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

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Abstract

Most forested landscapes have been strongly influenced by humans, and hence prediction of response to future perturbations or climate change requires understanding of the interaction among human influences and the abiotic environment. Environmental and anthropogenic influences on forest structure in *Larix decidua* Mill. stands were investigated in two watersheds of the central Italian Alps (Valtellina, SO). We related three data sets (forest structure, anthropogenic influences, and topography) using ordination methods. Path models of correlative and causal relationships between these sets of variables were developed and used to differentiate the two watersheds with respect to levels of historical human influence. The two study areas (Musella and Ventina) were characterized by strong climatic and topographic gradients as well as a long history of human settlement, although historical intensity of agricultural activities was much greater for Musella. We hypothesized a weaker influence of abiotic variables on forest structure where the intensity of the primary human disturbance factors, forest thinning and cattle grazing, had been strongest. Stand structure types varied from sparse, larch-dominated forests at high elevations, to denser stands at lower elevations dominated by spruce. Correlations of environmental variables with dominant trends in stand structure were low with the exception of elevation. Anthropogenic variables were unimportant at Ventina, whereas the interactive effects of both anthropogenic and abiotic variables were needed to explain stand structure in Musella. The best-fit model indicated a negative effect of elevation and anthropogenic variables on overall tree size. Stands with greater tree density and canopy height layer diversity were located further from roads. Both watersheds were characterized by a strong dominance of larch stands, but their structure and spatial pattern differed greatly. Sparse larch forests were exclusively associated with moraines and upper elevations at Ventina, but were also common near low-elevation farms at Musella. Historical human influences were difficult to measure and may play a greater role in determining forest structure than was suggested. Our study emphasizes the importance of landscape context for interpreting the relative strengths of anthropogenic and abiotic influences on stand development pathways.

Key words

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

1. Introduction

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

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

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

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

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

In this research we investigated the relative importance of natural and anthropogenic factors for shaping forest structure of two watersheds of the central Italian Alps, which represented different historical land use intensities. We conducted a landscape level analysis of the distribution of stand structural types, classified using hierarchical cluster analysis, in order to evaluate the relative influences of anthropogenic disturbances and biophysical factors. Path analysis was used to elucidate direct and indirect effects of anthropogenic and abiotic influences on forest structure. We expected a weaker influence of abiotic variables on forest structure where the intensity of the primary human disturbance factors, forest thinning and cattle grazing, had been strongest.

2. Methods

2.1. Study area

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

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

#Figure 1 approximately here#

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

2.2. Sampling design and data collection

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

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

2.3. Stand descriptors

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

#Table 1 approximately here#

2.4. Data analysis

Three data sets were used in this study: forest structure data collected in the field, anthropogenic variables derived from thematic maps, and topographic variables derived from a 10-m resolution digital elevation model (DEM). Proximities to man-made features (buildings and roads) were calculated in ArcGIS using Euclidean distances and considered proxy variables for human pressure (Roath and Krueger, 1982, Nakamura et al., 2000, Kawamura et al., 2005). Buildings were classified as “malghe” (a local name for shepherd’s huts) and “other buildings.” A greater weight was assigned to malghe because they represent an important source of grazing disturbance. The roads category comprised a network of roads and trails data derived from maps or photo-interpreted. Both indices were linearly rescaled from 0 to 100 so as to obtain a comparable measurement. Topographic variables included elevation, aspect, slope steepness, solar radiation and snow index. Aspect as circular data (degrees) was transformed to linear data following a method based on the interaction of slope and aspect to indicate the relative solar insolation (Clark, 1990). The snow index was a snow redistribution measure influenced by separate exposure, elevation-slope and aspect effects (Baker and Weisberg, 1995). Solar radiation was a direct clear-sky short-wave radiation measurement based on latitude, season, time interval and a DEM (Kumar et al., 1997; Zimmermann, 2000). Each dataset was relativized by the standard deviate in order to put variables, that were measured in different units, on an equal footing (McCune and Grace, 2002).

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

Principal components analysis (PCA) was used to explore the correlation structure of variables and to identify key factors underlying spatial patterns of stand structure variation. Two data matrices for each study site including eleven stand structure variables (Table 1) and seven topographic and anthropogenic variables (elevation, aspect, slope, solar radiation, snow index, distance from roads, distance from buildings) were processed using the statistical package PcOrd (McCune and Mefford, 1999). We used biplots to assess the correlation of environmental variables with the underlying gradients of stand structure (PCA axes). Moreover PCA was used to extract two synthetic descriptors of stand structure then used as focus variables in the path analysis. Relationships between stand structure, environmental and anthropogenic sets of variables were analyzed using path analysis, a specialized version of Structural Equation Models (Shipley, 2000). With path analysis, the cause-and-effect relationships between the putative causal variables (environmental and anthropogenic) and the hypothesized effect variables (first two stand structure principal components) were tested (Leduc et al., 1992, Cuevas, 2003, Weisberg, 2004, Houle, 2007). This method permits modeling of both directly observed (manifest) and unmeasured (latent) variables. A graphical model is presented using diagrams where arrows symbolize cause-and-effect relationship between variables that are represented by rectangles (manifest) and ellipses (latent). Path analysis allowed us to quantify and graphically illustrate relative influences of topographic, climatic and anthropogenic variables on stand structure, which was our response variable. Several hypothetical models were built under the underlying concept that environmental and anthropogenic variables interact together in shaping forest structure (Figure 2). Alternative models considered subsets of the full model (Figure 2), including the interactive effects of the various combinations of variable groups, Topographic (T), Anthropogenic (A) and Climatic (C): T-C-A, T-A, T-C, T and A only.

#Figure 2 approximately here#

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

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

3. Results

3.1. Multivariate Analyses of Forest Structure and its Environmental Relationships

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

#Table2 approximately here#

PCA was used to relate stand structure to environmental and anthropogenic influences. A biplot of the first two components at Musella showed a strong negative correlation of elevation (r = -0.74) with the dominant axis, while distance from roads was weakly and positively correlated with the second axis (r = 0.23; Figure 3). The first and second principal components accounted for 40% and 18% of the total variation, respectively. The ordination of plots revealed a clear grouping related to clusters 1 (sparse larch dominated stands with small trees, at higher elevations) and 4 (dense, larch dominated stands with mean size trees, at lower elevations). A perpendicular position of the elevation vector relative to distance from roads indicated that these variables were uncorrelated. The first component (axis 1) reflected variations of diameter, basal area and tree height; the second was related to density and vertical evenness (Table 3). Sites further from roads tended to have greater tree density and diversity of canopy height layers, although the statistical relationship was weak (Figure 3).

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

#Figures 3, 4 and Table 3 approximately here#

3.2. Causal Models of Forest Structure

We tested alternative path models for two synthetic descriptors of stand structure derived from the PCAs: overall tree size (PC 1) and tree density and vertical complexity (PC 2). Four alternative models emerged as having significant support (Table 4); two each for the Musella and Ventina study areas, respectively. Models for tree size (PC 1) only are shown (Figure 5) because of their better predictive ability and similar behavior to the models based on the second principal component. The two models for Musella differed in that the first included only topographic and anthropogenic factors (Figure 5 – M1), while the second additionally included the explicit influences of climatic variables (Figure 5 – M2). Both models included the interaction of anthropogenic and abiotic influences in that the negative effect of site aspect on proximity to buildings (β = -0.31) was explicitly represented. Elevation was strongly negatively associated with tree size in both models (β = -0.83 and β = -0.90). A weak negative effect on tree size was also observed for the anthropogenic variables (proximity to buildings and roads). Slope was weakly but positively associated (β = 0.20 and β = 0.22) with tree size. In the second model (Figure 5 – M2), a direct positive effect (β = 0.23) of solar radiation on tree size was slightly reduced by indirect effects mediated by snow depth (total effect = 0.15).

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

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

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

4. Discussion

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

#Figure 6 and 7 approximately here#

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

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

The Ventina site has historically been less disturbed by human land uses. Therefore, it is not surprising that anthropogenic variables failed to emerge as important in the most parsimonious path models. Stand structure in this relatively pristine landscape of complex topographic gradients is best explained by abiotic variables. More complex models including the interactive effects of anthropogenic influences and abiotic factors were needed to explain stand structure in the Musella watershed. At Musella, stands that were likely to have experienced historically more intense anthropogenic disturbance currently have smaller trees and sparser, less diverse stand structures. Both watersheds are characterized by a strong dominance of larch stands, but their structure and spatial pattern differ greatly. At Musella, sparse stands are mainly located at higher elevations, but are also common near low-elevation farms. At Ventina, this pattern differs in that sparse forests are exclusively associated with moraines and upper elevations. Vegetation dynamics at Ventina represent primary succession in the path of the retreating glacier, whereas at Musella past and present human actions (grazing and unmanaged thinning) contribute to maintain a more open canopy and even-aged forest at lower and moderate elevations. Another indicator of the relative importance of anthropogenic disturbance in the two study areas is maximum larch age, which is estimated at greater than 1000 years at Ventina and less than 500 years at Musella (Nola, 1994; Nola and Motta, 1996). A high level of anthropogenic disturbance can also explain the scarcity of Swiss stone pine at Musella, where larch trees were likely favored by humans due to their ability to form sparse pastured woodlands. Larch has a light canopy and is resistant to grazing. The stone pine was considered a competing species and an obstacle to traditional agroforestry practices. Seedling removal of stone pines was a common practice in the Western Alps until the first half of the twentieth century (Motta and Lingua, 2005; Motta et al., 2006).

Historical human influences are difficult to measure and may play a greater role in determining forest structure than is suggested by these analyses. It would be valuable to develop accurate spatial datasets for such human influences, including more explicit proxy variables for human influences that are independent of abiotic, topographic variables. Spatially explicit data on native and nonnative plant species diversity could be a useful integrated measure of anthropogenic disturbance, especially cattle grazing (Dullinger et al., 2003; Vacher et al., 2007). Remote sensing and GPS tracking could also be used to better understand cattle distribution and behavior for assessment of grazing intensity (Kawamura et al., 2005). Historical data regarding cattle density and their distribution in the pastures, as well as individual-based models of grazing animal behavior (Dumont and Hill, 2001), could be used to estimate historical grazing intensity.

Unfortunately, long-term data on historical forest harvesting and density and spatial distribution of cattle were not available for our study areas. For this reason, map-derived data (distances from roads and buildings) were used as proxy indices of potential human impact on the forest structure of the two study areas.

Path analysis provides an analytical tool that allowed us to partition the interacting factors involved in shaping forest structure in our complex mountain region with a long history of human impacts. Land abandonment is currently the main cause for forest increase in the Alps. However, over the long term, the importance of climate change in large scale vegetation dynamics will clearly increase because forests will fill anthropogenic gaps below and above the treeline (Walther, 1986; Dale, 1997; Gehrig-Fasel et al., 2007).

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

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Tables

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

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

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

		Stand structure types	Plots (n)	Ri (n)	Do (%)	De (n/ha)	DBH-Me (cm)	DBH-Sd (cm)	BA (m2/ha)	He (m)	CC (%)	NNI	VE	AGE (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

Table 3 - Principal component loadings for the first two principal components for both study areas. Loadings greater than 0.4 are indicated in bold.

	MUSELLA		VENTINA	
Axis	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

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

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

Figure captions

Figure1 - Location of the 70 plots (●) in two watersheds of Malenco valley.

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

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

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

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

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

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

Figure 1

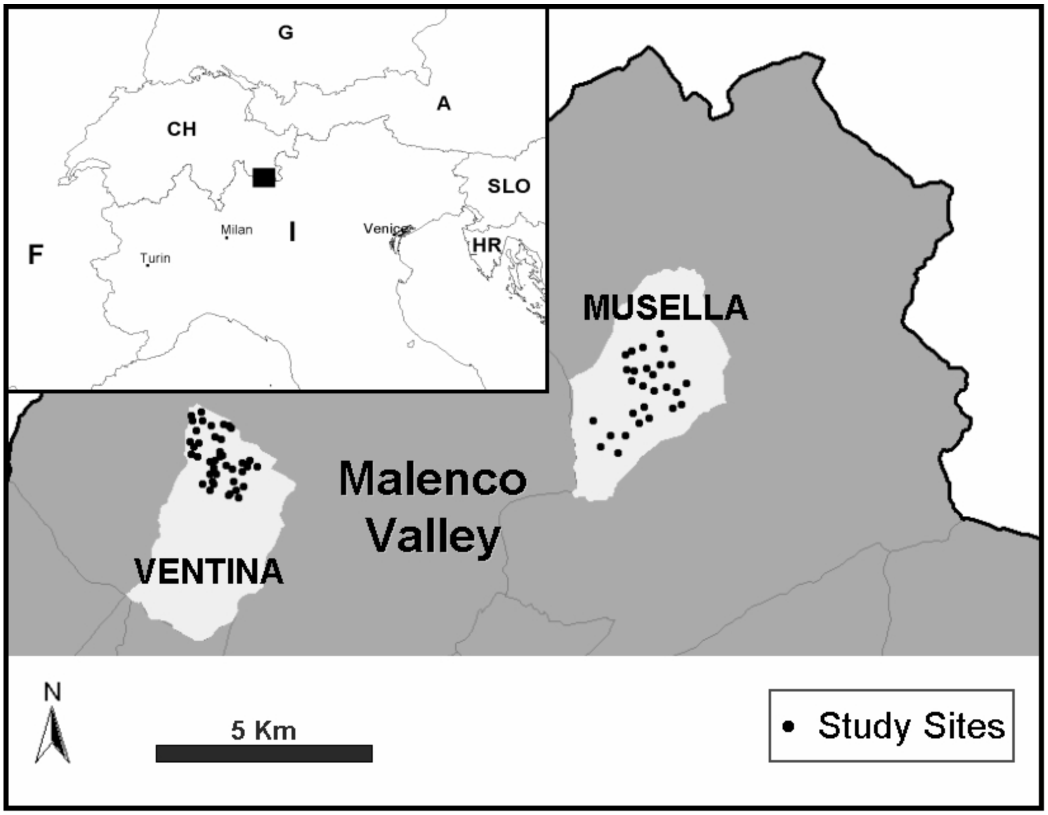


Figure 2

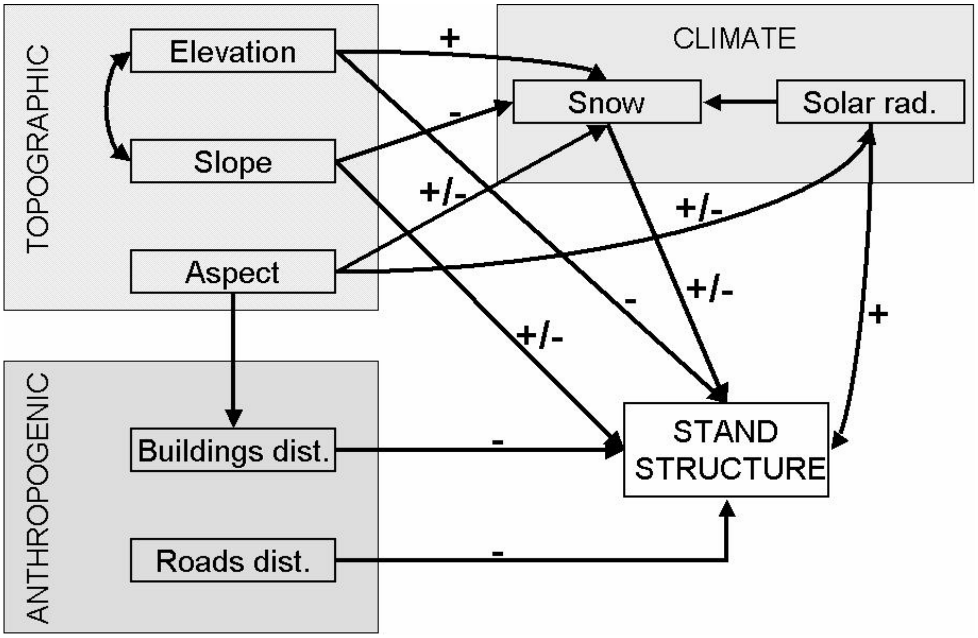


Figure 3

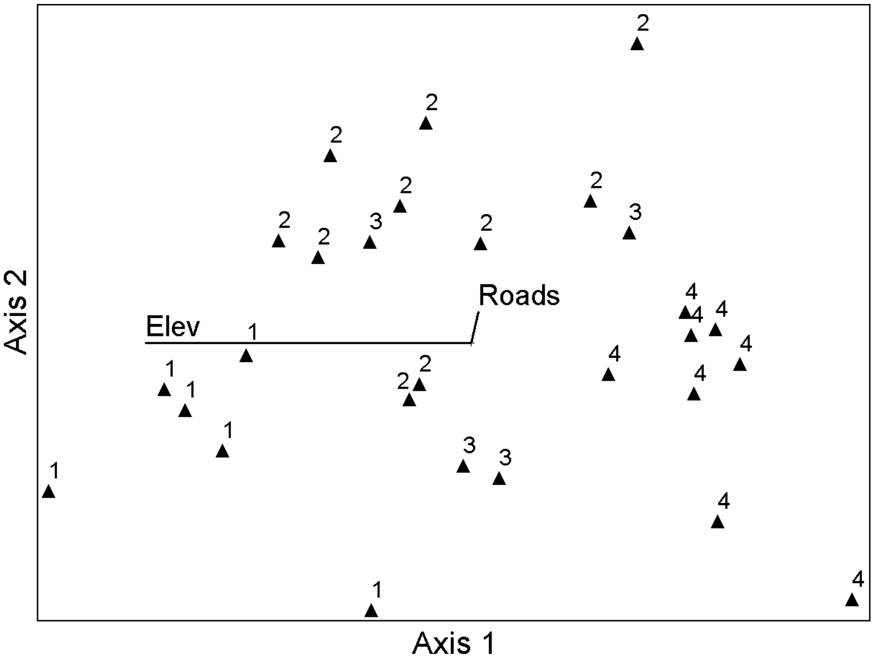


Figure 4

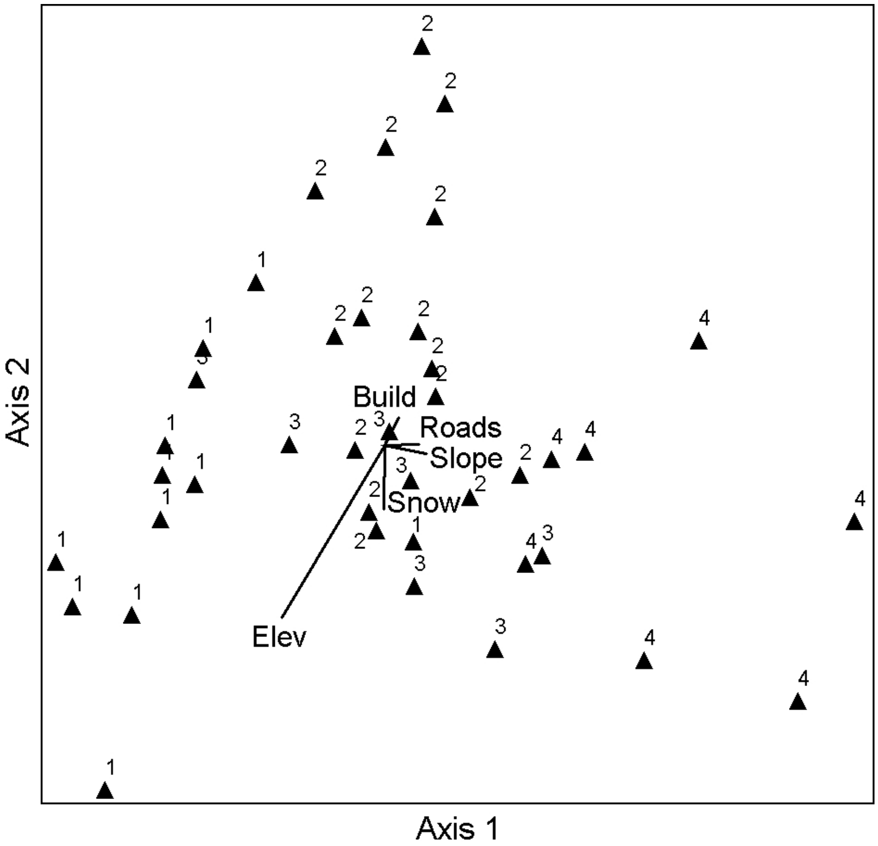
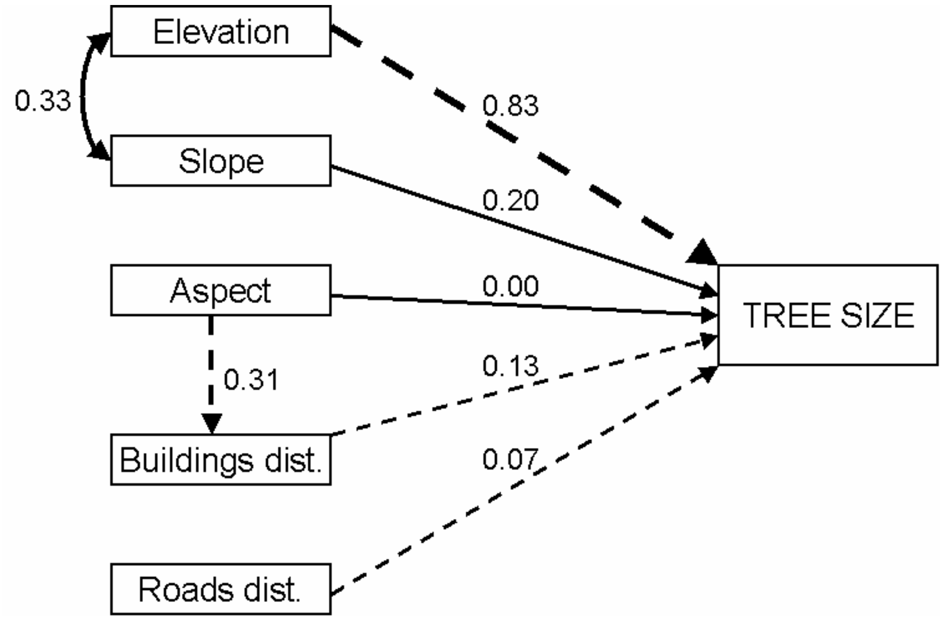
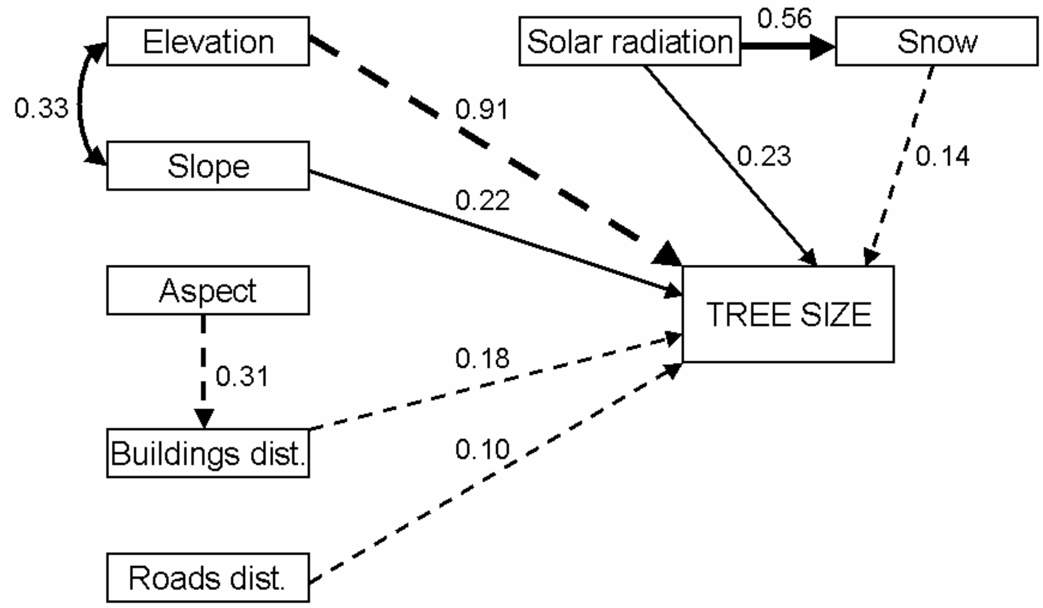
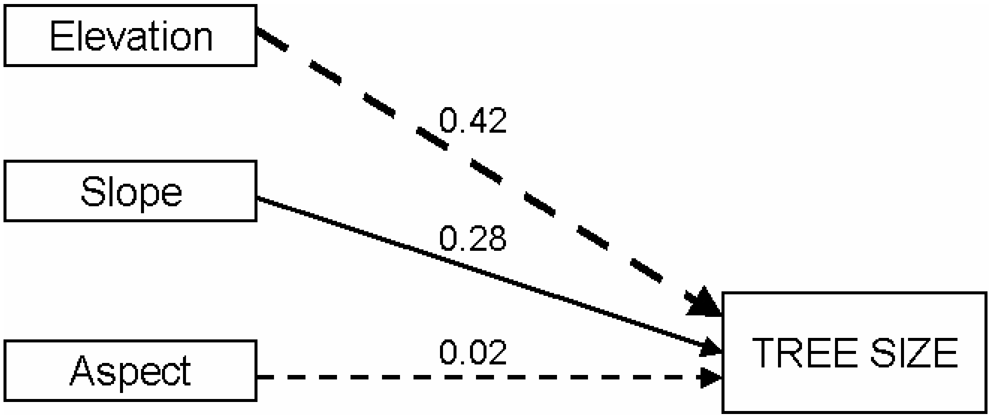


Figure 5 (M1, M2, V1, V2)



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Slope
Aspect
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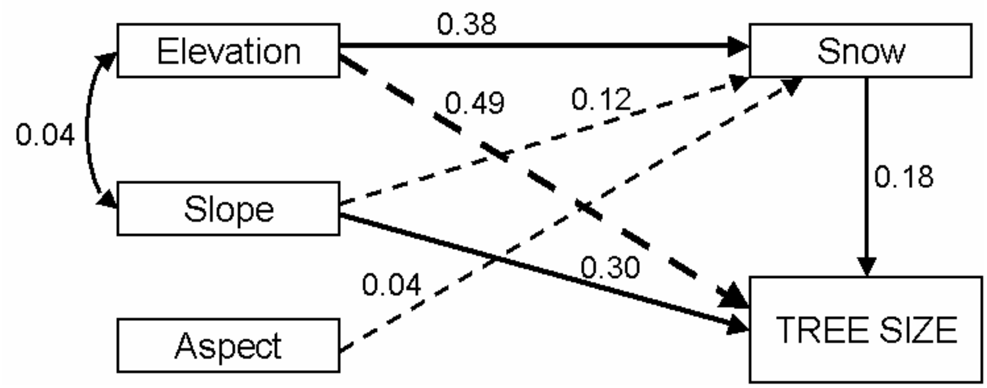
0.28
0.02
TREE SIZE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Snow
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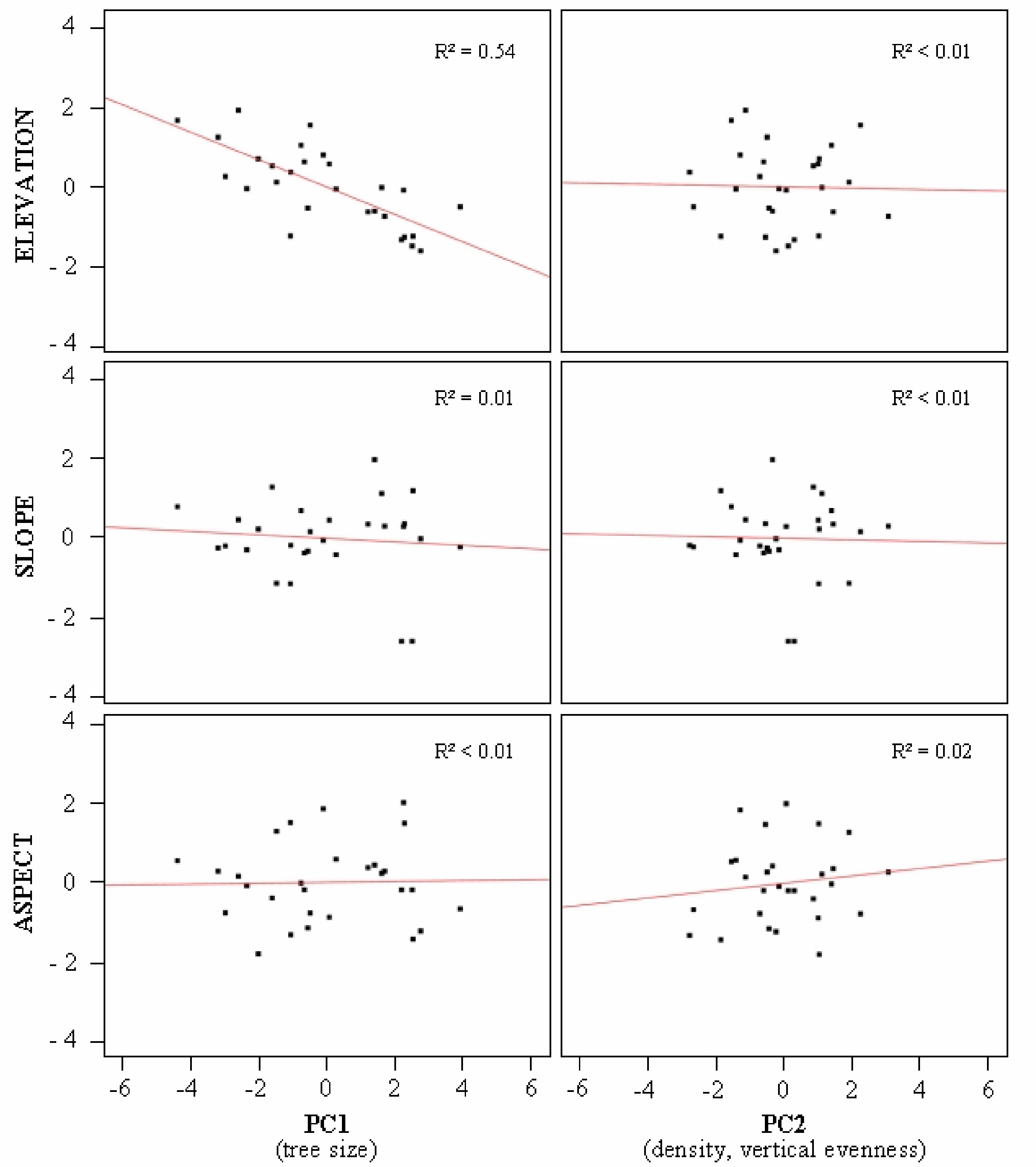
0.12
0.04
0.18
Slope
0.04
0.30
Aspect
TREE SIZE

Figure 6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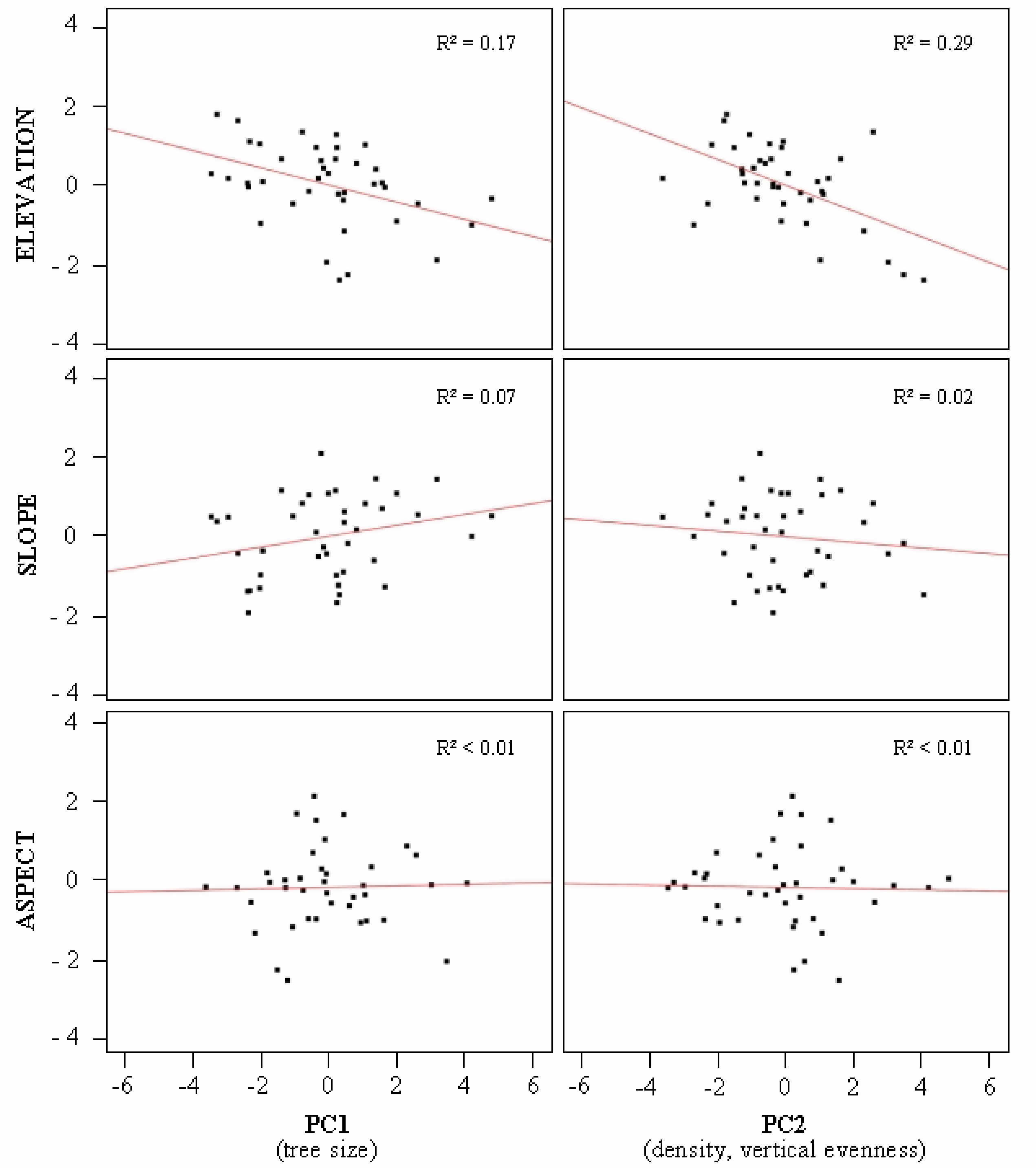
R² < 0.01
R² = 0.01
R² < 0.01
R² < 0.01
R² = 0.02
ELEVATION
SLOPE
ASPECT
4
2
0
- 2
- 4
-6
-4
-2
0
2
4
6
PC1
(tree size)
PC2
(density, vertical evenness)

Figure 7


ELEVATION
SLOPE
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R² = 0.02
R² < 0.01
R² < 0.01
4
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0
- 2
- 4
-6
-4
-2
0
2
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PC1
(tree size)
PC2
(density, vertical evenness)