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1 **Interacting effects of physical environment and anthropogenic disturbances on the structure**
2 **of European larch (*Larix decidua* Mill.) forests**

3

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5

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13

14 **Abstract**

15 Most forested landscapes have been strongly influenced by humans, and hence prediction of
16 response to future perturbations or climate change requires understanding of the interaction among
17 human influences and the abiotic environment. Environmental and anthropogenic influences on
18 forest structure in *Larix decidua* Mill. stands were investigated in two watersheds of the central
19 Italian Alps (Valtellina, SO). We related three data sets (forest structure, anthropogenic influences,
20 and topography) using ordination methods. Path models of correlative and causal relationships
21 between these sets of variables were developed and used to differentiate the two watersheds with
22 respect to levels of historical human influence. The two study areas (Musella and Ventina) were
23 characterized by strong climatic and topographic gradients as well as a long history of human
24 settlement, although historical intensity of agricultural activities was much greater for Musella. We

25 hypothesized a weaker influence of abiotic variables on forest structure where the intensity of the
26 primary human disturbance factors, forest thinning and cattle grazing, had been strongest.
27 Stand structure types varied from sparse, larch-dominated forests at high elevations, to denser
28 stands at lower elevations dominated by spruce. Correlations of environmental variables with
29 dominant trends in stand structure were low with the exception of elevation. Anthropogenic
30 variables were unimportant at Ventina, whereas the interactive effects of both anthropogenic and
31 abiotic variables were needed to explain stand structure in Musella. The best-fit model indicated a
32 negative effect of elevation and anthropogenic variables on overall tree size. Stands with greater
33 tree density and canopy height layer diversity were located further from roads. Both watersheds
34 were characterized by a strong dominance of larch stands, but their structure and spatial pattern
35 differed greatly. Sparse larch forests were exclusively associated with moraines and upper
36 elevations at Ventina, but were also common near low-elevation farms at Musella. Historical
37 human influences were difficult to measure and may play a greater role in determining forest
38 structure than was suggested. Our study emphasizes the importance of landscape context for
39 interpreting the relative strengths of anthropogenic and abiotic influences on stand development
40 pathways.

41

42 **Key words**

43 Stand structure, *Larix decidua*, Path analysis, anthropogenic disturbances, central Italian Alps.

44

45 **1. Introduction**

46 An important goal of ecology is to clarify causal relationships that determine plant species
47 distribution and forest structure over broad spatial scales. A traditional approach to this topic,
48 stemming from efforts of early biogeographers to map the world's biomes (von Humboldt, 1808;

49 Hawkins et al., 2003), is to consider the abiotic template (climate and topography) as the principal
50 constraint acting on vegetation dynamics and plant successional processes (Curtis and McIntosh,
51 1951; Bray and Curtis, 1957; Stephenson, 1990; Urban et al., 2000). However, for most regions of
52 the world anthropogenic influences play a critical role (Leduc et al., 1992). The resulting cultural
53 landscapes are semi-natural systems developed as a result of the tight interaction between human
54 traditions and the natural environment (Antrop, 1997; Naveh, 1982, 1995).

55 Such cultural landscapes have only recently become a focus of ecological study, despite their
56 prevalence and importance. In Europe and North America, a disproportionate number of studies is
57 conducted in areas that have only been minimally influenced by humans (Spies et al., 1990;
58 Peterken, 1992, 1996; Bradshaw et al., 1994; Bergeron and Harvey, 1997), notwithstanding the
59 difficulty in generalizing from such pristine study areas to the more prevalent condition (i.e.
60 human-dominated landscapes). In the European Alps, human-induced disturbances have been
61 profound and of long duration (c. 5000 years) (Stern, 1983; Carcaillet, 1998; Motta and Nola,
62 2001; Motta et al., 2002). In North America, there is a growing understanding that many if not
63 most contemporary landscapes can only be understood in the context of historical human land use
64 and disturbance, in some cases predating Euro-American settlement (White and Mladenoff, 1994;
65 Hunter, 1996; Swetnam et al., 1999; Parshall et al., 2003). Native American influences were
66 important for many forested landscapes, particularly with regard to vegetation management using
67 fire in the western United States (Barrett and Arno, 1982; Baker, 2002; Whitlock and Knox, 2002;
68 Hessburg and Agee, 2003). Although the time span of Euro-American impact has been relatively
69 short (c. 200-400 years), many studies concerning cultural influences on ecological systems have
70 since been conducted, particularly in the northeastern United States (Marsh, 1864; Foster, 1992;
71 Turner and Meyer, 1993; Motzkin et al., 1999; Turner et al., 2001; Hall et al., 2002; Foster et al.,
72 2003).

73 A decline in traditional agricultural practices, due to depopulation and marginalization of
74 mountainous areas, is documented in many European countries (Baldock et al., 1996; MacDonald
75 et al., 2000; Dullinger et al., 2003; Bätzing, 2003; Gellrich and Zimmermann, 2007).
76 Marginalization is "a process driven by a combination of social, economic, political and
77 environmental factors by which in certain areas farming ceases to be viable under an existing land
78 use and socio-economic structure and no other agricultural options are available, so the process
79 ends at land abandonment" (Baldock et al., 1996). This process has been particularly relevant in
80 the southern side of the European Alps (Bätzing et al., 1996; Lehringer et al., 2003; Lingua et al.,
81 2007). Since land abandonment, encroachment of tree and shrub species into former agricultural
82 pastures has severely modified those landscapes that had been intensively managed. At high
83 altitudes, in the subalpine belt of the European Alps, secondary succession following cessation of
84 grazing is causing widespread changes for extensive areas of sparsely wooded "larch meadow"
85 vegetation types (Piussi, 2000) that were traditionally grazed in the past (Didier, 2001; Maurer et
86 al., 2006; Bolli et al., 2007).

87 It is well accepted that the abiotic template and natural and anthropogenic disturbances act
88 together to constrain biological processes. Both human-dominated and biophysical systems exhibit
89 complex nonlinear dynamics (Ellis and Swift, 1988; Sprugel, 1991; Wu and Loucks, 1995;
90 Carpenter et al., 1999). The key factors that create vegetation mosaic structures in cultural
91 landscapes are therefore a challenge to disentangle (Leduc et al., 1992) and generalizations have
92 been elusive.

93 In this research we investigated the relative importance of natural and anthropogenic factors for
94 shaping forest structure of two watersheds of the central Italian Alps, which represented different
95 historical land use intensities. We conducted a landscape level analysis of the distribution of stand
96 structural types, classified using hierarchical cluster analysis, in order to evaluate the relative

97 influences of anthropogenic disturbances and biophysical factors. Path analysis was used to
98 elucidate direct and indirect effects of anthropogenic and abiotic influences on forest structure. We
99 expected a weaker influence of abiotic variables on forest structure where the intensity of the
100 primary human disturbance factors, forest thinning and cattle grazing, had been strongest.

101

102 **2. Methods**

103 2.1. Study area

104 The research area consists of two watersheds of the upper Val Malenco, an inner valley of
105 Valtellina (Central Alps, Lombardy, Italy). The Musella study area occupies 1150 ha in the eastern
106 Malenco valley (45° 27' N; 28° 41' E) and elevation ranges from 1650 m a.s.l. and 3050 m a.s.l.
107 The Ventina study area occupies 1124 ha in the western Malenco valley (45° 26' N; 28° 33' E)
108 with an elevation range from 1650 m a.s.l. to 3570 m a.s.l. (Figure 1).

109 Musella has 470 ha of forested area, Ventina 170 ha. Moraines and glaciers cover a majority of
110 the Ventina watershed, which is steeper than Musella. The bedrock is silicate and serpentine is the
111 predominant rock. Both study areas are inner valleys of the “endalpic district” (Del Favero, 2002)
112 characterized by a continental climate. Annual precipitation from 1921 to 1990 has varied from
113 668 mm to 1551 mm, averaging 974.9 mm (Lanzada, 1000 m a.s.l.). In both catchments European
114 larch (*Larix decidua* Mill.) is the dominant tree species with Norway spruce (*Picea abies* (L.)
115 H.Karst), Swiss stone pine (*Pinus cembra* L.) and mountain pine (*Pinus mugo* subsp. *uncinata*) as
116 co-dominant species throughout the subalpine zone. Two subalpine shrub species are locally
117 abundant: dwarf mountain pine (*Pinus mugo* subsp. *mugo* Turra) and green alder (*Alnus viridis*
118 (Chaix) D.C.) ones.

119

120 #Figure 1 approximately here#

121 Grazing activity existed in the area even before 1447 (Bergomi, 2006). Cattle grazing was
122 commonly limited by stockyards within the alpine pastures, while goats were permitted to roam
123 freely as long as they did not damage pastures. Grazing data from the beginning of twentieth
124 century (Società Agraria di Lombardia, 1901) revealed that grazing pressure was much higher at
125 Musella than Ventina: 4.1 and 1.1 LUha⁻¹ respectively (Livestock Units; i.e. 600 kg body weight
126 according to BL/BUWAL, 1994). During the 1978-80 period, grazing declined in both areas (to
127 0.6 LUha⁻¹ at Musella and 0.5 LUha⁻¹ at Ventina). More recently, grazing activity has ended at
128 Ventina (Della Marianna et al., 2004). Previously grazed open stands that have developed without
129 grazing pressure for decades coexist with newly established forests on the glacial moraines.
130 However, forests at Musella are still partially grazed with varying intensities. A substantial
131 increase of livestock units (to 1.1 LUha⁻¹) in 2006 was likely a consequence of a recent restoration
132 policy applied to mountain pastures throughout the Lombardy region. For this reason we expected
133 a weaker influence of abiotic variables on forest structure at Musella, where anthropogenic
134 disturbances are still intense.

135 2.2. Sampling design and data collection

136 High resolution (50-cm) color aerial orthoimages (Sondrio province, 2003) were photo-interpreted,
137 and a stratified random sampling was applied to locate sample plots. An object-oriented image
138 analysis, based on homogeneous patches and not on single pixels, was implemented in eCognition
139 (v. 4.0) software to perform a segmentation of the aerial orthoimages (Benz et al., 2004; Weisberg
140 et al., 2007). The “image objects” resulting from segmentation were then manually photo-
141 interpreted. The segmentation process facilitated separation of homogeneous patches of forest
142 from non-forest land uses. This binary classification was developed over a “patch” scale (scale
143 parameter = 10; 0.8 ha mapping resolution) and a centroid from each forested patch was derived in
144 a GIS environment.

145 Approximately seventy circular plots (40 for Ventina and 28 for Musella) were established by
146 using the patch centroids as center points for sample plots. Plots of 12-m radius were used for the
147 tree (DBH \geq 5 cm) layer survey, and subplots with a radius of 6 m were established within each
148 plot for the understory and sapling (DBH <5 cm and height >10 cm) layers. The following
149 parameters were measured for all trees: diameter at 1.30 m, total height, crown length and crown
150 radius projection to the ground in four directions. For saplings, only density, composition and
151 height were collected. Cover and abundance of understory shrub species were recorded for each
152 subplot. All trees were mapped and the three larches with the greatest diameter were cored upslope
153 at a height of 50 cm in order to estimate stand age.

154 2.3. Stand descriptors

155 A combination of structural diversity indices and classical stand structure measures was used to
156 classify different stand types (Table 1). Diversity and structural diversity measures included
157 species richness, relative dominance of larch, diameter standard deviation, and vertical evenness
158 (Neumann and Starlinger, 2000). An index of aggregation (Clark and Evans, 1954; Neumann and
159 Starlinger, 2000) was used to measure the horizontal structure within each plot. Vertical structure
160 was assessed with the Vertical Evenness Index that applies the Shannon evenness formula to the
161 proportions of crown projection area of four height layers (Neumann and Starlinger, 2000).

162

163 #Table 1 approximately here#

164 2.4. Data analysis

165 Three data sets were used in this study: forest structure data collected in the field, anthropogenic
166 variables derived from thematic maps, and topographic variables derived from a 10-m resolution
167 digital elevation model (DEM). Proximities to man-made features (buildings and roads) were
168 calculated in ArcGIS using Euclidean distances and considered proxy variables for human

169 pressure (Roath and Krueger, 1982, Nakamura et al., 2000, Kawamura et al., 2005). Buildings
170 were classified as “malghe” (a local name for shepherd’s huts) and “other buildings.” A greater
171 weight was assigned to malghe because they represent an important source of grazing disturbance.
172 The roads category comprised a network of roads and trails data derived from maps or photo-
173 interpreted. Both indices were linearly rescaled from 0 to 100 so as to obtain a comparable
174 measurement. Topographic variables included elevation, aspect, slope steepness, solar radiation
175 and snow index. Aspect as circular data (degrees) was transformed to linear data following a
176 method based on the interaction of slope and aspect to indicate the relative solar insolation (Clark,
177 1990). The snow index was a snow redistribution measure influenced by separate exposure,
178 elevation-slope and aspect effects (Baker and Weisberg, 1995). Solar radiation was a direct clear-
179 sky short-wave radiation measurement based on latitude, season, time interval and a DEM (Kumar
180 et al., 1997; Zimmermann, 2000). Each dataset was relativized by the standard deviate in order to
181 put variables, that were measured in different units, on an equal footing (McCune and Grace,
182 2002).

183 A hierarchical cluster analysis was performed on the stand structure data, using Ward’s clustering
184 method based on a Euclidean distance matrix. Sixty-eight sample plots were grouped according to
185 similarity in stand structure using cluster dendrograms and a 50% threshold for total variance
186 explained.

187 Principal components analysis (PCA) was used to explore the correlation structure of variables and
188 to identify key factors underlying spatial patterns of stand structure variation. Two data matrices
189 for each study site including eleven stand structure variables (Table 1) and seven topographic and
190 anthropogenic variables (elevation, aspect, slope, solar radiation, snow index, distance from roads,
191 distance from buildings) were processed using the statistical package PcOrd (McCune and
192 Mefford, 1999). We used biplots to assess the correlation of environmental variables with the

193 underlying gradients of stand structure (PCA axes). Moreover PCA was used to extract two
194 synthetic descriptors of stand structure then used as focus variables in the path analysis.
195 Relationships between stand structure, environmental and anthropogenic sets of variables were
196 analyzed using path analysis, a specialized version of Structural Equation Models (Shipley, 2000).
197 With path analysis, the cause-and-effect relationships between the putative causal variables
198 (environmental and anthropogenic) and the hypothesized effect variables (first two stand structure
199 principal components) were tested (Leduc et al., 1992, Cuevas, 2003, Weisberg, 2004, Houle,
200 2007). This method permits modeling of both directly observed (manifest) and unmeasured
201 (latent) variables. A graphical model is presented using diagrams where arrows symbolize cause-
202 and-effect relationship between variables that are represented by rectangles (manifest) and ellipses
203 (latent). Path analysis allowed us to quantify and graphically illustrate relative influences of
204 topographic, climatic and anthropogenic variables on stand structure, which was our response
205 variable. Several hypothetical models were built under the underlying concept that environmental
206 and anthropogenic variables interact together in shaping forest structure (Figure 2). Alternative
207 models considered subsets of the full model (Figure 2), including the interactive effects of the
208 various combinations of variable groups, Topographic (T), Anthropogenic (A) and Climatic (C):
209 T-C-A, T-A, T-C, T and A only.

210
211 #Figure 2 approximately here#
212 PCA was also employed to reduce the number of stand structure response variables to a smaller
213 subset of integrative, synthetic variables for use in the path models. Quantitative model
214 comparisons used a combination of Akaike's Information Criterion (AIC) statistic and the Root
215 Mean Square Error of Approximation (RMSEA). The latter is a goodness-of-fit index that is
216 relatively independent of sample size. A model with $RMSEA < 0.06$ was considered a good fit

217 (Hu and Bentler, 1999). All such models were computed and the models with the smallest AIC
218 statistic were selected as the most parsimonious models (Hu and Bentler, 1999). Path analyses
219 were conducted using Mx software that works with covariance matrices as input data and a
220 maximum likelihood (ML) fit function (Neale, 1994).

221

222 **3. Results**

223 3.1. Multivariate Analyses of Forest Structure and its Environmental Relationships

224 The cluster analysis performed on the stand structure data set (11 stand descriptors) produced four
225 structural types in each study area (Table 2). Stand structural types varied from sparse, larch-
226 dominated forests with young trees at high elevations (Type 1), to denser stands at lower
227 elevations where spruce is more common (Type 2). Ventina had slightly more sites belonging to
228 Type 1 (28% vs. 21%), while Musella had more sites belonging to Type 3 (29% vs. 18%), mixed-
229 species stands with large trees.

230

231 #Table2 approximately here#

232 PCA was used to relate stand structure to environmental and anthropogenic influences. A biplot of
233 the first two components at Musella showed a strong negative correlation of elevation ($r = -0.74$)
234 with the dominant axis, while distance from roads was weakly and positively correlated with the
235 second axis ($r = 0.23$; Figure 3). The first and second principal components accounted for 40% and
236 18% of the total variation, respectively. The ordination of plots revealed a clear grouping related to
237 clusters 1 (sparse larch dominated stands with small trees, at higher elevations) and 4 (dense, larch
238 dominated stands with mean size trees, at lower elevations). A perpendicular position of the
239 elevation vector relative to distance from roads indicated that these variables were uncorrelated.

240 The first component (axis 1) reflected variations of diameter, basal area and tree height; the second

241 was related to density and vertical evenness (Table 3). Sites further from roads tended to have
242 greater tree density and diversity of canopy height layers, although the statistical relationship was
243 weak (Figure 3).

244 The PCA biplot of 40 plots established at the Ventina study area showed a strong influence of
245 elevation on stand structure (Figure 4). The first and second principal components accounted for
246 33% and 24% of the total variance, respectively. As for the Musella study area, the first
247 component represented diameter and tree height, while the second represented tree density, canopy
248 cover and vertical evenness (Table 3). The first component was positively influenced by distance
249 from roads and slope, and negatively influenced by elevation. The second component was
250 negatively influenced by elevation and snow and positively influenced by distance to buildings.
251 The ordination of plots revealed a clear grouping related to cluster 1 (sparse larch dominated
252 stands with small trees) exclusively. Such stands occurred at high-elevation, snowy sites.

253

254 #Figures 3, 4 and Table 3 approximately here#

255 3.2. Causal Models of Forest Structure

256 We tested alternative path models for two synthetic descriptors of stand structure derived from the
257 PCAs: overall tree size (PC 1) and tree density and vertical complexity (PC 2). Four alternative
258 models emerged as having significant support (Table 4); two each for the Musella and Ventina
259 study areas, respectively. Models for tree size (PC 1) only are shown (Figure 5) because of their
260 better predictive ability and similar behavior to the models based on the second principal
261 component. The two models for Musella differed in that the first included only topographic and
262 anthropogenic factors (Figure 5 – M1), while the second additionally included the explicit
263 influences of climatic variables (Figure 5 – M2). Both models included the interaction of
264 anthropogenic and abiotic influences in that the negative effect of site aspect on proximity to

265 buildings ($\beta = -0.31$) was explicitly represented. Elevation was strongly negatively associated with
266 tree size in both models ($\beta = -0.83$ and $\beta = -0.90$). A weak negative effect on tree size was also
267 observed for the anthropogenic variables (proximity to buildings and roads). Slope was weakly but
268 positively associated ($\beta = 0.20$ and $\beta = 0.22$) with tree size. In the second model (Figure 5 – M2), a
269 direct positive effect ($\beta = 0.23$) of solar radiation on tree size was slightly reduced by indirect
270 effects mediated by snow depth (total effect = 0.15).

271 Significant models for Ventina did not include effects of anthropogenic variables. Only
272 topographic variables contributed significantly to the first model (Figure 5 – V1). Elevation was
273 the only variable strongly but negatively related to stand structure ($\beta = -0.42$). The second model
274 for the Ventina site was more complex and included snow as a predictor variable. Snow depth was
275 positively associated with tree size, and in turn mediated the effects of the various topographic
276 variables on tree size, as each of these variables also influenced snow depth (Figure 5 – V2). For
277 example, a direct negative effect ($\beta = -0.49$) of elevation on tree size was slightly reduced by the
278 positive effect of increasing elevation on snow depth (total effect = -0.42).

279 Elevation had a similar influence on tree size in all the models tested, but it was particularly strong
280 for the Musella study area (models M1 and M2). The anthropogenic variables had a similar,
281 slightly negative effect on tree size in the two Musella models, but were not important predictors
282 of stand structure for the Ventina study area. Aspect had weakly negative direct effects at Ventina,
283 and negative indirect effects through “proximity to buildings” at Musella.

284

285 #Figures 5 – M1, M2, V1, V2 and Table 4 approximately here#

286 **4. Discussion**

287 Abiotic environmental gradients, described by simple topographic variables including elevation,
288 slope, and aspect, proved to be good predictors for forest structure even in forests that are still

289 recovering from recent, intensive human influence. This is likely a result of the extreme
290 environmental gradients that characterize these mountainous landscapes. Furthermore, the effects
291 of the physical environment are largely independent of anthropogenic influences, except for the
292 positive association between building density and aspect observed at the Musella site.
293 Correlations of environmental variables with components describing dominant trends in stand
294 structure were relatively low, with the exception of elevation (Figure 6 and 7). This indicates that
295 either the effect of elevation is so strong as to swamp other effects, or that the anthropogenic and
296 abiotic variables measured were only weakly related to the true underlying gradients driving forest
297 development processes. Tree size, and especially basal area, emerged as a good, integrative
298 descriptor for forest structure and diversity as exemplified by many other studies (Neumann and
299 Starlinger, 2000; Solomon and Gove, 1999; Staudhammer and LeMay, 2001; Houle, 2007).

300

301 #Figure 6 and 7 approximately here#

302 Predictor variables in vegetation modeling can be classified as representing indirect gradients
303 (topographic variables) or direct or resource gradients (bioclimatic variables; Austin, 1980, 1985;
304 Guisan and Zimmermann, 2000). Our models were constructed using mainly indirect gradients
305 (topographic variables) rather than direct or resource gradients (bioclimatic variables). Use of such
306 indirect predictors to infer complex combinations of resource and direct gradients generally favors
307 model precision instead of generalizability (Guisan et al., 1999; Guisan and Zimmermann, 2000).
308 Path models developed within the present research may not be directly applicable to other study
309 areas and different climatic conditions. However, the general relationships described by the
310 conceptual model should be valid. A certain level of misclassification and uncertainty of the model
311 can be explained by the use of proxy or DEM-derived data (Tappeiner et al., 1998), particularly
312 with regard to snow, which is only weakly predicted by topography (Tappeiner et al., 2001).

313 Despite the importance of abiotic factors in shaping forest structure, anthropogenic influences play
314 a critical role for most regions of the world. For some areas in the Italian Alps, historical human
315 influences are important for understanding current patterns of forest structure across mountain
316 landscapes (Motta et al., 2006). In these areas culture-landscape interactions are multifaceted and
317 it is essential to consider human impacts on the environment (Naveh, 1995).

318 The Ventina site has historically been less disturbed by human land uses. Therefore, it is not
319 surprising that anthropogenic variables failed to emerge as important in the most parsimonious
320 path models. Stand structure in this relatively pristine landscape of complex topographic gradients
321 is best explained by abiotic variables. More complex models including the interactive effects of
322 anthropogenic influences and abiotic factors were needed to explain stand structure in the Musella
323 watershed. At Musella, stands that were likely to have experienced historically more intense
324 anthropogenic disturbance currently have smaller trees and sparser, less diverse stand structures.

325 Both watersheds are characterized by a strong dominance of larch stands, but their structure and
326 spatial pattern differ greatly. At Musella, sparse stands are mainly located at higher elevations, but
327 are also common near low-elevation farms. At Ventina, this pattern differs in that sparse forests
328 are exclusively associated with moraines and upper elevations. Vegetation dynamics at Ventina
329 represent primary succession in the path of the retreating glacier, whereas at Musella past and
330 present human actions (grazing and unmanaged thinning) contribute to maintain a more open
331 canopy and even-aged forest at lower and moderate elevations. Another indicator of the relative
332 importance of anthropogenic disturbance in the two study areas is maximum larch age, which is
333 estimated at greater than 1000 years at Ventina and less than 500 years at Musella (Nola, 1994;
334 Nola and Motta, 1996). A high level of anthropogenic disturbance can also explain the scarcity of
335 Swiss stone pine at Musella, where larch trees were likely favored by humans due to their ability
336 to form sparse pastured woodlands. Larch has a light canopy and is resistant to grazing. The stone

337 pine was considered a competing species and an obstacle to traditional agroforestry practices.
338 Seedling removal of stone pines was a common practice in the Western Alps until the first half of
339 the twentieth century (Motta and Lingua, 2005; Motta et al., 2006).
340 Historical human influences are difficult to measure and may play a greater role in determining
341 forest structure than is suggested by these analyses. It would be valuable to develop accurate
342 spatial datasets for such human influences, including more explicit proxy variables for human
343 influences that are independent of abiotic, topographic variables. Spatially explicit data on native
344 and nonnative plant species diversity could be a useful integrated measure of anthropogenic
345 disturbance, especially cattle grazing (Dullinger et al., 2003; Vacher et al., 2007). Remote sensing
346 and GPS tracking could also be used to better understand cattle distribution and behavior for
347 assessment of grazing intensity (Kawamura et al., 2005). Historical data regarding cattle density
348 and their distribution in the pastures, as well as individual-based models of grazing animal
349 behavior (Dumont and Hill, 2001), could be used to estimate historical grazing intensity.
350 Unfortunately, long-term data on historical forest harvesting and density and spatial distribution of
351 cattle were not available for our study areas. For this reason, map-derived data (distances from
352 roads and buildings) were used as proxy indices of potential human impact on the forest structure
353 of the two study areas.
354 Path analysis provides an analytical tool that allowed us to partition the interacting factors
355 involved in shaping forest structure in our complex mountain region with a long history of human
356 impacts. Land abandonment is currently the main cause for forest increase in the Alps. However,
357 over the long term, the importance of climate change in large scale vegetation dynamics will
358 clearly increase because forests will fill anthropogenic gaps below and above the treeline (Walther,
359 1986; Dale, 1997; Gehrig-Fasel et al., 2007).

360 Our study highlights the importance of landscape context for modeling and interpreting influences
361 of anthropogenic disturbances on forest structure. A model that is able to partition natural and
362 anthropogenic effects on stand structure can provide a robust method for discriminating between
363 anthropogenically disturbed sites and areas where natural disturbances and climate change are the
364 primary driving forces. Such an approach can be informative for developing conservation
365 priorities in relation to those cultural landscapes that are disappearing in many Alpine regions
366 (Margules et al., 1994; Guisan and Zimmermann, 2000; Maurer et al., 2006). It is important to
367 identify cultural landscapes (e.g. the *Larix* forest) in order to calibrate an integrated forest
368 management strategy where some areas are actively restored and managed while others are merely
369 monitored. Cultural landscapes in the Italian Alps are complex mosaics characterized by a greater
370 diversity of forest structural types than may otherwise be found in less disturbed systems
371 (MacDonald et al., 2000). However, the two types of landscapes with different levels of historical
372 human influence can occur in close proximity to each other, as is the case for Ventina and
373 Musella. Future research should attempt to identify and model the two kinds of areas *a priori*, as
374 these are likely to exhibit different stand dynamics and different potential responses to global
375 change.

376

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382

383

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594 **Tables**

595 Table 1 - Descriptors and measures used in the stand structure classification.

596

STAND DESCRIPTORS	Symbols	Measures and references
Richness of trees	Ri	n. of trees' species
Dominance	Do	relative density of larch stems
Density	De	n. of stems per hectare
Diameter (mean)	Dbh-Me	diameter at 130 cm (mean value)
Diameter (standard dev.)	Dbh-Sd	diameter at 130 cm (standard deviation)
Basal Area	BA	basal area per hectare
Height	He	mean height
Canopy Cover	CC	canopy cover (following Crookston and Stage 1999)
Nearest neighbor Index	NNI	Clark-Evans Index of aggregation (Clark and Evans, 1954)
Vertical Evenness	VE	vertical evenness following Neumann and Starlinger, 2001
Age of larch	AGE	age estimation of the 3 largest-diameter larches

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599 Table 2 - Mean values of the 11 descriptors for each structure type obtained by cluster analysis at Musella and Ventina sites.

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Stand structure types		Plots	Ri	Do	De	DBH-Me	DBH-Sd	BA	He	CC	NNI	VE	AGE
		(n)	(n)	(%)	(n/ha)	(cm)	(cm)	(m ² /ha)	(m)	(%)			(yrs)
Musella	1 Sparse; larch dominated; small trees	6	1.50	0.83	301.67	11.75	5.95	4.28	6.05	28.33	0.60	0.65	77.17
	2 Mean density; mixed; mean size trees	4	2.00	0.18	541.00	17.85	12.30	18.83	9.63	43.25	0.64	0.64	123.00
	3 Mean density; mixed; big trees	8	1.88	0.50	480.38	29.23	15.25	38.68	15.79	59.13	0.74	0.62	163.67
	4 Dense; larch dominated; mean size trees	10	2.00	0.84	689.20	15.33	10.80	19.75	8.13	54.90	0.65	0.73	163.00
Ventina	1 Sparse; larch dominated; small trees	11	1.64	0.92	266.73	11.48	5.80	4.02	5.05	18.45	0.60	0.59	84.30
	2 Mean density; mixed; mean size trees	7	2.43	0.43	252.21	19.52	17.96	12.55	7.16	21.14	0.69	0.62	273.29
	3 Mean density; mixed; big trees	7	2.14	0.90	249.33	36.66	20.96	50.93	12.98	42.71	0.79	0.59	298.57
	4 Dense; larch dominated; mean size trees	15	2.33	0.88	640.90	17.76	12.09	20.43	8.54	54.80	0.74	0.74	185.67

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603 Table 3 - Principal component loadings for the first two principal components for both study areas.

604 Loadings greater than 0.4 are indicated in bold.

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Axis	MUSELLA		VENTINA	
	PC 1	PC 2	PC 1	PC 2
% of variance	40.27	17.88	32.84	24.42
Ri	0.143	0.244	0.127	0.398
Do	-0.253	-0.050	0.016	-0.088
De	0.110	0.637	0.023	0.549
Dbh-Me	0.423	-0.230	0.449	-0.209
Dbh-Sd	0.397	-0.196	0.447	-0.105
BA	0.448	0.062	0.380	0.081
He	0.438	-0.121	0.441	-0.063
CC	0.306	0.345	0.251	0.451
NNI	0.186	0.196	0.230	0.172
VE	-0.171	0.483	-0.027	0.447
AGE	0.130	0.179	0.356	-0.183

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613 Table 4 - Path models comparison by means of their fit indices. Akaike's Information Criterion
614 (AIC) statistic and the Root Mean Square Error of Approximation (RMSEA) together with degrees
615 of freedom (df), Maximum Likelihood chi-squared fit function value (ML χ^2) and its probability
616 (P) are reported.

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Models	Goodness-of-Fit statistics				
	ML χ^2	df	P	RMSEA	AIC
M1	4.440	9	0.880	<0.001	-13.560
M2	14.847	19	0.732	< 0.001	-23.153
V1	0.981	3	0.806	< 0.001	-5.019
V2	0.927	3	0.819	< 0.001	-5.073

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631 **Figure captions**

632 Figure 1 - Location of the 70 plots (●) in two watersheds of Malenco valley.

633 Figure 2 - Conceptual model to be tested for both study areas through path analysis. The full
634 model includes topographic, climatic and anthropogenic variables associated through positive or
635 negative causal paths. “Stand structure” refers to the first principal component (PC 1) defined as
636 tree size.

637 Figure 3 - Biplot from Principal Components Analysis of 28 plots at Musella. Site scores are
638 shown as triangles; stand structure types are reported as number (1-4). Correlations of
639 environmental variables with PCA axes are shown as linear vectors. Vectors are shown only for
640 correlations > 0.05 . The first and second principal component accounted for 40% and 18% of the
641 total amount of variation, respectively.

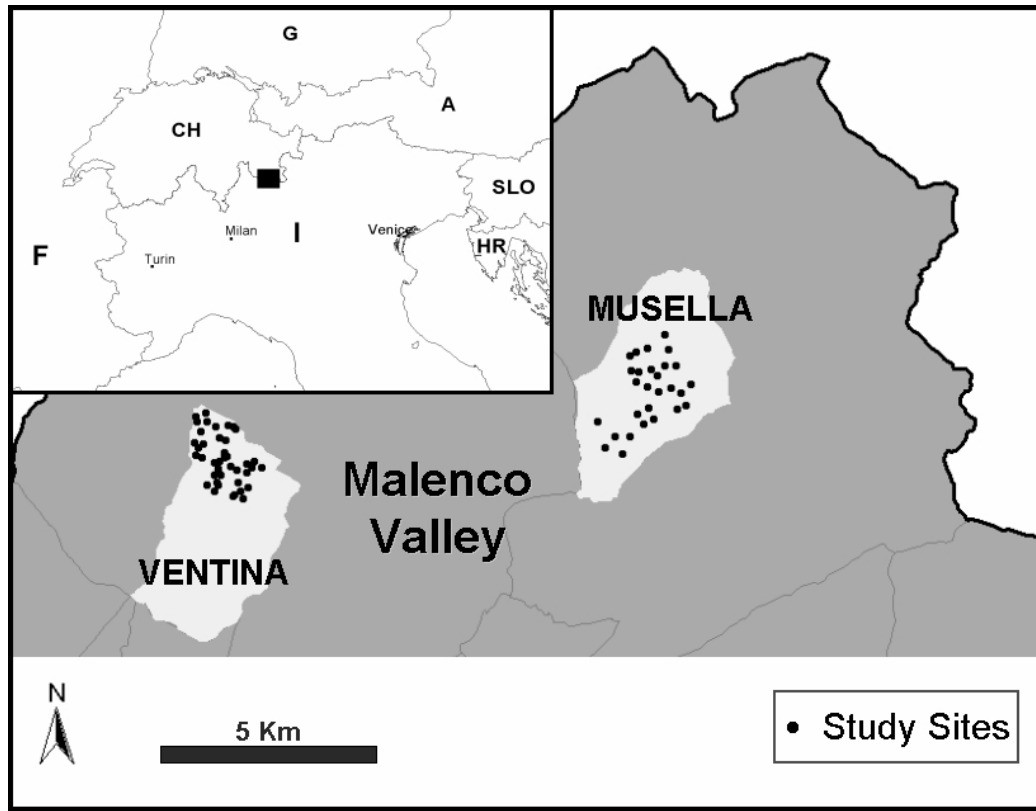
642 Figure 4 - Biplot from Principal Components Analysis of 40 plots at Ventina. Site scores are
643 shown as triangles; stand structure types are reported as number (1-4). Correlations of
644 environmental variables with PCA axes are shown as linear vectors. Vectors are shown only for
645 correlations > 0.05 . The first and second principal component accounted for 33% and 24% of the
646 total amount of variation, respectively.

647 Figure 5 - Path diagrams for Musella (M1, M2) and Ventina (V1, V2). Continuous lines: positive
648 paths; dotted lines: negative paths; single arrow lines: causal paths; double arrow lines: covariance
649 paths. Thickness of causal path vectors corresponds to the strength of effect. Only significant path
650 coefficients are presented next to each path.

651 Figure 6 - Bivariate scatter plots of selected environmental variables vs. the stand structure PCs at
652 Musella. Only relationships significant for the SEM analyses are shown.

653 Figure 7 - Bivariate scatter plots of selected environmental variables vs. the stand structure PCs at
654 Ventina. Only relationships significant for the SEM analyses are shown.

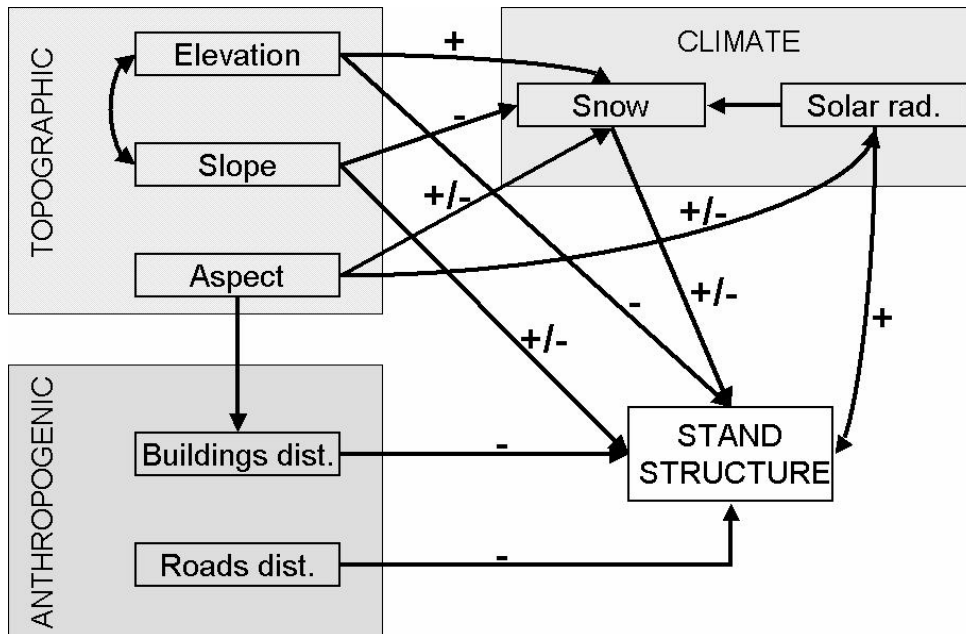
655 Figure 1



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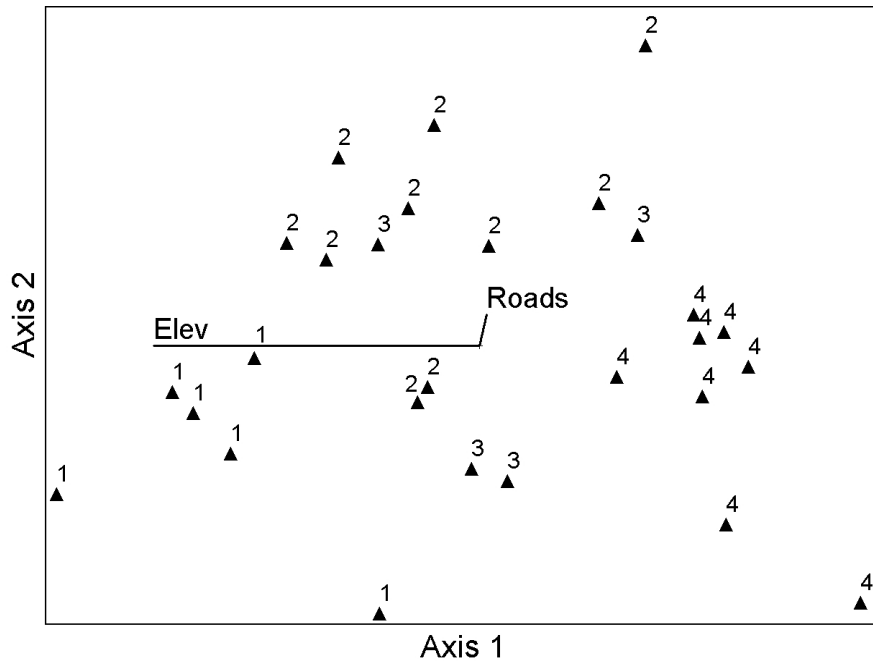
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658 Figure 2



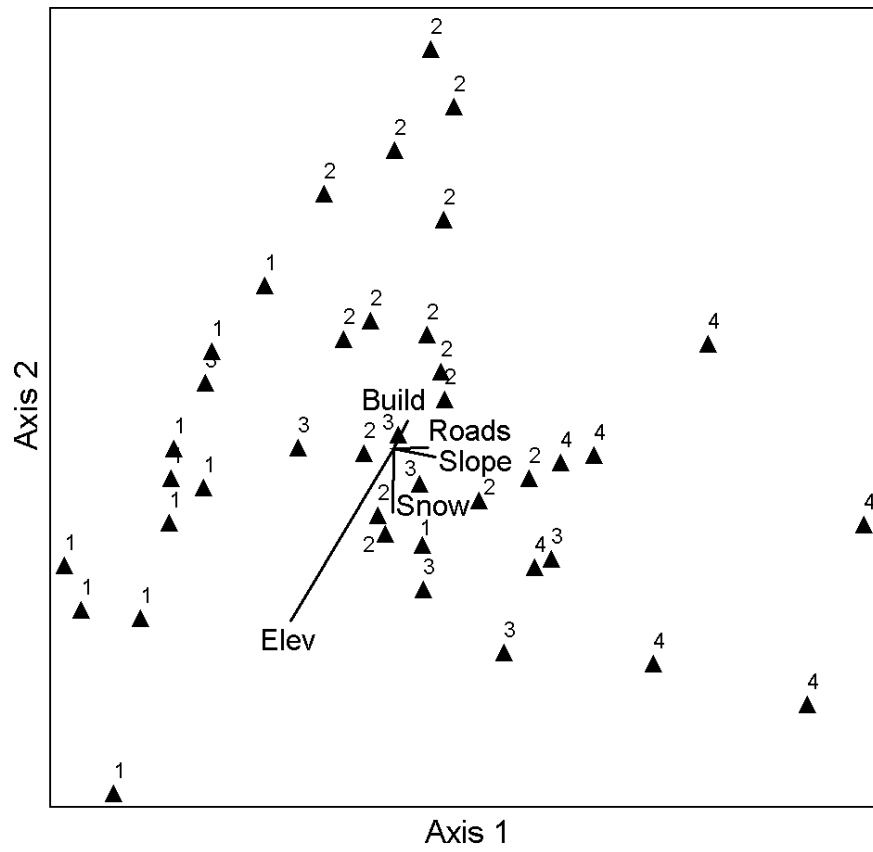
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660 Figure 3



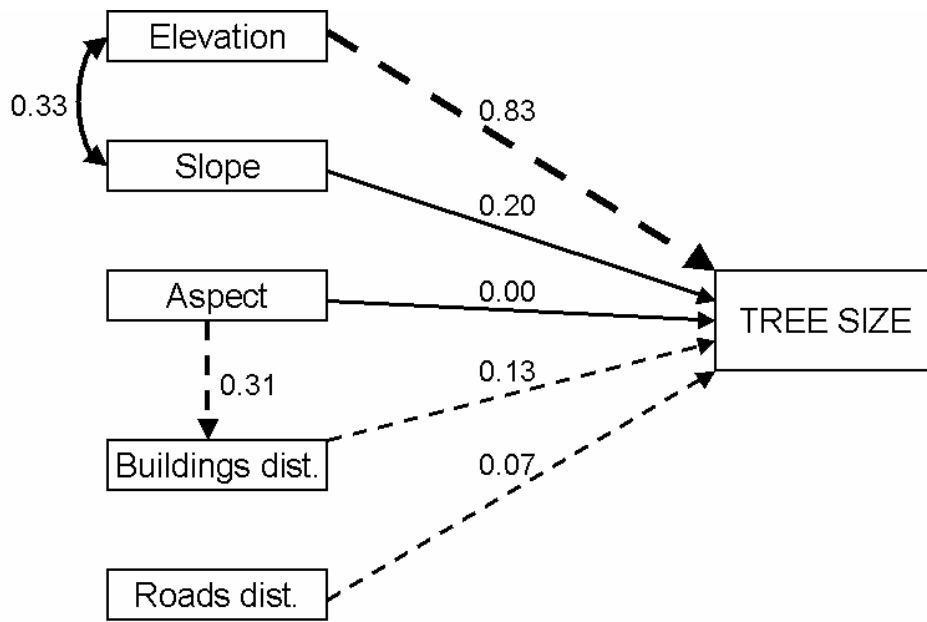
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662 Figure 4



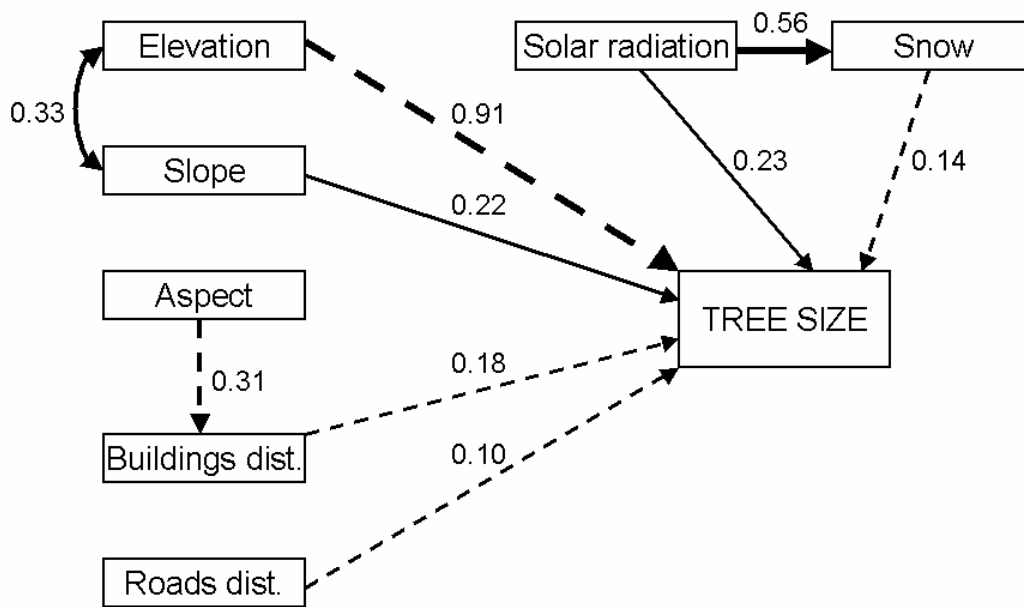
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664 Figure 5 (M1, M2, V1, V2)



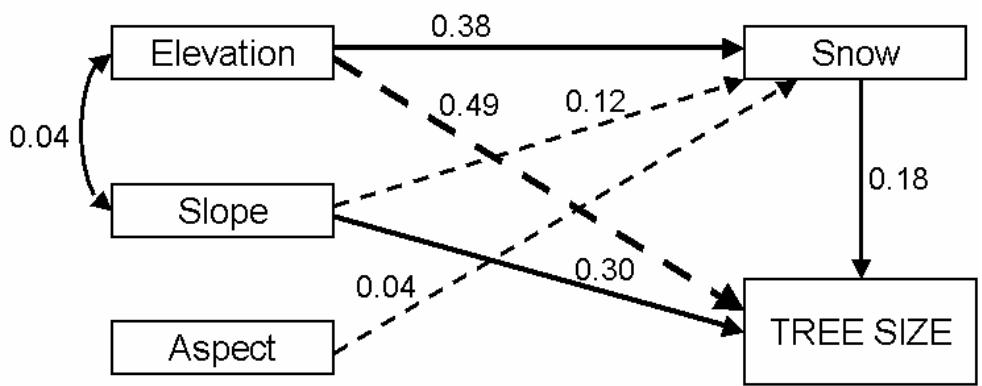
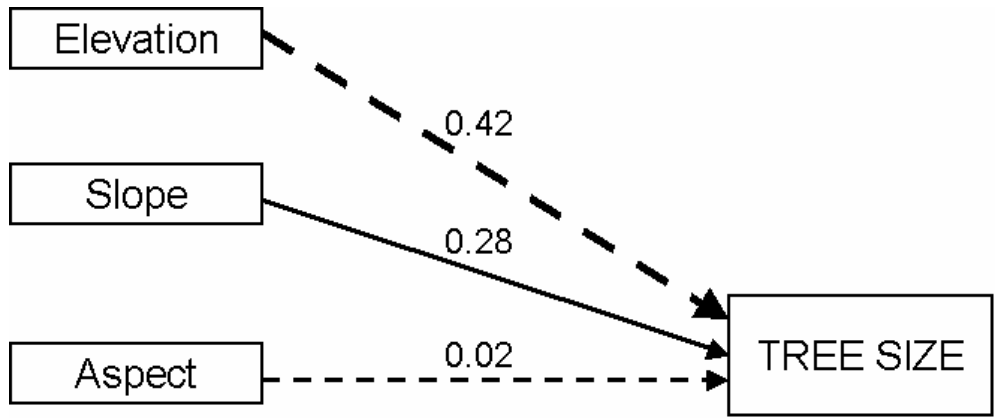
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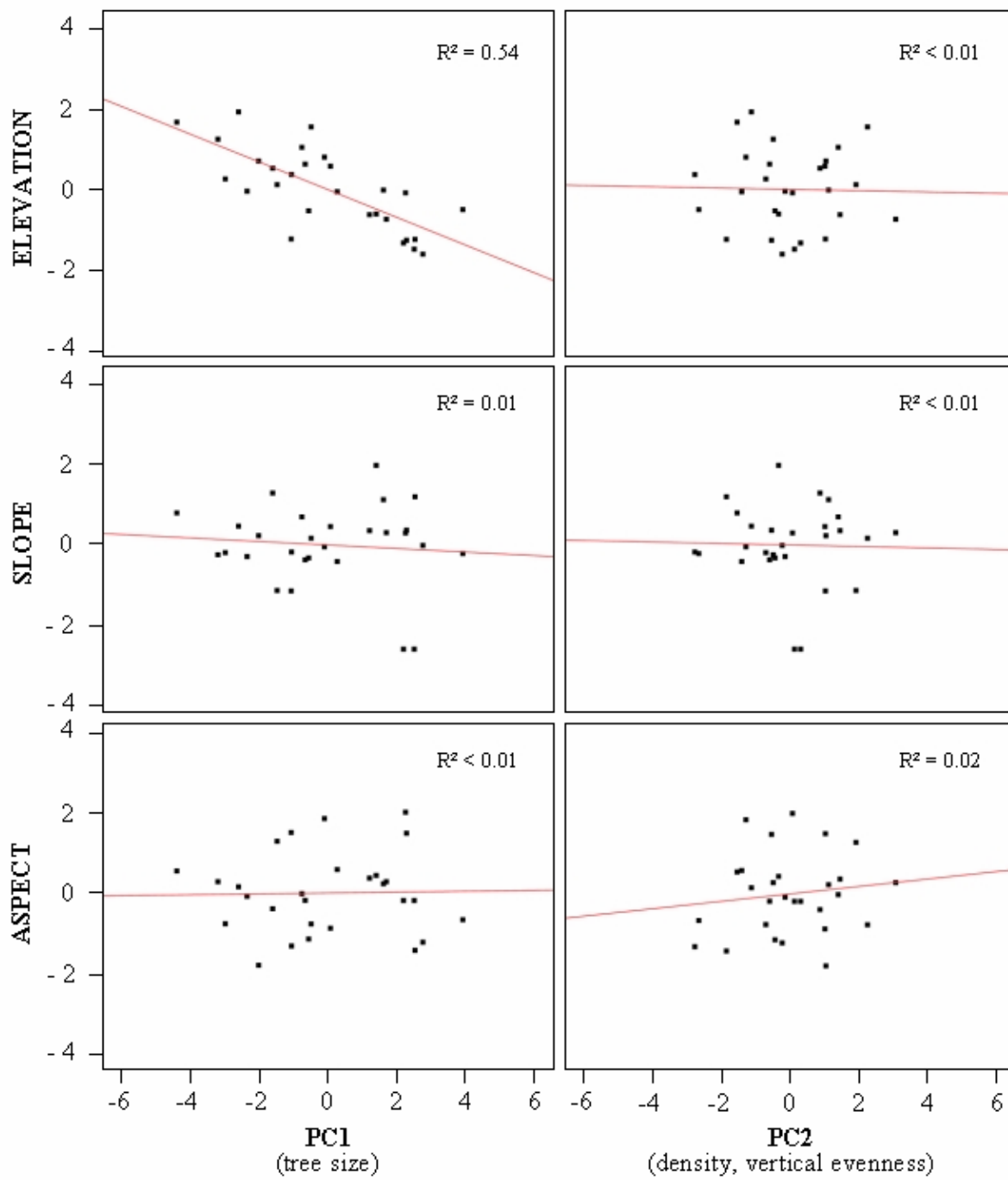
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683 Figure 6

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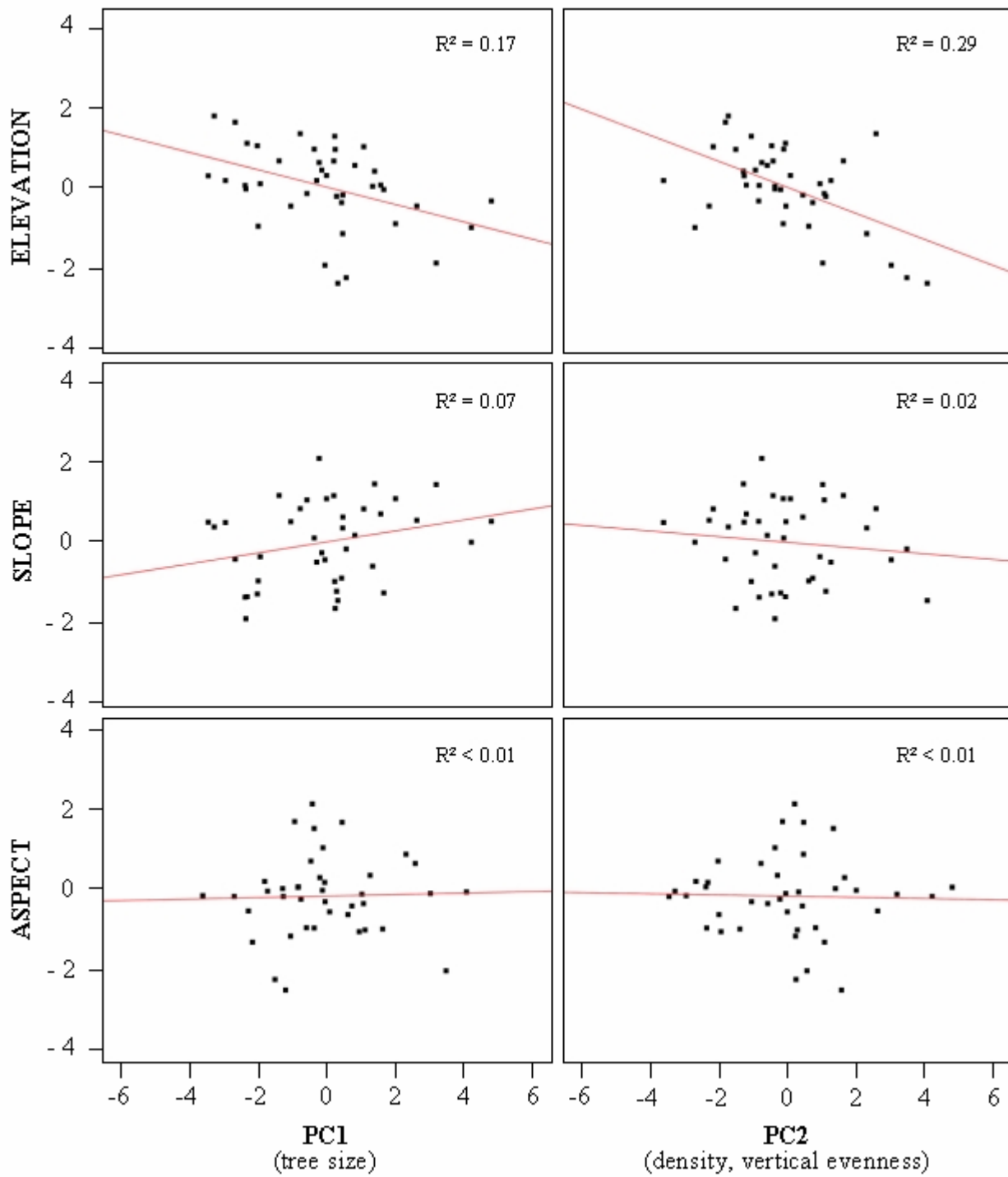
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689 Figure 7

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