# Vascular plant richness along an elevation gradient at Monte Velino (Central Apennines, Italy)

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## SUMMARY

Species richness was studied during two years in 100 m elevation bands along an altitudinal transect from 1100 m up to 2487 m asl on the south-western slope of Monte Velino. The 1300 to the 2200 m elevation bands have a similar area in the range of 0.36 to 0.40 $km^2$. A total of 636 taxa (species and subspecies) was recorded. Each species was attributed a life form, an elevation category and a chorotype. The richness per elevation band decreases monotonously along the transect with a plateau between 1300 and 1600 m asl. Because of the similarity of the area of the elevation bands between the 1300m and the 2200 m elevation band, the richness pattern along the transect is not merely a function of the area. The rejection of the area hypothesis, at least between 1300 and 2300 m asl, is also demonstrated by the species traits. Most of them show a monotonous pattern with elevation, either decreasing or increasing. The cumulative increase of species richness along the transect follows the Arrhenius' power function $S = C \times A^z$ with a z value of 0.291. Endemics peak at an intermediate elevation in the 2000 m elevation band and follow the isolation-area hypothesis. In that the species-density matches the adiabatic decrease of air temperature, we consider the latter as the driving factor for the pattern of the species richness in relation to elevation. Colder temperatures (a) reduce the species pool in relation to elevation due to an increasingly colder and shorter vegetation period; (b) drive geomorphological processes that both reduce habitats number and spatial heterogeneity, and enhance their convergence and homogenization (temperature-physiography hypothesis). Therefore, area, temperature and isolation are the three main parameters to explain plant richness with elevation for Monte Velino.

## INTRODUCTION

Patterns of plant diversity along elevational gradients have always been a topic of interest in biogeography. Different hypotheses have been put forward to explain elevational patterns including space limitation (area), range width of species, ecological and historical factors (Lomolino, 2001; MacArthur, 1972; Rahbek, 1995; Stevens, 1992). Usually a decrease in plant species richness is observed with increasing altitude (e.g. for high European mountains Ozenda, 1985, 1997; Grabherr et al., 1995; Körner, 2000; Theurillat et al., 2003) but sometimes species richness peaks at mid-altitudes (Rahbek, 1995; Grytnes,

2003; Lomolino, 2001). Several hypotheses like the "mid-domain effect" hypothesis (Colwell et al., 2004; Grytnes, 2003; Hawkins et al., 2005), the "temperature-physiography" hypothesis (Theurillat et al., 2003) and, to some extent, the "elevation effect" (Steenis, 1961; Engeveld, 1985) and the "mass effect" (Shmida and Wilson, 1985) have been developed to explain diversity gradients with elevation. Two hundred years ago Willdenow wrote "the warmer the climate, the greater the number of growing plants" (in Lomolino, 2001). Today, apart from energy, there is no definitive agreement about the mechanisms driving plant distribution with elevation (Lomolino, 2001).

Climate being fundamentally responsible for the distribution of both vascular plants and vegetation (Walter, 1985), mountain systems (orobiomes) often have a much higher diversity of vascular plants than the surrounding lowlands (e.g. Körner, 2002; Körner and Spehn, 2002; Nagy et al., 2003a;b). Mountains, and especially high mountains, form particular climatic systems grouping, over an elevation extension of a few kilometers, climatic variations which occur over latitudinal distances 1000 times greater (Walter, 1985). The direct consequence of the altitudinal extension of the relief is a decrease of the mean air temperature according to a universal adiabatic gradient of about 0.55 K for 100 m in elevation (MacArthur, 1972), which is equivalent to a latitudinal shift of 100 km toward the poles.

The Central Apennines are known for their great diversity of vascular plants. More than 1000 species and subspecies of plants have been recorded there above 1400 m asl, 12,7% of which are endemic (Lucchese and De Simone, 2000). There are several causes for this richness including elevation, extension of the relief, and historical factors such as the role played by the mountains of southern Europe during the Quaternary glaciations. These mountains acted as a refuge for ancient species, at the same time isolating them and thus favoring the development and preservation of endemics. Besides climate and historical factors, land-use is another factor that has an influence on diversity, particularly in the Mediterranean region (Blasi, 1998). For millennia forest and pastoral activities have profoundly modified natural vegetation and the distribution of species.

After two years of study, we document here for the first time for Central Italy the general pattern of plant richness along a transect extending more than 1300 m in elevation on the south-western aspect of Monte Velino.

METHODS

Study area. The study area is located in the Central Apennine (Abruzzo region) on the regular slope of the south-western aspect of Monte Velino (Fig. 1). The elevational transect has an area of 5.336 km²; it is 2 km wide, going from 1100 m asl at its base to 2487 m asl at the summit of Monte Velino (Fig. 2). The area, situa-
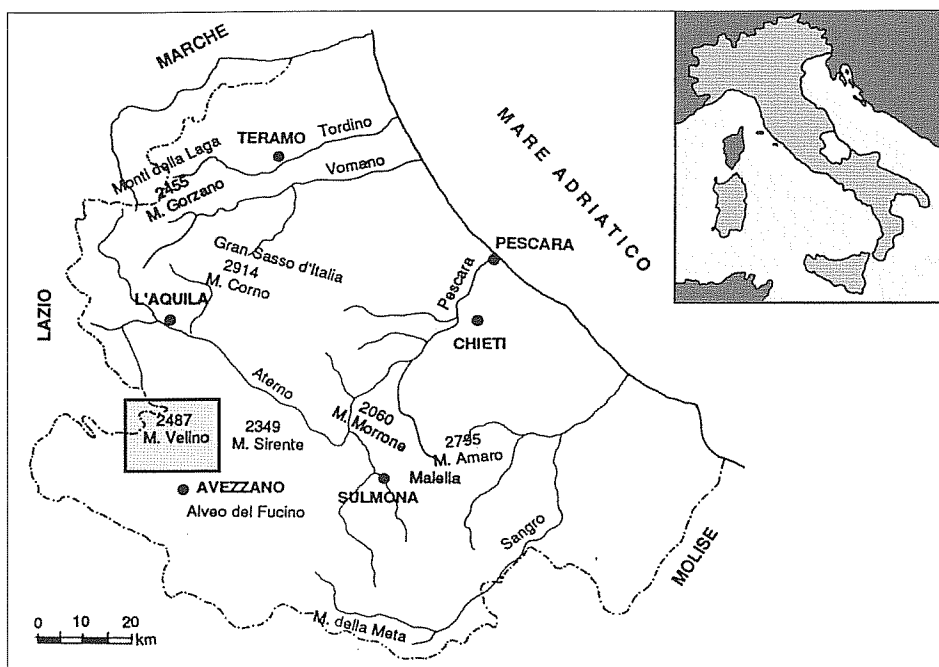
Fig. 1 - Localisation of the study area (Monte Velino) in the Abruzzo Region of Central Appenines

ted entirely on limestone, is characterized by a sub-mediterranean climate. It is almost totally deforested and has been subject to pasturing for millennia (Avena and Blasi, 1980; Petriccione, 1993). The lowest part of the transect, up to ca. 1600 m asl, belongs to the supramediterranean (or montane) vegetation belt, the middle part to the oromediterranean (or subalpine) vegetation belt (ca. 1600-2300 m asl), and the highest part above 2300 m asl to the cryoromediterranean (or alpine) vegetation belt.

Sampling. The transect is divided into 100 m elevation bands along the contours. Due to differences in the steepness of the slopes and the fact that the transect reaches the crest line at 2210 m asl, the areas of the 100 m elevation bands vary within the transect (Tab. I). In each 100 m elevation band all the vascular plants were sampled during the vegetation period 2005 and 2006. The elevation was estimated during recording with the help of Thommen 6000 m altimeter (error $\pm 10$ m).

Plant taxa (species and subspecies; thereafter species for the sake of simplicity) were determined using mainly Pignatti (1982) and Tutin et al. (1964-1980; 1993), with the help of specialized literature (Foggi et al., 1998; 2003; Lattanzi and Tilia, 2002; Lucchese, 1987; Tondi, 2002; Small and Jomphe, 1989; Zohary and Heller, 1984). Each species was attributed a life form, an
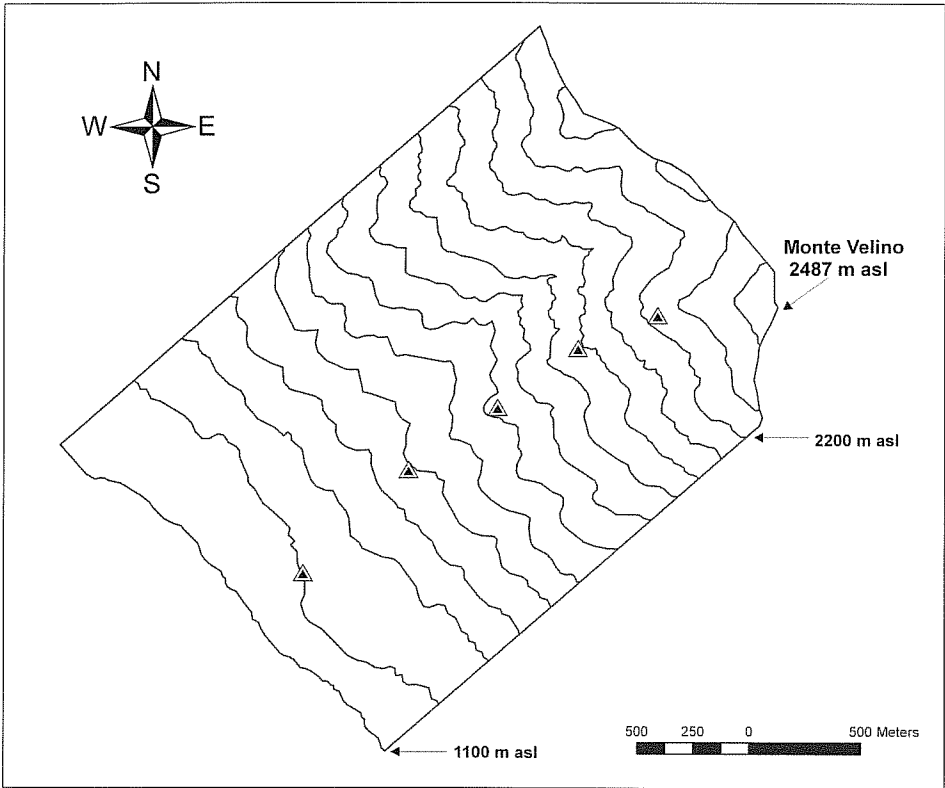
151

Fig. 2 - The elevational transect on the south-western aspect of Monte Velino with the 100 m elevation bands starting at 1100 m asl up to the summit (2487 m asl). The delimitation of the elevation bands follows the contour lines of the 1:25000 topographic map Carta Tecnica Regionale, quadrante 145-II, Regione Abruzzo. The triangles indicate the locations of temperature and precipitation measurements at 1207, 1482, 1728, 1978 and 2238 m asl. UTM E050 coordinates at 1728 m asl: 365090/4667099

elevation category and a chorotype. Life forms and elevation-based categories were taken from Pignatti (1982) and Pignatti (2005); chorotypes from Pignatti (1982) and Aeschimann et al. (2004). Six elevation-based categories were distinguished: colline (0-800 m asl), colline-montane (0-1500 m asl), colline to subalpine (0-2200 m asl), colline to alpine (0 to over 2200 m asl), montane-subalpine (800-2200 m asl) and subalpine-alpine (>1500 m asl), i.e. true oreophytes. Chorotypes have been grouped in seven main categories: (i) cosmopolitan, (ii) Arctic-Alpine and circumboreal, (iii) endemics, (iv) Eurosiberian and Eurasiatic, (v̇) Mediterranean s.l. (including montane-Mediterranean, Mediterranean-West or Central Asiatic, Mediterranean-Turanian), (vi) European s.l. (including South European, Europaeo-Caucasian, Europaeo-West Asiatic) and (vii) South European oreophytes (mainly montane South-European).

Tab. I - Data for each 100 m elevation bands of the transect (1100- : elevation band 1100-1199 m asl)

| Elevation band | 1100- | 1200- | 1300- | 1400- | 1500- | 1600- | 1700- | 1800- | 1900- | 2000- | 2100- | 2200- | 2300- | 2400- | total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Area (km²) | 0.649 | 0.608 | 0.404 | 0.402 | 0.395 | 0.388 | 0.384 | 0.366 | 0.378 | 0.364 | 0.381 | 0.404 | 0.173 | 0.04 | 5.336 |
| richness (observed) | 354 | 305 | 265 | 286 | 286 | 204 | 194 | 159 | 149 | 159 | 113 | 119 | 93 | 51 | 636 |
| richness (interpolated) | 354 | 332 | 321 | 328 | 317 | 256 | 232 | 205 | 188 | 176 | 134 | 125 | 96 | 51 | - |
| richness (cumulated) | 354 | 409 | 448 | 489 | 525 | 540 | 567 | 579 | 591 | 611 | 620 | 630 | 635 | 636 | - |
| % phanerophytes | 12.71 | 11.75 | 11.53 | 10.37 | 9.15 | 8.98 | 6.47 | 5.37 | 4.79 | 3.98 | 2.24 | 1.60 | 1.04 | 0 | 60 |
| % chamaephytes | 12.43 | 12.65 | 13.08 | 12.20 | 13.25 | 17.97 | 20.26 | 18.54 | 20.74 | 23.30 | 21.64 | 22.40 | 23.96 | 31.37 | 75 |
| % hemicryptophytes | 43.50 | 47.89 | 49.84 | 51.22 | 52.05 | 50.00 | 54.31 | 58.54 | 57.45 | 60.80 | 65.67 | 69.60 | 67.71 | 62.75 | 323 |
| % geophytes | 8.47 | 10.54 | 11.53 | 12.50 | 12.62 | 12.89 | 9.05 | 7.32 | 6.91 | 5.68 | 5.97 | 5.60 | 6.25 | 3.92 | 70 |
| % terophytes | 22.88 | 17.17 | 14.02 | 13.72 | 12.93 | 10.16 | 9.91 | 10.24 | 10.11 | 6.25 | 4.48 | 0.80 | 1.04 | 1.96 | 108 |
| % endemics | 3.95 | 4.82 | 5.92 | 5.79 | 6.94 | 8.98 | 11.21 | 12.68 | 14.36 | 17.05 | 20.15 | 22.40 | 26.04 | 19.61 | 49 |
| % cosmopolitan | 9.60 | 9.04 | 8.10 | 7.62 | 7.89 | 5.08 | 4.74 | 5.37 | 5.32 | 3.98 | 3.73 | 2.40 | 2.08 | 0 | 43 |
| % arctic-alpine and circumb. | 0.85 | 1.51 | 1.87 | 2.74 | 2.84 | 3.13 | 3.45 | 2.93 | 3.19 | 3.41 | 4.48 | 6.40 | 6.25 | 11.76 | 19 |
| % eurasiatic and eurosiberian | 15.25 | 15.96 | 17.13 | 18.60 | 15.77 | 16.80 | 15.09 | 13.66 | 13.83 | 10.80 | 5.97 | 7.20 | 3.13 | 0 | 101 |
| % european | 27.68 | 30.12 | 29.91 | 28.96 | 28.39 | 28.13 | 25.43 | 23.41 | 22.34 | 19.89 | 16.42 | 16.80 | 14.58 | 15.69 | 156 |
| % mediterranean | 38.98 | 32.53 | 29.60 | 27.13 | 23.97 | 19.53 | 16.81 | 14.15 | 11.70 | 8.52 | 6.72 | 4.00 | 3.13 | 3.92 | 172 |
| % oreophytes S-european | 3.67 | 6.02 | 7.48 | 9.15 | 14.20 | 18.36 | 23.28 | 27.80 | 29.26 | 36.36 | 42.54 | 40.80 | 44.79 | 49.02 | 96 |
| % colline | 10.45 | 6.02 | 4.98 | 3.35 | 2.86 | 1.95 | 2.16 | 0.98 | 1.06 | 1.14 | 0.75 | 0 | 0 | 0 | 46 |
| % colline-montane | 54.52 | 54.22 | 49.53 | 46.34 | 40.63 | 33.98 | 28.02 | 22.44 | 19.15 | 15.34 | 7.46 | 6.40 | 4.17 | 3.92 | 266 |
| % colline-montane-subalpine | 26.27 | 28.31 | 31.15 | 33.84 | 35.24 | 36.72 | 33.62 | 34.15 | 30.85 | 23.86 | 21.64 | 18.40 | 14.58 | 9.80 | 160 |
| % colline-alpine | 6.21 | 7.23 | 7.79 | 9.45 | 12.70 | 15.23 | 18.53 | 20.98 | 23.40 | 26.14 | 27.61 | 28.80 | 31.25 | 25.49 | 66 |
| % montane-subalpine | 1.98 | 3.01 | 4.67 | 5.18 | 6.35 | 7.81 | 6.47 | 8.29 | 8.51 | 9.66 | 8.21 | 8.00 | 7.29 | 11.76 | 34 |
| % subalpine-alpine | 0.56 | 1.20 | 1.87 | 1.83 | 2.86 | 4.30 | 11.21 | 13.17 | 17.02 | 23.86 | 34.33 | 38.40 | 42.71 | 49.02 | 64 |

Climatic data. Along the transect, precipitation, air and soil temperatures were measured at regular elevation intervals of ca. 250 m starting at 1200 m asl (see Fig. 2), mainly during the vegetation period. Liquid precipitation was measured monthly by taking the mean of a pair of gauges placed at soil level. Vaseline (paraffinum liquidum) was used to prevent evaporation in the gauges. Air and soil temperatures were measured respectively at 2 m above and -10 cm under soil level, using Grant thermistor probes (one measure every minute, registration of the mean every 10 minutes with Grant Squirrel data loggers).

Statistical analyses. Linear regressions (SPSS 13.0 for Windows) were performed on exploratory account only, as the 100 m elevation bands being adjacent along the elevation gradient, the data are not independent and the results of regression analysis are not valid (Veech, 2000). Assuming that the absence of a species between two elevation bands is due most probably to a lack of observation of only two years rather than a real absence, the data were interpolated thus providing potential ranges.
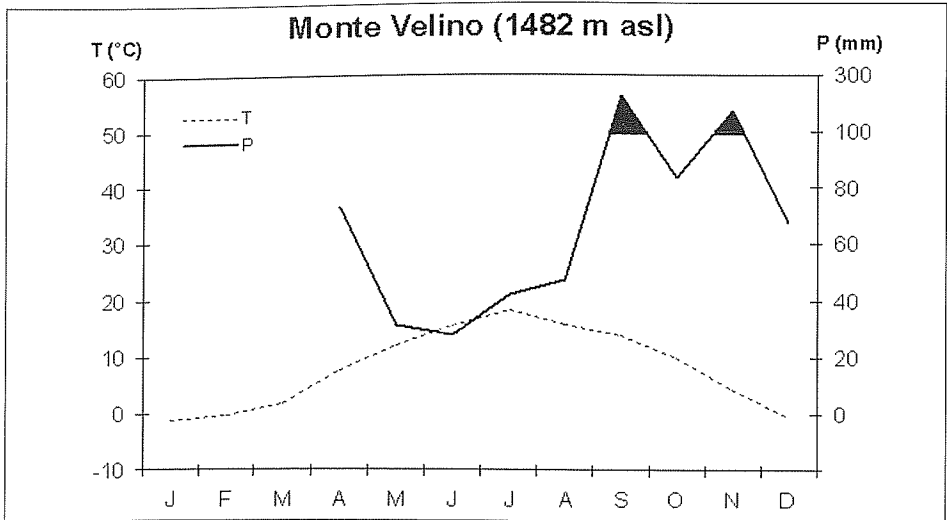
153

Fig. 3 - Ombroclimatic diagram at 1482 m asl for the period July 2005-September 2006. Temperature: mean 2005-2006 for July-September. Precipitation: mean 2005-2006 for July-November; December: precipitation 2006

## RESULTS

### Climatic data

For the two vegetation periods (July 2005-September 2006) of measurement, the ombroclimatic diagram at 1482 m asl (Fig. 3) shows a typical Mediterranean pattern with a summer decrease of precipitation, although with a negligible aridity, and a wetter period in autumn (data for months with snow are not available). For the measurement period, the annual mean air temperature is 8.07 °C (Tab. II).

The adiabatic decrease of air temperature is not regular along the south-western slope of Monte Velino during the vegetation period, with a lower gradient between 1207 and 1482 m asl than at higher elevation (Fig. 4). The mean gradient is 0.47 K/100 m between 1207 and 1482 m asl for the 111 days of measurements, 0.94 K 100 m between 1482 and 1978 m asl for 127 days of measurements and 0.85 K between 1978 and 2238 m asl for 86 days of measurements (from data of Tab. III). In the same way, the pattern of the mean of minima and maxima of air temperature is not regular with elevation

Tab. II - Air temperature data measured at 1482 m asl at 2 m above soil level during the vegetation period 2006 (for location see Fig. 2)

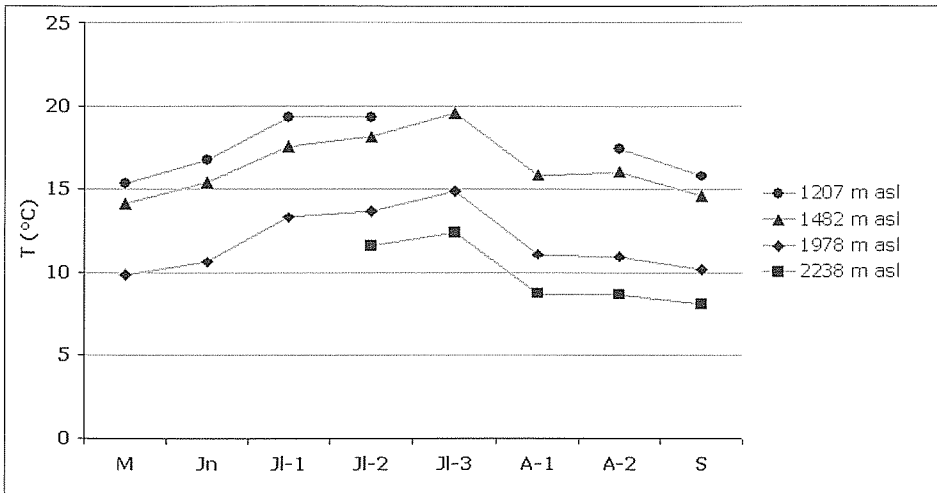| 1482 m | J | F | M | A | M | J | J | A | S | O | N | D | mean |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| T | -1.39 | -0.26 | 1.83 | 7.62 | 11.94 | 15.38 | 18.40 | 15.72 | 13.84 | 10.003 | 4.21 | -0.49 | 8.07 |
| P | | | | 73.08 | 30.67 | 27.52 | 42.18 | 46.90 | 221.64 | 83.92 | 173.67 | 68.11 | - |

154

Fig. 4 - Air temperature pattern at 2 m along elevation during the vegetation period 2006

Tab. III - Air temperature data at 2 m above soil level during the vegetation period 2006 along the altitudinal transect (for location see Fig. 2). Measurement period: M = 26-31 May, Jn = 1-30 June, Jl-1 = 1-5 July, Jl-2 = 6-23 July, Jl-3 = 24-31 July, A-1 = 1-8 August, A-2 = 9-31 August, S = 1-29 September

| Month-Elevation (asl) | 1207 m | 1482 m | 1978 m | 2238 m |
|---|---|---|---|---|
| M | 15.36 | 14.18 | 9.84 | |
| Jn | 16.76 | 15.38 | 10.61 | |
| Jl-1 | 19.30 | 17.59 | 13.32 | |
| Jl-2 | 19.32 | 18.13 | 13.73 | 11.61 |
| Jl-3 | | 19.56 | 14.87 | 12.43 |
| A-1 | | 15.86 | 11.08 | 8.77 |
| A-2 | 17.40 | 16.07 | 10.96 | 8.66 |
| S | 15.78 | 14.61 | 10.16 | 8.07 |

during the vegetation period. In particular, the minima at the lowest elevation (1207 m asl) are slightly lower than those at 1482 m asl, corresponding to a mean increase of the minima of 0.15 K per 100 m (Fig. 5). Higher up, the mean decrease of the minima with elevation is regular with 0.83 K/100 m between 1482 and 1978 m asl for 127 days of measurements and 0.82 K between 1978 and 2238 m asl for 86 days of measurements (data not shown). The elevation pattern for the maxima is regular but shows a stronger decrease at low elevation with a mean gradient of 1.29 K/100 m between 1207 and 1482 m asl, 1.16 K/100 m between 1482 and 1978 m asl and 0.97 K between 1978 and 2238 m asl (data not shown). Precipitation pattern shows that there is little increase in precipitation toward higher elevation during the vegetation period (Fig. 6, Tab. IV). This implies that the summer decrease in precipitation persists with elevation, although there is no aridity.
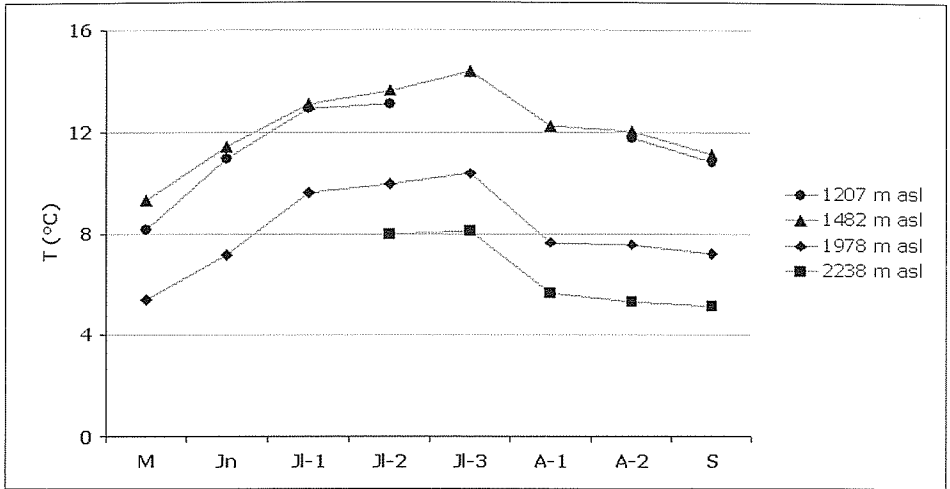
Fig. 5 - Pattern of mean air temperature minima at 2 m along elevation for the vegetation period 2006

Tab. IV - Precipitation at soil level from April to October 2006 along the altitudinal transect (for location see Fig. 2). Mean M-O: mean from May to October

| Elevation (asl) -Month | A | M | J | J | A | S | O | Mean M-O |
|---|---|---|---|---|---|---|---|---|
| 1207 m | 61.35 | 28.42 | 24.81 | 48.31 | 51.25 | 186.91 | 72.17 | 68.65 |
| 1482 m | 73.08 | 30.67 | 27.52 | 42.18 | 46.90 | 221.64 | 83.92 | 75.47 |
| 1728 m | 80.30 | 26.16 | 37.89 | 37.44 | 45.32 | 219.24 | 81.67 | 74.62 |
| 1978 m | | 31.58 | 53.68 | 43.31 | 42.54 | 216.66 | 81.44 | 78.20 |
| 2238 m | | 32.03 | 108.72 | 42.72 | 36.13 | 216.73 | 69.91 | 84.37 |
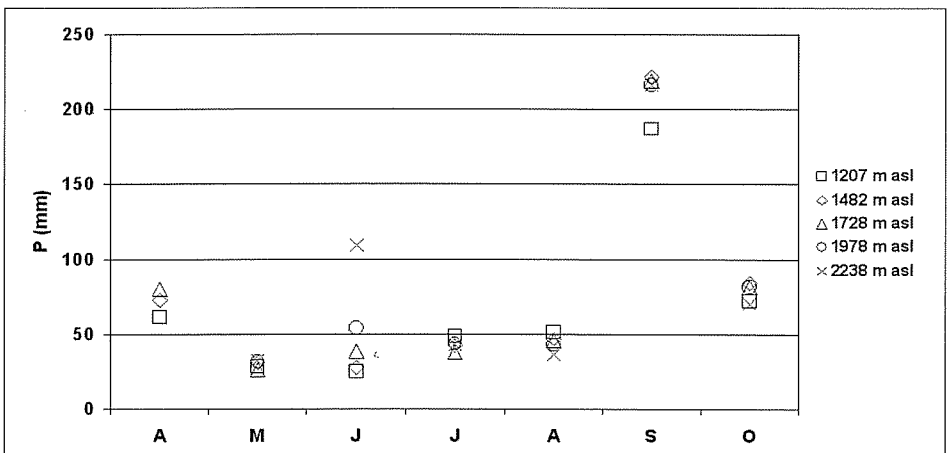


Fig. 6 - Precipitation pattern along elevation for the vegetation periods 2005 and 2006 (mean between 2005 and 2006 for July to October)

## Floristic data

A total of 636 taxa have been recorded for the altitudinal transect (Tab. I). The pattern of vascular plant richness per 100 m elevation band shows a monotonous decrease from the bottom of the transect (1100 m asl) to the top (2487 m asl) with a plateau between 1300 and 1600 m asl (Tab. I, Fig. 7). However, for the first five 100 m elevation bands the decrease in richness (interpolated data) is weak with a mean decrease of -6.3 species/100 m of elevation relative to the upper part of the transect with a mean decrease of -22.9 species/100 m elevation.

The pattern of the percentage of life forms within each 100 m elevation band (interpolated data; Fig. 8, Tab. I) shows a monotonous increase of hemicryptophytes up to 2200 m elevation band ($r^2$ = 0.889) and of chamaephytes ($r^2$ = 0.876). On the other hand, there is a regular decrease of phanerophytes ($r^2$ = 0.988) and therophytes ($r^2$ = 0.922). The proportion of geophytes increases slightly up to the 1600 m elevation band and then decreases monotonously.

The pattern of the percentage of the six elevation-based-categories (Fig. 9, Tab. I) shows that low elevation species (colline, 0-800 m asl) are found until the 2100 m elevation band. Low to mid elevation species (colline-montane, 0-1500 m asl), which form the largest group in absolute value (41.8% of all the species) show a regular decrease with elevation ($r^2$ = 0.980). However, the high elevation species (10% of all the species), i.e. the oreophytes (subalpine-alpine, >1500 m asl) show a strong increase from the 1600 m elevation band upward ($r^2$ = 0.983).
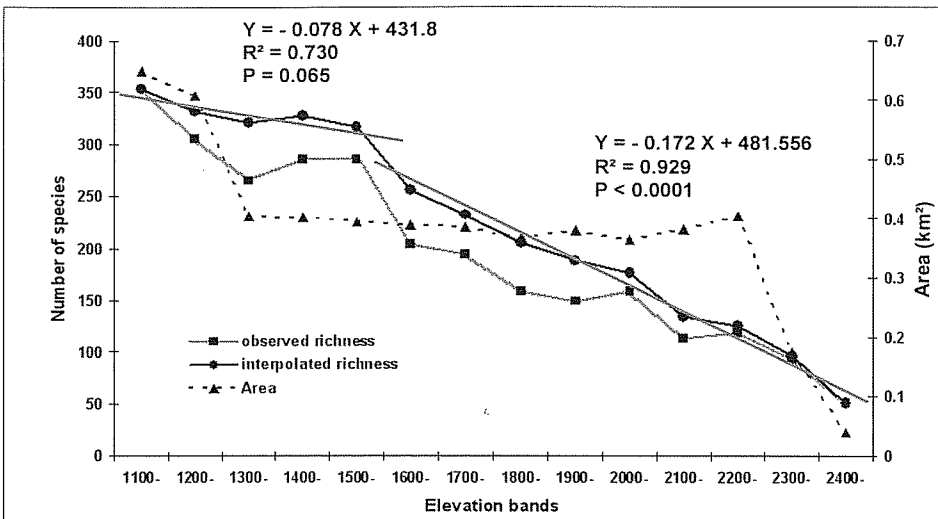


Fig. 7 - Pattern of the number of plant species per 100 m elevation band along the altitudinal transect. The area (km²) of each 100 m elevation band is indicated
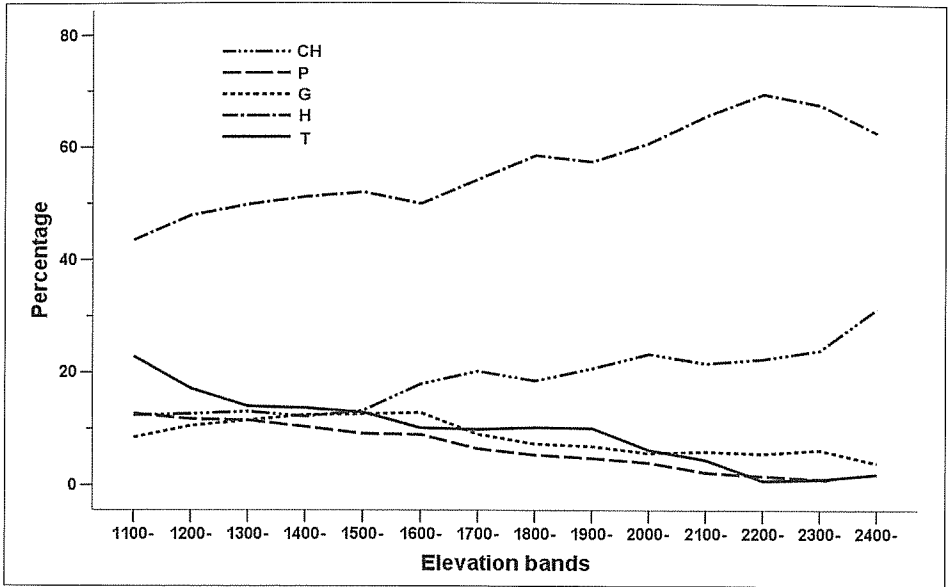
Fig. 8 - Distribution pattern of the percentage of the life forms per 100 m elevation band (interpolated data)
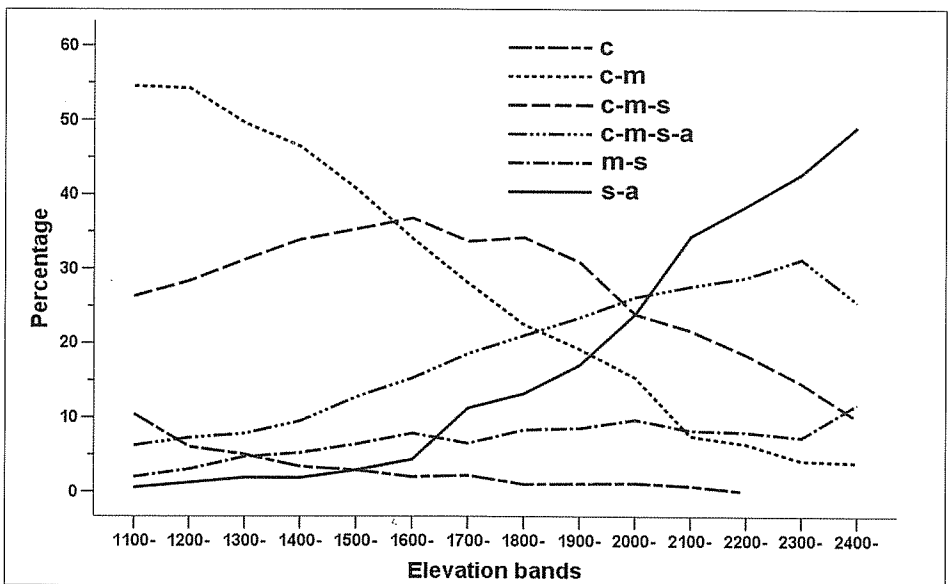


Fig. 9 - Distribution pattern of the percentage of the elevation-based-categories per 100 m elevation band (interpolated data). Categories: c = colline (0-800 m asl); c-m = colline-montane (0-1500 m asl); c-m-s = colline to subalpine (0-2200 m asl); c-m-s-a = olline to alpine (0 to over 2200 m asl); m-s = montane-subalpine (800-1500 m asl); s-a = subalpine-alpine (> 1500 m asl)
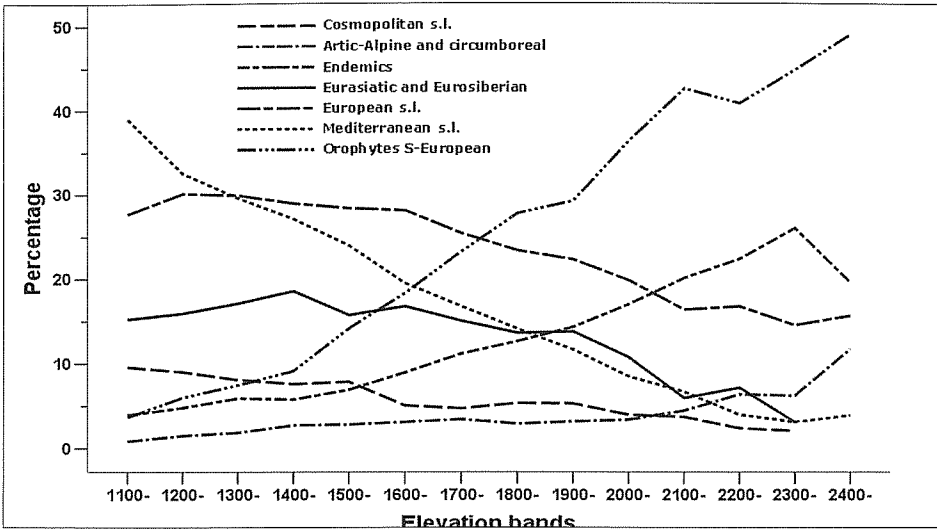
158

Fig. 10 - Distribution pattern of the percentage of the chorotypes per 100 m elevation bands (interpolated data)

In the same way, the proportion of the species with a large range (colline to alpine, 0 to over 2200 m asl) increases regularly with elevation up to the 2300 m elevation band ($r^2 = 0.986$) but the proportion of mid to high elevation species (montane-subalpine, 800-2200 m asl) increases irregularly. For their part, the colline to subalpine (0-2200 m asl) species (25% of all the species) have an unimodal distribution, peaking in the 1600 m elevation band.

The chorological analysis (Fig. 10, Tab. I) shows that the percentage of three categories increases more or less regularly with elevation, i.e. the oreophytes of the mountains of southern Europe (15% of all the species; $r^2 = 0.984$), the endemics up to the 2300 m elevation band ($r^2 = 0.949$) and the Artic-Alpine and circumboreal species ($r^2 = 0.697$). The proportion of all other chorotypes decreases with elevation. Mediterranean s.l. (27% of all the species) and cosmopolitan species decrease regularly (respectively $r^2 = 0.970$ and $r^2 = 0.940$). European s.l. species (24% of all the species) and Eurasiatic and Eurosiberian (16% of all the species) decrease monotonously (respectively $r^2 = 0.900$ and $r^2 = 0.775$).

The cumulative increase of the vascular plant richness (interpolated data) from the lowest 100 m elevation band to the summit follows the power function $S = C \times A^z$ of Arrhenius (1921) with S = number of species, A = area (Figs 11 and 12) in the form

$$S = 7.096 \, A^{0.291} \qquad \text{(eq. 1)}$$

i.e. $\log S = 0.851 + 0.291 \log A \qquad r^2 = 0.992, \, p < 0.0001 \qquad$ (eq. 2)

159

When taking the cumulative increase of plant richness only for a partial transect from the 1600 m elevation band to the 2200 m elevation band (Figs. 11 and 12), i.e. with a similar area for each elevation band and the transect being located entirely within the oromediterranean vegetation band (Fig. 7), the accumulation curve differs and corresponds in the log form to eq. 3.
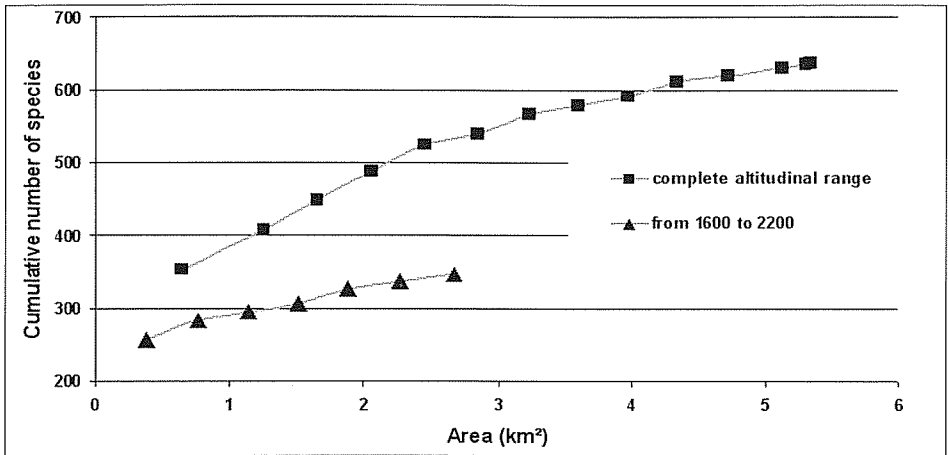


Fig. 11 - Cumulative plant species richness with cumulative area along the altitudinal transect for the complete range (i.e. from the 1100 m elevation band upward) and for the partial range from the 1600- to the 2200 m elevation band (both interpolated data). Area is a surrogate for the 100 m elevation bands
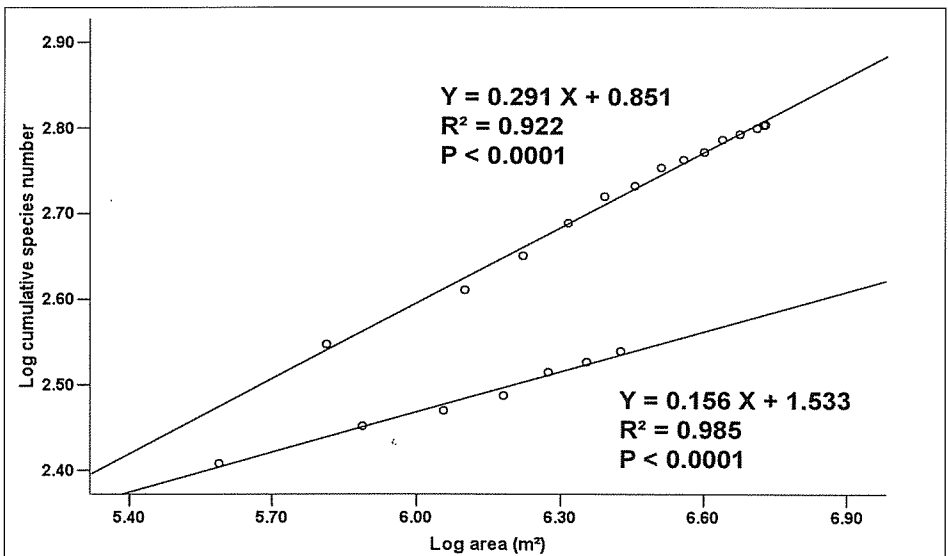


Fig. 12 - Log-transformed cumulative plant species richness (interpolated data) to log-transformed cumulative area for the entire altitudinal transect (upper line) and for a partial transect from the 1600- to the 2200 m elevation bands (lower line)

160

$$\log S = 1.533 + 0.156 \log A \qquad r^2 = 0.985, p < 0.0001 \qquad \text{(eq. 3)}$$

Conversely, the cumulative increase for the partial transect from the 1100 m elevation band up to the 1500 m elevation band, the accumulation curve is very similar to eq. 2:

$$\log S = 0.851 + 0.291 \log A \qquad r^2 = 0.977, p < 0.002 \qquad \text{(eq. 4)}$$

DISCUSSION

In his "Elevation gradients of species-density: historical and prospective views", Lomolino (2001) presented several hypotheses that can be confronted by our results. The area of the 100 m elevation bands being very similar between the 1300 m and the 2200 m elevation band (Fig. 7), the richness pattern is not merely a function of the area. Our results show that the species-density at the regional scale decreases with elevation, rejecting the null hypothesis that species-density does not change significantly (Lomolino, 2001). In the same way, although an identical distribution pattern of richness would probably be found at the mountain range and be correlated to the total area per 100 m elevation band, the area hypothesis can be rejected by our results, at least between 1300 and 2300 m asl. This is also demonstrated by the species traits. Some of the species traits (life forms, elevation types, chorotypes) show a monotonous, decreasing pattern with elevation like richness. These are traits corresponding mainly to a low elevation or a warm climate, i.e. phanerophytes, geophytes and therophytes among the life forms, colline, colline-montane species for the elevation types, and cosmopolitan, Eurasiatic and Eurosiberian, European s.l. and Mediterranean s.l. species for the chorotypes (Figs. 8, 9 and 10) and they would support an area hypothesis. However, there are traits showing a reverse pattern, especially up to the 2300 m elevation band, i.e. they increase with elevation. These traits correspond mainly to high elevation or a cold climate. They are hemicryptophytes and chamaephytes for the life forms, colline to alpine, montane-subalpine and subalpine-alpine species for the elevation types, and South European oreophytes, Arctic-Alpine and boreal species for the chorotypes. In addition, there are traits showing a hump-shaped pattern like the colline to subalpine elevation type. From the upper subalpine upward, the proportion of hemicryptophytes ($>60\%$) and chamaephytes ($>20\%$) matches the results from comparable studies in other mountain ranges (Agakanjanz and Breckle, 1995; Theurillat et al., 2003), as well as a more general pattern for high mountain ranges (see Nagy et al., 2003b).

On the other hand, the distribution pattern of endemics and cosmopolitan species follows the isolation-area hypothesis (Lomolino, 2001). Endemics peak in the 2000 m elevation band with 30 species (data not shown), i.e. at an intermediate elevation, and the proportion increases with elevation, as shown also for

161

the Majella (Central Apennines) by Stanisci et al. (2005). The decrease in the 2400 m elevation band results most probably from the very small area of the elevation band. Cosmopolitan species have the maximum number in the lowest elevation band and the proportion decreases constantly with elevation. According to Lomolino (2001), the feedback among zonal communities could explain peaks in species-density at intermediate elevation. Although this is not the case with our results, the plateau observed between the 1300 and 1500 m elevation bands, i.e. in the upper part of the mesomediterranean (montane) vegetation belt, could result from such an effect with the appearance of subalpine-alpine species extending downward from the next oromediterranean vegetation belt.

The altitudinal pattern of species richness is often compared to the latitudinal pattern, although the two variables are not fully comparable (Chapin and Körner, 1995; Rahbek, 1995). According to Rosenzweig (2002), the latitudinal pattern of the species richness outside of the tropics could simply reflect a decreasing gradient of tropical species extending outside the tropical zone. By taking away these species, the gradient could disappear as the global areas of the extra-tropical climatic zones are comparable. Applying this reasoning in our particular case, one could expect that, by taking away the low elevation species in the 100 m elevation bands of comparable area within the bioclimatic oromediterranean (subalpine) vegetation belt between 1600 and 2300 m asl, the richness of the 100 m elevation bands would become the same. We tested this hypotheses by taking away (a) the low- to mid-elevation species (colline, colline-montane elevation types) and (b) additionally the colline to subalpine type (Fig. 13). In the first case, the species-density continues to decrease, although only slightly for the next two 100 m elevation bands. In the second case, the species-density increases up to the 2000 m elevation band and then decreases. The decrease of the species-density in the oromediterranean vegetation belt cannot be simply attributed to the decrease of low elevation species. The species-area relationship still holds, however, in both cases (Fig. 14), that is the cumulative number of species still increases, with:

$$\log S = 0.984 + 0.219 \log A \qquad r^2 = 0.986, p<0.0001 \qquad \text{(eq. 5)}$$

when taking away the colline and colline-montane species, and

$$\log S = -0.246 + 0.374 \log A \quad r^2 = 0.984, p<0.0001 \qquad \text{(eq. 6)}$$

when taking away the colline, colline-montane and colline to subalpine species. The mean decrease of 22.9 species per 100 m in the oromediterranean (subalpine) belt matches the order of magnitude (15-47) found in other mountain ranges (Körner, 2001; Nagy et al., 2003b).

In relation to the species-area relationship, mountain summits are considered to be a special case of islands (MacArthur, 1972; Lomolino, 2001). The richness-area relationship holds with the elevation (Figs. 11 and 12) and the z

values of 0.291 for the total transect is in the range of the island values (0.25-0.35; Rosenzweig, 2002). This is not the case for the z value of 0.156 for the partial transect between the 1600 and 2200 m elevation band which would relate to a mainland value (0.13-0.18). The increase of richness with the cumu-
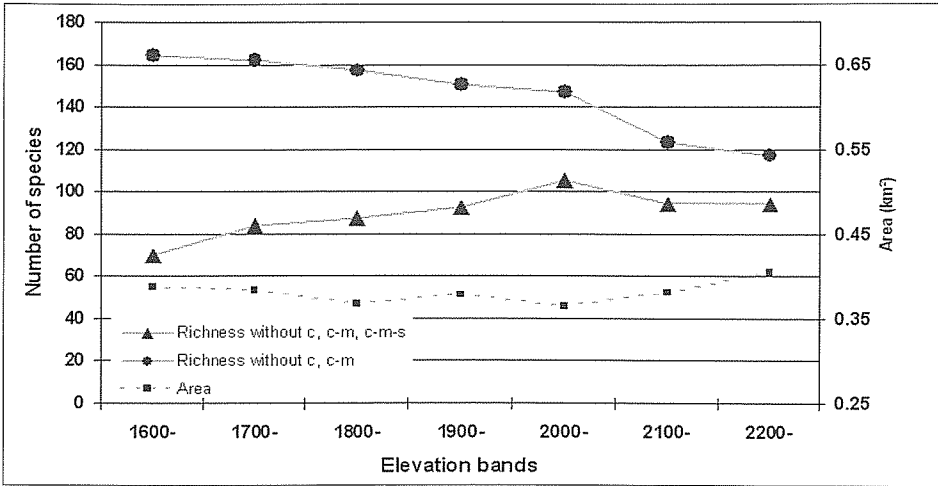


Fig. 13 - Pattern of reduced species-density between the 1600- and 2200 m elevation band by taking away colline and colline-montane species (circles) and colline-montane-subalpine species in addition (triangles)
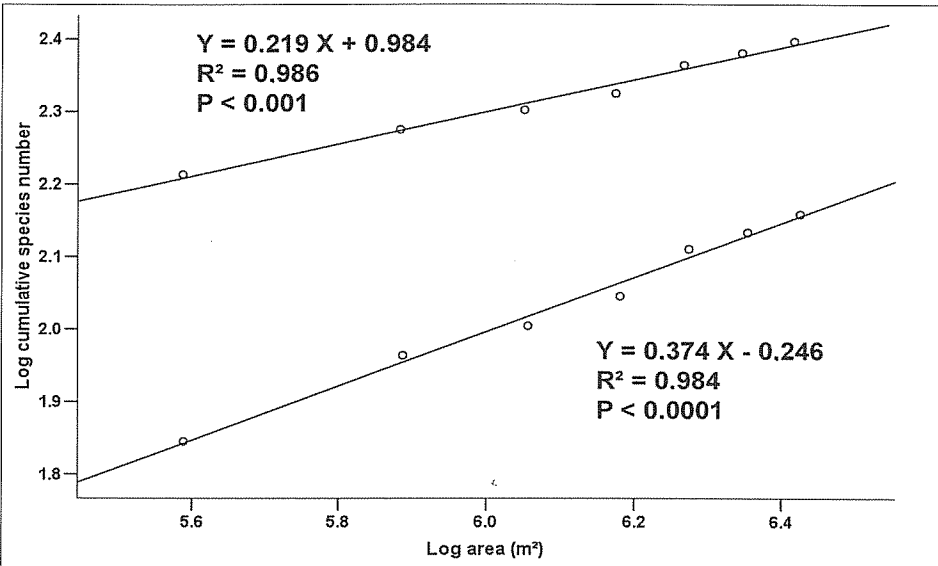


Fig. 14 - Log-transformed of a reduced cumulative plant species richness (interpolated data) to log-transformed cumulative area for the 1600- to the 2200 m elevation bands. Upper line: richness without colline and colline-montane species. Lower line: richness without colline, colline-montane and colline to subalpine species.

163

lative area along the altitudinal transect (Figs 11 and 12) is somehow counterintuitive when looking at the richness pattern per elevation band (Fig. 7). That means that, even if species-density decreases, new habitats are added with elevation, at least in the sense of those discriminated by the species themselves (Rosenzweig, 2002). That is, for instance, cold rock faces or boulders at high elevation respectively to warm rock faces or boulders at low elevation. Therefore, even if habitat types or habitat numbers per se decrease with elevation in high mountains, the species pool may still increase up to the limit of plant life.

Recently, several energy-related hypotheses have been put forward to explain global richness gradients (e.g. Evans et al., 2005; Hawkins et al., 2003; Kalmar and Currie, 2006; O'Brien, 2006). For elevation patterns, Rahbek (1995) and Theurillat et al. (2003) consider temperature, an energy-related factor, as the driving factor associated with physiographic factors (the temperature-physiography hypothesis, Theurillat et. al, 2003). Indeed, because of the adiabatic decrease, temperature is an appealing factor. In our particular case, the weak decrease in richness up to the 1500 m elevation band (-7.4 species/100 m, interpolated data; -13.6 species/100 m, observed data) corresponds to the weak adiabatic decrease of 0.47 K/100 m between 1207 and 1482 m asl (Fig. 4). The stronger decrease in richness upward (-26.6 species/100 m, interpolated data; -23.5 species/100 m, observed data) corresponds to the stronger adiabatic decrease of 0.94 K 100 m between 1482 and 1978 m asl and 0.85 K between 1978 and 2238 m asl. The weak adiabatic gradient up to 1500 m is probably a consequence of the inversion phenomena for the minima in this part of the transect, the means being higher at 1482 m asl than at 1207 m asl (Fig. 5), and the slightly stronger gradient for the maxima not being able to compensate for such an inversion.

With elevation, the temperature decrease has a direct effect at the biological level (Körner, 2003), selecting increasingly the better cold-adapted species, i.e. those that can live with a shorter vegetation period. At the community level, colder temperatures reduce productivity and thus habitat diversification. At the physiographic level of the nano- and microrelief (respectively 1-100 cm, 1-100 m), they reduce habitats through geomorphological processes like fluvial processes that decrease with an increasing winter length, and periglacial processes, that increase with colder temperature. At the same time, all these processes, and often also an increase of steep slopes with elevation (Theurillat and Guisan, 2001; 2002) enhance habitat convergence. Along the elevation transect, a landscape analysis (unpublished data) reveals an increasing homogenization (finer grain) and a reduced spatial heterogeneity, i.e. less mosaic through fragmentation, of the habitats with elevation. In addition, a reduced productivity and a shorter vegetation period reduce the human influence, a source of secondary habitats.

The observed decrease of the species-density with elevation at the regional level in the Central Apennines fits the temperature-physiography model which

assumes that colder temperature reduces (a) the species pool with elevation due to an increasingly colder and shorter vegetation period and (b) the habitat availability by influencing geomorphological processes, providing that other limiting ecological factors, e.g. like water, do not play a part. However, the cumulative richness with elevation indicates that new species are added at the highest elevations, especially endemics, and thus isolation also plays a part. Therefore, the variation of plant richness with elevation for Monte Velino depends on three main parameters, area, temperature and isolation, fitting the global model found by Kalmar and Currie (2006) for birds.

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