1   **Diachronic analysis of individual-tree mortality in a Norway spruce stand in the**

2   **eastern Italian Alps**

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Abstract

- Understanding tree mortality processes across time requires long term studies. Spatiotemporal patterns of mortality in a 200 years-old mono-layered Norway spruce stand were evaluated to determine what factors affected individual-tree mortality.

- We performed an analysis on two surveys (1993 and 2005) in a 1-ha permanent plot in the Paneveggio forest (Eastern Italian Alps). Tree diameter and age distribution between surveys were compared. We examined spatial patterns of living and dead trees before 1993, in 1993 and in 2005 using univariate and bivariate Ripley's $K(d)$ function, and a kernel estimator of local crowding. A logistic model was used to assess the effects of diameter, age, recent growth and competitive pressure on tree mortality.

- Spatial pattern analysis indicated mortality was associated to tree neighbourhood (neighbour effect at 2-5 m). An increment of regularization of tree spatial pattern occurred due to density-dependent mortality. Logistic regression showed tree diameter and recent growth were determinant on mortality risk during the monitoring period.

- Even if the stand is relatively aged, mortality dynamics are those typical of stem exclusion stage. Mortality was related to competitive dynamics, and small suppressed trees with slow growth rate had higher probability to die.

Introduction

Understanding and predicting tree mortality is critical in forest ecology (Franklin et al., 1987). Knowledge about mortality processes is required to increase the understanding of stand structural dynamics, improve the accuracy of forest growth models (e.g. gap models, Bugmann, 2001) and facilitate the design of sustainable management operations (Aakala et al., 2007). Moreover it is essential for ecosystem conservation, since deadwood represents an important factor for biodiversity (Harmon et al., 1986). Tree mortality is one of the most contradictory and least measurable processes of plant population development (Taylor and MacLean, 2007). Difficulty in interpreting tree death in forests is attributed to the complexity of natural mortality processes (Monserud, 1976), that could be allogenic, i.e., due to exogenous abiotic or biotic factors, and autogenic, i.e., due to tree ageing and competitive dynamics (Peet and Christensen, 1987). More often, actual mortality patterns result from the interaction of multiple agents (Harper et al., 2006).

At the individual level, survival mostly depends on the location of immediate neighbors (Ford and Diggle, 1981): the probability of mortality is increased by proximity to trees affected by disease or pests (Taylor and MacLean, 2007), and vulnerability to windstorm may increase in absence of protection from neighbouring trees (Nagel and Diaci, 2006). Similarly, individual competition depends on distance from neighbours, hence autogenic mortality involves trees standing too close to competitors (Goreaud et al., 2002; Olano et al., 2009). However, most studies on mortality have been conducted on large plot networks (Monserud and Sterba, 1999), where explicit spatial information was not available, therefore actual tree spatial pattern was rarely taken into account.

70 Individual-tree mortality models have shown mortality of Norway spruce (*Picea abies*

71 (L.) Karst.) to be influenced by diameter, recent growth pattern (Bigler and Bugmann,

72 2003; Lännenpää et al., 2008), age (Monserud and Sterba, 1999) and competition by the

73 overstory (e.g. Eid and Tuhus, 2001). In the present study we analyzed the process and

74 pattern of individual-tree mortality in a subalpine Norway spruce stand in the Valbona

75 Forest Reserve (Paneveggio-Pale di San Martino Natural Park, Trentino, Italy). We

76 chose a pure stand, undisturbed since the 1940's, growing in quite homogeneous site

77 conditions, in order to minimize confounding factors that might mask mortality

78 processes. No signs of heavy external disturbances such as large wind-throws, wildfires,

79 rockfalls, insects attacks, pathogens, etc. were observed. Our aim was to evaluate what

80 factors determine individual-tree mortality in a mature recently-unmanaged Norway

81 spruce stand. The analysis was conducted in a 1-ha long-term monitoring plot located

82 inside the reserve, comparing data from two surveys (1993 and 2005).

83 Considering the prevalence of standing dead trees, we examined dead trees

84 characteristics and mortality spatial pattern to verify whether mortality was induced by

85 competition. Moreover, we evaluated changes in tree spatial pattern across time.

86 Finally, a logistic regression was used to assess the influence of diameter, age, recent

87 growth and proximate competitive pressure on tree mortality in the 12-years monitoring

88 period.

89

90 **Materials and methods**

Study site and field measurements

The study is focused in the Valbona Forest Reserve (latitude 46° 18' N, longitude 11° 45' E), a 123 ha subalpine Norway spruce forest included in the Paneveggio-Pale di San Martino Natural Park (Trentino, Italy). The phytocoenosis is classified as *Homogyno-Piceetum subalpinum myrtilletosum*. Rainfall is 1157 mm/year at Passo Rolle (2002 m a.s.l.), approximately 3 km from the study site, and 1104 mm/year at Paneveggio (1508 m a.s.l.), approximately 2 km from the study site. Annual mean temperature is 2.7 °C at Passo Rolle and 3.7 °C at Paneveggio. The bedrock is porphyry and sandstone, and soils are podsols and rankers.

Most of the Reserve is characterized by monolayered Norway spruce stands, heritage of past management. The stand analyzed herein is a monolayered pure Norway spruce stand at an elevation of 1815 m a.s.l. Slope (47%), aspect (north) and microtopography appear quite homogeneous. It is relatively far from forest roads and has developed without anthropogenic influence since the 1940's, when all thinning and harvesting operations were over. Most individuals established between 1790 and 1850 (Motta et al., 1999). In 1993 a 1-ha (100x100 m) sample plot was established to initiate long-term forest dynamics monitoring. All live trees with diameter at breast height (dbh) > 7.5 cm were identified, labelled with numbered tags and mapped. Dbh was measured for each tree. In 2005 the measurement was repeated, and dead trees with dbh > 7.5 cm were added to the inventory. Stand characteristics are summarized in Table 1.

Dendrochronological analysis

In 1998 an increment core was taken upslope at a height of 50 cm from each live tree

with dbh > 7.5 cm. In order to calculate the year of establishment of dead trees, in 2005

an increment core was taken upslope from all dead trees at a height of 50 cm. Ring

width was measured to the nearest 0.01 mm. Data were collected and stored using a

LINTAB device and the TSAP package (Frank Rinn, Heidelberg). The cores were

cross-dated against available site chronologies (Motta, 2002; Motta et al., 2002) in order

to ensure the assignment of the correct year to each annual ring. The analysis was

carried out both on cores that included a pith and on those falling short of the pith,

whose position could be estimated by means of a graphical device (pith locator), hence

the number of missing innermost rings can be calculated (Josza, 1988). In order to

calculate the year of establishment, it was necessary to take into account the time to

reach coring height. Since previous studies conducted in Paneveggio (Motta et al.,

2002) showed that Norway spruce took an average of 18 years to reach a height of 50

cm, we subtracted this number to the year corresponding to the inmost ring at sampling

height.

Comparison between inventory years

We used *t*-test and Kolmogorov-Smirnov (KS) two-sample test to compare dbh and age

distributions of dead trees between inventory years (1993 and 2005), i.e. to assess if

mortality involved trees having similar dbh and age. For mortality observed in 1993, we

considered only snags, because logs in 1993 were regarded as snags fallen due to

136 decomposition processes (snapped dead) (Storaunet and Rolstad, 2004), hence dead in

137 previous period.

138 We used a combination of different spatial analysis techniques to investigate mortality

139 processes. We analyzed the spatial structure of dead trees in two periods (1993 and

140 2005) and of live trees in three periods: before 1993, in 1993, and in 2005. For the

141 "before 1993" analysis we considered as live all the trees and the standing dead trees

142 present in the 1993 inventory (Zhang et al., 2009).

143 For each period we computed the univariate Ripley's $K(d)$ (Ripley, 1976) in order to

144 evaluate if the spatial arrangement of live and dead trees was random, aggregate or

145 regular. We used a square-root transformation $L(d)$ that linearizes $K(d)$ and stabilizes its

146 variance and has an expected value of approximately zero under the Poisson assumption

147 (Diggle, 1983). We conducted the analysis from 1 to 50 m (half the length of the plot

148 side), applying a 1 m lag distance. The Monte Carlo technique (Besag and Diggle,

149 1977) (999 randomizations) was used to assess the deviation from the Complete Spatial

150 Randomness (CSR) assumption. A correction algorithm was used to account for edge

151 effects (Haase, 1995).

152 In order to evaluate spatial relationships between dead and live trees, and to assess the

153 spatial extent of inter-tree mortality interactions, we used the $L_{12}(d)$ function, which is a

154 generalization of $L(d)$ for a bivariate point process (Lotwick and Silverman, 1982).

155 Since mortality in a forest stand is an event affecting *a posteriori* the individuals of a

156 population (Getzin et al., 2006), the null model employed to detect this event was

157 random labelling (Diggle, 1983; Goreaud and Pélissier, 2003). Mortality agents

158 determine the patterns of dead trees but these can only work within the limits set by the

159   distribution of living trees prior to the mortality events themselves (Aakala et al., 2007).

160   In order to calculate the 99% confidence intervals, the position of all trees were

161   maintained, but the labels 'dead' and 'survivor' for each tree were randomly assigned in

162   each of the 999 Monte Carlo simulation (Diggle, 1983). Univariate and bivariate

163   Ripley's *L(d)* were calculated using the software SPPA 2.0 (Haase, 2001).

164   In order to analyze variation of local density through time we calculated local crowding

165   intensity before 1993, in 1993 and in 2005 estimating a kernel function, i.e., a moving-

166   window estimate of the non-constant first-order intensity $\lambda^R(x, y)$ computed as follows:

167

168   [1] $$\lambda^R(x, y) = \frac{\text{Points}\left[C_{(x,y)}(R)\right]}{\text{Area}\left[C_{(x,y)}(R)\right]}$$

169

170   where $C_{(x, y)}(R)$ is a circular moving window with radius R that is centered in cell (x, y),

171   the operator Points[X] counts the points in a region X, and the operator Area[X]

172   determines the area of the region X. Analyses were performed using the grid-based

173   software Programita (Wiegand and Moloney, 2004). Plot surface was divided into a 1x1

174   m grid and the moving window radius was set at 10 m. A smaller moving window

175   would too closely mimic the original pattern, while a larger one approximates CSR

176   (Wiegand and Moloney, 2004). A first-order intensity map showing $\lambda^R(x, y)$ values for

177   all grid cells (1 m) in the plot was obtained for each period. Skewness and kurtosis of

178   cell frequency distributions were scrutinized to evaluate the change of local density

179   through time.

180

Mortality model

Since mortality is a discrete event, the logistic function is widely used to determine the

influences of explicatory variables on individual tree mortality (Monserud, 1976). We

performed a binomial logistic regression to evaluate probability of survival in the

observation period (1993-2005) using the software SPSS 16.0 (SPSS Inc., Chicago IL):

[2] $\quad PS = \left(1 + e^{-\beta' X}\right)^{-t}$

where PS is the probability of survival over a period of t years. β' X is a linear

combination of parameters β and the explicatory variables X. Independent variables

were entered by a stepwise process. Models accuracy was evaluated as the percentage of

dead trees correctly classified and as the overall accuracy (prediction for dead and live

trees) (Bigler, Bugmann, 2004). Nagelkerke's R^2 and Hosmer-Lemeshow goodness-of-

fit were used as well (see Crecente-Campo et al., 2009 for further details).

The aim of this analysis was to evaluate the effects of dbh, age, recent growth and

neighbourhood on mortality probability (complementary of probability of survival, 1 -

PS). Diameter of focal trees is generally included in mortality models, since density-

dependent mortality usually involves smaller trees. Age is related to juvenile mortality

or senescence. Recent growth was calculated as the Basal Area Increment (relBAI) of

focal trees in 1993. RelBAI assesses individual tree vitality before the analysis period

(Bigler, Bugmann, 2004). Since in many suppressed and dead trees growth rings were

extremely narrow (Cherubini et al., 1996), and several missing rings occurred, we

calculated relBAI for 10 and 30 years before 1993 (Antos et al., 2008). Tree survival

finally depends on the location of immediate neighbours (Ford and Diggle, 1981). We

203 assessed neighbourhood as the sum of basal area (BA) of trees located within the area of

204 influence (Kenkel, 1988) of each focal tree. Analysis was performed using kriging

205 interpolation implemented with ArcView® geographic information system software.

206 The radius of the area of influence was estimated from bivariate Ripley's $K(d)$ function.

207 An adjustment for edge effect was applied.

208 We tested three models: in the first one we included dbh, age and BA of neighbours,

209 while in the second and in the third model relBAI (1964-1993 and 1984-1993

210 respectively) was also included.

211 Even if competition had a long-term negative impact on growth rate in this plot

212 (Castagneri et al., 2008), tree rings are integrator of biotic and abiotic influences, and it

213 is hard to distinguish neighbour effect signal. To analyse neighbour effect on mortality,

214 we used model 1.

215 Moreover, dendrochronological analysis is time demanding, and simulation studies

216 normally rely on the predicted rather than on measured increment (Crecente-Campo et

217 al., 2009), thus we tested model 1 not including recent growth information. However,

218 tree-rings are more informative than competitive measurement on whole growth history

219 of a tree (Bigler and Bugmann, 2003), and a higher performance of model 2 and 3 was

220 expected.

221

222 **Results**

223 **Comparison between inventory years**

224 In the 12 years monitoring period mortality rate has been 0.8% year^{-1} (48 snags and 4

225 uprooted logs on 557 live trees) (Table 1). Trees dead before 1993 were smaller in dbh

226 (mean value: 19.5 cm) than trees dead after 1993 (26.2 cm) (t-test, $p < 0.001$) and their

227 size distributions differed significantly (KS test, $p < 0.001$).

228 We determined the establishment year of 31 out of 53 trees dead before 1993 and of 37

229 out of 52 trees dead between 1993 and 2005. t-test and KS test did not indicate

230 significant differences in the mean and frequency distribution of tree ages.

231 The spatial pattern of live trees deviated significantly from CSR at short distances,

232 exhibiting pronounced changes across time. Ripley's $L(d)$ function showed a regular

233 distribution of live trees at distances < 4 meters before 1993, and more so in the

234 following inventory years (Fig. 1). Trees dead before 1993 were aggregated at $d = 5$ to

235 15 m, but the pattern did not significantly deviate from a random one in the following

236 period (Fig. 1).

237 In the monitoring period we observed a positive association between live and dead

238 trees. Bivariate analysis based on random labelling null model showed a significant

239 positive correlation in 1993 for distances < 3 m, and an even stronger positive

240 correlation in 2005 for distances < 6 m (Fig. 2).

241 Local crowding maps (Fig. 3) showed a decrease in heterogeneity across time. This

242 trend was confirmed by statistical analysis of local density values. Mean cell value

243 decreased with time, from 17.82 trees in the 10 m moving window before the first tally

244 to 15.00 in 2005, because of mortality. Standard deviation decreased from 4.22 to 3.40.

245 Local density value had a leptokurtic distribution at all tallies. Pearson's kurtosis value

246 was higher in 2005 (0.273) and in 1993 (0.264) than before 1993 (0.134), indicating a

247 decrease in the frequency of low- and high- density across time. Moreover, cell

248 distributions in 1993 and in 2005 shifted to low values (Skewness value = 0.032 before

249 1993; 0.207 in 1993; 0.431 in 2005).

250

251 **Mortality model**

252 Model 1 correctly predicted the status of 75.7% of dead trees and 77.8% of living trees,

253 and overall accuracy was 77.6% (Table 2). Hosmer-Lemeshow p was higher than 0.05,

254 but fit of the model was quite low. Model 2 (relBAI 1984-1993) and 3 (relBAI 1964-

255 1993) had a higher number of both dead and live trees correctly predicted than model 1,

256 hence a higher overall accuracy occurred (85.1%; 83.7% respectively). Moreover,

257 Nagelkerke's R^2 and Hosmer-Lemeshow p were higher. Model 2 had a slightly better

258 overall accuracy and R^2 than model 3.

259 Dbh was a highly significant variable in all models, indicating that mortality involved

260 mainly small size classes. Age was never significant. In both model 2 and 3 relBAI was

261 highly significant, indicating that recent growth strongly improved the model. However

262 in model 2 odds ratio was lower than in model 3, indicating relBAI 1984-1993 had a

263 stronger positive effect in survival probability.

264 In model 1, BA of neighbours was significant ($p < 0.05$). However, it was not

265 significant in models including relBAI, probably because those variables were

266 correlated (r = -0.229; $p < 0.01$ with relBAI 1984-1993). Since recent growth is caused

267 by different factors that are also responsible of survival probability, it is a best

268 descriptor of tree condition than neighbourhood alone, hence in the stepwise selection it

269 was preferred to neighbour BA.

270

Discussion

In the study plot pre-1993 mortality mostly involved small diameter classes, while in the following period it focused on mid-size trees as well. Tree mortality heavily changed the forest structure, since smaller diameter classes were almost absent from the last inventory.

Mortality observed in 1993 was clustered, while mortality in 2005 was not. However, that result alone is not sufficient to infer the cause of mortality, because cluster mortality could be due to allogenic mortality causes (Cherubini et al., 2002; Dobbertin et al., 2001), or to self-thinning in an heterogeneous environment (Getzin et al., 2008) or in a non-homogeneously distributed stand (Wiegand and Moloney, 2004).

The positive interaction between live and dead trees in the plot indicated death probability was not the same for all individuals but it depended on neighbours (Goreaud and Pélissier, 2003). At small spatial scale dead trees were positively associated to live trees due to the death of trees standing too close to competitors, pointing out the importance of small-scale competition in mortality dynamics (Hou et al., 2004; Wolf, 2005). The space around an individual where mortality is higher than expected under random conditions delineates the "area of influence", where the effect of competition is intense enough to determine mortality of neighbours (Kenkel, 1988; Ward et al. 1996).

The mean area of influence increased during the observation period, indicating an increase in competitive pressure as the stand developed. Several suppressed trees 2 to 5 m apart from competitors were alive in 1993, but they died in the following period.

Results were consistent with those in dense mature Norway spruce stands in Czech

293 Republic (neighbour effect at 2-5 m) (Vacek and Lepš, 1996), and in open-canopy

294 mature *Picea-Betula* stands in Finland (neighbour effect at 0-4 m) (Doležal et al., 2006).

295 As a result of mortality, local density pattern changed in the observation period. There

296 was an increment of regularization at distance lower than 6 m, as a consequence of

297 mortality of suppressed trees close to neighbours. Moreover we observed a decrease of

298 high-density patches and consequently an increment of medium-low density patches,

299 resulting in a more homogeneous spatial pattern. Many studies on spatial pattern

300 development have shown a shift from aggregated or random distribution in early stand

301 phases to uniform or over-dispersed distribution in later stages, as competition for

302 limiting resources negatively affects survival in close proximity of other trees (Wolf,

303 2005). This trend is consistent with that observed in the stand analyzed herein.

304 Spatial analyses supported prediction about mortality process, i.e. mortality observed in

305 the plot between 1993 and 2005 was mainly caused by competition. Considering that,

306 we discuss the effect of descriptive variables on tree mortality.

307 Models prediction accuracy was comparable to similar works on Norway spruce

308 mortality (Bigler and Bugmann, 2004; Eid and Tuhus, 2001). Several descriptive

309 variables were available, including dendrochronological and spatial pattern information.

310 However models were fitted on a restricted dataset (1 ha), and general conclusion on

311 Norway spruce mortality can not be inferred.

312 Diameter was a critical variable in determining mortality likelihood in our plot, as

313 usually observed in mortality of Norway spruce stands (Monserud and Sterba, 1999).

314 The effect of tree size on competitiveness and survivorship is consistent with density-

315   dependent mortality patterns: mortality rate increases as size decreases, since small trees

316   have lower chances of competing for resources (Uriarte et al., 2004).

317   Trees dead in the observation period were coeval of live trees, indicating that

318   establishment period did not influence death probability. In the even-aged stand

319   analyzed herein, where most individuals established across a time span of 60 years,

320   senescence did not significantly influence mortality risk, and mortality involved smaller

321   but not younger trees.

322   In high density stands individual mortality is related to the size of competitors. Majority

323   of mortality models were computed over large areas using non-spatial models, and

324   competition was expressed as the size of competitors in the plot (e.g. BA of trees larger

325   than focal tree, Eid and Tuhus, 2001). However, density-dependent mortality was

326   related to neighbourhood around individual (Goreaud and Pélissier, 2003). Our analysis

327   demonstrated that individual survival likelihood depended on the size of neighbours

328   within the area of influence of the focal tree.

329   Recent growth was an important indicator of survival likelihood. Tree rings provide

330   information about recent history of the focal tree (Cherubini et al., 2002; Dobbertin,

331   2005; Wyckoff and Clark, 2000). They are a direct measurement of the constraints

332   experienced by the tree during growth, thus they are more informative than indirect

333   measurements, such as the size of neighbours. However, in absence of

334   dendrochronological data, neighbourhood indices can provide information about

335   competitive pressure on the trees, indicating trees more likely to die.

336

337   **Conclusion**

338 The importance of long term and repeated studies of forest stand is well recognized

339 (Turner et al., 2003). Mortality dynamics are best observed by repeatedly tallying

340 populations for a decade or more, and this usually reveals characteristic pulses and

341 trends in spatial patterns through time (Peterken, 1996).

342 Even if the stand is relatively aged (most of the trees have more than 180 years) the

343 competitive mortality dynamics observed in the plot are those typically observed in the

344 last phases of the stem exclusion stage (Oliver and Larson, 1996). Our analysis showed

345 variations in live and dead trees pattern across time, and indicated that probability of

346 tree death depended on local crowding. Trees having low chances to acquire resources

347 (small dbh) and with slow growth rate had higher probability to die. Moreover we

348 observed a regularization of spatial structure both at individual and at plot scale, so we

349 can infer that intraspecific competition was the primary cause of mortality during recent

350 decades.

351 In upcoming years, we expect an increment of competitive pressure (Castagneri et al.,

352 2008) and mortality involving mainly suppressed trees in the "area of influence" of

353 bigger neighbours. Besides we expect an increment of the allogenic mortality involving

354 the creation of gaps as already observed in the Reserve (Motta et al., unpublished data),

355 thus an increment of deadwood biomass and a levelling or decline of live biomass as

356 mortality breaks up the dominant canopy of trees (Smith, Long, 2001).

357

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496 **Tables**

497 Table 1. Stand characteristics of the permanent plot.

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	1993	2005	Variation %
Trees (n ha^{-1})	557	510	-8.4
Basal area (m^2 ha^{-1})	65.9	73.7	+11.8
Quadratic mean dbh (cm)	38.8	42.9	+10.6
Mean height (m)	28	29.6	+5.7
Snag density (n ha^{-1})	53	101	+90.6
Snag basal area (m^2 ha^{-1})	1.9	4.9	+167.8
Snag quad. mean dbh (cm)	21.4	24.6	+14.9

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513　Table 2. Estimated parameters and fit statistics of the logistic models.

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Model		1	2	3
Variables				
Intercept	Estimate	-1.663	2.963	3.455
	Sig.	0.183	0.103	0.067
Dbh 1993	Estimate	-0.129	-0.059	-0.081
	Sig.	0.000	0.014	0.001
	Odds ratio	0.879	0.942	0.922
BA neighbours	Estimate	0.017	0.000	0.003
	Sig.	0.040	0.986	0.710
	Odds ratio	1.017	n.s.	n.s.
Age 1993	Estimate	0.012	-0.009	-0.009
	Sig.	0.125	0.390	0.392
	Odds ratio	n.s.	n.s.	n.s.
RelBAI 1984-1993	Estimate		-0.338	
	Sig.		0.000	
	Odds ratio		0.713	
RelBAI 1964-1993	Estimate			-0.079
	Sig.			0.000
	Odds ratio			0.924
Producer's accuracy dead %		75.7	80.6	83.3
Producer's accuracy living %		77.8	85.5	83.7
Overall accuracy		77.6	85.1	83.7
Nagelkerke R^2		0.244	0.459	0.424
p (Hosmer-Lemeshow)		0.078	0.628	0.849

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518 **Figure captions**

519 Fig. 1. Univariate Ripley's K analysis for alive trees and snags in different periods. The

520 solid line represents $L(d)$; the two broken lines represent the Monte Carlo envelope

521 constructed at 99% confidence level. Values above confidence limit indicate clustering,

522 whereas values below indicate hyperdispersion. Analyses were performed from 1 to 50

523 m. Over 25 m functions did not diverge from null hypothesis, thus only results up to 25

524 m were shown.

525

526 Fig. 2. Bivariate Ripley's K_{12} analysis in different periods tested against random

527 labelling null hypothesis. The solid line represents $L_{12}(d)$; the two broken lines

528 represent the Monte Carlo envelope constructed at 99% confidence level. Values above

529 confidence limit indicate positive spatial interactions between live trees and snags,

530 whereas values below indicate negative spatial interactions. Analyses were performed

531 from 1 to 50 m. Over 25 m functions did not diverge from null hypothesis, thus only

532 results up to 25 m were shown.

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534 Fig. 3. Kernel density of living trees in the three periods (a, c, e) and location of snags

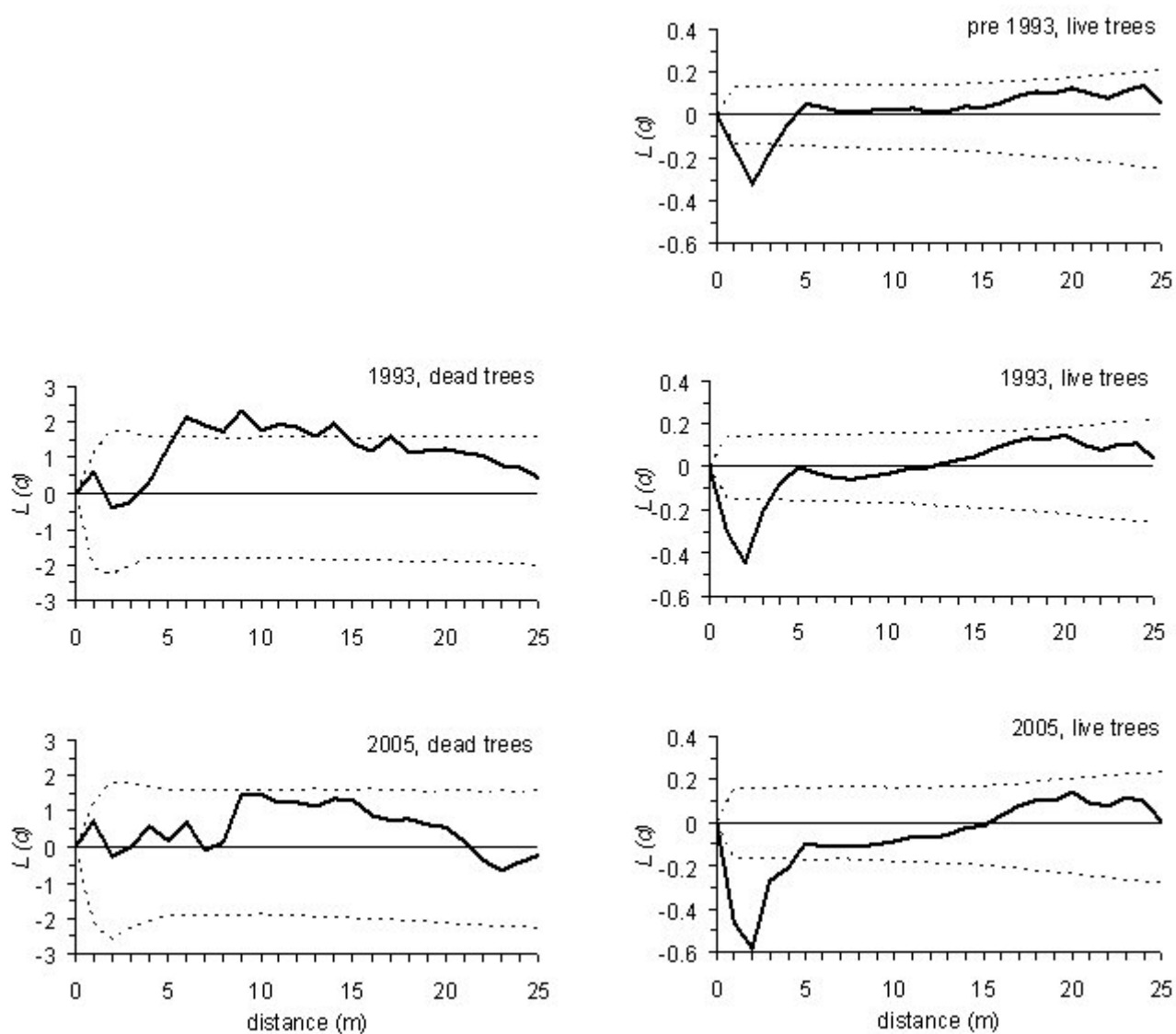535 observed in 1993 (b) and in 2005 (d). Pixel size is 1m x 1m.
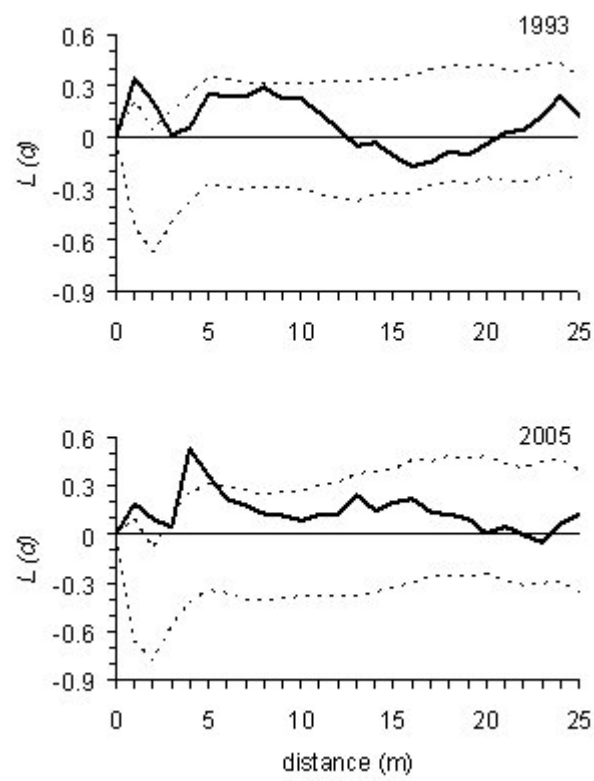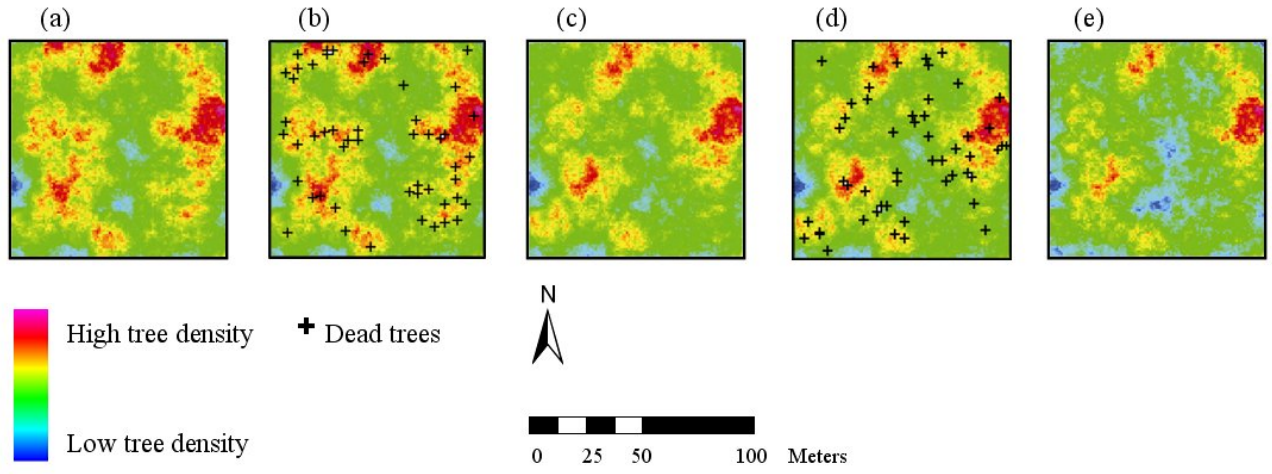
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Figure 1

Figure 2

Figure 3

(a) (b) (c) (d) (e)

High tree density   + Dead trees

Low tree density

N

0   25   50   100   Meters

REFEREE 1

General opinion and decision

Nevertheless, conclusions are too descriptive (too qualitative) and results are not so new: authors are illustrating the self-thinning process (where tree density and associated competition for resources is higher, tree mortality is higher) and they don't give enough value to their large data-set including many dendrometric measurements.

To reach their objectives of a better understanding of mortality process and of more accurate forest dynamics models, authors should develop a more quantitative approach and compare their results with other studies on Spruce mortality.

I then recommend a major revision for this paper. It would be acceptable if it included a mortality model analysing explicitly the effects of size, age, neighborhood and past radial growth on mortality probability (through a multivariate logistic model for example).

We developed a logistic model including size, age, neighbourhood and past radial growth. Past radial growth was calculated using dendrochronological data.

We included more quantitative information, e.g. mean dbh of dead trees (line 226-227), and we stress our quantitative results on neighbour effect (2-5 m) at line 290.

We compared our results with other studies on Norway spruce mortality (line 292-294).

Main remarks

- These results deserve to be presented in the revised version of the manuscript but as general results introducing a more in-depth study. As for example, the distance of 3 and 6 m found by the authors could be used for the computation of a Neighborhood Competitive Index to be included in a mortality model (Uriarte et al., 2004).

We developed a mortality logistic model considering results from spatial pattern analysis, e.g. the extent of neighbour effect at 2-5 m to calculate neighbourhood.

Results are too descriptive:

- The effect of competition on tree mortality has already been demonstrated and quantified (Monserud, 1976; Wunder et al., 2007; Bigler and Bugmann, 2003; Dobbertin, 2005; Kobe and Coates, 1997; Wyckoff and Clark, 2000).

- Your issue is of interest: there is a need to differentiate the effects of size, growth, neighborhood and age on tree mortality. But the statistical methods you used were not

sufficient to do so as you principally tested one effect independently of the others.
- It would be better to quantify the effect of each of this covariates in a multivariate analysis.
In accordance to referee suggestion, we quantified effects of covariates (size, age, neighbourhood and past radial growth) all together in the logistic model.

Secondary remarks
- What about fallen dead trees? It is not so surprising to see an effect of crowding on mortality as you identified standing dead trees only.
We included fallen dead trees for the period 1993-2005 (line 224). We modified introduction and research objective because 48 on 52 dead trees were standing dead trees, and competitive mortality could be expected.
For mortality observed in 1993, we considered logs as snags fallen due to decomposition processes, since they were highly decomposed and appeared to be fallen dead (i.e. snapped dead). Logs were excluded from analyses because they originated from trees dead before snags, and we can not investigate mortality episodes too distant in time. Moreover, logs are decomposed (1) and they could be moved from they original location (2), hence analyses on size and dendrochronological samples (1), and spatial pattern analyses (2) could not be performed.

- In sub-alpine spruce forests, mortality due to external disturbances is of high importance (wind-throws, avalanches, rockfalls, insects attacks, pathogens, etc.) and can be taken into account through the DBH of the tree.
No external disturbances were observed in our plot (line 78).

References suggested
Suggested references were taken into account and in some cases cited.

REFEREE 2

The tree-ring study by Paolo Cherubini and Fritz Schweingruber that looked at patterns of stand development in this area should probably be cited.

Dendrochronological analysis by Cherubini et al. 1996 were considered and the paper cited (line 200).

Line 31. The language used here is wrong. There were not two subsequent surveys. Rather, there was an initial survey in 1993, and a subsequent one in 2005.

We corrected the paragraph following referee suggestion.

Line 55. The situation is not as clearcut as the separation between allogenic and autogenic processes suggests. It is not a matter of "or", as most mortality processes involved in the decline and death of a tree involve both allogenic and autogenic processes. I would refer the authors to Manion's decline spiral. The authors acknowledge the complexity in line 68, but the statements on line 55 should be less definitive.

We replaced "or" with "and", and we concluded the paragraph with the sentence "More often, actual mortality patterns result from the interaction of multiple agents".

Line 89. Please specify what these "given mortality agents" are, as the hypothesis will only hold true for a few such agents.

Introduction was partially modified and this sentence was deleted.

Line 143. How reliable is the pith locator technique? Its use here for ageing trees seems to introduce a potential source of uncertainty? In how many trees did the authors fail to core the pith?

To calculate the year of establishment we needed to estimate the pith and the number of missing rings. A variety of methods exist. We adopted the graphical procedure using the pith locator. We are aware that this technique can introduce an error, however it is widely used to estimate missing innermost rings. E.g. R Motta, P Nola, Journal of Vegetation Science, 2001; PT Soule, PA Knapp, HD Grissino-Mayer, Ecological Applications, 2004;   M Savage, JN Mast, Canadian Journal of Forest Research, 2005;   JD Bakker, Canadian Journal of Forest Research, 2005.

Moreover, this technique was already used in previous analysis in Paneveggio forest (R Motta, P Nola, P Piussi, Journal of Ecology, 2002).

Line 166. What is the rationale for doing this? Why would a standing dead tree in 2005, that was not recorded in 1993, have died prior to 1993? This suggests that there were major differences in the inventory techniques between the two surveys, and these need to be explained.

In 1993 dead trees were not recorded. A standing dead tree in 2005, that was not recorded in 1993, was already dead in 1993. Otherwise it would be recorded as live tree in 1993. We believe this procedure could lead to a misunderstanding, so we simplified description of data collection. The other measurement protocol applied in the surveys were fully consistent.