

Why and where do adult trees die in a young secondary temperate forest? The role of neighbourhood

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Abstract

- The density and identity of tree neighbourhood is a key factor to explain tree mortality in forests, especially during the stem exclusion phase.
- To understand this process, we built a logistic model for mortality in a spatially explicit context, including tree and neighbourhood predictors. Additionally, we used this model to build mortality risk frequency distributions. Finally, we tested this model against a random mortality model to predict the spatial pattern of the forest.
- Annual mortality rate was high for pedunculate oak (*Quercus robur*, 6.99%), moderate for birch (*Betula celtiberica*, 2.19%) and Pyrenean oak (*Q. pyrenaica*, 1.58%) and low for beech (*Fagus sylvatica*, 0.26%). Mortality risk models for pedunculate oak and birch included stem diameter, tree height, canopy position and neighbourhood. Mortality was affected by the specific nature of the neighbourhood showing a clear competitive hierarchy: beech > pedunculate oak > birch. Models based on random mortality and logistic regression model were able to predict the spatial pattern of survivors although logistic regression predictions were more accurate.
- Our study highlights how simple models such as the random mortality one may obscure much more complex spatial interactions.

Résumé – Pourquoi et où les arbres adultes meurent dans une jeune forêt tempérée ? Le rôle du voisinage.

- La densité et l'identité des arbres du voisinage sont un facteur clé pour expliquer la mortalité d'arbres dans les peuplements forestiers, surtout pendant la phase d'exclusion du tronc.
- Pour comprendre ce processus, nous avons construit un modèle logistique pour la mortalité dans un contexte spatialement explicite, en incluant l'arbre et des prédicteurs de voisinage. De plus, nous avons utilisé ce modèle pour construire des distributions de fréquence de risque de mortalité. Finalement, nous avons évalué ce modèle par rapport à un modèle de mortalité aléatoire pour prédire la structure spatiale de la forêt.
- Le taux de mortalité annuelle était élevé pour le chêne pédonculé (*Quercus robur*, 6.99 %), modéré pour le bouleau (*Betula celtiberica*, 2.19 %) et le chêne tauzin (*Q. pyrenaica*, 1.58 %) et faible pour le hêtre (*Fagus sylvatica*, 0,26 %). Les modèles de risque de mortalité pour le chêne pédonculé et le bouleau intégraient le diamètre du tronc, la hauteur de l'arbre, la position du houppier et le voisinage. La mortalité a été affectée par la nature spécifique du voisinage montrant une hiérarchie claire dans l'aptitude compétitive : hêtre > chêne pédonculé > bouleau. Les modèles basés sur une mortalité aléatoire et le modèle logistique ont été capables de prédire la répartition spatiale des survivants bien que les prédictions du modèle logistique étaient plus précises.
- Notre étude montre comment des modèles simples basés sur une mortalité aléatoire peuvent obscurcir des interactions spatiales beaucoup plus complexes.

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1. INTRODUCTION

Despite the demographic role of adult tree mortality is as relevant as recruitment for population dynamics and persistence (Harper, 1977), there is a huge asymmetry in the effort invested in explaining recruitment compared to tree mortality. Probably, this is related to the fact that adult mortality is a rare event in long-lived species (García and Zamora, 1993). The large sample sizes and long periods of time required to obtain an appropriate number of mortality events supposes a high setback for this type of research (Hood and Bentz, 2007; Wyckoff and Clark, 2000). Not surprisingly, much of the current effort to explain causes and processes of tree mortality has been devoted to catastrophic events such as wildfires (Reggelbrugge and Conard, 1993), hurricanes (Uriarte et al., 2004; Wolf et al., 2004), root rot (Dobbertin et al., 2001) or drought (Suarez et al., 2004), where tree mortality peaks, but comparatively less effort has been dedicated to explore mortality in non-perturbed forest stands (Aakala et al., 2007; Bigler and Bugmann, 2004).

However, unveiling factors that promote regular mortality of adult trees is a central issue to understand and model forest dynamics (Hawkes, 2000). Mortality driven changes in canopy composition play a key role in shaping forest composition and structure. This fact may be especially relevant in some forest stand stages such as at the stem exclusion phase (Oliver and Larson, 1996), where the highest competition levels and tree death rates occur (Peet and Christensen, 1987).

Regular tree mortality has been related to a set of predictors such as species identity, tree size, position in the canopy, but also growth rate and growth trend (Bigler and Bugmann, 2004; Das et al., 2008; Olano and Palmer, 2003). Characteristics of tree neighbourhood are closely related to competition intensity and mortality risk (Hubbell et al., 2001; Uriarte et al., 2004). However, most of the research has been carried out on monospecific stands (Dobbertin et al., 2001; Drobyshev et al., 2007; Monserud and Sterba 1999), with relative less attention being focused on mixed forests where the effect of neighbour identity creates a much more complex picture (Hubbell et al., 2001; Yao et al., 2001; Zhao et al., 2004).

In addition, predictions of individual mortality risk based on field data are necessary to improve the rules of individual-based forest models (Grimm and Railsback, 2005). To this extent, analyses based on individual risk of death allow to distinguish and weight the effect of different factors and to obtain death risk estimates for individual trees. Application of this type of technique in a spatially explicit context allows not only to assess the factors promoting tree mortality, but also to predict the spatial pattern of survivors. Moreover, estimation of individual hazards provides a tool to cope with the effect of different population structures on mortality risk distribution (Zens and Peart, 2003).

Here, we present a study that aims to model adult tree mortality during stem exclusion phase in a mixed temperate forest in Northern Spain. We built an individual based mortality model, which included the effect of intrinsic factors such as tree size and height but also neighbourhood identity. In addition, we used these models to analyze mortality risk fre-

quency distribution for birch and pedunculate oak. Finally, we checked the ability of these mortality models to predict the spatial pattern of each species, comparing their results to that of a model of random mortality.

2. MATERIALS AND METHODS

2.1. Materials

The study site was a ca 2.5 ha forest stand located in the Urkiola Natural Park (Bizkaia, Spain, 43° 86' N, 28° 39' W) at 550 m altitude on a steep slope (28°). Rock parent material is sandstone and the soil is acidic and very shallow. Climate is temperate-oceanic with a high annual rainfall (1 655 mm on average) and a mean annual temperature of 11 °C (climatic data from the Urkiola Pass, 2 km far from the forest).

The tree layer is unusually rich (12 species) for temperate European stands and dominated by birch (*Betula celtiberica* Rothm. & Vasc.), beech (*Fagus sylvatica* L.), Pyrenean oak (*Quercus pyrenaica* Willd.) and pedunculate oak (*Q. robur* L.), which together account for 93% of the total basal area (Herrera et al., 2001). The understorey layer is also very rich, and especially diverse in shrub and vines.

A detailed dendrochronological study showed this forest suffered two major silvicultural actions along the 20th century (Herrera et al., 2001). In 1948, most of the existing trees were cut, and immediately thereafter *Pinus radiata* D. Don was planted at very low density. These pines were harvested in 1967. Following this perturbation, the stand underwent secondary succession, and at the moment it is a secondary forest in a stem exclusion stage, exhibiting a strong decrease in radial growth for many trees. Most of the birches were recruited in a short period after the 1967 perturbation, while pedunculate oak continued establishing during the next two decades. The presence of different seed trees that survived the first forest cut, allowed beech to establish shortly after the perturbation, maintaining a continuous establishment rate since (Herrera et al., 2001).

In 1999, a tract of this forest of 1.9 Ha monitoring plot of irregular shape (maximum length = 260 m) was mapped. Every individual with diameter at breast height (DBH) larger than 2 cm or higher than 1.4 m was mapped and permanently marked. DBH, height with a clinometer, vital state (living or dead) and number of stems were measured for each tree. In 2005, all the trees were re-measured, including newly recruited individuals. In multi-stem individuals (12% of the trees) we measured all the stems. DBH for the whole individual was the equivalent DBH for a single stem with the same area as the sum of the individual stems. Position for multi-stemmed trees was located at the midpoint between stems.

2.2. Statistical analysis

Mortality rate was calculated on a 6-year period and then transformed it to an annual rate with the formula

$$\sigma(x) = 1 - (1 - m(x))^{1/n} \quad (1)$$

where $\sigma(x)$ is the annual mortality rate function, $m(x)$ the 6 years mortality rate and n the number of years. We built mortality models for the two species (pedunculate oak and birch) with the highest number of death trees with a logistic regression (Legendre and Legendre, 1998).

Two groups of variables were selected to predict mortality. A first group considered individual tree characteristics (DBH and height), and a second group included several surrogates of its neighbourhood. The density and nature of neighbourhood was measured using the influence index of Woods (2000)

$$I_f = \sum_{(\text{dist} < 10\text{m})} D_n / \text{dist}_{n,f} \quad (2)$$

where D_n is the DBH of an individual neighbouring tree and $\text{dist}_{n,f}$ the distance between the neighbouring and the focal tree. Influence indices were calculated separately for beech (I_{F_s}), birch (I_{B_c}) and pedunculate oak (I_{O_r}) and for all the tree species pooled (I_T). Canopy position was also estimated by the number of trees higher than the focal individual in a radius of 10 m.

Variables were included in the model by the Wald forward stepwise selection. Cut-off value for inclusion in the model was 0.05, and 0.1 to exclude a previously included variable. Overall model significance was evaluated using log likelihood ratio (Hosmer and Lemeshaw, 2000). Additionally, we employed Receiver Operating Characteristic curve (ROC curve) to test the validity of the logistic regressions. ROC curves provide an evaluation of the model sensitivity (rate of true positives) and specificity (rate of false positives). The validity is estimated by the C statistics that measures the area under the curve and compares it with a null hypothesis (Hosmer and Lemeshaw, 2000).

We used the logistic models to describe mortality risk distribution for birch and pedunculate oak and their variation across time due to growth and changes in the neighbourhood related to death of surrounding trees. Our models were used under three different circumstances: three data sets and conditions: (a) all individuals alive in 1999 to evaluate mortality risk at the onset of the study, (b) the subset of individuals surviving in 2005, but under 1999 stand conditions, to evaluate the distribution risk at that time and (c) the previous subset of survivors, but under 2005 stand conditions, to evaluate the changes in mortality risk due to growth and changes in their neighbourhood. Models predicted mortality risk for a six year period, 1999–2005 for scenarios (a) and (b), and 2005–2011 for scenario (c).

The spatial pattern of each species was analysed with Ripley's K function (Ripley, 1988). More specifically, $\lambda K(r)$, where λ is the intensity (i.e. the density) of the pattern, was used to estimate the expected number of points within a distance r of any point of the pattern. As a preliminary visual exploration of the forest pattern suggested the existence of first-order effects (i.e. the intensity of the pattern is not constant over the study site), we used the inhomogeneous K function (Baddeley et al., 2000; Liu et al., 2007; Wiegand et al., 2007). We estimated the intensity function $\lambda(x, y)$ (i. e. the spatially varying intensity) parametrically, using the maximum pseudolikelihood algorithm of Baddeley and Turner (2005).

For each species, we fitted heterogeneous Poisson models with the intensity function estimated as a log-linear function of second order polynomials of spatial coordinates x and y (Baddeley and Turner, 2006; De la Cruz, 2006; Liu et al. 2007). This results in a non-stationary intensity function that accounts for the underlying spatial trend of each species, allowing the inhomogeneous K function to correctly estimate second order spatial dependencies. Edge effects were accounted for with the border method (i.e. the reduced sample estimator (Ripley, 1988)). For ease of interpretation we transformed the inhomogeneous K function in the frequently used L function $L(r) = [K(r)/\pi]^{1/2} - r$.

We evaluated if the resulting spatial structure of each species could be predicted by two potentially alternative models: (a) random

mortality with equal mortality risk for all the individuals (Goreaud and Pelissier, 1999; Kenkel, 1988; Sterner et al. 1986), (b) mortality based on logistic models, where individual mortality risk depends on individual characteristics and neighbourhood (Batista and Maguire, 1998; Hubbell et al., 2001; Yao et al., 2001). We tested each model comparing the observed inhomogeneous L function with the 99% envelopes, i.e. the 0.5% and 99.5% quantiles, of the inhomogeneous L functions generated by 999 MonteCarlo simulations of each model. Each simulation consisted in a random thinning of the whole pattern of dead and living trees according to a prescribed probability of deletion. In the random mortality model, the probability of deletion was the same for all trees and equal to the proportion of dead trees. In the logistic mortality model, the probability of deletion for each tree was the fitted value of the logistic model. In both scenarios, the number of dead trees was the same as that observed during the 1999–2005 period.

Statistical analyses were performed in the R environment (R Development Core Team, 2007). Spatial analyses were performed with the *spatstat* R-package (Baddeley and Turner, 2005). A function to automate the computation of envelopes of the inhomogeneous K function simulating from the fitted values of a logistic model has been included in the *ecspa* package (De la Cruz, 2008).

3. RESULTS

Stand basal area increased from 21.1 m² ha⁻¹ in 1999 to 21.8 m² in 2005, whereas stem density decreased from 925 to 705 stem ha⁻¹. Diameter distribution in 1999 was close to a normal distribution in oaks and birch, but beech showed its maximum at the smallest DBH class (Fig. 1). Diameter distribution in 2005 showed a decrease in the smaller DBH classes in birch and oaks due to mortality, while recruitment augmented this class in beech (Fig. 1). Mortality rates differed among species (Tab. I). Pedunculate oak showed the highest rate, a third of the individuals died between 1999 and 2005. Birch and Pyrenean oak showed moderate mortality rates and it was very low for beech.

Logistic regressions were only performed for birch and pedunculate oak because mortality events were too low in the Pyrenean oak and beech. Four parameters were included in the logistic regression for pedunculate oak and three for birch (Tab. II). Mortality risk in pedunculate oak was related to DBH, canopy position, beech and birch influence indices (I_{F_s} and I_{B_c}). As expected pedunculate oak mortality risk decreased as DBH increased, but also in areas with more birches (I_{B_c}) and increased when it was surrounded by taller trees and also as the number of beeches in the focal tree neighbourhood (I_{F_s}) increased. ROC curve showed that the logistic regressions predicted mortality risk accurately ($C = 0.825$; $p < 0.001$). Results for the logistic regression for birch were rather similar (Tab. II). Birch mortality risk decreased with tree height and DBH and increased in areas with more beeches. ROC curve showed that the logistic regressions predicted mortality risk accurately ($C = 0.871$; $p < 0.001$).

Distributions of mortality risk frequency were rather different in 1999 for pedunculate oak and birch (Fig. 2). Mortality risk was highly skewed (skewness = 2.373) to low values in birch, but it was more evenly distributed in pedunculate oak

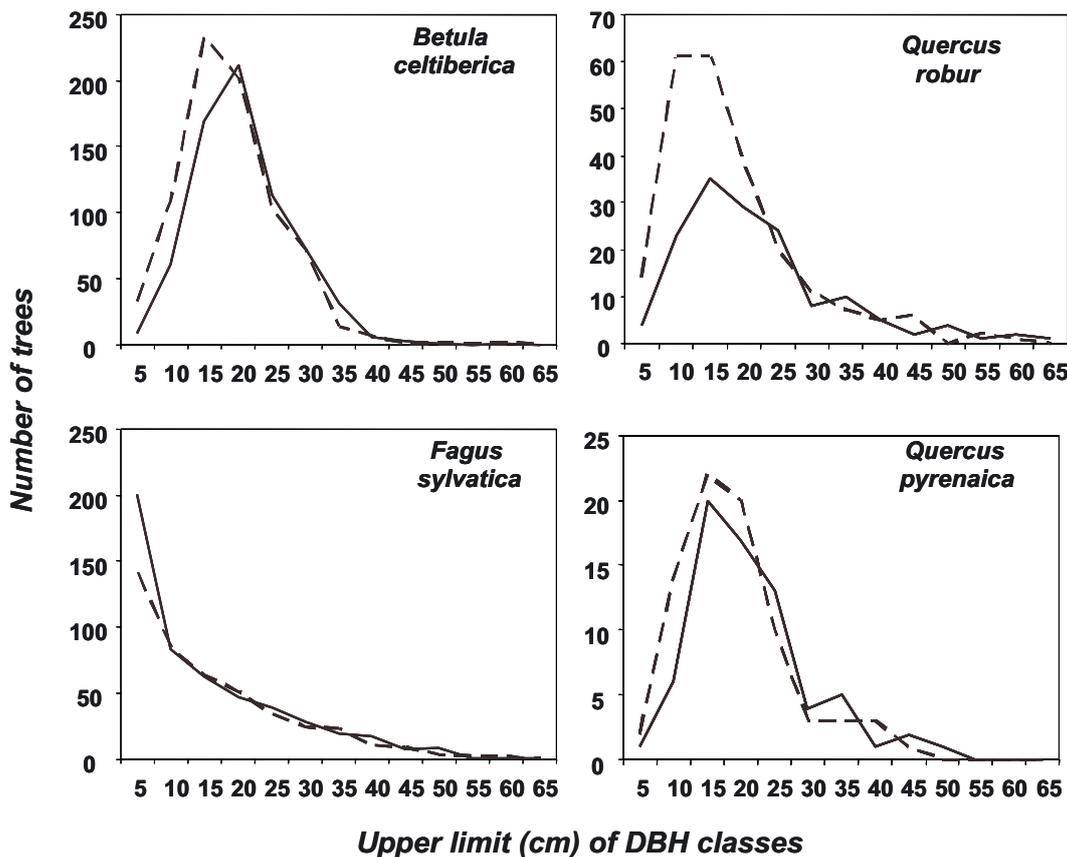


Figure 1. DBH distribution for birch, pedunculate oak, Pyrenean oak and beech in 1999 (dashed line) and 2005 (continuous line).

Table I. Living trees in 1999, number of survivors in 2005 and annual mortality rate ($\sigma(x)$). Only species with more than 50 individuals in 1999 are considered.

Species	Living trees (1999)	Survivors (2005)	$\sigma(x)$ in %
<i>Betula celtiberica</i>	772	676	2.19
<i>Fagus sylvatica</i>	447	440	0.26
<i>Quercus robur</i>	227	147	6.99
<i>Quercus pyrenaica</i>	77	70	1.58

(skewness = 0.452). Skewness of mortality risk frequency increased for both species in 2005 (birch = 3.154, pedunculate oak = 0.903), suggesting that mortality risk became more concentrated in part of the tree population. An estimate of mortality rates based on the logistic models for the next six years (2005–2011) period suggested a decrease in mortality rate for both species, from 6.99% to 4.26% in pedunculate oak, and from 2.19% to 1.40% in birch.

The spatial pattern of both species in 2005 was consistent with the predictions of the random mortality model (Fig. 3). For both species, and for all analysed scales r , the observed $L(r)$ function remained within the 99% generated from a random thinning of the 1999 pattern. This means that both surviving pedunculate oak and surviving birch trees were neither

Table II. Logistic regression for pedunculate oak and birch mortality. β is the coefficient for each of the parameters.

Species	Number of trees	Model p	Parameters in the model	Parameter P	Parameter β
<i>Quercus robur</i>	227	< 0.001	Constant	0.832	-0.187
			DBH	0.003	-0.118
			Canopy position	0.007	0.091
			I_{Fs}	0.016	0.037
<i>Betula celtiberica</i>	772	< 0.001	I_{Bc}	0.039	-0.027
			Constant	0.001	2.108
			Height	0.005	-0.161
			DBH	0.001	-0.219
			I_{Fs}	0.001	0.041

more, nor less clustered than what would have been expected by chance alone.

The 2005 spatial pattern was also consistent with the logistic mortality model (Fig. 3). The envelopes generated by applying the logistic mortality model as a thinning function over the initial pattern of live trees almost completely surrounded the empirical L function for both pedunculate oak and birch (areas significantly exceeding the confidence envelopes seem to emerge at distances of 3 and 13 m in pedunculate oak). However, in this case, the envelopes were tighter for most of the scales than those of the random mortality model,

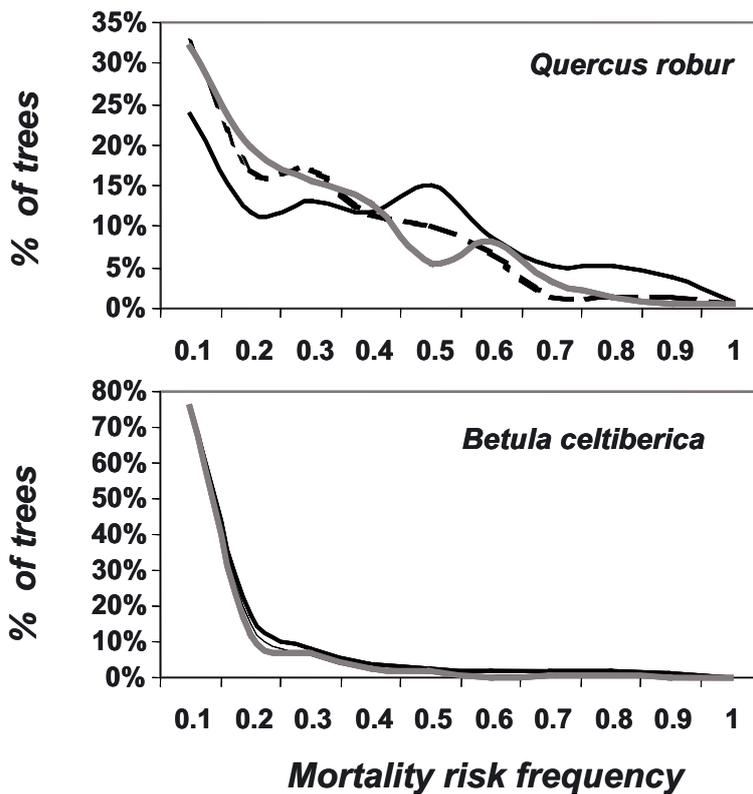


Figure 2. Mortality risk frequency distributions for pedunculate oak and birch. For all individuals alive in 1999 (black line), for the subset of individuals surviving in 2005, under 1999 conditions (dashed black line) and for the subset of individuals surviving in 2005, under 2005 conditions (grey line).

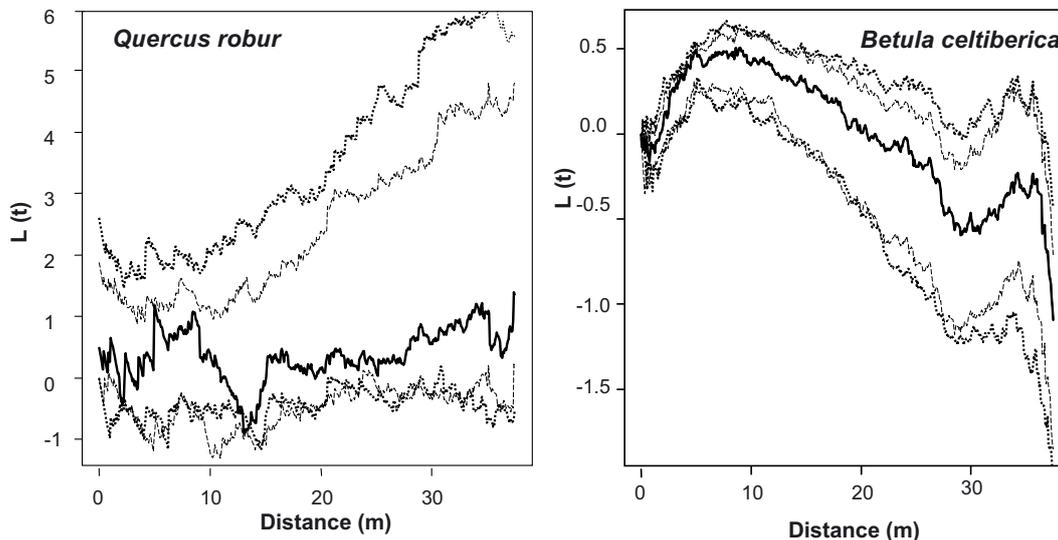


Figure 3. Inhomogeneous L functions of the 2005 tree pattern for pedunculate oak and birch. The solid black line represents the empirical inhomogeneous L-function. Dotted lines are the 99% envelopes, i.e. the 0.5% and 99.5% quantiles, of the inhomogeneous L functions of 999 simulations of the random mortality model over the 1999 tree pattern. Dashed lines are 99% envelopes computed from 999 simulations of the logistic mortality models over the 1999 tree pattern.

suggesting that the logistic model had more power to describe the evolution of the spatial structure of both species.

4. DISCUSSION

The annual mortality rate in the studied forest (2.21%) stays within the range of regular mortality processes in other studied forests (Lugo and Scatena, 1996; Oliver and Larson, 1996; Wyckoff and Clark, 2002). However, mortality showed strong differences among species. The low annual mortality rate in beech may be related to its late successional status and the opposite holds for the pioneer birch. However, the high mortality rate of pedunculate oak, well above birch, is higher than expected for temperate forests (Drobyshev et al., 2008). Specially, since no catastrophic events occurred during the studied period.

Birch and pedunculate oak mortality rates were related both to tree intrinsic factors and to the nature of neighbourhood. The negative relationship between DBH and mortality risk has been documented repeatedly (Coomes et al., 2003; Lorimer, 1983; Piovesan et al., 2005), especially in stem exclusion phase (Luis and Fonseca, 2004). Size is a good estimator for competitive ability and physiological status, especially in even-aged stands where small differences in size may suppose strong changes in canopy position once competitive hierarchies are established (Peet and Christensen, 1987). This fact is supported by the inclusion of height in both models. Nevertheless, there are differences in the way height entered in the models. The model for birch height is included without considering the role of neighbourhood, whereas the model for pedunculate oak considers the position of the individual tree in the local canopy. This suggests a much stronger relevance of local environment for oak survival. In any case, the pooled neighbourhood is never included in the models, suggesting that competition is not dependent on the total biomass in the area, but on the specific nature of the neighbourhood. In spite of the higher pedunculate oak mortality, both models suggest a clear competitive hierarchy: beech > pedunculate oak > birch that matches classic pioneer-dominant successional theory for European temperate forest vegetation (Ozenda, 1985). The displacement of oak and birch by beech has been related to the canopy structure generated by beech, but also to additional mechanisms such as a higher efficiency in nutrient uptake (Leuschner et al., 2001). The positive effect of birch on pedunculate oak has been observed in other mixed forests (Paluch and Bartkiewicz, 2004), and can be attributed to the less dense canopy generated by birch. In fact, in our forest, there is a negative correlation between canopy cover and birch influence index (I_{Bc} : Kendall's $\tau = -0.14$; $P < 0.01$) suggesting that a birch neighbourhood is a more favourable environment for oaks.

The results also highlight the relevant effect of arrival sequence on the local successional pathway. Birch is a good colonizer, with dense seed bank (Olano et al., 2002) and seed rain (unpublished data), therefore its population was able to establish in high numbers immediately after the last stand perturbation in 1967 (Herrera et al., 2001). Moreover, its inability

to emerge on litter and almost null survivorship under low light regimes (Laskurain, 2008; LePage et al., 2000) limited the temporal extent of this establishment window. On the other side, pedunculate oak has a limited dispersal ability and irregular seed production reducing the initial establishment after the perturbation, but oak seeds are able to establish in litter and grow under lower light regimes, thus extending establishment period over a longer time window (Laskurain, 2008). Consistently, birch DBH distribution is shifted toward bigger trees with few individuals with in low DBH classes, whereas pedunculate oak shows a greater contribution of small DBH classes. The rapid establishment of beech trees after the disturbance (Herrera et al., 2001) generated a hostile environment that limits the chances of small pedunculate oaks to reach the canopy. However, the differences in mortality rate between pedunculate oak and birch are not only attributable to size distribution. There is also a certain spatial segregation between both species. Pedunculate oaks are surrounded by more beech and less birch trees (I_{Fs} : $Z = -2.45$, $p = 0.01$; I_{Bc} : $Z = -3.39$, $p < 0.001$), suffering a more competitive environment. Consequently, there are both temporal and spatial processes involved in the mortality pattern observed.

The use of mortality risk frequency distributions provides a synthetic view of how this process is affecting to pedunculate oak and birch populations, giving a hint on the evolution of the forest in the nearby future. The selective filtering of mortality on the most sensitive individuals drives population to lower mortality rates, even if the factors promoting mortality remain constant (Zens and Peart, 2003). As a result a decrease in mortality rate for the period 2005–2011 is predicted for pedunculate oak and birch, a fact that would slow down the pace of species replacement.

The spatial pattern of birch and pedunculate oak in the stand could be adequately described by the random mortality hypothesis (Kenkel, 1988; Sterner et al., 1986). The observed L functions remain almost completely surrounded by the randomly simulated envelopes at all analysed scales (i.e. from 0 to 40 m.). This suggests that neither of those species is experiencing self-thinning, as intra-specific density dependence should have resulted in a pattern more regularly spaced what is expected under random mortality (He and Duncan, 2000; Kenkel, 1988). However, mortality is not random. The logistic model describes even better (i.e. with tighter envelopes) the evolution of the spatial structure of the stands. Batista and Maguire (1998) found a similar result studying the spatial pattern of mortality in a tropical forest, and concluded that a thinning function dependent on subject tree attributes and neighbourhood could reasonably model the spatial pattern of tree mortality. Our results show that what appears as a random mortality process could in reality be driven by complex causal relationships. In fact, our spatial models corroborate the importance of inter-specific vs. intra-specific competition as no influence index for the focal species was included in the logistic regression models. The adoption of a random mortality model would have implicitly assumed that neither intra- nor inter-specific competition were relevant for the dynamics of the stand. All this suggests that the analysis of spatial patterns

of mortality (or of survival) would benefit from focusing on explicit mortality causes (see De la Cruz et al., 2008).

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