

1 Analysis of intraspecific competition in two subalpine Norway spruce (*Picea abies* (L.) Karst.)  
2 stands in Paneveggio (Trento, Italy)

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8

9 Abstract

10

11 As a consequence of the recent change in human land-use intensity in mountain territories in the  
12 Italian Alps, many Norway spruce (*Picea abies* (L.) Karst.) subalpine forests have recently  
13 developed without significant anthropogenic disturbance. Even so, their structure and dynamics are  
14 still influenced by past human activity. In order to analyze the interactions between past  
15 management and current stand dynamics, competition among trees was studied in two 1-ha  
16 permanent plots in the Valbona Forest Reserve, located within the Paneveggio-Pale di San Martino  
17 Natural Park (eastern Italian Alps). The plots were established in 1993 in two stands with similar  
18 age, density and structure but different management history. Tree measurement was repeated in  
19 2005.

20 We carried out the analysis both on the stand- and on the individual tree scale. We computed  
21 maximum Stand Density Index (SDI) for Norway spruce in Paneveggio Park (SDI<sub>max</sub> 1380) based  
22 on an ancillary sample plot network. The intensity of stand-level competition and its course through  
23 time was assessed in each study area computing percent relative SDI (SDI%) for the two inventory  
24 years.

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25 Competition at individual level was studied using known individual-based Competition Indices  
26 (CIs) as well as a new set of Crown Area Indices (CAI), all of them based on tree variables such as  
27 dbh, height, crown area and inter-tree distance. We assessed the performance of each index by  
28 evaluating its explanatory power in forecasting individual tree basal area growth ( $\Delta g$ ) in a 10-year  
29 period.

30 In the more recently thinned plot, competition did not induce mortality rates comparable to the  
31 second plot, that has been unmanaged for the last 60 years. We expect the intensity of competition-  
32 induced mortality of the two stands to increase its similarity in the next future.

33 Individual CIs based solely on tree diameter produced the best performance in plot 1 (e.g., Daniels'  
34 CI,  $R^2_{adj} = 0.580$ ). In plot 2 different CIs, including tree height, crown area and inter-tree distance as  
35 base variables also, proved the most explanatory ones, including  $CAI_6$  ( $R^2_{adj} = 0.553$ ), which not  
36 consider dbh.

37 We attributed the differential role of tree spatial location and dominance-related descriptors in  
38 predicting growth to the time when the stand experienced the last anthropogenic disturbance. The  
39 competition relationships still experience the effect of the artificial alteration of forest structure:  
40 after human disturbance, mature Norway spruce subalpine forests need several decades to approach  
41 more natural dynamics.

42

43 Keywords

44 Norway spruce; Forest dynamics; Subalpine forest; Competition; Individual based competition  
45 indices; Stand Density Index.

46

47 1. Introduction

48

49 Competitive dynamics between trees is a key factor in shaping forest stand evolution (Tilman,  
50 1982; Brand and Magnussen, 1988). This process arises when neighboring plants share limited

51 resources, leading to a reduction in survivorship and/or growth rate (Clements, 1929; Grime, 1979;  
52 Begon et al., 1996; Oliver and Larson, 1996). For this reason, competition has long been known as  
53 a primary process governing population size, community structure and diversity (Oliver and Larson,  
54 1996; Newton and Jolliffe, 1998; Simard and Sachs, 2004; Simard and Zimonick, 2005).

55 In order to understand competitive dynamics, several competition indices (CI) have been developed  
56 through time to assess the competitive intensity taking place either in whole stand or acting on  
57 individual trees. Stand-level competition indices reflect the degree of tree crowding per unit area  
58 (Husch et al., 1982), allowing to compare competitive status in different stands (Hynynen and  
59 Ojansuu, 2003). Individual-based CIs reflect the local density of competitors interacting with an  
60 individual tree (Tomé and Burkhardt, 1989). They quantitatively assess the intensity of competition  
61 experienced by focal trees and allow to quantify the influence of neighboring individuals on the  
62 growth of the subjects (Hynynen and Ojansuu, 2003). They may or may not rely on spatial tree  
63 location, hence they are usually classified as distance-dependent or distance-independent (Biging  
64 and Dobbertin, 1995). The interpretation of the outcome of competition can depend critically on the  
65 way competition is measured (Freckleton and Watkinson, 1999). No index has been found  
66 universally superior, but rather CIs need to be tested on local species and conditions to determine  
67 their applicability (Burton, 1993; Weigelt and Jolliffe, 2003). Moreover, the natural course of  
68 competition through time is often influenced by exogenous disturbance events, either natural or  
69 anthropogenic. All forest stands in the Italian Alps have been affected by humans in some way,  
70 either through direct periodic harvesting or by more subtle forms of land-use. Nevertheless, in the  
71 last decades there has been a noticeable reduction of the anthropogenic disturbance and, as a  
72 consequence, many forest stands have developed naturally even if their composition and structure  
73 still reflect past human activity (Guisan and Theurillat, 2000; Bachofen and Zingg, 2001; Motta and  
74 Lingua, 2005).

75 The Norway spruce (*Picea abies* (L.) Karst.) forest in Paneveggio-Pale di San Martino Natural Park  
76 (Trentino Alto Adige, Italy) represents an example of the aforementioned process. Historical

77 evidence **shows** that the forest has been intensively managed for centuries. Following World War II,  
78 the frequency of silvicultural operations decreased and, in the Valbona valley, came to a complete  
79 end in 1990, when a forest reserve was established (Motta et al., 2006). The present study focuses  
80 on two long-term forest monitoring plots located inside the reserve, characterized by a varying time  
81 since last disturbance. **Our aim was to analyze interactions between past management and current**  
82 **stand dynamics. We expected competition dynamics to be still influenced by past human activities**  
83 **in the more recently disturbed plot. This effect was expected to be observed both at stand and at**  
84 **individual level, i.e. on mortality rate and on individual growth rate respectively.** The objectives of  
85 this work were: comparing competitive dynamics at the stand level (1) and at the individual level,  
86 analyzing the influence of competition on tree growth using existing individual-based CIs (2) and  
87 new competition indices (3), devised using biologically representative variables, i.e., the variables  
88 determining the competitive ability of the trees and shaping the outcome of inter-tree relationships.

89

## 90 2. Methods

91

### 92 2.1. Study site

93

94 The study is focused on two stands in the Valbona Forest Reserve (latitude 46° 18' N, longitude 11°  
95 45' W), a **123 ha** subalpine Norway spruce forest included in the Paneveggio-Pale di San Martino  
96 Natural Park (Trentino, Italy). The phytocoenosis is classified as *Homogyno-Piceetum subalpinum*  
97 *myrtilletosum* (Di Tommaso, 1983).

98 Rainfall is 1157 mm/year at Passo Rolle (2002 m a.s.l.), approximately 3 km from the study site,  
99 and 1104 mm/year at Paneveggio (1508 m a.s.l.), approximately 2 km from the study site. Annual  
100 mean temperature is 2.7 °C at Passo Rolle and 3.7 °C at Paneveggio. The bedrock is porphyry and  
101 sandstone, and soils are podsol**s** and rankers.

102 Both stands are pure and monolayered; spatial pattern of adult tree stems is random (Motta, 2002).  
103 The first stand was established after a logging that removed parts of the previous stand around year  
104 1820. This stand was affected by moderate and major disturbances during 19<sup>th</sup> century, and again  
105 during the period 1915-1924. The plot is located a few hundreds meters from a forest road, and was  
106 quite accessible for thinning and harvesting operations, that lasted until 1980-1984. The second  
107 stand was established after a logging around year 1790. This stand is relatively faraway from forest  
108 roads and has developed without anthropogenic influence since the 1940s, when all thinning and  
109 harvesting operations were over (Motta et al., 1999) (stand characteristics on Table 1).

110

## 111 2.2. Field measurements

112

113 During 1993, two 1-ha (100x100 m) sample plots were established and all live and dead standing  
114 trees with diameter at breast height (dbh) > 7.5 cm, logs, and stumps were identified, labelled with  
115 numbered tags and mapped. Dbh was measured for each tree. The inventory was repeated in 2005.  
116 We measured diameter at 50 cm height, dbh, total height, crown radii in the four cardinal directions,  
117 and height of the lowest living branches (upslope and downslope).

118 The trees chosen for competition analysis (focus trees) were taken in a 60x60 m subplot placed at  
119 the center of the permanent plot in order to avoid edge effects. A stratified random sampling was  
120 carried out in each subplot by splitting the trees ( $n_1 = 179$ ,  $n_2 = 157$ ) in 3 equal groups based on dbh  
121 class. A random sample of 20 trees was selected from each size class.

122 An increment core was taken upslope from focus trees at a height of 50 cm. In the lab, following  
123 optimization of surface resolution, we measured radial increments of the last 40 years to the nearest  
124 0.01 mm. Data were collected and stored using a LINTAB device and the TSAP package (Rinn,  
125 1996). All the cores were cross-dated against available site chronologies (Motta, 2002; Motta et al.,  
126 2002) in order to ensure the assignment of the correct year to each annual ring. We successfully  
127 cross-dated 58 cores from plot 1 and 55 from plot 2.

128

### 129 2.3. Stand-level competition analysis

130

131 We used Reineke's Stand Density Index (SDI) (Reineke, 1933) to analyze competition intensity in  
132 the two stands. SDI describes stand density as the number of 25 cm-dbh stems per hectare required  
133 to express an equivalent degree of crowding. We calculated SDI in plot 1 and plot 2, using the  
134 summation method proposed by Shaw (2000) as the generalization of Reineke's formulation for all  
135 stand structures:

136

$$137 \quad \text{SDI} = \sum_{i=1}^n \left( \frac{d_i}{25} \right)^b \quad (1)$$

138

139 were  $d_i$  is the dbh of the  $i$ -th tree in the sample (cm), and  $b$  is the self-thinning coefficient. The value  
140 of the coefficient, representing the negative slope of a species' self-thinning line, has been debated  
141 (for a review see Pretzsch and Biber, 2005). Nevertheless, Reineke's suggested value of 1.6 can be  
142 considered a reasonable approximation for all species when broad ecological dynamics are  
143 investigated (Shaw, 2006).

144 A species' maximum SDI represents the boundary of all possible size-density combinations attained  
145 by stands of that given species. Relative density, i.e., the percent ratio between observed stand  
146 density and this theoretical maximum, describes the intensity of competition acting in the stand, and  
147 can be linked to specific stand developmental stages (Drew and Flewelling, 1979; Long, 1985).

148 Maximum SDI values proposed in literature for Norway spruce are not consistent with one another,  
149 ranging from 1057 to 1571 in Austria (Sterba, 1981; Monserud et al., 2005), to 1609 for non-  
150 planted spruce forests in Southern and Central Germany (Pretzsch, 2005). The maximum SDI for  
151 Norway spruce in the Paneveggio-Pale di San Martino Natural Park (forested area: 2970 ha) was  
152 calculated from dataset of 291 sample plots already available. The plots have a surface area ranging

153 from 400 to 452 m<sup>2</sup> and are located on elevations ranging from 1600 to 2200 m a.s.l. Plots with less  
154 than 5 sample trees, or less than 80% of total basal area accounted for Norway spruce, were  
155 excluded from further analysis in an effort to draw plots from nearly pure stands (Long and Shaw,  
156 2005). 138 plots were used for SDI calculation, based on the dbh of sample trees (equation 1). The  
157 98<sup>th</sup> percentile of the SDI distribution was assumed as maximum SDI for Norway spruce in the  
158 study area (Shaw, personal communication). We obtained percent relative density in the two  
159 permanent plots for both inventory years through the ratio between observed and maximum SDI. In  
160 order to compare stand development with the self-thinning trajectory of undisturbed stands (Long,  
161 1985), we plotted SDI resulting from both inventories (years 1993 and 2005) on log-log axes and  
162 calculated the average self-thinning slope between the two points.

163

#### 164 2.4. Individual-based competition indices

165

166 In order to analyze competition dynamics in the plots and find out the variables effectively  
167 determining the competitive relationships between trees, we used individual-based competition  
168 indices (CIs). The explicative power of a competition index is usually tested by how well it predicts  
169 the growth of subject tree (Stadt et al., 2002). The set of indices (Table 2) was selected from the  
170 literature in such a way to represent different combinations of tree variables (diameter, height,  
171 crown area, inter-tree distance) involved in determining a tree's competitive status.

172 We included both distance-dependent and distance-independent CIs. The latter can be very useful  
173 because they require less information than spatially explicit CIs, even if they are not appropriate for  
174 the analysis of tree spatial pattern in the plot (Zhao et al., 2006).

175 The first step to calculate individual-based competition indices was the identification of the trees  
176 actively competing with the focus tree. Many methods for competitors selection are available (for a  
177 complete review see Biging and Dobbertin, 1992; Alvarez Taboada et al., 2003; Corral Rivas et al.,  
178 2005). We recurred to the influence-zone concept proposed by Stæbler (1951), i.e., the

179 bidimensional surface within which trees compete for environmental resources (Ottorini, 1978).  
180 Competition is assumed to exist when the zones of influence of two trees overlap. Since larger trees  
181 may compete at greater distances than smaller trees (Martin and Ek, 1984), we deemed the methods  
182 that take into consideration the size of the subject and competitor trees as the most appropriate.  
183 Many authors defined the zone of influence as a circular area surrounding the tree with a radius  
184 equal to the crown radius of an open-grown tree of the same diameter (Holmes and Reed, 1991;  
185 Larocque, 2002; Corral Rivas et al., 2005) or the same height (Ek and Monserud, 1974). We chose  
186 tree height, rather than dbh, as the predictor variable because it is less influenced by the degree of  
187 crowding experienced during tree development (Assmann, 1970), and therefore it is a better  
188 expression of a tree's maximum crown size (Strand, 1972). In order to calculate the size of open-  
189 grown crowns, we used the allometric equations proposed by Hasenauer (1997) for Norway spruce  
190 in the Austrian Alps, an area both geographically and climatologically similar to the one studied  
191 herein:

$$193 \ln(cw) = a_0 + a_1 \cdot \ln(h) \quad (2)$$

194  
195 where  $cw$  is crown width of an open-grown tree (m),  $h$  is total tree height (m), and  $a_0, a_1$  are  
196 respectively the intercept and the slope of the regression line. The trees whose zone of influence  
197 intersects the open-grown crown of focal tree were chosen as competitors; this selection method  
198 was applied to all the CIs used.

199 The explicative power of each CI was tested examining his relationship with 10-year basal area  
200 increment ( $\Delta g$ ) of focus trees, defined by

$$202 \Delta g = \pi \left[ d_{0.5h} \Delta r - (\Delta r^2) \right] \quad (3)$$

203



204 where  $\Delta g$  is individual basal area increment ( $\text{cm}^2$ ),  $\Delta r$  is the last 10-year radial increment (cm),  $d_{0.5h}$   
205 is diameter at 0.5 m height.

206  $\Delta g$  distribution was normalized by logarithmic transformation; the logarithm of  $\Delta g$  is considered  
207 one of the best variables reflecting the nonlinear curve of tree growth (Cole and Stage, 1972; Zeide,  
208 1993; Wykoff, 1990) and has got desirable properties with the error structure, e.g., homogeneous  
209 variance (Monserud and Sterba, 1996).  $\Delta g$  was modeled as an exponential function of tree size and  
210 competition indices by a number of studies (e.g. Cole and Lorimer, 1994).

211 The following linear regression model was used to investigate the performance of each competition  
212 index:

213

$$214 \ln(\Delta g) = b_0 + b_1 \cdot \ln(CI_i) \quad (4)$$

215 where  $CI_i$  is the value of the competition measure being used for the  $i$ -th focal tree and  $b_0$ ,  $b_1$  are  
216 respectively the intercept and the slope of the regression line. We examined overall goodness-of-fit  
217 of each regression model (RMSE and adjusted- $R^2$ ) in order to assess the most informative  
218 competition measure. The analyses were made both on all focus trees at a time and separately for  
219 each study area. All analysis were performed using the software SPSS 13.0 (SPSS Inc., Chicago  
220 IL).

221 To better understand the relationship between different variables and the actual competition in the  
222 two study areas, we devised a new competition index including biologically representative  
223 variables, i.e., the variables determining the aboveground competitive relationships of trees: inter-  
224 tree distance, crown area, tree height. The new index was designed excluding diameter at breast  
225 height as a predictor, since this variable is strongly related to subject tree's  $\Delta g$  (Holmes and Reed,  
226 1991). Moreover, dbh is related more to the age and the past competitive status of trees (Prévosto  
227 and Curt, 2004) than to their current social position and ability to intercept light or shade other  
228 competitors.

229 An individual's ability to intercept light and to shade other competitors also depends on its crown  
230 area (Hatch et al., 1975; Doyle, 1983; Holmes and Reed, 1991). As suggested by Alvarez Taboada  
231 et al. (2003), we examined the role of crown cross-sectional area calculated by four crown radii,  
232 summing the ratios between the *i*-th competitor and the subject's projected crown areas but  
233 excluding spatial information (CAI<sub>1</sub>) (Tab. 2). A second index (CAI<sub>2</sub>) was designed to reflect the  
234 asymmetry of aboveground competition (Weiner, 1990): a squared ratio enhances size differences  
235 between focus and competitor trees.

236 Next, we added total tree height, to explicitly consider the relative social position of the subject tree  
237 compared with its neighbors, again using a simple (CAI<sub>3</sub>) and a squared (CAI<sub>4</sub>) ratio. Last, we  
238 added spatial information to these height-weighted crown area ratios, creating CAI<sub>5</sub>, and finally,  
239 using a squared ratio, we created CAI<sub>6</sub>.

240

### 241 3. Results

242

#### 243 3.1. Site description

244 Plot 2 had an higher density and mean diameter compared to plot 1 (Table 1). Diameter class  
245 distributions had a gaussian shape, supporting evidence of an even-aged structure (Fig. 1). In the  
246 last ten years, a few trees overcame the lower dbh measurement threshold (7.5 cm) in both plots.  
247 There was an increase in frequencies of the higher diameter classes and a decrease in the medium-  
248 lower ones.

249 In plot 1 density had slightly decreased since the first inventory because of the death of smaller  
250 trees. In plot 2 density had clearly decreased, and mortality involved lower and medium-lower  
251 diameter classes (Fig. 1).

252

#### 253 3.2. Stand-level competition

254

255 The maximum SDI for Norway spruce in Paneveggio-Pale di S. Martino Natural Park was 1380.  
256 Stand Density Index in plot 1 was 1051 (76.2% relative density) in 2005 and 935 (67.7%) in 1993.  
257 In plot 2, SDI values were 1178 and 1098 respectively (i.e., 85.4% and 79.6% in relative terms).  
258 The average slope of the self-thinning trajectory was -4.802 in plot 1, and -1.139 in plot 2 (Fig. 2).  
259 Especially in plot 1, the obtained value was far from -0.6, i.e., the suggested slope for the maximum  
260 self-thinning line (Reineke, 1933).

261

### 262 3.3. Individual-level competition

263

264 Results obtained by correlation between individual-based CIs and basal area increment (Table 3)  
265 show that spatial independent Daniels and NSCIM indices had better  $R^2_{adj}$  in both plots (except  
266 NSCIM for plot 2).

267 Indices performance improved as dbh ratio was taken into greater account i.e. from R.K.<sub>1</sub> to  
268 Hegyi's index to R.K.<sub>2</sub>. R.K.<sub>2</sub> was the distance-dependent index having the best  $R^2_{adj}$  value in both  
269 plots. All the distance-dependent indices had an higher  $R^2_{adj}$  in plot 2 than in plot 1, but also an  
270 higher RMSE, including those using crown area as a variable. The  $R^2_{adj}$  value of Crown Area  
271 Indices proposed herein increased when accounting for competition asymmetry (CAI<sub>2</sub> better than  
272 CAI<sub>1</sub>) and including the height variable (CAI<sub>3</sub>, CAI<sub>4</sub> better than CAI<sub>1</sub> and CAI<sub>2</sub> in both plots). In  
273 plot 2, inter-tree distance improved index performance more than in plot 1, and CAI<sub>5</sub> and CAI<sub>6</sub>  
274 performed as the best spatial indices (a few lower  $R^2_{adj}$  and a few higher RMSE than R.K.<sub>2</sub>).

275

## 276 4. Discussion

277

278 The intensive and diversified exploitation that occurred in the past complicates the study of natural  
279 forest dynamics. Understanding the dynamics of forest stands with strong past anthropogenic

280 disturbances is particularly difficult because the different types of human impact typically vary in  
281 time and space.

282 At the beginning of the study period, relative density in both plots was already above the 60%  
283 threshold, which represents complete resource exploitation and marks the onset of the self-thinning  
284 process (Drew and Flewelling, 1979). It is notable that relative density limits marking specific  
285 developmental stages are usually broad indications and are not to be considered accurate numerical  
286 estimates. Moreover, relative density has been calculated from  $SDI_{max}$  of a local sample, and may  
287 not represent the species' maximum density.

288 In 1993, about ten years later the last thinning operations, SDI in plot 1 was 68% of the maximum.  
289 During the observation period, relative density increased up to 76%; the observed mortality  
290 involved mostly small size classes, in agreement with the self-thinning hypothesis (i.e.,  
291 competition-induced death of suppressed trees).

292 Stand 2 developed in a similar way, increasing its relative density by 6 percentage points and  
293 showing a comparable rise of tree mean size, promoted by an active growth of the surviving trees.

294 Since more time has passed from the last silvicultural operation in the second stand, its current  
295 development may be considered closer to natural conditions. In the last ten years, the unthinned plot  
296 suffered sustained competition-induced mortality; such dynamics seem to have been continuously  
297 taking place, since several standing dead trees were already found in the stand at the time of the first  
298 measurement.

299 Current density of plot 1 is close to the initial degree of crowding in plot 2. Even so, percent  
300 frequency of standing dead trees in the former situation is too low if compared to the latter to be  
301 imputed only to relative density differences (i.e., 2% and 10% respectively).

302 The low mortality rate can be related to the effect of past thinning. Even when average size and  
303 density are equal, thinned stands do not behave the same as stands grown without thinning  
304 (Farnden, 1996). Low thinning imply that suppressed trees – that in undisturbed stands would  
305 generally lose competition and die – are removed all at once.

306 Plot 1 is characterized by a different diameter and height distribution as compared to plot 2. The  
307 slope of self-thinning trajectory in plot 1 is far from the asymptotic self-thinning slope, while in plot  
308 2 this parameter is closer to the reference  $-0.6$ , although mean tree size is similar in the two sites.  
309 This means that the latter stand is currently experiencing a higher mortality rate than plot 1 (higher  
310 mortality per unit size increase); the self-thinning process is fully operating and involves both lower  
311 and medium size classes. According to Newton (2003), the size-density trajectory of a recently  
312 thinned stand diverges from that of a stand that had naturally evolved to a comparable density level.  
313 In the last 10 years, plot 1 was approaching the more natural trajectory plotted by plot 2. The treated  
314 stand will need some additional time to adjust its competitive relationships, i.e., to attain the natural  
315 mortality rate typical of its relative density. In absence of exogenous disturbance, we expect  
316 mortality rate in plot 1 to approach an incidence closer to the one in plot 2 in the next future.

317 The differences shown by stand-level measures of competition were consistent with individual CIs  
318 measurement. For each CI used in this study, we analyzed the trend in average CI value per dbh  
319 class (data not shown). We observed that competitive pressure decreased more rapidly with  
320 increasing tree size in plot 2. Here, more intense stand competition dynamics determined stronger  
321 inequalities in individual social relationships, while in plot 1 individuals belonging to different  
322 diameter classes seemed to suffer a more uniform competitive pressure.

323 Existing individual based distance-independent CIs (Daniels and NSCIM) use dbh squared to  
324 represent subject tree size. Since dbh is correlated with basal area increment, these indices were  
325 expected to show a strong relationship with  $\Delta g$ .

326 Even if site characteristics (climate, micromorphology) seem to be similar to plot 1, all distance-  
327 dependent competition indices showed a better  $R^2_{adj}$  in plot 2. The higher RMSE in plot 2 was due  
328 to the higher variability. In plot 1, giving a greater weight to competitor distance (e.g., R.K.<sub>2</sub> to  
329 R.K.<sub>1</sub>) or adding spatial data to the indices' formulation (e.g., CAI<sub>3</sub> to CAI<sub>5</sub>) did not improve the  
330 predictive ability of the indices. Current tree spatial pattern is influenced by recent anthropogenic  
331 interference (more than in plot 2), due to recent logging activities. The likely outcome of this

332 disturbance factor is that natural spatial structure, i.e., the one originated by natural stand dynamics  
333 as inter-tree competition, is masked, hence the little role played by spatial location of neighbouring  
334 competitors. Past studies have shown that superiority of distance-dependent competition indices is  
335 not a rule (e.g., Biging and Dobbertin, 1995). Competitive influence on spatial structure is  
336 complicated by the confounding effect of spatial micro-site variability (Fox et al., 2001), and by  
337 possible human activities, misleading interpretation of individual CIs (Fox et al., 2007).

338 Diameter is used in the formulation of many competition indices (e.g., Hegyi, 1974; Lorimer,  
339 1983). Spatial indices using dbh as the main predictor variable (e.g., R.K.<sub>2</sub>) showed a good  
340 performance in both plots, differently than the other CIs used. Success of these indices was  
341 probably due to the correlation existing between subject tree's diameter growth and its dbh, as  
342 suggested by Holmes and Reed (1991); such correlation might introduce ambiguity in the  
343 expression of the effect of competitive stress (Brand and Magnussen, 1988; Larocque, 2002).

344 Moreover, diameter is related to the age and past competition history of the tree (Prévosto and Curt,  
345 2004; Fox et al., 2007), rather than to actual social position. Past competitive status was a good  
346 predictor of the current one in both plots (see also Cole and Lorimer, 1994).

347 Inequalities in height within a population can result in the pre-emption of resources (light) by taller  
348 individuals (D'Amato and Puettmann, 2004). In monolayered populations, relative height of the  
349 subject tree expresses his current social status compared with the neighbors (Holmes and Reed,  
350 1991). Indices using tree height had good performance in plot 2, and quite good in plot 1. The  
351 worse performance in plot 1 is consistent with the behaviour of all spatial-dependent indices, where  
352 distance has a lower predictive power because of the recent treatments. Tree height still represents a  
353 good descriptor of competitive dynamics, retaining a close relationship to 10-year increment. This  
354 can also be seen by considering the improvement in index performance when using CAI<sub>3</sub> in place of  
355 CAI<sub>1</sub>.

356 Logging activities could also explain the lower performance of CIs using crown area ratio in plot 1  
357 as compared to plot 2. These activities were carried on already mature individuals (tree age

358 averaged 160 years at the time). Ageing trees, especially softwoods (Williams, 1996), lose the  
359 ability to expand crown to fill in newly created gaps (Waller, 1986; Zeide, 1987; Piussi, 1994;  
360 Juodvalkis et al., 2005). In plot 1 the trees likely did not adapt their crown to the new canopy  
361 conditions created by thinning operations; actual crowns are not related to their current competitive  
362 status.

363 As Lorimer (1983) pointed out, growth cannot be predicted from stem spatial pattern alone and  
364 requires some indication of the crown class or competitive status of the subject tree, especially  
365 when predicting recovery from competition when a competitor is removed (e.g., by thinning,  
366 Vanclay, 1994).

367 The satisfactory performance of the Crown Area Indices proposed herein in plot 2 confirmed that  
368 crown area, tree relative height, and spatial information are useful variables to understand and  
369 describe competition in a stand experiencing natural dynamics and undisturbed by man in the recent  
370 past. The three predictors were simultaneously used in CAI<sub>5</sub> and CAI<sub>6</sub>. The fairly good performance  
371 of latter indices shows their ability to adequately represent the competitive status of a tree. CAI<sub>5</sub> and  
372 CAI<sub>6</sub> might be used in future researches to test their usefulness in competition analysis of Norway  
373 spruce forests.

374 Not many years have passed since the interruption of forest management in the Valbona forest  
375 reserve. We found the influence of past silvicultural operation to be still determinant in shaping  
376 current competitive dynamics. The plots analyzed herein showed limited differences in stand  
377 density, tree age or environmental factors, but competition was likely influenced the most by recent  
378 thinning, that altered forest structure and tree spatial relationships. In the first study plot, that has  
379 been developing without human disturbances since 1984, the intensity of competition between trees  
380 (stand level analysis) and the role of its mediators (individual level analysis) seem to be deeply  
381 influenced by past disturbance. In this case, only CIs using diameter as a predictor variable have the  
382 ability to reflect competitive relationships. Conversely, self-thinning dynamic in the more natural  
383 developed plot is closer to natural's, and competition can be efficiently modeled by indices based on

384 **dominance-related tree variables**. These effectively represent competitive relationships between  
385 individuals when natural dynamics are the main drivers of stand development. We suggest that  
386 following human activities, including moderate logging, mature subalpine Norway spruce stands  
387 will require several decades to restore mortality rates and tree competitive relationships  
388 characterizing naturally developed forests.

389

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563 Tables

564 **Table 1**

565 Stand characteristics

	Plot 1 (1993)	Plot 1 (2005)	Variation %	Plot 2 (1993)	Plot 2 (2005)	Variation %
<b>Elevation (m a.s.l.)</b>	<b>1695</b>			<b>1815</b>		
<b>Slope (%)</b>	<b>30</b>			<b>47</b>		
<b>Aspect</b>	<b>North</b>			<b>North</b>		
Trees (n ha <sup>-1</sup> )	484	476	-1.7%	557	510	-8.4%
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	55.9	64.6	+15.6%	65.9	73.7	+11.8%
Quadratic mean dbh (cm)	38.4	41.6	+8.3%	38.8	42.9	+10.6%
Mean height (m)		31.1			29.6	
Volume (m <sup>3</sup> ha <sup>-1</sup> )	820	946	+15.4%	874	977	+11.8%
Snag density (n ha <sup>-1</sup> )	0	9	*	53	101	+90.6%
Snag volume (m <sup>3</sup> ha <sup>-1</sup> )	0	5.5	*	21.9	59.9	+173.5%

566 \* For Plot 1 it was not possible to calculate Snag density and Snag volume **percent** increment.  
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576 **Table 2**

577 Competition indices and corresponding equations <sup>a</sup>

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Index	Source	Variables	Equation
Daniels	Daniels et al. (1986)	Dbh	$\frac{d_i^2 \cdot n}{\sum_{j=1}^n d_j^2}$
<b>NSCIM</b>	<b>Corona, Ferrara (1989)</b>	Dbh	$\frac{\sum_{j=1}^n d_j^2}{d_i^2}$
<b>CAI<sub>1</sub></b>	<b>This work</b>	Crown area	$\sum_{j=1}^n \frac{a_j}{a_i}$
<b>CAI<sub>2</sub></b>	<b>This work</b>	Crown area	$\sum_{j=1}^n \left( \frac{a_j}{a_i} \right)^2$
<b>CAI<sub>3</sub></b>	<b>This work</b>	Crown area, height	$\sum_{j=1}^n \left( \frac{a_j \cdot h_j}{a_i \cdot h_i} \right)$
<b>CAI<sub>4</sub></b>	<b>This work</b>	Crown area, height	$\sum_{j=1}^n \left( \frac{a_j \cdot h_j}{a_i \cdot h_i} \right)^2$
Staebler	Staebler (1951)	Distance	$\sum_{j=1}^n l_{ij}$
Hegyí	Hegyí (1974)	Distance, dbh	$\sum_{j=1}^n \frac{d_j}{d_i \cdot (l_{ij} + 1)}$
R.K. <sub>1</sub>	Rouvinen, Kuuluvainen (1997)	Distance, dbh	$\sum_{j=1}^n \frac{d_j / d_i}{l_{ij}^2}$
R.K. <sub>2</sub>	Rouvinen, Kuuluvainen (1997)	Distance, dbh	$\sum_{j=1}^n \frac{(d_j / d_i)^2}{l_{ij}}$
P.K.	Pukkala, Kolström (1987)	Distance, height	$\sum_{j=1}^n \arctan \frac{(h_j - h_i)}{l_{ij}}$
CCS	Alvarez Taboada et al. (2003)	Distance, crown area	$\sum_{j=1}^n \frac{a_j}{a_i \cdot l_{ij}}$
CAI <sub>5</sub>	This work	Dist., crown area, height	$\sum_{j=1}^n \frac{\left( \frac{a_j \cdot h_j}{a_i \cdot h_i} \right)}{l_{ij}}$



CAI<sub>6</sub>

This work

Dist., crown area, height

$$\sum_{j=1}^n \frac{\left( \frac{a_j \cdot h_j}{a_i \cdot h_i} \right)^2}{l_{ij}}$$

579 <sup>a</sup>  $n$  number of competitors,  $d_i$  subject tree dbh (cm),  $d_j$  competitor tree dbh (cm),  $l_{ij}$  distance between  
580 competitor ( $j$ ) and subject ( $i$ ) tree (m),  $h_i$  subject tree height (m),  $h_j$  competitor tree height (m),  $a_i$   
581 subject tree crown area (m<sup>2</sup>),  $a_j$  competitor tree crown area (m<sup>2</sup>).

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583 Table 3

584 Contribution of competition indices to individual tree basal area growth models (logarithmic linear  
585 regression)<sup>a</sup>

Index	Plot 1		Plot 2	
	R <sup>2</sup> <sub>adj</sub>	RMSE	R <sup>2</sup> <sub>adj</sub>	RMSE
Daniels	0.580	0.480	0.598	0.646
<b>NSCIM</b>	0.531	0.507	0.537	0.693
CAI <sub>1</sub>	0.056	0.719	0.295	0.855
CAI <sub>2</sub>	0.079	0.711	0.344	0.825
CAI <sub>3</sub>	0.169	0.675	0.475	0.738
CAI <sub>4</sub>	0.188	0.667	0.499	0.721
Staebler	0.030	0.729	0.292	0.857
Hegyí	0.393	0.577	0.508	0.715
R.K. <sub>1</sub>	0.095	0.704	0.176	0.924
R.K. <sub>2</sub>	0.529	0.508	0.581	0.660
P.K.	0.387	0.580	0.503	0.718
CCS	0.082	0.709	0.384	0.799
CAI <sub>5</sub>	0.191	0.666	0.527	0.701
CAI <sub>6</sub>	0.214	0.657	0.553	0.681

586 <sup>a</sup> Pukkala and Kolström's index was computed considering not only trees taller than subject as

587 competitors (as suggested by Prévosto and Curt, 2004), but the totality of the neighboring

588 individuals. The calculated values can be either positive or negative; therefore tree's index value

589 was not log-transformed.

590

591 Figure captions

592

593 Fig. 1.

594 Comparison between 1993-2005 diameter distribution in the study plots.

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596 Fig. 2.

597 Plots self-thinning trajectory in the inventory period. Solid line represents maximum SDI. Dash-dot

598 line represents 60% of maximum SDI.