	–
Abies M	43.1***	+	83.4***	+	20.7***	+	13.7***	+
Fagus A	n.s. (0.3)		n.s. (0.3)		6.1*	–	6.9**	–
Fagus L	6.0*	–	14.8***	–	23.6***	–	30.3***	–
Fagus M	17.5***	+	44.2***	+	8.3**	+	25.0***	+
Buxus A	n.s. (0.1)		n.s. (0.4)		n.s. (0.0)		n.s. (0.0)	
Buxus L	43.1***	–	83.5***	–	5.5*	–	8.1**	–
Buxus M	14.8***	+	45.2***	+	n.s. (0.7)		n.s. (1.9)	
df2	390		307		139		96	

* < 0.05; ** < 0.01; *** < 0.001

Table 4. Values of the *F*-statistic and significance levels of logistic regression of target tree states (alive or dead, in individual columns) vs. the number of neighbouring individuals of different species, at 0 - 4 m and 0 - 8 m scales, after accounting for the influence of neighboring conspecific trees ('intraspecific competition'). For each target species, the live neighbours smaller and larger were used as predictors of tree survival. Negative signs indicate that survival probability decreases with the density of larger neighbours of other species; first sign in each parenthesis if for neighbor trees larger than the target tree (for details see Methods). df2 = residual df for each response variable.

	Abies < 4 m	*Abies* < 8 m	*Fagus* < 4 m	*Fagus* < 8 m
Abies			4.6*	8.2**
			(–, +)	(–, +)
Fagus	0.7	0.3		
Buxus	15.9***	5.4**	3.7	3.8
	(–, +)	(–, +)		
df2	387	304	138	94

* < 0.05; ** < 0.01; *** < 0.001

conspecifics at the range of 0 - 8 m. Compared with live *Abies*, dead *Abies* had also significantly more live *Fagus* trees of larger sizes at both neighbourhood radii. The presence of larger *Buxus* shrubs was also significantly associated with a higher rate of *Abies* mortality. The probability of *Fagus* survival was lower in regions with increased conspecific tree density, and decreased most strongly with the density of taller neighbours at the range of 0 - 8 m (Table 3). *Fagus* survival was also lower in denser patches of taller individuals of *Abies* and *Buxus*. *Fagus* with close and taller neighbours of *Abies* and *Buxus* had significantly higher mortality rates than conspecifics with no, or smaller neighbours of these species.

The results of neighbourhood analyses with single predictor variables listed in Table 3 indicate that both intra- and interspecific interference with overstory trees and understorey shrubs influence the survival of tree species in this stand. However, when we further explored the relationship between survival and density and had statistically checked the influence of neighbouring conspecific trees, the previously strong negative correlation between *Abies* survival and *Fagus* density was no longer significant at any neighbourhood radius (Table 4). The probability of *Abies* survival remained lower in denser patches of larger *Buxus* shrubs. On the contrary, *Fagus* survival remained significantly lower in denser patches of taller *Abies* after adjustment for intraspecific interference, but was no longer related to the shrub density.

Discussion

Colonization by *Abies alba* and *Fagus sylvatica* was influenced by the presence of few older trees, remnants of the grazed open-canopy forest. Since there were mature trees on the pasture before establishment of new cohorts, colonization may have occurred by dispersal of seeds from these source individuals rather than from the surrounding forests, leading to clustering of new recruits around their parent trees. Indeed, both *Abies* and *Fagus* initially had clumped distributions of conspecifics at one or more spatial scales (Fig. 1). Other important factors causing intraspecific aggregation were interactions between invading trees and shrub vegetation. *Buxus* shrubs were more abundant at lower slopes, which were readily accessible for livestock and intensively grazed in the past. *Buxus*, with evergreen leaves unpalatable to livestock, is resistant against grazing and hence a frequent pioneer species in old-field and old-pasture successions in a calcareous, sub-Mediterranean part of SW Europe (Debussche & Lepart 1992; Rousset & Lepart 1999). In the Central Pyrenees, the *Buxus* layer in the forest understorey is one of the first potential barriers to tree regeneration (Villar et al. 1993), and it can be viewed as a filter that tree seedlings must pass through.

Buxus appeared to have influenced establishment of *Abies* and *Fagus* differently, thereby controlling future canopy composition and spatial structure. *Abies* initially formed denser patches on elevated sites less occupied by *Buxus* shrubs, whereas *Fagus* preferentially established within shrub patches (Table 2). A strong initial tendency for repulsion between *Buxus* and *Abies* saplings and smaller trees indicates that establishment of invading *Abies* was inhibited by the shrub understorey. This is in agreement with several studies where ground vegetation and continuous cover of litter adversely affected establishment in smaller-seeded *Abies*, whose seedling survival was restricted to emergent sites such as rotting logs and tree stumps, or local areas where mineral soil remains exposed (Takahashi 1997). Unlike *Abies*, invading *Fagus* was located significantly closer to *Buxus* than expected at random (Table 2), as was predicted in case *Buxus* facilitates establishment of *Fagus*. *Buxus* shrubs may promote establishment of *Fagus* under their canopies by reducing seed predation rates and by providing protection against grazing. Rousset & Lepart (2000) found that *Buxus* reduces the growth of naturally established seedlings of *Quercus humilis* during old-pasture succession, but promotes seedling survival by protecting them against sheep grazing and summer drought. *Fagus* with relatively soft, nutritious leaves is preferred forage compared to the other tree species and because low-intensity livestock grazing is still practised in Ordesa Valley, and forest vegetation is

also browsed by wild herbivores (García-Gonzales & Cuartas 1996), its successful establishment may depend on protection by *Buxus*. Ultimately, *Fagus* colonized shrub-free areas less than *Abies*. Better dispersal and resistance to grazing may explain the higher abundance of *Abies* invasion in this area, even though there were more mature *Fagus* trees before new cohorts established.

Both spatial and neighbourhood analyses indicate that initial aggregations of conspecific trees increased the proportion of interactions that were intra- rather than interspecific. Intraspecific interactions led to self-thinning, with higher rates of mortality in denser patches of conspecifics. The high-density *Abies* population experienced substantial thinning that resulted in smaller numbers of regularly spaced survivors (Figs. 1 and 2), and greater relative dominance of *Fagus*. Obviously, shaded saplings and smaller trees were the first to die (Hara 1985), while the remaining dominant trees became more evenly spaced (Vacek & Lepš 1996). As in other studies, spacing of trees became more regular as succession proceeded and competition for resources increased (Tagawa 1965). Indeed, competition has been implicated as the cause of regular spacing in all reported instances of this phenomenon in natural communities (Chapin et al. 1989). The largest increases in regularity at a scale of 2 (1 - 4) m in *Abies* and of 3 (1 - 7) m in *Fagus* indicate roughly the mean radius of 'competitive zone' of an individual, which is in agreement with that reported earlier (Kenkel 1988; Vacek & Lepš 1996; He & Duncan 2000).

Abies had most strongly reduced survival in denser patches of overstory conspecifics (Table 3). Moreover, having accounted for these intraspecific effects, its survival remained significantly lower under *Buxus* shrubs, but was no longer affected by *Fagus* density in the overstory (Table 4). In contrast, *Fagus* survival was no longer negatively influenced by shrub density, after we checked for intraspecific effects, but it remained significantly lower in denser patches of canopy *Abies*. This suggests that the higher-density *Buxus* patches prevented *Abies* from recruiting to the canopy by reducing its survivorship in the understorey, whereas denser patches of *Abies* reduced canopy recruitment of *Fagus*. This agrees with other studies where pioneer shrubs and trees become dominant and prevent recruitment of other species (Peterson & Squiers 1995). Due to the higher mortality of *Abies* under larger clones of *Buxus*, surviving *Abies* saplings and smaller trees were rather concentrated in shrub-free areas (Fig. 3). Also, the higher mortality of *Fagus* in denser patches of *Abies* (but not *vice versa*) results in spatial segregation of surviving individuals of these two species (Fig. 4), a pattern arising from asymmetric interspecific competition. The results are in agreement with the forest dynamic models that predict spatial segregation among 'strategically similar species' (Pacala 1997) due to local

dispersal and competition into monospecific neighbourhoods, which may lead to coexistence of species at the community level (Tilman & Kareiva 1997).

Occurrence of dead *Abies* was not associated with the higher densities of live *Fagus* saplings (Table 3); self-thinning in *Abies* did not open up the forest canopy creating gaps and promoting the establishment of *Fagus*. Consequently, self-thinning in a dominant competitor, a process known to promote succession or plant co-existence (e.g. Faliński 1988), is not likely the main factor structuring the community. Since the variation in abiotic conditions in our area is small, there are reasons to believe that *Buxus* is a factor promoting tree species coexistence. The differential effects of *Buxus* on establishment and survival of *Abies* and *Fagus* show that the shrub understorey has the potential to influence the composition of future forest. Our data imply that, in the absence of shrubs, the rapidly invading *Abies* would outcompete *Fagus*, or to substantially slow down its recruitment rate until canopy disturbance would create light openings large enough for successful establishment and growth.

Positive spatial associations between *Buxus* and taller *Abies* and *Fagus* trees (Fig. 3) indicate that the shrubs can coexist with tree species in old-growth stages. Rousset & Lepart (2000) reported that *Buxus* remains positively associated with *Quercus humilis* in later stages of old-pasture succession, because its seedlings have higher survival rates under oak canopies than in adjacent grass-dominated areas. Positive association between *Buxus* and older *Abies* suggests that competition is not the only interaction between these two species. In general, positive and negative interactions or competitive hierarchies among species involved in succession can vary with their development stage, aspect of the site, or successional phase (Rejmánek & Lepš 1996; Callaway 1998). Although *Buxus* reduced the understorey survival of *Abies*, its competitive effect was not sufficiently strong to prevent conifers from establishing freely in the stand. That is, *Buxus* did not form a continuous cover, neither fully coalescing patches. *Buxus* is a relatively weak competitor compared to other clonal dominants colonizing old pastures, which often block succession for a long time (Prach et al. 1996). Other factors than *Buxus* dominance (e.g. adverse microclimate, avalanches and erosion on deforested pastures) will have hindered succession toward forest after cessation of intense grazing. Aggregations between *Buxus* and older trees probably originated from the period of intense land use when the shrubs facilitated tree seedling survival, possibly by protecting them against grazing and soil erosion (Camarero & Gutiérrez 1999), and by suppressing herb cover beneath their canopies (Rousset & Lepart 1999, 2000). These positive associations are likely to intensify in

mature stands where survival of shrubs is higher under open canopies of older trees with higher understorey light levels, than in dense patches of young trees. This may explain the common occurrence of *Buxus* in relict old-growth forests in the Central Pyrenees (Villar et al. 1993), and also why the association *Buxo-Fagetum* is a frequent climax vegetation in this region on colluvial soils (Villar & Benito 2001).

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