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BIODIVERSITY RESEARCH

Plant species richness and diversity along an altitudinal gradient in the Sierra Nevada, Mexico

Arturo Sánchez-González[1,]† and Lauro López-Mata[1,]*

[1]*Programa de Botánica, Colegio de Postgraduados, Km. 36.5 Carretera México-Texcoco, C.P. 56230, Montecillo, Texcoco, Estado de México, México*

*Correspondence: Lauro López-Mata, Programa de Botánica, Colegio de Postgraduados; Km. 36.5 Carretera México–Texcoco, C.P. 56230, Montecillo, Texcoco, Estado de México, México. Fax: (55 +595) 95 20 247; E-mail: lauro@colpos.mx
†Present address: Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo (UAEH), Ciudad Universitaria, Carretera Pachuca-Tulancingo Km 4.5, Pachuca CP 42184, Hidalgo, México

ABSTRACT

This article presents an analysis of plant species richness and diversity and its association with climatic and soil variables along a 1300-m elevation gradient on the Cerro Tláloc Mountain in the northern Sierra Nevada in Mexico. Two 1000-m^2 tree sampling plots were created at each of 21 selected sampling sites, as well as two 250-m^2 plots for shrubs and six 9-m^2 plots for herbaceous plants. Species richness and diversity were estimated for each plant life form, and beta diversity between sites was estimated along the gradient. The relationship between species richness and diversity and environmental variables was modelled using simple linear correlation and regression trees. Species richness and diversity showed a unimodal pattern with a bias towards high values in the lower half of the elevation gradient under study. This response was consistent for all three life forms. Beta diversity increased steadily along the elevation gradient, being lower between contiguous sites at intermediate elevations and high – the species replacement rate was nearly 100% – between sites at the extremes of the gradient. Few species were adapted to the full spectrum of environmental variation along the elevation gradient studied. The regression tree suggests that differences in species richness are mainly influenced by elevation (temperature and humidity) and soil variables, namely A_2 permanent wilting point, organic matter and horizon field capacity and A_1 horizon Mg^{2+}.

Keywords

Beta diversity, environmental gradients, Mexico, regression tree analysis, Sierra Nevada, temperate forests, Trans-Mexican Volcanic Belt.

INTRODUCTION

One of the most important challenges facing ecologists and biogeographers is to understand patterns of spatial and temporal variations in species richness and diversity (MacArthur, 1972; Lomolino, 2001). Latitudinal gradients in species richness and diversity, and the species–area relationships are among the most discussed and documented of these (Rahbek, 1997; Whittaker *et al*., 2001; Willig *et al*., 2003). Richness and diversity patterns on elevation gradients are, however, little understood, and have only been documented recently (Rahbek, 1995, 1997; Vetaas & Grytnes, 2002; Wang *et al*., 2002; Bhattarai & Vetaas, 2003), calling into doubt the hypothesis that species richness and diversity decrease monotonically with increasing elevation. Rahbek (1995), after a thorough review of the literature, showed that although species diversity tends to decrease with increasing elevation, the trend is not monotonic. Maximum species richness was observed at intermediate or low elevations in 50% of the studies examined.

With this finding, a re-evaluation of the nature of species richness and diversity along altitudinal gradients has become one of the focal points of research on mountain ecosystems. Lomolino (2001) suggests that the species diversity–elevation relationship (increase, decrease or spikes at intermediate elevations) depends basically on covariation patterns and interactions with specific environmental and biogeographical variables. In the opinion of Pausas and Austin (2001), for advances in understanding patterns in species richness along environmental gradients to be achieved, studies that involve multiple variables should be carried out, take interactions between them into account and utilize linear and nonlinear statistical techniques.

Due to human activities, the temperate subhumid zone typical of mountainous regions in Mexico (Rzedowski, 1978), particularly those of the Sierra Nevada forests adjoining the Valley of Mexico (one of the largest, most populated metropolizes in the world), show considerable variation in their composition, abundance and distribution (Toledo & Ordóñez, 1993; Challenger, 1998). In spite of the importance of the direct and indirect benefits provided by these forests, few studies have covered the full elevation gradient in enough detail to precisely describe existing variations in their structure and composition (Velázquez, 1994;

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Sánchez-González & López-Mata, 2003). Nevertheless, patterns in species richness and diversity and their relationship with soil and climate factors are not known.

Species richness and diversity patterns in the northern Sierra Nevada were analysed between 2800 and 4100 m elevation using plant distribution data. The study attempted to answer the following questions: Does species richness and diversity vary significantly with elevation along the gradient studied? Are variations along the elevation gradient in these structural attributes monotonic, unimodal or otherwise? What are the main environmental variables associated with these variations? The answers to these questions seek to contribute to knowledge about species richness and diversity patterns in the temperate subhumid zone that surrounds the Valley of Mexico.

METHODS

Study area

The study area was located within the Trans-Mexican Volcanic Belt (Ferrusquía-Villafranca, 1993) between 19°23′43″ and 19°28′37″ N, and between 98°42′51″ and 98°48′12″ W in the northern Sierra Nevada. The highest peaks in the area are the Popocatépetl Volcano (5453 m), the Iztaccíhuatl Volcano (5285 m), the Cerro Tláloc Mountain (4100 m) and the Cerro Telapón Mountain (4060 m). The predominant climate is temperate subhumid, with annual summer rainfall in excess of 1000 mm and average temperatures ranging between 3 and 22 °C. On the slopes of the Sierra Nevada, temperature decreases an average of 0.49 °C per 100 m increase in elevation. The annual 700-mm isohyet skirts the base of the mountains, while precipitation reaches 1200 mm on their slopes (García, 1968). Above 4000 m, the climate ranges from cold to very cold, with occasional snow in winter (Madrigal, 1967; García, 1968; Toledo & Ordóñez, 1993). Six natural vegetation types grow between 2800 and 4100 m a.s.l. along the western slope of the Cerro Tláloc: scrub–oak, oak forest, mixed forest, fir forest, pine forest and alpine grassland (Sánchez-González & López-Mata, 2003). The lower limit of the elevation gradient was set at 2800 m, as vegetation below this level is strongly affected by humans. It has been extensively grazed, burned to stimulate pasture regrowth, replaced by farmland, selectively logged, and harvested for plant species with a variety of traditional uses (Lauer, 1978; Rzedowski, 1978; Challenger, 1998).

Field work and data analysis

Twenty-one sites between 2800 and 4000 m were selected. Two 1000-m^2 (50 × 20 m) plots were chosen at random to sample the tree layer; two 250-m^2 plots to sample the shrub layer, and six 9-m^2 plots to sample the herbaceous layer. Species richness was calculated as the total number of species at each sampling site. The density of each species was calculated as the number of individuals per sampling site. Shannon's natural logarithm based index (H′), Simpson's inverse index ($\lambda = D^{-1}$) and Fisher's α index (Fisher *et al.*, 1943) were used as measures of diversity. The Fisher's α index is not influenced by the size of the sampling area and is less affected by an abundance of rare species than the other measures (Magurran, 1988).

Beta diversity (β), was calculated on the basis of the species replacement rate (Wilson & Schmida, 1984; Koleff *et al.*, 2003), using the formula:

$$\beta = \frac{g(H) + l(H)}{2\alpha}$$

where β = beta diversity, α = average number of species in the samples (average alpha), $g(H)$ = number of species gained along an environmental gradient and $l(H)$ = number of species lost along the same gradient. The number of species shared among the six vegetation types through the gradient studied was also estimated. Species diversity indices were calculated using the ESTIMATES 6b1a program (Colwell, 2001).

Soil characteristics measured at each sampling site were O horizon litter thickness (cm) and A_1 horizon depth (cm). The A_1 and A_2 horizon characteristics measured were field capacity (FC) (%), permanent wilting point (PWP) (%), porosity (%), clay (%), acidity (pH) and organic matter (OM) (%), exchangeable calcium (Ca^{2+}) (cmol kg^{-1}), magnesium (Mg^{2+}) (cmol kg^{-1}), sodium (Na^{+}) (cmol kg^{-1}) and potassium (K^{+}) (cmol kg^{-1}), and for the litter, O horizon, total nitrogen (N) (%), phosphorus (P) (%), potassium K (%), calcium (Ca) (%) and magnesium (Mg) (%). Measurements were made using the methodology described by Black *et al.* (1965) and Aguilera (1989). Elevation (m), slope (%) and exposure (degrees) were also recorded. Climatic variables were average temperature and total annual precipitation. Their values were estimated using data gathered from the nine closest weather stations to the study region (Quintas, 2000), except for elevations above 3300 m, where there are no weather stations. According to García (1968), Rzedowski (1978) and Toledo and Ordoñez (1993), in the mountains surrounding the Valley of Mexico, average annual precipitation ranges between 600 and 800 mm and average annual temperature between 3 and 5 °C at elevations above 4000 m. Daily temperatures fluctuate enough to make frosts possible at any time of the year. The values suggested by these authors were used as likely values for the summit of the Cerro Tláloc Mountain.

The relationship between species richness and diversity and environmental factors was analysed by linear correlation, polynomial regression and regression trees using the S-PLUS 2000 program. Regression tree analysis (RTA), which does not involve *a priori* assumptions about any particular type of relationship between the variables, are useful for capturing nonlinear relationships and facilitating interpretation of the results, something which cannot be achieved through the use of linear models (Iverson & Prasad, 1998; McCune & Grace, 2002). Recently, it has been demonstrated that RTA effectively modelled much of the spatial variability and autocorrelation inherent in the original data (Cablk *et al.*, 2002). The number of colonizing and native Mexican species was estimated for each life form and in total, based on Calderón de Rzedowski & Rzedowski (2001). A plant colonizer here is defined as a species whose occurrence is favoured by habitat disturbances, and includes native and alien plants. Nevertheless, out of the 618 alien species recorded for Mexico by

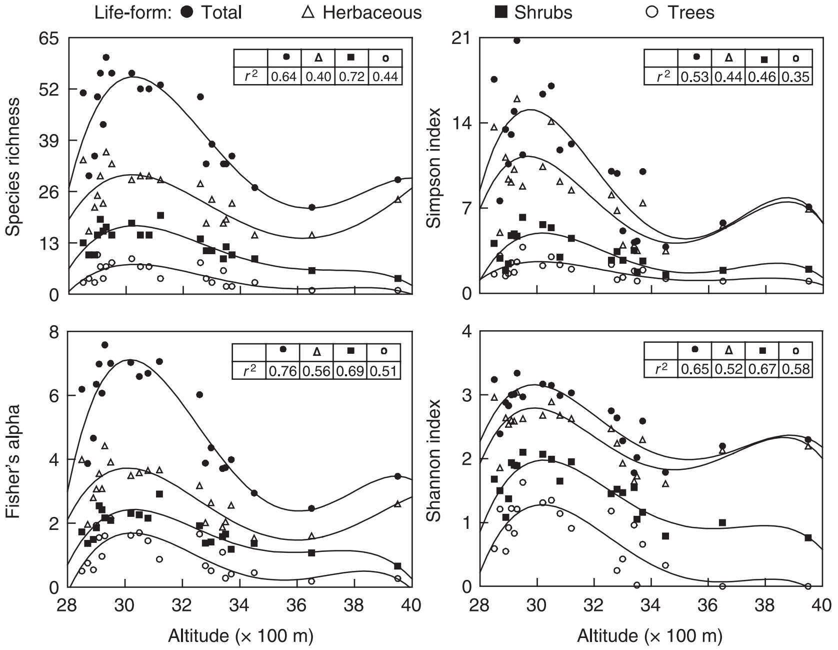

Figure 1 Species richness and diversity indexes by growth form along the elevation gradient in the Sierra Nevada, Mexico ($P < 0.01$ in all cases and life forms).

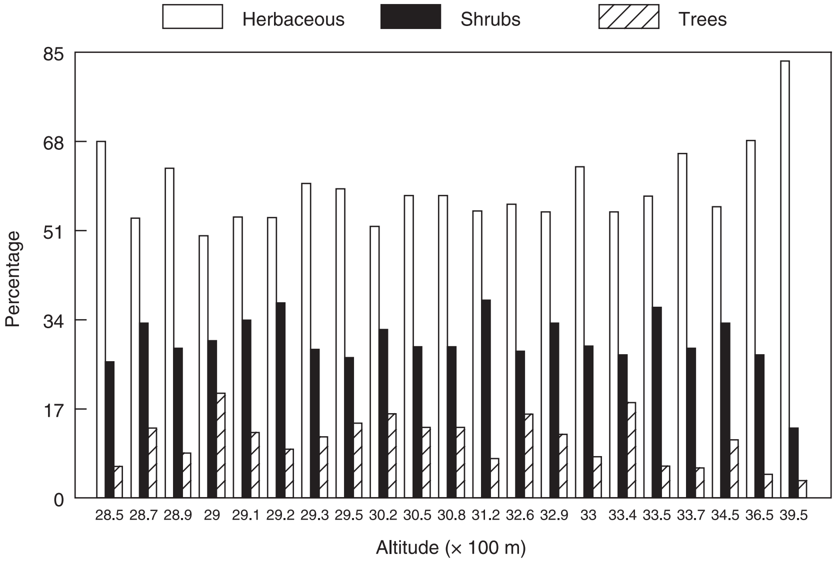

Figure 2 Percentage of herbaceous, shrub and tree species at each sampling site.

Villaseñor and Espinosa-Garcia (2004), only two alien species (*sensu* Richardson *et al.*, 2000) were present along the gradient studied: *Solanum tuberosum* L. and *Reseda luteola* L.

RESULTS

Total species richness and diversity followed a unimodal pattern along the elevation gradient in all vegetation strata, and a fourth order polynomial regression showed a significant fit to the trend of the variation (Fig. 1). Species richness and diversity were intermediate at elevations below 2950 m, high between 2950 and 3200 m, low between 3200 and 3500 m and very low at elevations above 3500 m. The proportions of herbaceous, shrub and tree species at each sampling site were similar; herbaceous forms predominated, followed by shrub forms, with tree forms least prevalent. At sites 20 and 21, where elevation was above 3500 m, the number of herbaceous species was higher and that of tree species lower (Figs 1 & 2).

A linear correlation analysis showed that both species richness and diversity were negatively correlated with elevation and positively correlated with the degree of slope. Colonizing and native species richness were significantly associated ($P < 0.01$) with total species richness. The number of colonizing species decreased abruptly in the upper limit of the elevation gradient. A number of soil variables were significantly associated ($P < 0.05$) with species richness or diversity (or both). A_1 horizon permanent wilting point, clay, Mg^{2+}, Na^+ and K^+; A_2 horizon N^+ and K^+ and O horizon P, Ca and Mg percentages showed a positive correlation. A_1 horizon depth and A_2 field capacity and organic matter were negatively correlated (Fig. 3). Although there is not enough climatic

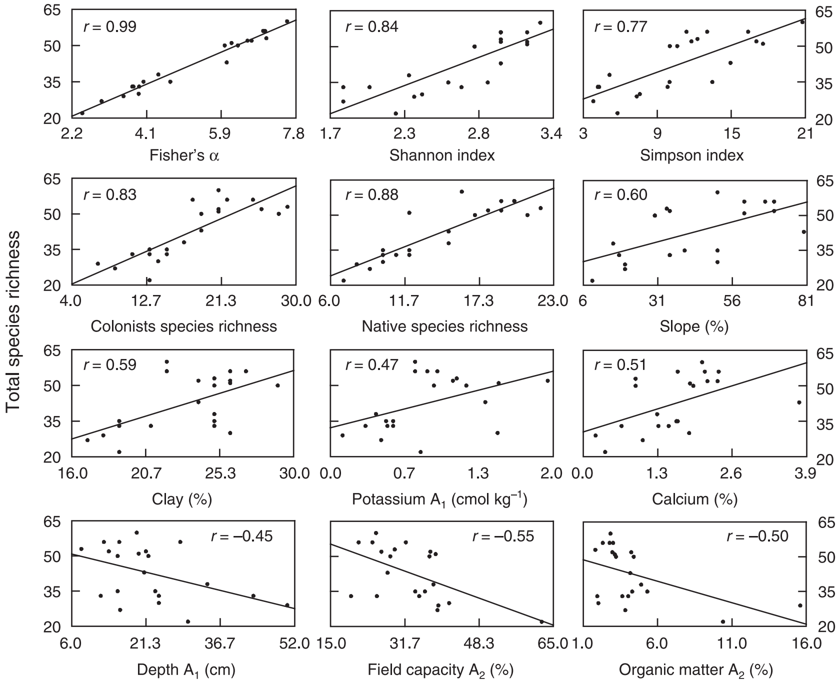

Figure 3 Environmental variables with greatest linear correlation ($P < 0.05$) with total species richness ($A_1 = A_1$ soil horizon; $A_2 = A_2$ soil horizon).

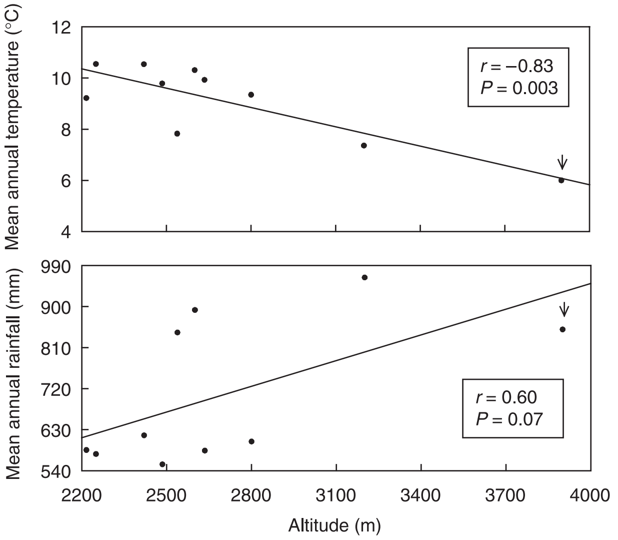

Figure 4 Annual average temperature and precipitation values. Data from 10 weather stations near the study zone. The last point, indicated with an arrow in both graphs, is a probable value reported for Sierra Nevada at elevations above 3900 m.

information available on the study zone, data from the literature and nearby weather stations show a significant negative linear association between temperature and elevation. Precipitation, in contrast, increases with elevation, reaching a maximum at approximately 3200 m and then decreasing (Fig. 4), as it has been suggested by García (1968), Rzedowski (1978) and Toledo and Ordoñez (1993). However, non-significant correlation occurs between total rainfall and elevation ($P < 0.07$); moreover, second, third, or fourth order polynomial regressions were not statistically significant ($P > 0.28$).

Since the correlation between species richness and diversity indexes was highly significant ($P < 0.01$) (Fig. 3), species richness was used as the target variable (Fig. 5). The regression tree analysis indicated that the factors that best explained observed species richness values were elevation, A_2 permanent wilting point, organic matter and field capacity and A_1 Mg^{2+}. Elevation was the most important variable; the regression tree structure indicated two options according to greater or lesser species richness. The first option suggests that maximum species richness values were found at elevations below 3270 m, at sites where A_2 permanent wilting point and organic matter were less than 22.1 and 3.1%, respectively. Species richness was somewhat less but still quite high at sites where A_2 organic matter was greater than 3.1%. Where A_2 permanent wilting point was above 22.1%, species richness had intermediate values. The second option suggests that sites at elevations above 3270 m have low to intermediate species richness; when elevation was above 3410 m, species richness was low, and when A_1 field capacity was greater than 52.6% (arrows with dashed lines), it was even lower. When elevation was below 3410 m, species richness took on intermediate values.

The results of the regression tree analysis were consistent; the direction of the effect of each variable on species richness was the same for every vegetation stratum. The regression tree allows species richness to be described using a few predictor variables. The highest values of species richness were invariably found in mixed forest between 2900 and 3200 m, at sites where A_2 permanent wilting point and organic matter varied between 13.1 and 20.8% and 1.80 and 4.4%, respectively. Species richness was lower in the scrub–oak between 2750 and 2850 m, at sites where A_2 permanent wilting point and organic matter were between 21.8 and 3.1%, respectively, and A_1 Mg^{2+} concentration was 4.7 cmol kg^{-1}. Intermediate species richness values were observed in oak forest between 2850 and 2950 m at sites where A_2 permanent

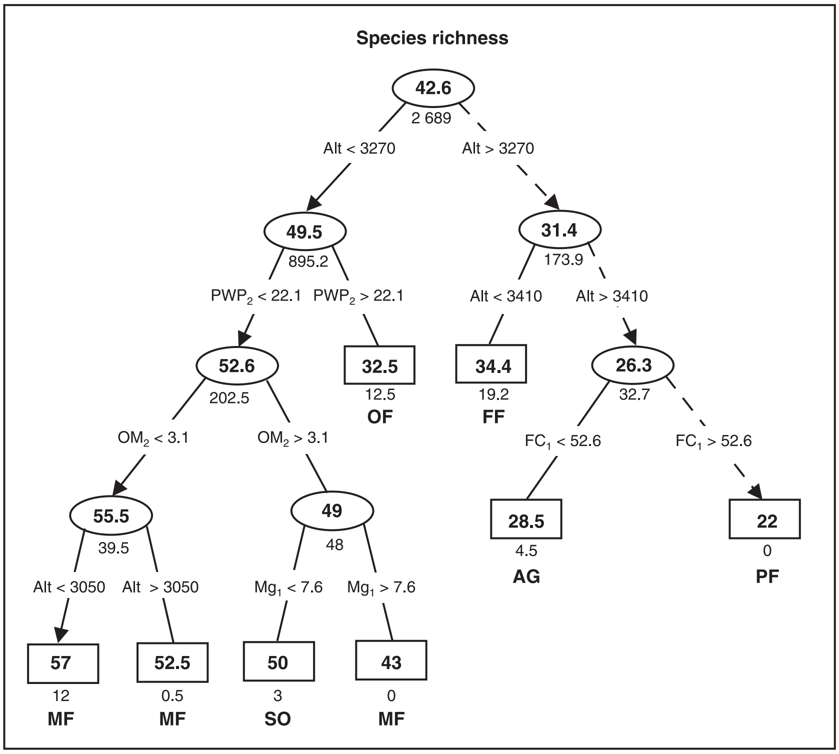

Figure 5 Regression tree for species richness variation along an elevation gradient at Sierra Nevada, Mexico. Rectangles and ellipses represent terminal and non-terminal nodes, respectively. The number inside each rectangle or ellipse represents average sample species richness values which go along the branches of the tree towards a particular terminal node. The number underneath each rectangle or ellipse is the sum of squares associated with the arithmetic mean of all samples going towards the nodes. The numbers at the connections between nodes represent the decision criteria by which a particular environmental value provides the basis for a division. The vectors with solid lines represent the path of highest species richness along the regression tree. The vectors with dashed lines show the path of lowest species richness along the regression tree (Alt = altitude; FC = field capacity; Mg = magnesium; OM = organic matter; PWP = permanent withering point; MF = mixed forest; SO = scrub–oak; OF = oak forest; FF = fir forest; AG = alpine grassland; PF = pine forest).

wilting point was between 22.3 and 25.3%, and in fir forest at elevations between 3100 and 3500 m. The lowest values of species richness were observed in pine forest above 3650 m and in alpine grassland above 3900 m, where A_1 field capacity ranged between 34.9 and 60% (Fig. 5).

Beta diversity between contiguous sites was high except in sites in the intermediate portion of the altitudinal gradient, which shared a large number of species. The species replacement rate between sampling sites tended to be higher as elevation increased, surpassing 90% at elevation extremes (Table 1).

DISCUSSION

In the northern Sierra Nevada, species richness and diversity (both overall and by growth form) tend to have higher values as elevation increases. This trend is not monotonic but unimodal, with maximum values in the lower half and minimum values in the upper half of the elevation gradient. Empirical studies analysed by Rahbek (1995), and more recently the work of Wang *et al*. (2002) and Grytnes and Vetaas (2002) found that this pattern, in which species richness achieves maximum values in lower to intermediate elevations, is the most common one in a variety of ecosystems.

Certain historical, climate and local factors (i.e. soil variables) are significantly related to species richness and diversity along the elevation gradient. Geomorphology, pollen and climate studies consulted by Lauer (1978) confirm that over the last 40,000 years, the Sierra Nevada alternated between cold and hot periods and wet and dry periods, resulting in a diverse array of combinations. Vegetation maps show sharp changes in the distribution of vegetation by elevation over these periods, where temperature and moisture created the dynamic which shaped the most important limiting factors determined by climate.

The regression tree analysis selected elevation as the first criterion for division. This factor operated on an overall scale, while soil variables, operating at the local scale, were used for the decision rule towards the terminal nodes. Both the correlation and the regression tree analyses showed significant associations between species richness and diversity and elevation. Elevation gradients basically reflect precipitation and temperature gradients (Pavón *et al*., 2000; Whittaker *et al*., 2001; Wang *et al*., 2002). The observed unimodal species richness pattern suggests that it could have resulted from the influence of local physical variables (i.e. soils) combined with a non-random pattern (*sensu* Lomolino, 2001) in temperature and precipitation variations along the elevation gradient.

Hamilton and Perrot (1981) believed that the structure and distribution of plant communities on the highest portions of mountain slopes often seem to be related to temperature and other climatic factors, while those at lower elevations may be determined by more benign biotic or abiotic factors. Pausas and Austin (2001) state that the main factors determining species richness patterns at the local level are resource availability and responses to environmental variables that have a direct physiological impact on plant growth or on resource availability.

The relationship between elevation and rainfall in the Valley of Mexico is not a simple linear one. Maximum total annual precipitation and the greatest number of days with measurable rainfall have been recorded at elevations between 2900 and 3200 m (Madrigal, 1967; García, 1968). This is significant, because the

Table 1 Number of species per site (main diagonal, in bold), number of shared species (above main diagonal) and beta diversity (below main diagonal) between the 21 sampling sites along elevation gradient studied (SS = sampling sites)

	Number of shared species																				
SS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	**51**	17	13	12	5	5	6	12	12	8	12	12	8	3	3	3	3	3	3	3	1
2	0.58	**30**	16	20	12	13	13	19	22	17	18	18	18	11	10	9	7	8	8	7	3
3	0.70	0.51	**35**	15	11	12	12	16	15	14	16	13	12	7	8	8	7	8	5	5	2
4	0.76	0.50	0.65	**50**	26	19	27	29	31	23	27	25	25	18	20	15	17	17	14	7	4
5	0.91	0.72	0.76	0.51	**56**	26	37	36	34	33	30	28	29	25	23	16	20	25	18	6	3
6	0.89	0.64	0.69	0.59	0.47	**43**	30	28	31	28	25	28	26	20	18	16	17	21	13	7	1
7	0.89	0.71	0.75	0.51	0.36	0.42	**60**	37	36	33	34	29	32	24	23	16	20	25	15	7	3
8	0.78	0.56	0.65	0.45	0.36	0.43	0.36	**56**	38	31	40	34	35	21	21	16	18	20	15	9	3
9	0.78	0.49	0.67	0.42	0.39	0.37	0.38	0.32	**56**	35	38	33	39	25	23	16	21	24	18	8	3
10	0.84	0.59	0.68	0.55	0.39	0.41	0.41	0.43	0.35	**52**	33	35	31	20	18	17	20	23	16	9	2
11	0.77	0.56	0.63	0.47	0.44	0.47	0.39	0.26	0.30	0.37	**52**	36	34	23	21	16	21	23	18	9	3
12	0.77	0.57	0.70	0.51	0.49	0.42	0.49	0.38	0.39	0.33	0.31	**53**	32	18	18	18	20	20	18	10	3
13	0.84	0.55	0.72	0.50	0.45	0.44	0.42	0.34	0.26	0.39	0.33	0.38	**50**	22	22	16	21	25	17	10	4
14	0.93	0.65	0.79	0.57	0.44	0.47	0.48	0.53	0.44	0.53	0.46	0.58	0.47	**33**	25	17	20	22	18	6	2
15	0.93	0.71	0.78	0.55	0.51	0.56	0.53	0.55	0.51	0.60	0.53	0.60	0.50	0.30	**38**	22	22	22	19	11	4
16	0.93	0.71	0.76	0.64	0.64	0.58	0.66	0.64	0.64	0.60	0.62	0.58	0.61	0.48	0.38	**33**	19	17	17	15	4
17	0.93	0.78	0.79	0.59	0.55	0.55	0.57	0.60	0.53	0.53	0.51	0.53	0.49	0.39	0.38	0.42	**33**	24	21	10	2
18	0.93	0.75	0.77	0.60	0.45	0.46	0.47	0.56	0.47	0.47	0.47	0.55	0.41	0.35	0.40	0.50	0.29	**35**	20	8	3
19	0.92	0.72	0.84	0.64	0.57	0.63	0.66	0.64	0.57	0.59	0.54	0.55	0.56	0.40	0.42	0.43	0.30	0.35	**27**	9	5
20	0.92	0.73	0.82	0.81	0.85	0.78	0.83	0.77	0.79	0.76	0.76	0.73	0.72	0.78	0.63	0.45	0.64	0.72	0.63	**22**	6
21	0.98	0.9	0.94	0.90	0.93	0.97	0.93	0.93	0.93	0.95	0.93	0.93	0.90	0.94	0.88	0.87	0.94	0.91	0.82	0.77	**29**
	Beta diversity																				

highest species richness and diversity in the northern Sierra Nevada are found precisely in the zone receiving the greatest precipitation. Moreover, the relative humidity and shaded microenvironment typical of forests is absent at elevations where alpine and subalpine vegetation grow. Here, solar radiation is direct and the evaporation rate tends to be higher than in the understorey of wooded environments.

It is likely that this elevation range is a transition zone in which the effects of temperature, moisture and local environmental factors (degree of slope, organic matter, water balance and soil nutrients) combine with contrasting spatial variation patterns (some increase with elevation while others decrease), resulting in a greater species interchange between communities. It is the elevation equivalent of the well known 'ecotone effect' (Lomolino, 2001).

Grime (1979) and Huston and DeAngelis (1994) found species richness to be lower where resources were lowest, it was high at intermediate levels, and decreased gradually as resource levels were higher. This pattern is not universal; the specific group of variables responsible for variations in species richness and diversity may be complex and may differ significantly between ecosystems and in different spatial an temporal scales (Pausas & Austin, 2001; Whittaker *et al*., 2001). It is also difficult to distinguish the local effects of physical and chemical soil characteristics on species richness and diversity, due to their dynamic, interactive nature. Organic matter is an important example; it is vital in determining the stability of soil aggregates, as it influences porosity and therefore gas and water exchanges, and thus the liberation and availability of nutrients (Schoenholtz *et al*., 2000).

Species richness and diversity values in the lower-middle portion of the gradient suggest that when temperature and moisture are not acting as limiting factors, the coexistence of a greater number of species is influenced by local variations in the relative quantity of nutrients, physical soil characteristics, topography and biotic factors. The highest values of species richness, the greatest number of colonizing and native species and a low species replacement rate are all found in this zone.

The lower species replacement rate between sites in the middle portion of the altitudinal gradient suggests that environmental conditions there favour the coexistence of a larger number of species (Lomolino, 2001; Wang *et al*., 2002). In contrast, the high species replacement rate between sampling sites — except in the lower-middle portion of the gradient — is indicative of wide environmental differences, and of adaptations between functional types (Wang *et al*., 2002). Few species can tolerate the full spectrum of environmental conditions at gradient extremes (Sánchez-González & López-Mata, 2003).

In the northern Sierra Nevada, elevation has a significant negative linear relationship with temperature (García, 1968; Sánchez-González, 2004) and a positive relationship with a number of other variables such as solar radiation, wind velocity and frost frequency (García, 1968; Rzedowski, 1978).

Lower levels of species richness at elevations above 3500 m can be explained as a function of ecophysiological pressures such as low temperatures, low productivity and shorter growing season (Rahbek, 1995; Brown, 2001; Vetaas & Grytnes, 2002). Added to this, as elevation increases, herbaceous species become more dominant. Their effect on habitat heterogeneity is low; gravitational processes are accelerated, relative humidity is lower and shaded microenvironments are less common (Colwell & Hurt, 1994; Vetaas & Grytnes, 2002; Theurillat *et al*., 2003). This combination of effects related to temperature and physiography suggests a negative effect on species richness.

Organic matter decays slowly in soils that are subjected to low temperatures, resulting in an excess accumulation of humus, which limits soil productivity (Prescott *et al*., 2000) and reduces vascular plant nutrient consumption (Waide *et al*., 1999). Water flow controls the movement of nutrients from the soil to the roots, while low temperatures reduce water conductivity (Cornwell & Grubb, 2003). At the top of the elevation gradient, moisture levels in the deep soil layers, with high field capacity in the A_1 and A_2 horizons, are high. The resulting oxygen deficiency combined with low temperatures is one of the main reasons for the low decomposition rate, resulting in a high accumulation of organic matter in the A_1 and A_2 horizons.

It is likely that low temperatures have contributed to increasing the species richness of specialized plants that can tolerate severe conditions on the Cerro Tláloc summit, and that these limiting conditions help reduce the competitive dominance of certain species. This would facilitate the recruitment of species with different resource restrictions, resulting in a local increase in diversity (Grime, 1979; Moody & Meentemeyer, 2001). Any factor that limits species dominance may promote the coexistence of specialized species at the same time, thereby increasing overall diversity. In addition, it would be expected that the maximum number of endemisms would occur at high elevations, due to isolation mechanisms (Vetaas & Grytnes, 2002). This is confirmed in the case of Mexican alpine grassland, where endemisms at the species level are estimated to be 75% (Challenger, 1998).

In spite of this complexity, in the present study, the regression tree allowed a simple interpretation of the relationship between species richness and environmental factors by reducing the number of variables involved in describing the relationship. The analysis suggested that elevation, A_2 organic matter and permanent wilting point, and A_1 Mg^{2+} and field capacity are the most important variables for explaining species richness patterns in the northern Sierra Nevada.

Sánchez-González (2004) states that the species composition in the temperate forests surrounding the endorheic basin of the Valley of Mexico is similar. Although it is likely that species richness, diversity and replacement rate patterns are also similar between these mountain zones, it is necessary to obtain quantitative data to confirm such an assumption before these forests disappear.

CONCLUSIONS

Species richness and diversity on the western slope of the Cerro Tláloc Mountain was consistently unimodal, both overall and by growth form, reaching maximum values in the lower half of the slope, between 2950 and 3200 m elevation. Beta diversity also increased gradually with elevation, with low values in a transition zone in the middle section of the elevation gradient. Few species were adapted to support the full spectrum of variation in environmental conditions; at the extremes of elevation studied, the species replacement rate was close to 100%. Differences in temperature and moisture along the elevation gradient explain the observed richness and diversity patterns. The lowest values of species richness were seen in the upper half of the gradient, where temperatures are lower. The highest rainfall values coincide with the elevation range exhibiting the highest values of species richness. The linear correlation and the regression tree show that elevation is the variable which best explains variations in species richness and diversity, and that local variables such as the degree of slope and soil organic matter and cations play a secondary role. It is necessary to assess the role of other variables on variations in species richness and diversity. One of these is the rate of human-induced perturbations, since it is likely that in the short term these are having a devastating effect on the vegetation structure of the northern Sierra Nevada, as has already happened in most of the forest zones adjoining the Valley of Mexico.

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