

STAND STRUCTURE AND REGENERATION OF A MIXED FOREST (*ABIES ALBA*-*FAGUS SYLVATICA*) IN THE CENTRAL PYRENEES, ORDESA NATIONAL PARK, SPAIN

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ABSTRACT.— The locations and biometrical characteristics of 2391 living and dead trees > 1.3 m tall of *Abies alba* and *Fagus sylvatica*, and the 378 understory shrubs of *Buxus sempervirens*, were mapped in a 1.4 ha plot on the northern slope of Ordesa Valley to evaluate several hypotheses about stand structural development, tree species regeneration and coexistence. The plot is located in relatively undisturbed old-growth forest, but contains areas at low elevation which were formerly pasture. *Abies* is typically represented by many young trees and gradually declining numbers of trees in successively older size classes, whereas *Fagus* has greater numbers of trees in larger size and older age classes. This would imply a shift in dominance from beech to fir if the two species have similar mortality rates. We tested two hypotheses about the coexistence of ecologically similar species: (1) based on differentiation of regeneration niches, and (2) by means of different life history strategies (preference for survivorship or fecundity). Redundancy analysis (RDA) was used to determine if the two species prefer different habitats. The analysis of spatial patterns and interspecific associations by Ripley's K-function was used to estimate the role of competition among trees in forest dynamics. The data provide empirical support for both tested hypotheses, although it has been shown that their importance varies depending on the degree of environmental heterogeneity along the slope across the plot. Different life history strategies appear critical to the success of coexistence in moderate environment at lower elevations, where co-dominant species have overlapping regeneration niches.

RÉSUMÉ.— Dans une parcelle de 1,4 Ha au versant nord de la vallée d'Ordesa nous avons cartographié à petite échelle et pris des données biométriques sur 2391 hêtres (*Fagus sylvatica*) et sapins (*Abies alba*) vivants ou morts mais tous s'élevant à plus de 1,3 m, ainsi que sur 378 arbustes de *Buxus sempervirens* dans le sous-bois. Puis nous avons tenté quelques hypothèses concernant la structure et la dynamique de la parcelle forestière, la régénération des arbres et leur coexistence. Bien que la parcelle fasse partie d'une vieille forêt peu altérée, dans sa partie inférieure quelques surfaces ont été pâturées. Le sapin montre beaucoup de jeunes individus et progressivement moins d'arbres de

grande taille; à l'opposé, le hêtre présente un plus grand nombre d'arbres appartenant aux classes de haute taille et de grande ancienneté. En supposant que les deux espèces aient des taux de mortalité similaires, cela indiquerait une tendance vers la dominance du sapin sur l'hêtre. Sur la coexistence de deux espèces écologiquement similaires, deux hypothèses peuvent être avancées: (1) différenciation de niches de régénération et (2) stratégies biologiques différentes (préférence pour la survivance ou la fécondité). Par la voie d'une analyse de type redundancy analysis (RDA) nous avons essayé de découvrir si les deux espèces préféraient des habitats différents. Pour évaluer le rôle de la concurrence entre arbres et son influence sur la dynamique de la forêt, nous nous sommes servis des modèles spatiaux et associations interspécifiques liées à la fonction K de Ripley. Il est vrai que les résultats obtenus peuvent supporter empiriquement les deux hypothèses précitées, mais nous avons démontré comment l'importance de chacune varie suivant le degré d'hétérogénéité environnemental du versant à travers la parcelle et de bas en haut. Les différentes stratégies de vie s'avèrent critiques pour le succès de la coexistence sur des pentes douces à basse altitude, précisément dans les zones où les espèces co-dominantes recouvrent leurs niches de régénération.

RESUMEN.— En una parcela de 1,4 ha de la vertiente N del Valle de Ordesa se cartografiaron detalladamente y se tomaron datos biométricos de 2391 árboles de haya (*Fagus sylvatica*) y abeto (*Abies alba*) vivos o muertos —todos ellos de altura superior a 1,3 m— así como de 378 arbustos de *Buxus sempervirens* en el sotobosque. Se tantearon después varias hipótesis sobre la estructura y dinámica de la parcela forestal, de la regeneración de los árboles y de su coexistencia. Aunque la parcela forma parte de un bosque viejo poco alterado, en su parte inferior alberga algunas áreas que fueron objeto de pastoreo. *Abies* muestra típicamente muchos individuos jóvenes y progresivamente menor número de árboles en las clases de mayor tamaño; opuestamente, *Fagus* presenta mayor número de árboles en las clases de mayor tamaño y de mayor edad. Suponiendo que ambas especies tuvieran tasas de mortalidad similares, ello indicaría una tendencia a dominar el abeto sobre el haya. Respecto a esta coexistencia de dos especies ecológicamente similares, hemos planteado dos hipótesis: (1) diferenciación de nichos de regeneración y (2) desarrollo de estrategias biológicas diferentes (preferencia por la supervivencia o por la fecundidad). Mediante análisis de redundancia (RDA) hemos intentado averiguar si las dos especies prefieren hábitats diferentes. Para estimar el papel de la competencia entre árboles de cara a la dinámica del bosque, usamos el análisis de modelos espaciales y asociaciones interespecíficas por medio de la función K de Ripley. Los datos obtenidos dan un soporte empírico a ambas hipótesis, pero hemos podido mostrar que la importancia de cada una de ellas depende del grado de heterogeneidad ambiental que se observa de abajo arriba en la ladera de la parcela. Así, en condiciones ambientales normales, a baja altitud, donde las especies codominantes solapan sus nichos de regeneración, desarrollar estrategias biológicas diferentes resulta crítico para el éxito de su coexistencia.

Key-words: *Abies alba*, *Fagus sylvatica*, interspecific associations, mixed temperate mountain forest, regeneration, spatial pattern, stand structure, Ordesa National Park, Spain.

1. Introduction

In the Central Spanish Pyrenees, the humid mountainous areas, more or less influenced by oceanic climate (Huesca and Lleida provinces), have been domi-

nated between 1200 and 1700 m by beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) (MONTSERRAT, 1966; RIVAS MARTINEZ, 1986; VILLAR & BENITO, 2001). However, these forests were impacted by timber extraction and grazing and were, in many cases, completely destroyed. Some forests were replanted recently, but not in the original composition. Beech and fir forests were also spontaneously colonized by *Pinus sylvestris* L. Most of the remaining fir-beech forests are relatively young, with trees 100-200 years old. Therefore, present-day examples of old-growth fir-beech forests are rare, and the information on the structure and regeneration of fir and beech in the original conditions is scanty (GIL PELEGRÍN *et al.*, 1989). Remnants of old-growth forests can still be found mainly on steep mountain slopes with northern or northwestern exposures (VILLAR *et al.*, 1993). Here, difficult accessibility prevented clear cutting, and the adverse microclimate made the forage less attractive for grazing.

Ordesa Valley in "Ordesa y Monte Perdido" National Park conserves some unique old-growth (i.e., unlogged and dominated by trees > 30 cm in diameter) fir-beech stands (VILLAR & BENITO, 2001). In 1998, we established a large permanent plot on a north-facing slope and recorded the locations and biometrical characteristics of all live and dead trees and shrubs > 1.3 m tall. The changes in the tree canopy and the shrub understory, dominated here by box *Buxus sempervirens* L., were recorded again in 2002. These stands grow on acid-to-neutral soils derived from sandstone bedrock and limestone rocks falling from the cliffs. Consequently, it is generally thought that these forests are exposed to recurring disturbances from stone and snow avalanches, landslides and wind-throws, which are important in maintaining their structural complexity (SOUSA, 1984; PICKETT & WHITE, 1985). Thus, these stands represent a wide range of environmental conditions enabling the study of environmental responses of tree species (OLIVER & LARSON, 1990). Silver fir saplings and smaller trees (dbh < 15 cm) are currently several-fold more abundant than those of beech (compare BONCINA *et al.*, 2003). Silver fir is typically represented by many young trees and gradually declining numbers of trees in successively older age classes. In contrast, there are greater numbers of beech trees in larger size and older age classes. The greater abundance of young fir in old-growth stands would imply a shift in dominance from beech to fir if the two species have similar mortality rates, and indeed fir-dominated stands are not difficult to find. In other old-growth stands, however, fir and beech coexist as dominant species.

The aim of this paper is to describe and analyze the forest structure and regeneration patterns of fir and beech in an old-growth forest. In particular, attempts have been made to reveal the mechanisms of small-scale coexistence (FOX, 1977). Two hypotheses were addressed in our research. The first is based on differentiation of regeneration niches (GRUBB, 1977; HARMS *et al.*, 2001). Regenerating fir and beech may prefer different habitats which would lead to separation of their adult trees. Such spatial segregation may promote coexis-

tence by avoiding interspecific competition (DUNCAN, 1991). The northern slopes vary considerably in topographic and substrate conditions. The valley forests terminate with limestone cliffs that impact upon the tree stands below through stone and snow avalanches. The slopes are frequently disrupted by avalanche gullies and corridors with mobile substrate and shallow soils on rock outcrops. Beech appears to dominate on rocky avalanche paths and coluvial soils, whereas young silver fir may attain the greater abundance on elevated locations with deeper soils. The second hypothesis of coexistence between beech and fir is based on different life history traits (GRIME, 1979). Differences in recruitment and survival rates may contribute to coexistence if fir and beech occur together on similar microsites, so that their regeneration niches overlap. For instance, the lower abundance of young beech in the forest understory can be balanced by its higher survival rate, faster and more flexible growth, and a greater resistance to disturbances as compared to silver fir. To evaluate the first hypothesis, the spatial distribution of silver fir and beech juveniles and adults was related to three environmental factors that vary considerably throughout the plot (slope steepness, surface rock cover, elevation). To examine if different life history strategies promote coexistence, we compared abundances, spatial patterns and mortality rates of silver fir and beech (juvenile and adult).

Our study plot was located on a hillside with the highest and lowest point differing in elevation by about 104 m. To enable gradient analysis, the plot was divided into three consecutive subplots that are environmentally relatively homogeneous. The intermediate and upper stands are located on a steep slope, representing an old-growth forest that does not appear to be greatly disturbed by anthropogenic factors, particularly logging of mature trees. The upper subplot has a wide avalanche gully surrounded by flat ridges. The lower subplot is located near the valley bottom on a gentle slope, and was formerly used for livestock grazing; it has been densely invaded by silver fir and to lesser extent by beech after cessation of intense grazing in the region. Some results from this stand have been already published (DOLEŽAL *et al.*, 2004). In this paper, we analyze data from all three subplots to determine if stands that differ in environmental characteristics and historical development vary in stand structural attributes.

2. Material and methods

2.1 Study site and field data collection

Research was conducted on the north-facing slope of Ordesa Valley on the left bank of the Arazas River near the Briet bridge, ca. 6 km northeast from the village of Torla, Spain. Ordesa is a glacial cirque of east-west orientation with

an altitude at the bottom of 1050-1350 m and reaching up to 2000-2200 m at the top crests. The region is influenced by an oceanic climate to the north and a continental perimediterranean climate to the south side. Mean annual temperature is about 5 °C; mean February and July temperatures are -1 and 12 °C respectively (Góriz meteorological station). Annual precipitation varies between 900 and 2000 mm. Seasonal distribution of precipitation is approximately winter (16%), spring (30%), summer (22%), and autumn (32%). The parent material in the study slope is composed of sandstone and limestone, transported downslope mostly by coluvial processes. Brown forest soil has developed from weathered bedrock and accumulated material.

The northern slopes between 1300 and 1700 m are now covered by mixed forest of *Fagus sylvatica* and fir *Abies alba*. The forest understorey is poor in herbaceous plants, but contains a shrub layer dominated by *Buxus sempervirens*. Old-growth characteristics exist throughout the forests particularly in terms of large diameter trees, a variety of diameter classes and canopy layers, gap formation, fallen logs and coarse woody debris on the forest floor. Some low-intensity livestock grazing is still practiced at the bottom of the valley and forest vegetation is also moderately grazed by native herbivores (GARCÍA-GONZÁLEZ & CUARTAS, 1996). From 1800 to 2200 m, the vegetation is subalpine, with a sparse forest of *Pinus uncinata* Ram. and an undergrowth of *Rhododendron ferrugineum* L. and *Vaccinium myrtillus* L. (GIL-PEREGRÍN & VILLAR-PÉREZ, 1988; CAMARERO & GUTIÉRREZ, 1999).

A 1.4 ha plot (70 m x 200 m) was established in 1998, with the longest side parallel to the maximum slope, and subdivided into 140 10 m x 10 m quadrats. The plot is located at an average elevation of 1401 m on slope with an average inclination of 15° and an elevation range of 104 m from the lowest to the highest point. The lower part of slope was formerly pasture where grazing ceased about 60 years ago (DOLEŽAL *et al.*, 2004). In the plot, all 2391 tree individuals (both living and dead) and 378 shrubs >1.3 m tall were mapped using metric tapes (x, y coordinates), and their biometrical parameters: dbh (diameter at breast height), total height, and crown length height measured. We defined as a sapling any individual with stem <6 m tall; a subcanopy tree 6-19 m; and canopy tree >19 m. We further distinguished unshaded dominant trees emerging above the main canopy (Table 1). The following was recorded for dead trees: species identification based on bark; whether standing, fallen, uprooted or wind-snapped; dbh and length of the log; the direction of log inclination. Shrubs of *Buxus sempervirens* had their positions recorded within the study area similarly as to trees, and determined state of vigor (alive or dead), number of stems per cluster, diameter at 10 cm above the ground, stem height, and crown diameters in two perpendicular directions. In every 10-m x 10-m quadrat, elevation, percentage surface rock cover and slope inclination were recorded.

Table 1. Canopy composition (number of living individuals) in the three stands (lower and intermediate of 70-m x 70-m, upper of 70-m x 60-m) on the northern slope of Ordesa Valley between 1350-1450 m altitude, counted for understory (1-6 m), subcanopy (6-19 m), main canopy (19-30 m), and emergent (unshaded dominant trees protruding above the main canopy) layers.

| | Stand | | |
|---------------------------|-------|--------------|-------|
| | lower | intermediate | upper |
| <u>Emergent layer</u> | | | |
| <i>Abies alba</i> | 52 | 26 | 4 |
| <i>Fagus sylvatica</i> | 29 | 24 | 45 |
| <i>Pinus sylvestris</i> | 10 | 8 | – |
| <u>Main canopy layer</u> | | | |
| <i>Abies alba</i> | 46 | 22 | 6 |
| <i>Fagus sylvatica</i> | 77 | 96 | 86 |
| <i>Sorbus aucuparia</i> | 1 | – | – |
| <i>Acer opalus</i> | – | – | 5 |
| <u>Subcanopy layer</u> | | | |
| <i>Abies alba</i> | 207 | 244 | 182 |
| <i>Fagus sylvatica</i> | 43 | 64 | 91 |
| <i>Acer opalus</i> | 1 | 1 | 3 |
| <u>Understory layer</u> | | | |
| <i>Abies alba</i> | 73 | 144 | 190 |
| <i>Fagus sylvatica</i> | 1 | 3 | 23 |
| <i>Acer opalus</i> | 2 | – | – |
| <i>Buxus sempervirens</i> | 167 | 140 | 61 |

2.2 Data analysis

We examined how the density of living and dead individuals, saplings and canopy trees of each species varied with elevation, slope inclination and rock cover by counting the number of stems in each of 140 100 m² quadrats, and then correlating stem density with environmental factors for these 140 quadrats. The relationship between species composition and environmental variables was evaluated by methods of multivariate ordination analysis using CANOCO for Windows package (TER BRAAK & ŠMILAUER, 1998). Redundancy analysis (RDA), ordination method based on the assumption of a linear species response to explanatory variables, was used as the data set was relatively homogeneous (we first carried out DCA with Hill's scaling and observed that the length of the first axis was 1.95, which permits the use of linear method). We conducted forward selection with three environmental variables and each variable was tested using 499 Monte Carlo permutations. Because the stand characteristics (tree densities and basal areas) obtained from the regular grid of 140 quadrats were not spatially independent, statistical significance was tested for by permutations restricted for rectangular grids (for details see TER BRAAK & ŠMILAUER,

1998). We first performed RDA for the entire plot, and then we carried out three separate analyses for individual subplots. Basal areas of living and dead trees of *Abies*, *Fagus* and *Buxus* were used as supplementary variables that do not influence the ordination axes, but their relationship to dependent and explanatory variables can still be judged from the ordination diagram.

To examine the spatial patterns of tree establishment and mortality, the mapped locations of the stems were analyzed by the $K(t)$ function and its derived variable the $L(t)$ function (RIPLEY, 1977; with the weighted edge correction given in DIGGLE, 1983, HAASE, 1995). In this approach, the type (clumped, random or regular) and intensity of stem distribution was determined by counting the number of neighbors within a circle of radius t of each individual in the study plot and then comparing the mean number with that derived from stem density per unit area. If the mean number of neighbors was higher than expected for given scale, the pattern was considered clumped at that scale, whereas if the number was smaller, the pattern was considered regular. Approximate 99% confidence limits were constructed from 99 randomly simulated point patterns using Monte Carlo technique (DIGGLE, 1983). For the analysis of spatial structure, individual trees were classified as juveniles (2-12 cm dbh) or adults (>12.1 cm dbh). To assess the spatial associations between groups of juveniles and adults, live and dead trees of fir and beech, a bivariate $K_{12}(t)$ function and its derived variable the $L_{12}(t)$ function were employed. In this approach, the either positive, neutral or negative associations were assessed by counting only neighbors of the other group within a circular area of radius t of each stem in the plot and then comparing the mean number with that expected under randomness (for details see LOTWICK & SILVERMAN, 1982). Monte Carlo simulation was used to construct approximate 99% confidence envelopes from the maximum and minimum values of function $L_{12}(t)$ generated from 99 toroidal shifts of one species with respect to the other (DIGGLE, 1983). The bivariate analyses indicated whether smaller trees prefer (shaded) sites next to adult trees, or (open) sites further away from adult trees (ŠRÚTEK *et al.*, 2002). $K(t)$ and $K_{12}(t)$ functions were computed at 1 m intervals up to 30 m, separately for each of three consecutive subplots, which are hereafter referred as lower (70 m x 70 m), intermediate (70 m x 70 m), and upper stand (70 m x 60 m).

3. Results

3.1 Composition and size structure

The current forest overstory is dominated by silver fir and beech, with subordinate Scots pine (*Pinus sylvestris* L.), mountain ash (*Sorbus aucuparia*

L.), and maple (*Acer opalus* Mill.) (Table 1). Fir, beech, pine, maple and ash dominated in order of abundance. Despite its lower numbers, beech had the highest DBH values, comprising 45-76% of the total basal area. Total stand basal area was respectively 56.3, 37.1 and 39.4 m²/ha in the lower, intermediate and upper subplots. Beech was most abundant among the main canopy and emergent trees, whereas silver fir dominated lower tree and sapling layers. Most Scots pines were found at the lower subplot (Table 1), all big trees with dbh from 40 to 60 cm and height from 26 to 34 m, representing the remnants from open-canopy grazed forest; no young individuals of this shade-intolerant species have established recently. In the long-term, it is assumed that these pines will die as a result of competition for light against beech and silver fir, the process observed at many other similar forests in the Central Pyrenees.

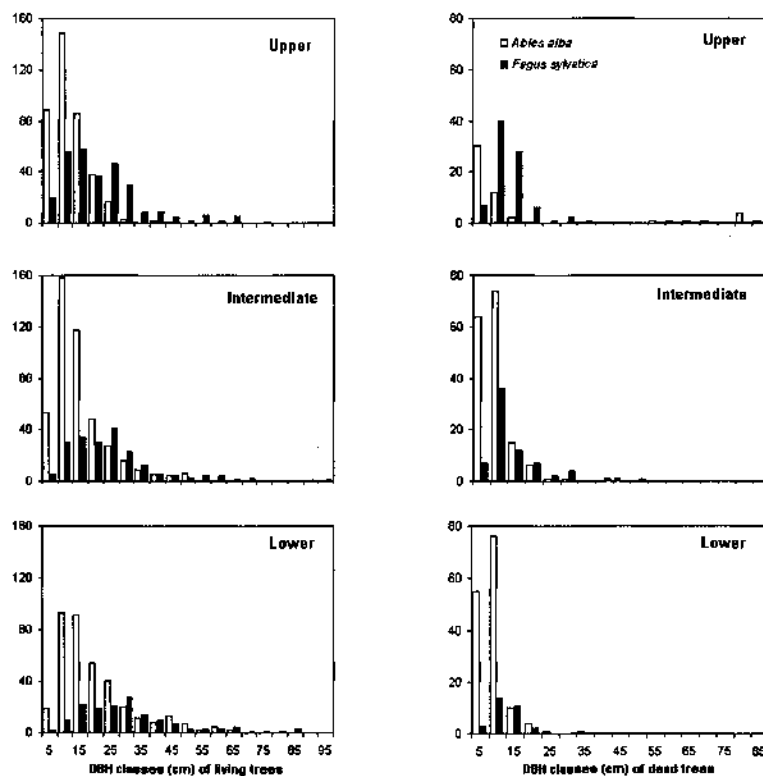


Figure 1. Size-class distributions of living and dead *Abies* and *Fagus* trees in three stands of a mixed mountain forest on a northern slope of Ordesa Valley, Central Pyrenees, Spain.

Fig. 1 shows the frequency distributions of stem diameters. At all three stands, the size structures of silver fir and beech populations were roughly similar, and were characterized by greater numbers of large canopy beech trees, and relatively few beech saplings and subcanopy trees. In contrast, silver fir populations were dominated by large numbers of saplings and subcanopy trees, proportionally fewer large trees, and no individuals as large as the largest beech. Thus, diameter distribution of silver fir trees exhibited a roughly negative exponential or inverse-J pattern, typical of uneven-aged population, with most trees with dbh <15 cm, indicating that most individuals established recently in the stand. The size-class data in silver fir suggest more or less continuous regeneration. The diameter-distribution of beech trees was unimodal or bimodal, which indicates discontinuous recruitment. The height class distributions of beech trees were consistently negatively skewed, with most stems being in 20-24 m height class, indicating that beech tend to grow taller rather than wider in closed-canopy forest conditions. The stem height of beech was higher than that of silver fir for the same dbh (analysis of covariance, $F_{1,1820} = 409.1$, $P < 0.001$). For instance, beech stems with 4-5 cm dbh had average height of 6.85 m, whereas silver fir stems of 4-5 cm dbh had average height of 4.41 m. This indicates that beech allocated more resources to height growth than diameter growth, presumably to escape shading from neighboring trees.

3.2 Tree mortality

The largest living beech tree had 94 cm dbh, and that of silver fir 61 cm dbh. Among dead individuals, the largest standing trees belonged to *A. alba*, with 80-90 cm dbh. Silver fir had many more dead trees than beech and overall accounted for 66.2% of stem mortality in the plot (Fig. 1). Silver fir had a much greater proportion of dead trees in the lower (79%) and intermediate (63.8%) stands compared with beech (16.1 and 28.6%), but a lower proportion of dead trees in the upper stand (38.1%) than beech (61.6%). Most dead silver fir stems were saplings and subcanopy trees with dbh less than 10 cm and stem height less than 10 m. The high mortality in young silver fir stems in the lower and intermediate stands increased relative abundance and dominance (basal area) for beech. Ninety three percent of 369 dead fir trees we measured were standing with the bark and branches relatively intact. Fallen trees were also concentrated in the smaller size classes; in most cases they were dead before they fell. It is unlikely that they were wind-snapped or uprooted owing to their small height and position under the main canopy. Uprooting caused tree death only in a few large canopy fir and beech trees. The canopy openings with uprooted trees and tree stumps (mostly of fir) occurred at the middle and upper subplots representing an old-growth forest, but none were

found at the lower subplot. Although we lack exact information on the proportion of gap area and the relative abundance of tree successors, our observations suggest that silver fir and *Buxus* are preferentially invading gaps and tree-fall piths.

3.3 Intraspecific spatial patterns

All types of spatial distribution of trees were found in the stands analyzed, but the dominating pattern was clumped (Table 2; Fig. 2). Statistically significant clumping occurred in both silver fir and beech at various scales, in particular when live and dead trees were taken together. When live trees or adult trees were tested separately, random or regular patterns were found in a few cases. There were two trends consistent for both the silver fir and beech distribution. The intensity of clumping decreased with stem size (i.e. was stronger in juveniles than adults), and decreased with mortality in small trees (Table 2; Fig. 3). These changes were most pronounced in the silver fir population at the lower stand, where higher mortality in denser patches of conspecifics shifted the pattern from clumped towards significantly regular. Decrease in intensity of clumping with removal of suppressed trees, and uniform pattern in the adult trees suggests intraspecific competition, i.e. decreased survival probability for individuals with very close neighbors (KENKEL, 1988; ŠRÚTEK *et al.*, 2002). The result was supported by analysis of intraspecific associations between juveniles and adults. These were initially positively associated at short distances. Post-mortality, however, association

Table 2. The results of $K(t)$ and $K_{12}(t)$ analyses of intraspecific spatial distribution patterns in *Abies alba* and *Fagus sylvatica* trees at three stands. "A" indicates significant aggregation or positive association (attraction) at the specified distances (m); "S" indicates hyperdispersion (regular pattern) or negative association (segregation); "random" indicates no deviation from 99 simulations of random point patterns; "*" indicates $K_{12}(t)$ analyses of intraspecific associations between juveniles and adults.

| | <i>Abies alba</i> | | | <i>Fagus sylvatica</i> | | |
|-----------------------------|-------------------|---------|--------|------------------------|--------|--------|
| | lower | middle | upper | lower | middle | upper |
| living + dead | A 2 | A 1-19 | A 1-18 | A 1-19 | A 1-30 | A 1-21 |
| living | S 1-6 | A 3-25 | A 1-18 | A 7-20 | A 1-30 | A 2-22 |
| living + dead (dbh < 12 cm) | A 1-15 | A 1-30 | A 1-16 | A 1-16 | A 2-29 | A 3-26 |
| living (dbh < 12 cm) | A 7-15 | A 1-30 | A 1-15 | A 2-5 | A 3-23 | A 3-30 |
| living (dbh > 12.1 cm) | S 4-8 | S 23-25 | random | A 8-20 | A 4-29 | A 7-24 |
| dead | A 1-5 | A 2-17 | A 2-7 | random | A 1-30 | A 2-9 |
| ad/juv living + dead* | A 1 | A 1-2 | A 1-7 | A 1-21 | A 2-7 | random |
| ad/juv living* | S 2-5 | random | A 1-8 | random | A 1-7 | random |

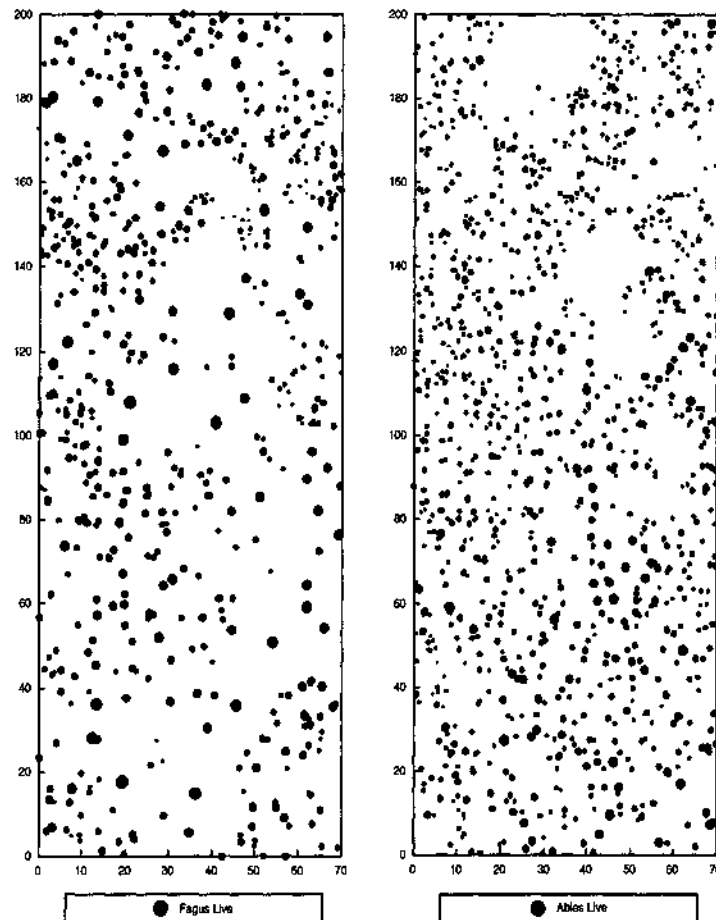


Figure 2. Stand map showing the locations of living individuals of *Abies alba* and *Fagus sylvatica*. Circle size is proportional to dbh. The longer size is parallel to the slope.

between juveniles and adults of silver fir became neutral (middle subplot) or negative (lower subplot) at small scales (Table 2). No cases of statistically significant shifts towards regularity (or repulsion) were found in silver fir at the upper subplot. Overall, there were more changes towards regularity (including changes from clumped pattern to random) in silver fir than in beech, and at the lower subplot than the other two ones. In beech, clumped patterns never changed into significantly regular patterns with the removal of suppressed trees. Similarly, initial positive associations between beech juveniles and adults did not shift to negative associations post-mortality.

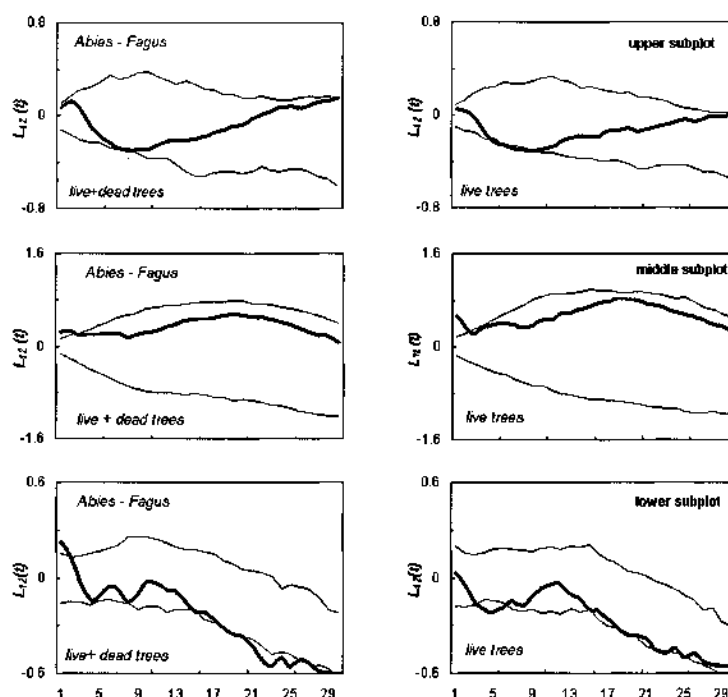


Figure 3. $L_{12}(r)$ showing spatial associations between the living trees of *Abies alba* and *Fagus sylvatica* at three stands of 1.4 ha study plot on the northern slope of Ordesa Valley. Thin lines gives ca. 99% confidence limits for independent distributions of two point patterns.

3.4 Interspecific associations

Distinct areas dominated by either species occurred more frequently at the upper part of study plot, with beech forming monospecific patches (ca. 400 - 900 m²) over larger areas than fir (Fig. 3). Mosaic patterns (i.e. forest composed of mono-dominant patches at small spatial scale, Fig. 4) became apparent as tree stands approached the rocky cliffs, a natural barrier for mixed fir-beech forests in Ordesa Valley. Consequently, with decreasing distance to the rock wall (along with increasing elevation and frequency of natural disturbances, e.g. snow avalanches), negative associations between silver fir and beech prevail (Table 3). Negative spatial relationships were found in both combined live and dead individuals or live individuals and adults analyzed separately. A strong tendency towards spatial segregation was found between juveniles, indicating that fir and beech tended to use different habitats for

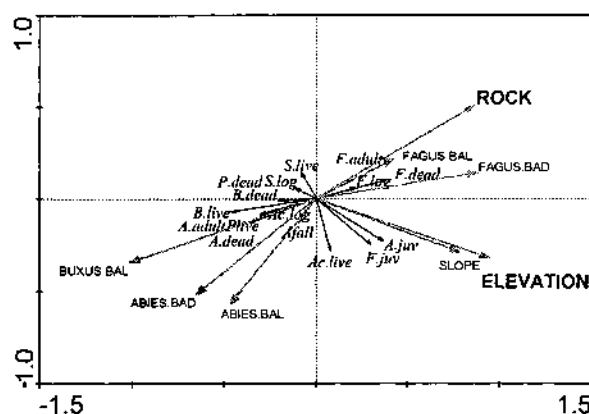


Figure 4. Ordination biplot of Redundancy analysis showing the relationship between tree species composition and environmental factors in 140 x 100 m² quadrats on the northern slope of Ordesa Valley. Abbreviations of dependent variables (thin arrows) are as follow: A - *Abies alba*, F - *Fagus sylvatica*, Ac - *Acer opalus*, P - *Pinus sylvestris*, B - *Buxus sempervirens*. live - living trees, dead - standing dead trees, log - fallen dead trees, juv - juveniles (dbh < 12 cm), adult - adult trees (dbh > 12.1 cm). Variables marked by dashed arrows (ABIES.BAL - basal area of living *Abies alba* trees, ABIES.BAD - basal area of dead *Abies alba* trees, FAGUS.BAL - basal area of living *Fagus* trees, FAGUS.BAD - basal area of dead *Fagus sylvatica* trees, and elevation) are supplementary variables.

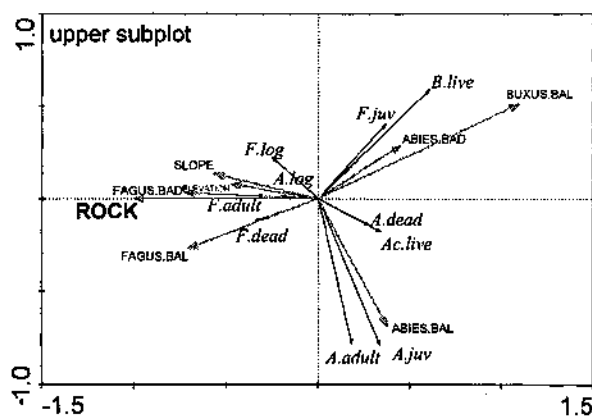


Figure 5. Ordination biplot of Redundancy analysis for the upper subplot: conventions as in Fig. 4

establishment. Consequently, at the upper part of the study plot, segregation of silver fir and beech into mono-specific patches likely resulted from different species responses to environmental heterogeneity rather than from interspecific competition. By contrast, the forest at the middle part of the

Table 3. Results of $K_{12}(t)$ analyses of interspecific spatial associations between *Abies alba* and *Fagus sylvatica*. "A" indicates significant positive association (attraction) at the specified distances (m); "S" indicates negative association (segregation); 'random' indicates no deviation from 99 simulations of random point patterns. "A juv" – *Abies alba* juveniles (dbh < 12 cm), "F adu" – *Fagus sylvatica* adults (dbh > 12.1 cm).

| | <i>Abies alba</i> - <i>Fagus sylvatica</i> | | |
|---------------------------|--|--------------|--------|
| | lower | middle | upper |
| live + dead | A 1-2 | A 1-2 | S 4-8 |
| live | S 3-7 | A 1-2 | S 7-8 |
| live + dead (12 cm < dbh) | S 18-23 | A 1-2, 20-30 | random |
| live (12 cm < dbh) | random | A 1-4, 25-30 | random |
| live (12.1 cm > dbh) | S 3-7 | A 1-2 | S 3-19 |
| dead | random | S 11-20 | random |

study plot lacks ridges and avalanche gullies and overall is environmentally less variable. Here, silver fir and beech were initially positively associated at short distances of 1 to 4 m, indicating the overlap of regeneration niches, and the intensity of aggregation between species even increased after mortality. An increase in interspecific aggregation in the course of self-thinning suggests the greater influence of intraspecific competition (thinning by a variety of mechanisms, most likely due to competition for light; LEP, 1990). Consequently, the forest at the middle part of the study plot can be characterized as converging to a uniformly mixed forest, with individual trees of silver fir and beech next to each other (see FRELICH & REICH, 1995). The opposite trend of increasing interspecific segregation in the course of self-thinning was found at the lower subplot. Here, silver fir and beech were initially positively associated at small scales, but post-mortality they showed negative association at short distances (Table 3 and Fig. 3). Thus, the forest at the lower part of the study slope seems to diverge into small monospecific patches.

3.5 Species-environment relationships

The dependence of species abundances on environmental variables was tested by the univariate regression and correlation analysis (Table 4), and by multivariate Redundancy analysis (RDA) (Table 5). We first conducted RDA with all 140 quadrats (analysis 1 in Table 5); surface rock cover and elevation remained significant explanatory variables after forward selection, explaining 16.2% variability in the species data. The ordination diagram produced by RDA shows that the density of silver fir and beech juveniles increases with elevation and slope steepness (these two variables are strongly correlated and hence it is difficult to separate their effects) and decreases with density of *Buxus* shrubs

(Fig. 4). Adult beech tree density increased with surface rock cover. Also the density of standing dead beech trees and fallen logs is positively correlated with rock cover. At the whole-plot level, silver fir and beech juveniles tend to be positively correlated, while adults are negatively correlated.

Table 4. Pearson correlation coefficients between tree density, percent slope and surface rock cover and shrub density. Significant correlations are in bold ($P \leq 0.05$).

| Species | State | lower | | Subplot middle | | | upper | | |
|------------------------|-------------|-------------|-------|----------------|-------|--------------|--------------|--------------|--------------|
| | | Elevation | Rock | <i>Buxus</i> | Slope | Rock | <i>Buxus</i> | Slope | <i>Buxus</i> |
| <i>Abies alba</i> | live + dead | 0.27 | -0.06 | -0.29 | 0.00 | -0.13 | -0.50 | -0.28 | -0.34 |
| | live | 0.30 | -0.18 | -0.42 | -0.11 | 0.07 | -0.43 | -0.26 | -0.31 |
| | dead | 0.05 | 0.11 | -0.11 | 0.16 | -0.36 | -0.32 | -0.15 | -0.19 |
| | juveniles | 0.33 | -0.26 | -0.32 | -0.07 | 0.29 | -0.21 | -0.22 | -0.37 |
| | adults | -0.03 | 0.19 | 0.10 | -0.10 | -0.22 | -0.46 | -0.22 | -0.14 |
| <i>Fagus sylvatica</i> | live + dead | 0.16 | -0.13 | 0.01 | -0.24 | 0.20 | 0.10 | -0.22 | 0.17 |
| | live | 0.12 | -0.17 | 0.02 | -0.30 | 0.16 | 0.13 | -0.33 | 0.00 |
| | dead | 0.03 | -0.01 | -0.03 | -0.07 | 0.22 | 0.00 | 0.13 | 0.47 |
| | juveniles | 0.10 | -0.14 | 0.27 | -0.19 | 0.03 | 0.13 | -0.28 | -0.39 |
| | adults | 0.07 | -0.03 | -0.11 | -0.31 | 0.24 | 0.11 | -0.21 | 0.36 |

Table 5. Summary of results of RDA analyses. r – is species-environment correlation on the first axis, %-1st axis is percentage of species variability explained by the first axis, %-all constrained is percentage of species variability explained by all the constrained axes, F -trace is the value of the overall F -statistic and is the corresponding probability level obtained by the Monte Carlo test. E - elevation, RC - rock cover.

| | Explanatory variables | r axis | %-1st constr. | %-all | F -trace | P |
|---|-----------------------|----------|---------------|-------|------------|-------|
| 1 | E, RC | 0.66 | 14.1 | 16.2 | 22.5 | 0.008 |
| 2 | RC | 0.78 | 15.3 | | 7.21 | 0.014 |
| 3 | RC | 0.54 | 5.5 | | 2.75 | 0.012 |
| 4 | E | 0.68 | 9.8 | | 5.13 | 0.012 |

A more detailed picture about species-environment relationships is provided by separate RDA analyses for individual subplots. In analysis of the upper subplot, rock cover remained the only significant explanatory variable, accounting for 15.1% variability in the species data (analysis 2 in Table 5). The density of adult trees (and hence basal area), fallen logs and standing dead trees of beech increase with rock cover whereas the density of beech juveniles decreases (Fig. 5). The diagram also shows that silver fir and beech juveniles tended to be negatively correlated. Such spatial segregation of juveniles may contribute to coexistence of species at the community level by decreasing inter-

ference among adult trees (TILMAN & KAREIVA, 1997). The RDA conducted for the middle subplot (Fig. 6) shows that rock cover explained much less variability than in the upper subplot; it likewise exhibited positive correlation with the basal area of beech and negative correlation with the basal area of silver fir (compare with Table). Consistent with the result of bivariate interspecific associations (Table 3), silver fir and beech showed positive correlation. There is a strong correlation between silver fir juveniles and adult beech trees (and fir juveniles and standing dead beech trees), suggesting that fir develop under beech canopy and colonize gaps created by the death of beech. The ordination diagram also shows that the box is unrelated to rock cover, and negatively related to silver fir density. In RDA of the lower subplot (picture not shown, see Table 4), elevation remained the only significant environmental variable after forward selection, accounting for 9.8% variability in the species data. The density of young silver fir trees is most strongly and positively correlated with elevation, whereas that of box shrubs is negatively correlated.

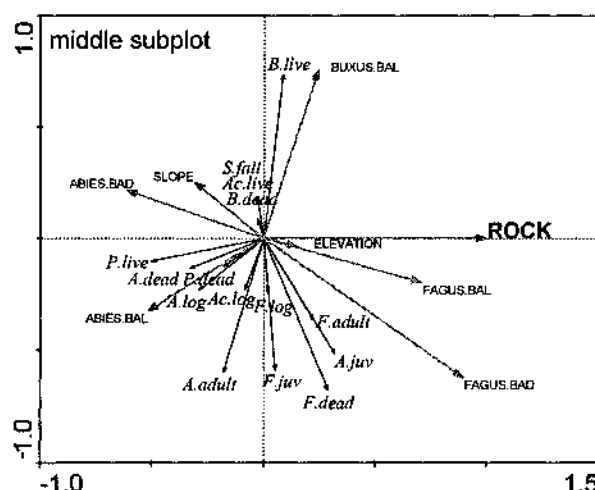


Figure 6. Ordination biplot of Redundancy analysis for the middle subplot: conventions as in Fig. 4.

4. Discussion

Tree distribution patterns, suggested by field observations and proven significant via statistical analyses, generated hypotheses about processes structuring the forest community and maintaining a particular level of diversity. The

hypothesis of habitat differentiation appears to be useful in explaining the coexistence of fir and beech in heterogeneous conditions of the upper part of the study slope, where significant correlations between species abundances and environmental factors were detected (Fig. 5, Table 4). The concept of niche differentiation is based on the assumption that important differences exist between coexisting species in their requirements for establishment and subsequent growth and survival (GRUBB, 1977; PEET, 1981). These differences in our study plot include the superior ability of beech to establish and survive in avalanche gullies, filled by stones falling from the cliffs and overlain by shallow soils. The predominance of adult beech in this unstable and repeatedly disturbed habitat could be explained by resistance to snow pressure, basal-slide avalanches, melting snow and solifluction. Beech growing in rocky gullies have typically curved stems up to height of 2-3 m, indicating the height of snow cover. HOMMA (1997) found that *Fagus crenata* exhibits the highest tolerance of tree trunks to snow pressure among six tree species in the mixed mountain forest in central Japan and was thus the predominant climax species in snow-rich regions at higher altitudes. Similar adaptation is known in *Fagus sylvatica* from the Central European Mountains (PLESNÍK, 1978; FANTA, 1981) and in *Fagus orientalis* from the Caucasus (DOLUKANOV, 1978).

The higher density of silver fir outside rocky avalanche gullies concurs with the general ecological requirements of this species. Deep-rooting silver fir prefers nutrient-rich deeper soils with higher water-holding capacity. Water deficit stress is usually higher on coarse-grained soils (JENNY, 1980). Fir is susceptible to conditions of low moisture in summer (ROLLAND *et al.*, 1999; BRÁZDIL *et al.*, 2002) and its tendency to achieve higher density on deeper and moister soils within our study plot (STASTNÁ, 2000) is consistent with how this species performs along the moisture gradient at larger spatial scales (ROLLAND *et al.*, 1999).

Beech often regenerates in small gaps where higher light levels ensure optimal development (YAMAMOTO *et al.*, 1995; COLLET *et al.*, 2001, 2002). It can also develop under the canopy of conspecific trees (KOOP & HILGEN, 1987). Beech seedlings in the British beechwoods develop under the crowns of mother trees but grow better at the border of the canopy (WATT, 1925). Young beech seedlings in the Fontainebleau forest occurred both beneath conspecific trees and in treefall gaps (PELTIER *et al.*, 1997), but most abundant were in semi-shade conditions under the crowns of mother trees, and where beech litter did not accumulate. In the Western Carpathians, shrubs and ferns form often dense understories under the relatively open canopies of old-growth fir-beech stands, and preclude tree regeneration (KORPEL, 1989; DOLEŽAL & ŠRÚTEK, 2002). Thus, in these forests inhibition of tree regeneration by ground-layer vegetation may result in exceedingly low densities of

young trees in large treefall gaps. Higher densities of beech saplings are often found in small gaps and canopy edges where the reduced fern and shrub cover occasionally permits successful seedling establishment.

Two principal factors that are thought to limit beech recruitment in our study plot are competition from overstory trees and reduced establishment in treefall gaps. The very recent canopy openings created by multiple windthrows in the middle part of study slope are now being filled by many box shrubs and some silver fir recruitment, including both new seedlings and released saplings, but very little (if any) beech seedlings became established. Consistent with this observation, beech juveniles and adults showed positive association at the middle and lower subplots, indicating that the prevalent mode of beech recruitment in these stands is beneath mother trees or in their vicinity rather than in treefall gaps. SWAGRZYK & CZERWCZAK (1993) likewise found in natural mixed-beech forests in East-Central Europe that gaps, created by the death of one or a few large trees, do not always promote successful recruitment of new individuals.

Competition from overstory trees is also likely to be responsible for the lack of recent beech recruitment into the larger diameter classes (Fig. 1); it has been shown that the survival probability of young beech in the lower stand is negatively correlated with density of both fir and beech canopy trees (DOLEŽAL *et al.*, 2004). From the population spatial and size structure, it can be assumed that stem recruitment in beech had several distinct episodes over the last 100-150 years and tended to occur in small, scattered patches, often in the proximity of older beech trees. These patterns suggest that infrequent natural disturbances form localized canopy openings (most probably with reduced litter and understory cover), damage older trees that may survive the event, and initiate the establishment of new trees that fill these openings. Ultimately, repeated observations coupled with dendroecological reconstruction will be required to fully understand spatio-temporal dynamics of tree populations in the region (e.g. TARDIF *et al.*, 2003).

The horizontal forest structure is a result of interactions between factors causing regularity in tree distribution (e.g. density-dependent competition) and factors causing clumping in tree distribution (e.g. environmental heterogeneity and windthrows) (BUSING, 1997; McDONALD *et al.*, 2003). Consistent with this general conclusion, our results show aggregation prevailing in heterogeneous environment at higher elevations (the upper subplot), whereas a tendency towards more regular patterns, or uniform spacing of adult trees, exists at lower elevations (the middle and lower subplots) where the more moderate environment may permit rapid resource acquisition and hence intense competition. In particular, silver fir colonization in open areas released after the cessation of grazing at the lower subplot seems to have experienced rapid resource acquisition, leading to intense intraspecific competition and self-thinning,

which changed the spatial distribution from initially clumped in colonizing trees to significantly regular in surviving trees (Table 2). This course of events has been repeatedly documented in young stands that initially dominate large disturbance openings (KENKEL, 1988; HE & DUNCAN, 2000). In natural old-growth forests, patterns consistent with density-dependent mortality are often confounded or masked by other forms of mortality like insect outbreaks and tree windthrows, many of which are random, density-independent events (PETERKEN, 1996). We ascribe the lack of regularity in silver fir distribution at the middle subplot to these kinds of interactions between density-dependent competition, environmental heterogeneity and random disturbances.

In recent years the concept of niche differentiation has been largely abandoned as a sole explanation for the coexistence of canopy tree species in natural forests (HARMS *et al.*, 2001). Alternative theories and models including intraspecific density-dependent regulations and differences in life history characters have been put forward (WILLS *et al.*, 1997). In the case of the present study, important differences in density-dependent and life history strategies between silver fir and beech seems critical to coexistence in the relatively homogeneous environment of the intermediate and lower part of the study plot, where the species seems to have overlapping regeneration niches. These differences include the greater establishment rate of silver fir, which accounted for 82% of the stems < 19 m in the plot. However, the much greater abundance of subcanopy trees of silver fir does not imply more frequent recruitment into the canopy, since silver fir accounted for only 29% of the stems > 19 m at the whole-plot level (and only 7% at the upper subplot). Its greater establishment rate compared to beech is therefore balanced by its greater mortality among saplings and subcanopy trees. This can be, at least in part, attributed to the clumped pattern of establishment. In young patches silver fir often reaches densities where resources (light) are limiting, which leads to intense intraspecific competition and self-thinning, so finally only a few individuals reach the upper canopy layer. The consistently lower frequency of beech in the understory and subcanopy strata is compensated for by its greater abundance in the canopy, which implies a lower mortality rate for beech during the recruitment from juvenile to adult stage, or greater survivorship and longevity in canopy trees.

Consequently, despite the predominance of silver fir in the subcanopy of this forest, it is unlikely that beech would be completely excluded and canopy dominance shift towards silver fir. Beech can maintain its present abundance because its lower recruitment rate is compensated for by a lower mortality rate among its juveniles and canopy members. Silver fir has a much greater recruitment rate, but its young conspecific patches suffered intense intraspecific competition and thinning. Moreover, silver fir seems to suffer higher mortality in denser patches of *Buxus sempervirens* compared to beech, at least at the lower stand (DOLEŽAL *et al.*, 2004). Thus, intraspecific competition and

thinning, together with the inhibitory effects of *Buxus sempervirens* shrubs, may play important roles in reducing the population size of silver fir. These density-dependent regulations may help to maintain a mixed composition in these stands. A number of studies have documented the coexistence of ecologically similar species by means of different life history strategies, where one species prefers survivorship and the other fecundity (VEBLEN, 1986; TAKAHASHI, 1997). Others studies have documented coexistence based on partitioning of the available niches (DUNCAN, 1991; HARA *et al.*, 1995; KUBOTA & HARA, 1996). The present study provides empirical support for both concepts in the mixed forest of fir and beech on the northern slope of Ordesa Valley.

In this study, we focused on the detailed mapping of a single large plot, as in other forest studies (KENKEL, 1988; HE & DUNCAN, 2000). Hence, we do not know if our results generalize to other fir-beech stands. It is likely that factors influencing forest structure and dynamics in our plot, including environmental heterogeneity and density-dependent interactions, will affect other fir-beech stands in similar way, although, it can be assumed that the relative importance of these factors may vary according to the aspect of the site, the history of human activities, and the forest development stage. Long-term observations and comparative studies are required to conclusively demonstrate to what extent the trends observed in this forest apply to other Pyrenean fir-beech stands.

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