ORIGINAL ARTICLE

Water–energy, land-cover and heterogeneity drivers of the distribution of plant species richness in a mountain region of the European Alps

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ABSTRACT

Aim To evaluate the relative importance of water–energy, land-cover, environmental heterogeneity and spatial variables on the regional distribution of Red-Listed and common vascular plant species richness.

Location Trento Province (*c.* 6200 km^2) on the southern border of the European Alps (Italy), subdivided regularly into 228 3′ × 5′ quadrants.

Methods Data from a floristic inventory were separated into two subsets, representing Red-Listed and common (i.e. all except Red-Listed) plant species richness. Both subsets were separately related to water–energy, land-cover and environmental heterogeneity variables. We simultaneously applied ordinary least squares regression with variation partitioning and hierarchical partitioning, attempting to identify the most important factors controlling species richness. We combined the analysis of environmental variables with a trend surface analysis and a spatial autocorrelation analysis.

Results At the regional scale, plant species richness of both Red-Listed and common species was primarily related to energy availability and land cover, whereas environmental heterogeneity had a lesser effect. The greatest number of species of both subsets was found in quadrants with the largest energy availability and the greatest degree of urbanization. These findings suggest that the elevation range within our study region imposes an energy-driven control on the distribution of species richness, which resembles that of the broader latitude gradient. Overall, the two species subsets had similar trends concerning the relative importance of water–energy, land cover and environmental heterogeneity, showing a few differences regarding the selection of some predictors of secondary importance. The incorporation of spatial variables did not improve the explanatory power of the environmental models and the high original spatial autocorrelation in the response variables was reduced drastically by including the selected environmental variables.

Main conclusions Water–energy and land cover showed significant pure effects in explaining plant species richness, indicating that climate and land cover should both be included as explanatory variables in modelling species richness in human-affected landscapes. However, the high degree of shared variation between the two groups made the relative effects difficult to separate. The relatively low range of variation in the environmental heterogeneity variables within our sampling domain might have caused the low importance of this complex factor.

Keywords
Calcareous bedrock, climate, conservation biogeography, elevation gradient, habitat heterogeneity, hierarchical partitioning, Red-Listed species, regional scale, spatial autocorrelation, urbanization.

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INTRODUCTION

The identification of the factors controlling the spatial variability of species richness is essential in order to determine the current status of biodiversity and to predict its likely response to global environmental change. A knowledge of the important driving variables is crucial for developing effective *in situ* conservation policies for sustainable land use (Gaston, 2000). The availability of extensive taxonomic surveys carried out on defined geographical units and their analysis in relation to environmental information are powerful tools to help us explore this issue at different spatial scales. Among the different taxonomic groups, plants are key elements of all terrestrial ecosystems, providing the primary production and being important structural elements (Kreft & Jetz, 2007).

Many hypotheses have been proposed to explain the regional distribution of plant species diversity (Fraser & Currie, 1996). Several of these have been shown to be more or less synonymous or not mutually exclusive, as they are based on different ecological processes which may act simultaneously in shaping diversity patterns (Palmer, 1994). Recently, the water–energy dynamics theory, as proposed by O'Brien (1993, 2006), has shown the potential to become a possible unifying theory (Vetaas, 2006), at least for modelling woody plant species richness (Bhattarai & Vetaas, 2003). The interaction between energy and water is known to be an important driver of diversity patterns for several taxonomic groups (Whittaker *et al.*, 2007), with effects dependent on latitude, i.e. at high latitudes energy represents the limiting component of the interaction, whereas at lower latitudes water is the key limiting component (Hawkins *et al.*, 2003). Mountain environments provide interesting study areas to explore the relationship between water variables, energy variables and species richness along vertical gradients (elevation) (Bhattarai & Vetaas, 2003, 2006), which might be expected to resemble the broader latitudinal gradient.

In addition to these climatic drivers, anthropogenic impacts through the effects of land-use change, leading to habitat modification and loss, are also acknowledged to be important factors affecting ecosystems world-wide. However, few modelling studies have addressed the interactions between climate and land-cover data on species diversity at broad spatial scales (Pearson *et al.*, 2004). Indeed, it is recognized that focusing only on climate will result in less accurate predictions of species distributions (Bakkenes *et al.*, 2002), and that incorporating land-cover variables into bioclimatic models will almost certainly improve their explanatory power significantly (Thuiller *et al.*, 2004).
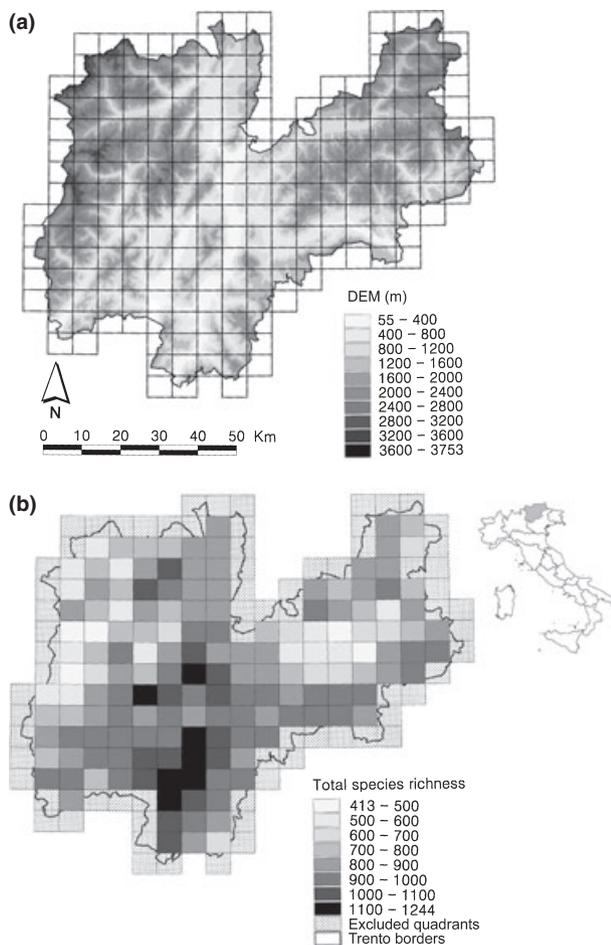
In studies relating the distribution of plant species richness to environmental factors, the variables within a given sampling domain have usually been calculated as the mean value for the sampling unit. However, more recently it has been suggested that the variability of the environmental variables within the domain should also be considered (Pausas & Austin, 2001; Ferrer-Castán & Vetaas, 2005). Environmental heterogeneity is of course known to be a key factor shaping diversity patterns (Shmida & Wilson, 1985; Currie, 1991; Nichols *et al.*, 1998). It influences important functions, ranging from population structure through community composition to ecosystem processes, and its effect is often scale dependent (Pickett & Cadenasso, 1995).

In this context, the European Alps are an interesting model system for testing the explanatory power of water–energy, land-cover and environmental heterogeneity variables on species diversity because of the simultaneous presence of a wide elevation gradient, relatively high human impact and large variation in topography. There have been several studies investigating the environmental drivers of plant species diversity at the regional scale in the European Alps (e.g. Wohlgemuth, 1998, 2002; Moser *et al.*, 2005). However, none has attempted to assess the relative contributions of different environmental and spatial variables, given the potential for interactions and shared explanatory power between the different factors. Recent developments in environmental modelling, including variation partitioning and hierarchical partitioning, allow the amount of shared variation to be assessed (Ferrer-Castán & Vetaas, 2005). Moreover, there has been no attempt to evaluate in a single study how much the relative importance of the different environmental factors varies between the Red-Listed and common plant species (i.e. all except Red-Listed species). As conservation planning based on the occurrence of rare species has been criticized as being too limited in scope to conserve biodiversity as a whole (Pearman *et al.*, 2006), it is important to investigate the determinants of distribution of common species in deriving effective management policies.

Thus, the aim of this work was to gain insights into the relationship between the distribution of Red-Listed and common plant species richness in a region of the southern Alps, and to assess the relative importance of water–energy, land-cover, environmental heterogeneity and spatial variables as potential drivers of these distributions. We fitted ordinary least squares (OLS) regression with variation partitioning (VP) (Borcard *et al.*, 1992), and hierarchical partitioning (HP) (Chevan & Sutherland, 1991), a relatively novel combination of procedures, in an attempt to identify the most likely factors among intercorrelated variables (Mac Nally, 2000; Luoto *et al.*, 2006). As ecological processes are often not spatially independent, we further evaluated the degree of spatial autocorrelation in our response variables and in the environmental model residuals.

Specifically, we addressed the following questions: (1) What is the relative importance of water–energy, land-cover and environmental heterogeneity drivers in explaining the distribution of plant species richness? (2) How much does the relative importance of the three sets of variables differ between the Red-Listed and common plant species? (3) Does the incorporation of spatial variables improve the explanatory power of the environmental models in explaining the distribution of plant species richness?

(a)

DEM (m)

55 – 400
400 – 800
800 – 1200
1200 – 1600
1600 – 2000
2000 – 2400
2400 – 2800
2800 – 3200
3200 – 3600
3600 – 3753

N

0 10 20 30 40 50 Km

(b)

Total species richness

413 – 500
500 – 600
600 – 700
700 – 800
800 – 900
900 – 1000
1000 – 1100
1100 – 1244
Excluded quadrants
Trento borders

Figure 1 The Trento Province (World Geodetic System 1984: 45°43.8′–46°28.3′ N, 10°31.9′–11°53.4′ E) subdivided regularly into 228 quadrants of 3′ × 5′. For the purposes of this study, we used only the 156 quadrants with more than 80% of the area within the province borders. (a) Digital elevation model (SIAT, Servizio Urbanistica e Tutela del Territorio, Provincia Autonoma di Trento, cell size 25 × 25 m) and (b) distribution of total plant species richness (edge quadrants filled with dots were those excluded from the analyses).

MATERIALS AND METHODS

Study area

The study area was the Trento Province (north-eastern Italy), an area of 6207 km^2 (World Geodetic System 1984: 45°43.8′–46°28.3′ N, 10°31.9′–11°53.4′ E) on the southern border of the European Alps (Fig. 1). The elevation range varies from 66 m (Lake Garda) to 3769 m a.s.l. (Mount Cevedale). The local climate depends primarily on altitude, and only secondarily on latitude, varying from sub-mediterranean conditions in the southern and central parts to continental conditions in the inner valleys. The annual rainfall averages *c.* 1000 mm year^{-1} and the annual mean temperature is *c.* 6.5°C.

Data on plant species distributions

Information on the distribution of plant species was extracted from a floristic inventory of the Trento Province (CFT Project, Prosser & Festi, 1993; COT project, Perazza & Decarli Perazza, 2005), which contained over 600,000 records in 2006. The province was subdivided into a regular grid of 228 quadrants, each of 3′ × 5′, corresponding to *c.* 35.7 km^2 (Fig. 1). The sampling effort in the different quadrants was related to the saturation level of the species accumulation curves, i.e. a quadrant was explored until the number of species tended to saturation. As with all taxonomic inventories, there is an inevitable incomplete count due to the subjectivity of botanists involved in the inventory, but we assumed that this error should be negligible and similar in each quadrant. For the purpose of this study, we omitted obvious edge quadrants and used only 156 quadrants with more than 80% of their area within the borders of the Province of Trento. The total species richness data set based on the inventory at December 2006 was used and separated into two subsets. The first subset contained the 'Red-Listed species' as defined in the provincial Red List (Prosser, 2001). This list includes 723 species, representing about one-third of the overall flora. The second subset, hereafter labelled as 'common species', was operationally defined as the difference between the total number of species and the number of Red-Listed species.

Explanatory variables

Water–energy

The water–energy variables were retrieved from continuous raster-based climatic maps with a resolution of 100 × 100 m. The climatic data were interpolated using 64 climatic stations located throughout the province (Sboarina & Cescatti, 2004). We considered the annual mean of minimum temperatures (Tmin) as a measure of available energy (Fraser & Currie, 1996), and the summer precipitation (PRE) as first indicator of water availability (Table 1). The mean value was obtained by averaging the values within the period 1990–99. As plant–water relationships are strongly dependent on the availability of soil water, we quantified soil moisture using the topographic wetness index (TWI, from Beven & Kirkby, 1979). The TWI was calculated from the digital elevation model of the province (25 × 25 m) using SAGA GIS (version 1.2, available at http://www.saga-gis.org/).

Land cover

The land-cover variables were derived from a vector-based land-use map (SIAT, Servizio Urbanistica e Tutela del Territorio, Trento, Italy). We defined the following five land-use classes: (1) built-up area (URB) covered by buildings, streets and other urban land uses; (2) farmland (AGR); (3) grassland (GRA), which consisted of permanent mown meadows or pastures; (4) forest (FOR), which included closed deciduous

Table 1 Descriptive statistics and abbreviations of the explanatory variables calculated for each of the 156 quadrants in Trento Province (Italy), and used in the analyses.

	Variable name and explanation	Unit	Mean	Min.	Max.
Water–energy					
Tmin	Annual average of minimum temperatures	°C	1.18	−4.89	7.06
TWI	Topographical Wetness Index	–	7.19	6.38	8.37
PRE	Mean summer precipitation (June–September)	mm year^{-1}	512	383	657
Land cover					
AGR	Area covered by farmland	%	6.09	0	50.07
GRA	Area covered by grasslands	%	13.36	0.13	46.56
FOR	Area covered by forest	%	60.95	7.04	89.26
URB	Area covered by built-up area	%	3.44	0	34.46
CAL	Area covered by calcareous bedrock	%	43.7	0	100
Environmental heterogeneity (within quadrant)					
Tmin-H	Standard deviation of Tmin	°C	1.54	0.53	2.62
PRE-H	Standard deviation of PRE	mm	11.86	1.41	45.91
SLO-H	Standard deviation of slope	Degree (°)	3.38	2.77	4.58
ELE-H	Elevation range (maximum–minimum)	m	1529	650	2230
BED-H	Shannon index of bedrock types	–	0.54	0	1.27
LC-H	Shannon index of land-cover types	–	0.95	0.38	1.42
Space					
X	Standardized longitude (Roma 40)	m	0	−44,049.86	58,656.67
Y	Standardized latitude (Roma 40)	m	0	−45,600.65	39,658.84

and coniferous forests; and (5) water bodies (WAT) comprising lakes and rivers. The vector-based data were converted to a raster model with a cell size of 25 × 25 m. Then, we calculated the proportion of the different land-use classes within each quadrant using FRAGSTATS (version 3.3; McGarigal *et al.*, 2002).

The bedrock variables were retrieved from the geological map (1: 200,000) of the province (Bosellini *et al.*, 1999). We classified each bedrock type into four main classes: (1) sedimentary calcareous bedrock; (2) volcanic and metamorphic acid bedrock; (3) volcanic basic bedrock; and (4) mixed debris.

Environmental heterogeneity

To provide measures of environmental heterogeneity within each quadrant, we derived a series of indices, as follows: (1) *water–energy heterogeneity* – we calculated the within-quadrant standard deviation of the minimum temperature (Tmin-H) and summer precipitation (PRE-H); (2) *habitat heterogeneity* – we used the Shannon diversity index (Magurran, 2004) calculated on the land-cover classes (LC-H) and on the bedrock types (BED-H). The Shannon index was computed using FRAGSTATS (version 3.3; McGarigal *et al.*, 2002); (3) *topographic heterogeneity* – we calculated the elevation range (ELE-H) and the within-quadrant standard deviation of slope (SLO-H). The standard deviation was calculated using SAGA GIS (version 1.2, available at http://www.saga-gis.org/).

Space

Besides environmental factors, the geographical location of the quadrant is likely to affect local patterns of species richness. In order to account for such a large-scale gradient, we performed a trend surface analysis based on the longitude (X) and latitude (Y) of each geographical centre within the quadrant. The spatial variables were calculated by including all terms for a cubic trend surface regression (X, Y, X^2, Y^2, XY, X^2Y, XY^2, X^3, Y^3). Before the analysis, the coordinates were centred on their respective means (Legendre & Legendre, 1998).

Data analysis

Environmental models with variation partitioning

To determine the relative influence of the three sets of variables on both Red-Listed and common plant species richness, we applied OLS regression with VP (Borcard *et al.*, 1992). First, we performed a separate stepwise forward selection within each of the three sets of explanatory variables (water–energy, land cover and environmental heterogeneity) using an *F*-test ($P < 0.05$) to select the significant predictors which best accounted for the variation in species richness. To allow for curvilinear effects of the explanatory variables, we incorporated their linear, quadratic and cubic terms. The significant variables were then further analysed by means of a VP approach to determine the relative influence of water–energy, land-cover and environmental heterogeneity variables on species richness. The variation in species richness was decomposed using a series of (partial) regression analyses implemented in the 'Vegan' package (Oksanen *et al.*, 2007) for R version 2.5.1 (R Development Core Team, 2004), using the estimation procedure proposed by Peres-Neto *et al.* (2006). All the partial regressions were tested for significance with a Monte Carlo permutation test ($n = 1000$). The total variation

in species richness was decomposed into seven components: the pure effect of water–energy (WE), land cover (LC) and environmental heterogeneity (HE), three first-order joint components (WE∩LC, WE∩HE and LC∩HE) and the joint component among the three groups (WE∩LC∩HE).

Spatial models and autocorrelation

To reveal the relative influence of environmental and spatial variables, we performed a further VP analysis incorporating the spatial variables in the environmental models. First, the species richness was regressed separately (1) against the environmental variables (all three sets together) and (2) against the nine terms of the trend surface analysis (Kivinen *et al.*, 2006). Then, the total variation explained was decomposed by means of partial regression into pure environmental, pure spatial structure and spatial component of the environmental influence. The analysis was repeated for both Red-Listed and common plant species richness.

Two approaches can be used to analyse the importance of spatial autocorrelation: (1) it can be integrated explicitly into the modelling procedure (e.g. Dormann, 2007; Kühn, 2007); or (2) it can be analysed in relation to the residual variation in environmental models. According to Hawkins *et al.* (2007), OLS estimates in grid data are unbiased by spatial autocorrelation and the biological interpretation of factors may not necessarily vary between spatial and non-spatial models (Ferrer-Castán & Vetaas, 2005). Thus, as water–energy and land-cover variables had a strong spatial structure due to the topography of our mountain system, we checked for spatial autocorrelation in the residuals of the models including the environmental variables (Hawkins *et al.*, 2007), instead of performing spatially explicit modelling. Hence, Red-Listed and common plant species richness and the residuals obtained from the environmental hybrid models (without spatial terms) were tested for spatial autocorrelation by means of Moran's *I*. Spatial correlograms were constructed using ten lag intervals. Each interval was 8-km wide, ranging from 0 to 80 km. The first lag distance allowed consideration, where possible, of the eight quadrants surrounding each quadrant in the grid. Moran's *I* values were tested for significance with a Monte Carlo permutation test ($n = 1000$) as implemented in the program ROOKCASE (Sawada, 1999). Each correlogram was tested for significance using a Bonferroni-corrected α of 0.01/10 = 0.001 (level of significance/number of tests).

Hierarchical partitioning

In addition to variation partitioning, HP (Chevan & Sutherland, 1991) was also used to identify the variables most likely to affect variation in species richness (e.g. Heikkinen *et al.*, 2005; Luoto *et al.*, 2006). HP allows the joint consideration of all the possible models in a multiple regression in attempting to identify the most likely causal factors (Mac Nally, 2000). This analysis splits the variation explained by each explanatory variable into a joint effect with the other explanatory variables

and an independent effect not shared with any other variable. HP was conducted using the 'Hier.Part' package (version 0.5–1, Mac Nally & Walsh, 2004) implemented in R version 2.5.1 (R Development Core Team, 2004). As HP needs monotonic relationships between response variables and explanatory variables, we transformed the explanatory variables when appropriate to improve the linearity of the relationships. 'Hier.Part' is restricted to run with only 12 variables, thus we excluded the spatial variables, PRE-H and Tmin-H, which accounted for the lowest explained variation in a simple linear regression with our response variables. As described by Mac Nally (2002), we tested for independent effects using a randomization routine ($n = 200$), which gives *Z*-scores for the generated distribution of randomized independent contributions and a level of statistical significance (*P*) based on this score. We used a normal error distribution and R^2 as a measure of goodness-of-fit.

RESULTS

The total species richness per quadrant varied from a minimum of 413 to a maximum of 1244, with a mean of 844 plant species; the richness of Red-Listed species was between 4 and 93, with a mean of 29, and the number of common species was between 408 and 1191, with a mean of 805.

Environmental models

The separate stepwise procedures performed on the three sets of explanatory variables (water–energy, land cover and environmental heterogeneity) for Red-Listed and common plant species richness selected several significant predictors in all the models (Table 2).

Red-Listed species

In the water–energy model, where 62.4% of the total variation was explained, species richness was significantly related to the mean of minimum temperature by a nonlinear function (Fig. 2a), which was selected as the best variable, and to the summer precipitation.

The land-cover model accounted for 59.5% of the total variation, and it included both the linear and quadratic terms of the proportion of urban elements, and the linear term of the proportion of calcareous bedrock. Quadrants with a high degree of urbanization and with a large cover of calcareous bedrock contained the greatest number of Red-Listed species. However, considering the simple relationship between species richness and URB, the positive influence seemed to become less pronounced at the largest proportions (Fig. 2b), while the response to CAL tended to be slightly unimodal (Fig. 2c).

The environmental heterogeneity model accounted for 43.2% of the total variation. Habitat heterogeneity was the first variable selected, followed by the elevation range, slope and temperature heterogeneity. The richest quadrants were

Table 2 Summary of the stepwise selection to build the separate multiple regression models for water–energy, land-cover and environmental heterogeneity variables for both Red-Listed and common plant species richness.

	F-value	P-value	Change in R^2	Model Adjusted R^2	d.f.	F-value	P-value
Red-Listed species							
Water–energy							
Tmin (+), Tmin^2 (+), Tmin^3 (+)	75.1	< 0.01	59.72	**62.36**	6, 149	43.8	< 0.01
PRE (+), PRE^2 (−), PRE^3 (+)	5.6	< 0.01	4.10				
Land cover							
URB (+), URB^2 (−)	81.4	< 0.01	51.55	**59.54**	3, 153	77.0	< 0.01
CAL (+)	33.6	< 0.01	8.77				
Environmental heterogeneity							
LC-H (+), LC-H^2 (−), LC-H^3 (+)	24.6	< 0.01	32.71	**43.21**	6, 149	20.6	< 0.01
ELE-H (−)	10.6	< 0.01	3.89				
SLO-H (+)	17.7	< 0.01	6.50				
Tmin-H (+)	6.3	0.01	2.31				
Common species							
Water–energy							
Tmin (+), Tmin^2 (−)	117.2	< 0.01	60.51	**59.99**	2, 153	117.2	< 0.01
Land cover							
CAL (+), CAL^2 (−)	51.3	< 0.01	40.12	**66.59**	6, 149	52.5	< 0.01
URB (+), URB^2 (−)	29.7	< 0.01	12.80				
FOR (+), FOR^2 (−)	34.7	< 0.01	14.97				
Environmental heterogeneity							
BED-H (+)	24.6	< 0.01	13.76	**22.08**	2, 153	23.0	< 0.01
SLO-H (+)	18.5	< 0.01	9.32				

The variable selection was performed within each group separately. The direction of the relationships is shown for the significant terms. The data came from 156 3′ × 5′ quadrants in the Italian Alps. Variables as given in Table 1.

those with the largest habitat heterogeneity (Fig. 2d). Overall, the environmental heterogeneity model explained the lowest proportion of variation in species richness. Except for elevation range, all the variables had a positive influence on the number of species.

The partitioning of the total variation explained indicated that the number of Red-Listed species was best explained by the explanatory variables reflecting water–energy (6.2%) and land cover (3.7%), whereas environmental heterogeneity (0.6%) did not have a significant effect on its own in partial regression (Table 3). The analysis also showed large fractions of variation shared between the different sets, i.e. variation, which cannot be attributed to any set exclusively. Among these shared components, the largest part was accounted for by the joint effect of the three sets and by the joint effect of water–energy and land cover. The first-order shared components involving the environmental heterogeneity variables were very low.
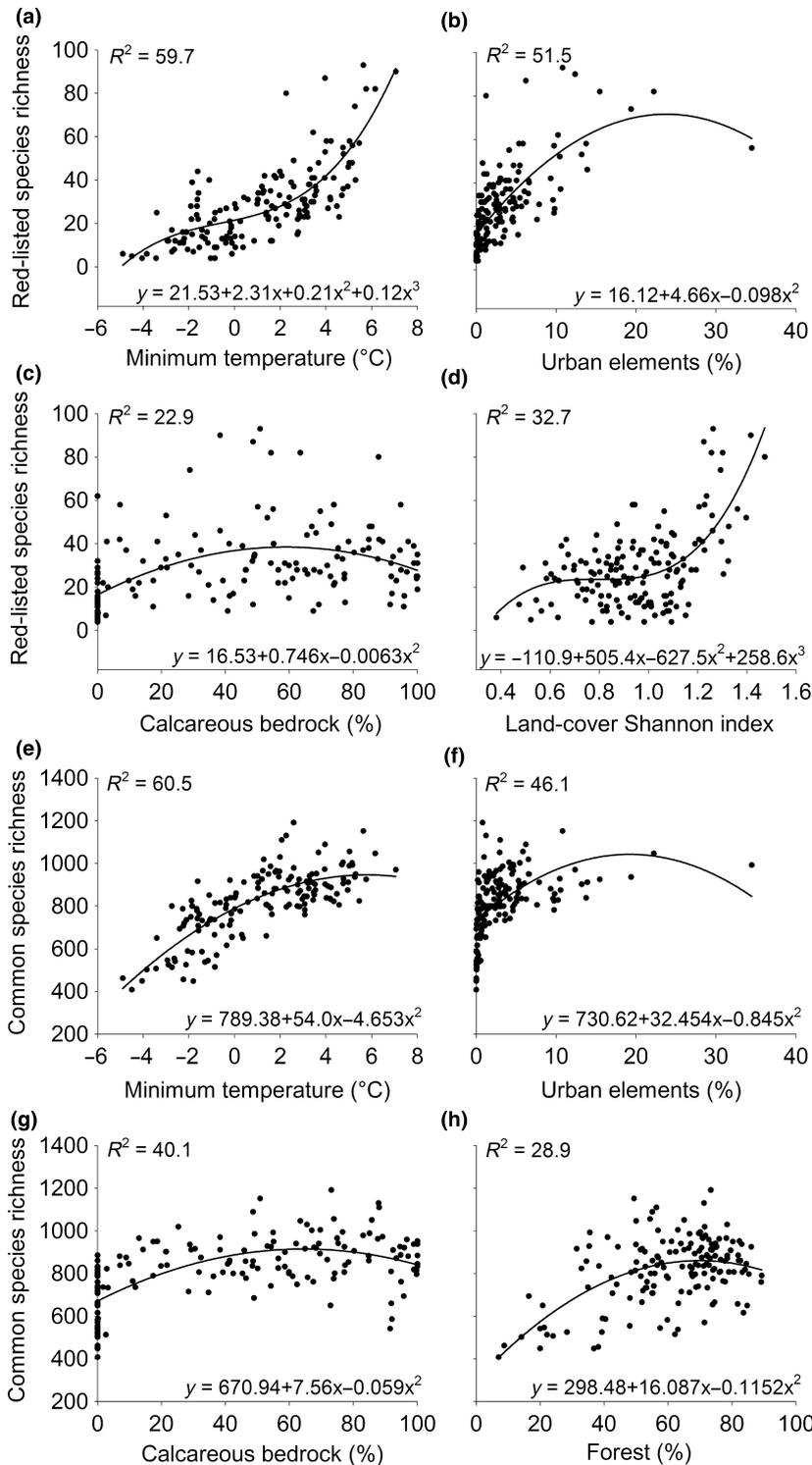
Common species

The water–energy model explained 60.0% of the total variation and species richness was significantly related only to the mean of minimum temperature. The shape of the relationship between temperature and common species richness (Fig. 2e) was rather different from that ascertained for the Red-Listed species.

The land-cover model accounted for 66.6% of the total variation and included three variables. The first variable included was the proportion of calcareous bedrock (linear and quadratic terms), then the linear and quadratic terms of the proportion of urban elements and forest were selected. Considering the simple relationships with the three significant land-cover variables, we found that species richness increased in a positive decelerating manner with the proportion of urban elements (Fig. 2f), calcareous bedrock (Fig. 2g) and forest (Fig. 2h).

The environmental heterogeneity model for common species accounted for 22.1% of the total variation. Bedrock heterogeneity was the first variable selected, followed by slope heterogeneity, both with positive linear influence on the number of species. Overall, the environmental heterogeneity model explained the lowest proportion of variation in species richness between the three groups.

The partitioning of the total variation explained by the three groups (70.6%) indicated that common plant species richness was best explained by the explanatory variables reflecting land cover (5.1%), and water–energy (2.8%), while environmental heterogeneity (1.0%) had a significant but very low pure effect. This analysis showed also large fractions of shared variation. Among these shared effects, the largest part was accounted for by the joint effect between water–energy and land cover and by the joint effect among the three groups (Table 3). The

Figure 2 Scatterplots of the number of Red-Listed plant species (a–d) and common plant species (e–h) vs. the most important explanatory variables quantified in the 156 quadrants. Trends are shown by fitting linear, quadratic and cubic functions when significant (*F*-test, $P < 0.01$).

first-order components involving the environmental heterogeneity variables were again low.

Spatial models and autocorrelation

The hybrid environmental models did not differ much in comparison with the separate models for each explanatory group considering both the total variation explained and the variables selected (Table 4). The separate spatial models of Red-Listed and common species richness included several significant terms and explained 34.9% and 45.3% of the total variation, respectively. However, after partialling out the environmental variables with VP, the variation in species richness exclusively explained by spatial variables showed significant but very low values (Fig. 3); i.e. the largest part of variation in species richness was explained by pure

Table 3 Variation partitioning of Red-Listed and common plant species richness into water–energy (WE), land-cover (LC) and environmental heterogeneity (HE) components (adjusted R^2 in %).

	Pure components*			Shared components*				
	WE	LC	HE	WE∩LC	WE∩HE	LC∩HE	WE∩LC∩HE	TVE
Red-Listed species								
	6.24 (0.001)	3.67 (0.001)	0.59 (0.380)	14.53	1.30	1.05	40.30	67.68 (0.001)
Common species								
	2.82 (0.001)	5.14 (0.001)	1.05 (0.024)	40.53	0.10	4.37	16.55	70.56 (0.001)

The data came from 156 3′ × 5′ quadrants in the Italian Alps. The *P*-values of the pure effects and of the total model with all variables are given in brackets (Monte Carlo permutation test, *n* = 1000).

*Adjusted fractions of total variation explained (TVE, in %) were estimated following the procedure of Peres-Neto *et al.* (2006).

Table 4 Summary of the stepwise selection to build the environmental hybrid model and the spatial model for both Red-Listed and common plant species richness.

				Model			
	F-value	*P*-value	Change in R^2	Adjusted R^2	d.f.	*F*-value	*P*-value
Red-Listed species							
Hybrid model							
Tmin (+), Tmin^2 (+)	101.8	< 0.01	57.09	**66.34**	8, 147	39.2	< 0.01
LC-H (+)	15.0	< 0.01	3.27				
PRE (+)	8.6	< 0.01	1.86				
URB (+), URB^2 (−)	4.5	0.01	2.00				
CAL (+)	9.7	< 0.01	2.10				
FOR (+)	8.3	< 0.01	1.80				
Spatial model							
Y	27.4	< 0.01	15.11	**34.90**	6, 149	14.7	< 0.01
X, X^2, X^3	14.1	< 0.01	17.82				
XY	9.7	< 0.01	4.07				
Common species							
Hybrid model							
Tmin (+)	195.0	< 0.01	55.86	**78.65**	8, 147	72.4	< 0.01
CAL (+)	44.9	< 0.01	6.20				
BED-H (+)	39.1	< 0.01	5.34				
Tmin-H (+), Tmin-H^2 (−)	20.7	< 0.01	5.72				
FOR (+)	16.6	< 0.01	2.29				
GRA (+)	17.8	< 0.01	2.46				
URB (+)	13.5	< 0.01	1.85				
Spatial model							
Y, Y^2, Y^3	15.7	< 0.01	23.63	**45.34**	7, 148	19.5	< 0.01
X, X^2, X^3	21.3	< 0.01	22.51				
X^{2}Y	5.2	0.02	1.84				

The hybrid model was obtained by regressing species richness against all environmental variables (three sets together), while the spatial model was created by regressing species richness against the nine terms of the trend surface analysis. The variable selection was performed within each group separately. The direction of the relations is shown for the significant terms. The data came from 156 3′ × 5′ quadrants in the Italian Alps.

environmental variables and by the joint effect between geographical location and environmental variables (spatially structured environmental variation).

The correlograms based on the Moran's *I* calculated on the response variables stressed a high positive spatial autocorrelation of species richness for both Red-Listed and common species (Fig. 4). Spatial autocorrelation in the residuals was reduced considerably after fitting the hybrid environmental models for both Red-Listed and common species. A substantial significant positive autocorrelation was found only at the shortest lag distance (8 km). At the second lag distance (16 km), the values decreased below 0.1, and in the following distance classes values were close to zero.

Hierarchical partitioning

Generally, the results of the HP analyses reflected those ascertained by the environmental VP analyses, but revealed
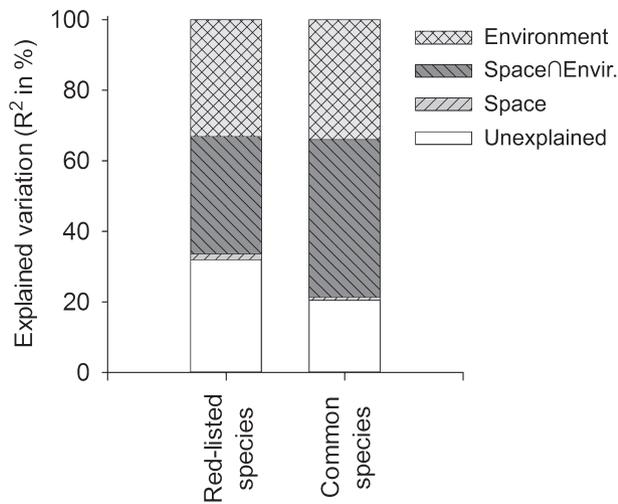
Figure 3 Variation partitioning of the model incorporating the variables selected in the hybrid environmental and spatial models (variables indicated in Table 4) for Red-Listed and common plant species richness. The total variation explained was split into non-spatial environmental variation (Environment), spatially structured environmental variation (Space∩Envir.), i.e. overlap between environmental and spatial components, spatial structure not explained by the environmental variables (Space) and unexplained variation.

slightly different results concerning the relative importance and the significance of some variables (Fig. 5). The minimum temperature and the proportion of urban elements were confirmed as important variables explaining large fractions of variation for both Red-Listed and common species, indicated by the large independent contributions. In contrast to the VP results, the proportion of farmland (AGR) was an important explanatory variable for both species groups. The relative importance of the other variables differed between the two groups considered.

For the Red-Listed species, additional important primary variables with relatively large independent effects were the TWI, habitat heterogeneity (LC-H) and secondarily the proportion of calcareous bedrock (CAL). Contrary to the former subset, additional variables with a large independent influence on common species were the area covered by forest (FOR) and the area covered by calcareous bedrock (CAL). Several other explanatory variables produced small significant independent effects.

DISCUSSION

Water–energy

Both VP and HP analyses showed that energy availability was a key determinant for the distribution of species richness of both Red-Listed and common plant species in the southern Alps. The synthesis of Hawkins *et al.* (2003) demonstrated that the relative importance of energy and water dynamics shifts latitudinally, such that energy places strong constraints on
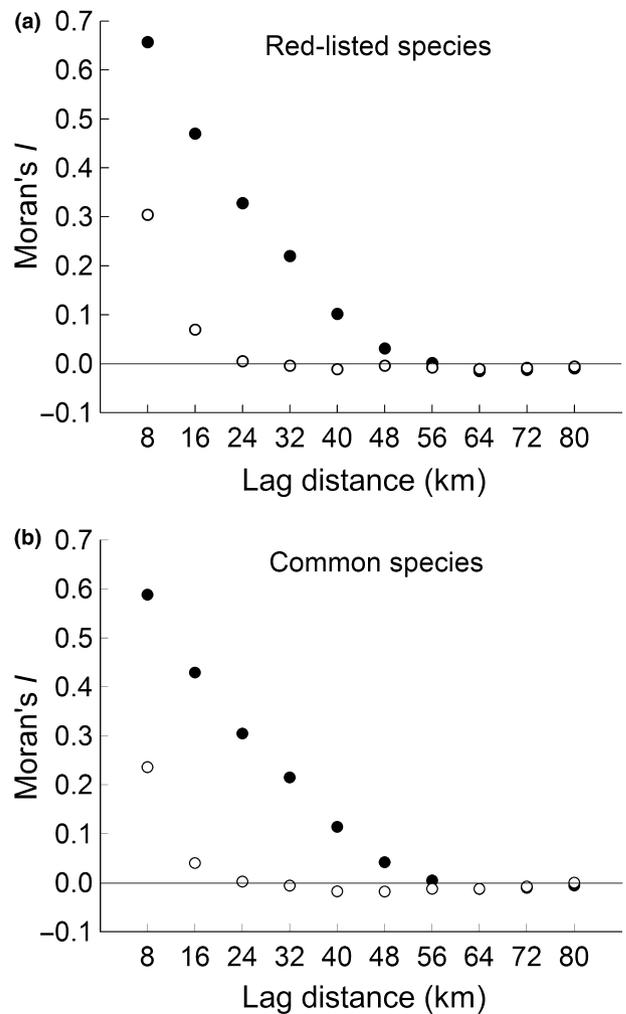
Figure 4 Spatial correlograms for (a) Red-Listed and (b) common plant species richness. Filled circles represent the original response variables and open circles the residuals after including all the significant environmental variables in the hybrid environmental models (see 'Data analysis' for more details). All correlograms were significant ($P < 0.01$); i.e. at least one coefficient was significant at the Bonferroni-corrected α (0.01/10 = 0.001).

plant species richness in the far north where energy inputs are low. Our results generally confirm this view with respect to mountain environments, i.e. temperature was the main limiting factor determining plant species richness due to the large elevation gradient. The finding of the lowest species richness levels at the low end of the temperature range conforms to previous studies in boreal and temperate mountain areas (Heikkinen & Neuvonen, 1997; Moser *et al.*, 2005). The non-significant relationship found by Wohlgemuth (1998) in similar environments was probably caused by incomplete sampling (truncated elevation gradient). In fact, this latter study excluded the alpine belt and was based on irregular, topographically defined mapping units. However, our general positive relationship between species richness and temperature along the elevation gradient might have taken a different shape if we had also considered the lowest part of the gradient (e.g.
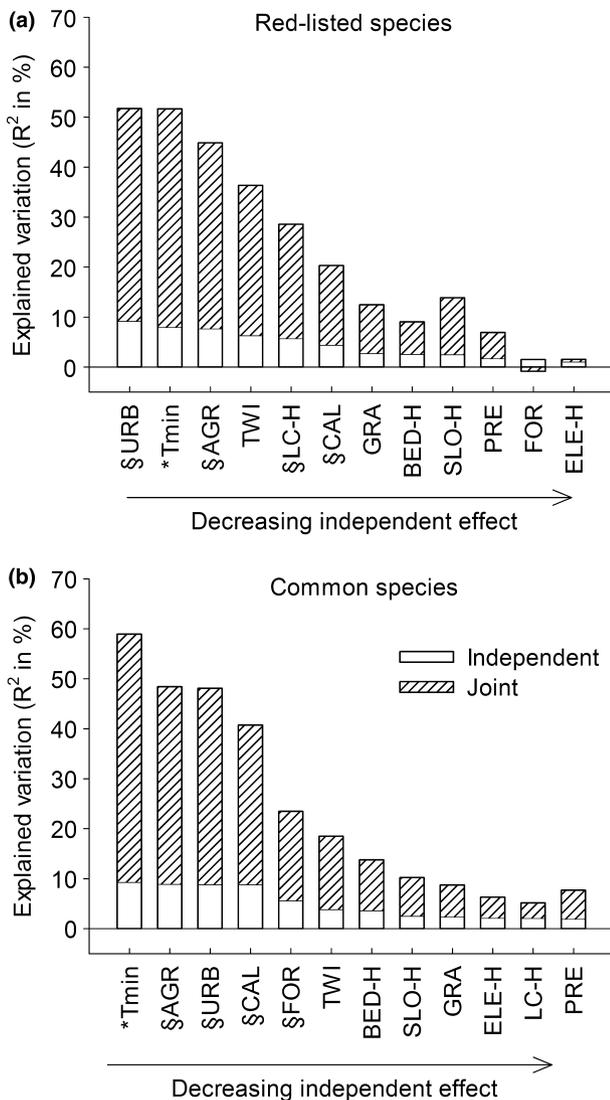
Figure 5 The independent and joint contributions (given as the percentage of the total explained variation) of each explanatory variable for the number of (a) Red-Listed and (b) common plant species, as estimated from hierarchical partitioning. Except for ELE-H [elevation range (maximum–minimum)] all the variables showed significant independent effects ($P < 0.01$), resulting from the z-randomization procedure ($n = 200$). Variable names as given in Table 1. § indicates power-transformed variables, *indicates log-transformed variables.

by extending the study area) (Lomolino, 2001; Bhattarai et al., 2004). Although numerous mechanisms that may drive such total species–energy relationships have been identified, knowledge about their relative contributions is scant and further research is needed to shed light on these processes (Evans et al., 2006a). Along with those underlying energy-driven factors, some water-related variables had significant but secondary effects on plant species richness. Among the water-related variables, the TWI had a relatively high independent relationship with the richness of Red-Listed species, i.e. quadrants with flat and concave topography supported

greater Red-Listed species richness, while this variable did not affect the occurrence of common species. However, these conclusions were likely to be related to the fact that many Red-Listed species were found in wetland habitats (e.g. mires, ponds, river banks or lakes) and in rural areas in the valley bottoms (Prosser, 2001). Precipitation on its own was not an important factor confirming the conclusions from other studies in 'cold' regions (e.g. Moser et al., 2005; Kivinen et al., 2006). This result might be attributed to the comparatively weak humidity gradient in our study area.

Land cover

Land-cover variables showed a high shared variation with temperature in explaining species richness. Red-Listed and common species responded differently to land-cover variables and the two analytical approaches (VP, HP) gave slightly different results. The HP results showed that both Red-Listed and common species richness were positively related to the proportion of urban elements (URB) and farmland (AGR). This finding is partially in contrast with the VP models, which did not include AGR in any model. The greatest number of Red-Listed and common species was concentrated in the highly urbanized valley bottoms, which were mainly used for agriculture, although the positive effect seemed to tend to saturation at large proportions. These findings conform to other studies, which show a general positive relationship between human population and biodiversity (Araújo, 2003; Evans & Gaston, 2005; Evans et al., 2006b). Considering the correlation between the proportion of urban elements and the minimum temperature ($r_s = 0.72$; $P < 0.01$), it is clear that the cities were concentrated in the most favourable areas. Our results concur with those of Pautasso (2007), who concluded that the broad-scale positive correlation between human presence and plant species richness suggests that people have preferentially settled and generally flourished in areas of high biodiversity and/or have contributed to it with species introductions and habitat diversification. Thus, highly urbanized areas are species rich probably not because of, but in spite of, urbanization (Kühn et al., 2004). Moreover, farmland retains at least some species-rich habitats, probably maintained by past and present traditional management practices and small-scale disturbances. However, the current change from the more traditional land-use practices to either more productive forms of agriculture or abandonment of marginal lands increases the risk of substantial species loss (Prosser, 2001).

Both VP and HP analyses also indicated that species richness of the common species was positively related to the proportion of forest. However, this relationship was not linear and at high proportions of forest the positive effect was less pronounced. This result is in agreement with several studies, which show that forest is a suitable land-cover type for many species (e.g. Kivinen et al., 2006). Forests may contain many different vegetation types with a large internal heterogeneity (Ellenberg, 1996), which is likely to support more ecological groups, for

example species related to clear-cuts, coniferous or broadleaf forest floors.

Both statistical approaches also highlighted the importance of underlying bedrock in controlling species diversity. The occurrence of calcareous substrates was of major importance in enhancing species richness, supporting the findings of the other studies in the European Alps (Wohlgemuth, 1998, 2002; Moser *et al.*, 2005). This influence was more pronounced for the common species than for the Red-Listed ones, and again the relationship was not linear. Overall, the Alpine flora contained more species restricted to calcareous bedrock than those related to acid substrates (Ewald, 2003). This well-known broad pattern of the European flora has been suggested to be the result of different processes such as: (1) species–area relationships caused by different substrate rejuvenation and range contraction between calcareous and siliceous bedrock caused by glaciations (Ewald, 2003); (2) speciation and extinction dynamics related to the prevalence of basic substrates in Europe (Grime, 2001); or (3) other potential factors confounding with calcareous bedrock (Wohlgemuth & Gigon, 2003).

Environmental heterogeneity

Environmental heterogeneity explained a relatively low amount of variation in species richness in both VP and HP analyses. This may be due to the fact that the study area had similar topography (see Fig. 1a), and thus the 156 quadrants had a relatively low range of variation in environmental heterogeneity variables. Moreover, the measures of within-quadrant variability used here were probably too coarse to capture the internal environmental heterogeneity at our sampling scale (*c.* 35 km^2) and study area extent (*c.* 6200 km^2). This could explain the low importance of this set of variables. The observed secondary role of environmental heterogeneity supports the results of Moser *et al.* (2005) for the Austrian Alps, but it is in contrast to the results obtained by Wohlgemuth (1998) for the Swiss Alps. This discrepancy was due to the fact that the former authors considered only mountain areas whereas the latter authors further included flatter areas, thereby increasing the range of variation of environmental heterogeneity among sampling units. Although environmental heterogeneity has been demonstrated to be of secondary importance, some of the heterogeneity variables had significant independent effects.

For the Red-Listed species, the Shannon index of land-cover types was the most important variable within the heterogeneity group. The habitat heterogeneity of entire landscape matrices has been shown to govern the movement of organisms, materials and energy, therefore contributing to the maintenance of greater diversity than more homogenous environments (Pickett & Cadenasso, 1995). Other contributing factors to environmental heterogeneity were the within-quadrant variability in slope and temperature. This result supports the heterogeneity theory, which predicts an increase of species richness with the increasing complexity of environmental

conditions (Shmida & Wilson, 1985). In contrast to our expectations, we found a small negative effect of elevation range. This is probably due either to the relatively low range in elevation of the most species-rich quadrants or to interactions with other selected predictors.

For the common species, bedrock heterogeneity was the most important heterogeneity variable. Quadrants with only one bedrock type had fewer species than quadrants with more diverse substrates. This was due to the co-occurrence of plant species related to both 'siliceous' and 'calcareous' substrates, i.e. the mixture of the two different species pools (Moser *et al.*, 2005).

Spatial structure and autocorrelation

The incorporation of spatial variables provided very low additional explanatory power when the geographical location of the quadrants was included in the environmental models. We found clear spatial trends in species richness distribution, but these strongly overlapped with our environmental factors. The species richness of both Red-Listed and common species increased southwards with a humped relationship with longitude. However, these spatial trends were already explained by the variables included in the environmental models, particularly by temperature, which was highly collinear with the spatial variables.

Regarding the spatial autocorrelation of the response variables, we applied a similar approach to that of Bhattarai & Vetaas (2003) and Virkkala *et al.* (2005). The inclusion of the environmental variables reduced the spatial autocorrelation drastically, which remained at a substantial level only at the shortest lag distance. The presence of positive short-distance spatial autocorrelation in the residuals of OLS regression is very common, but it has been demonstrated that it may not necessarily bias the parameter estimates or the biological interpretation of the predictors (Hawkins *et al.*, 2007). The spatial structure of species richness was mostly related to spatially structured environmental effects, as confirmed here by the trend surface analysis. The gradual changes in topography within our grid appeared to be the main cause underlying the spatial patterns in both response and explanatory variables.

CONCLUSIONS

Our findings suggest that the elevation range within our study region imposes an energy-driven control on the distribution of species richness, which resembles that of the broader latitude gradient. The low energy availability at high elevations seemed to be the most important factor controlling plant species richness in our mountain system. Both water–energy and land-cover variables showed significant pure effects in explaining plant species richness, indicating that climate and land cover should both be included as explanatory variables in modelling species richness in human-affected landscapes. However, the high degree of shared variation between the two groups made

the relative effects difficult to separate. Hence, further studies are necessary to quantify the magnitude of climate- and human-driven processes, and their possible interactions, as a basis for understanding the mechanisms underlying the distribution of plant species richness along elevation gradients.

Unravelling the relative importance of the factors that control the spatial variability of species richness is a crucial issue for predicting the response of biodiversity to global environmental change. As the greatest diversity of both Red-Listed and common species was concentrated on the highly urbanized and agriculturally exploited valley bottoms, conservation policies should be implemented in these areas in particular, as they are the most prone to species loss because of large-scale change in land use.

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