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Consistent Shifts in Alpine Plant Traits along a Mesotopographical Gradient

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Abstract

Despite an increasing interest in the study of functional diversity, there have been few attempts to link plant traits, habitat variation, and community structure in Alpine landscapes. These interrelationships were examined along a snowmelt and growing-season-length gradient determined by mesotopographical variations. The study site was chosen so as to encompass much of the floristic beta diversity encountered at the Alpine belt of the southwestern Alps. A three-table ordination technique, named RLQ, was used to unravel on a quantitative basis the co-structure of a plot-by-environmental-variable table, a plot-by-species table, and a species-by-traits table. The main covariations between traits and habitat were (1) an increased specific leaf area (SLA) and leaf nitrogen content on a mass basis (N_{mass}) in late-meting sites, (2) a trend toward upright and thick leaves in the most exposed, physically disturbed, early-melting sites, and (3) an increasing leaf area in the middle of the gradient, which also exhibits small-scale disturbance due to the Alpine marmot. The interplay of intermediate snow-melting dates and intense zoogenic disturbance appears to promote plant diversity and the persistence of species whose mean-elevation distribution is located much below the study site. The adaptive value of trait attributes along the mesotopographical gradient is discussed within the broader context of plant strategies in temperate Alpine grasslands.

Introduction

Plant strategies have been defined as sets of coadapted life-history traits, each set being designed to solve a particular ecological problem (Stearns, 1989). It is assumed that (1) habitat heterogeneity provides the template upon which evolutionary processes forge plant strategies and (2) species' functional traits are the outcome of a long-term history of adaptation (Southwood, 1988). At the ecological scale, a fundamental tenet is to consider the habitat template as a filter able to sort species according to their particular combination of traits (Keddy, 1992). Much effort has been devoted to the examination of variations in plant traits along resource and disturbance gradients, widely considered as the two main axes of the habitat template (Grime, 1977; Southwood, 1988). Consistent patterns of trait variations along these gradients are generally held as indirect evidence that ecological sorting was an important mechanism in determining current species assemblages (Ribera et al., 2001).

The establishment of Alpine plant communities of the European temperate mountains dates back to the last deglaciation, i.e., ca. 15,000 yr BP in the Alps (Frenzel et al., 1992). This short time period precludes any significant in situ local evolution, and the postglacial history of Alpine flora may reasonably be viewed as the history of colonization of a new habitat by a set of species with already-evolved traits. Therefore, Alpine plant communities are particularly suitable to test to what extent ecological sorting of species might have determined species assemblages.

Arctic and Alpine plant communities exhibit a high species turnover along mesotopographical gradients (e.g., Billings and Bliss, 1959; Kudo and Ito, 1992; Walker et al., 1993; Stanton et al., 1994; Onipchenko et al., 1998; Michalet et al., 2002). These gradients correspond to a mesoscale habitat heterogeneity (Billings, 1974) and typically range from snow-free, wind-exposed crests to long-lasting snowdrifts. In combination with wind, mesotopography controls snowpack accumulation and hence the growing-season length. Snow-cover duration has the potential to affect plant growth through its influence on temperature and light regime (review in Körner, 1999), wind exposure (Cernusca, 1976), soil-water content (Isard, 1986), nitrogen availability (Bowman, 1992), and disturbance regime (Komarkova, 1993). It is therefore widely recognized that consistent and repeated differences in snow-melting patterns largely determine the nature and intensity of stress and/or disturbance that plants have to cope with and, as such, are expected to be a strong ecological driver of species sorting for Alpine plant communities.

Although shifts in plant functional traits have been extensively investigated along gradients in elevation or latitude (reviews in Friend and Woodward, 1990; Körner, 1999), few attempts have been made to examine high-elevation species' traits along mesotopography (but see Kudo, 1992, 1996; Kudo et al., 1999). In particular, the problem has never been addressed in the framework of gradient analysis and plant-community structure. However, as outlined by Diaz et al. (1999), consistent linkages between habitat and functional diversity should rely on comparative and quantitative analyses, carried out at the community level.

Ecological data usually consist of three tables: a plot-by-species table (L) giving the abundances of the various species in each sample unit, a plot-by-environmental-variable table describing the habitat template (table R), and a species-by-traits table (Q) qualifying morphological or physiological features of species. Dolédec et al. (1996) proposed a generalized co-inertia analysis of tables R, L, and Q as a heuristic method to search for linkages between habitat and traits, a problem generally known as the "fourth corner" problem (Legendre et al., 1997). Relating life-history traits of species with the main sources of environmental variability has been successfully carried out by using the RLQ technique for both plant (Barbaro et al., 2000) and animal assemblages (Ribera et al., 2001; Hausner et al., 2003).

Whether it is possible to detect any significant relationship between traits and habitat obviously depends on the list of examined traits. A few traits—e.g., seed mass, specific leaf area (SLA), and height—may serve as surrogates for setting plant strategy (Westoby, 1998; Weiher et al., 1999). These traits are strongly related to the

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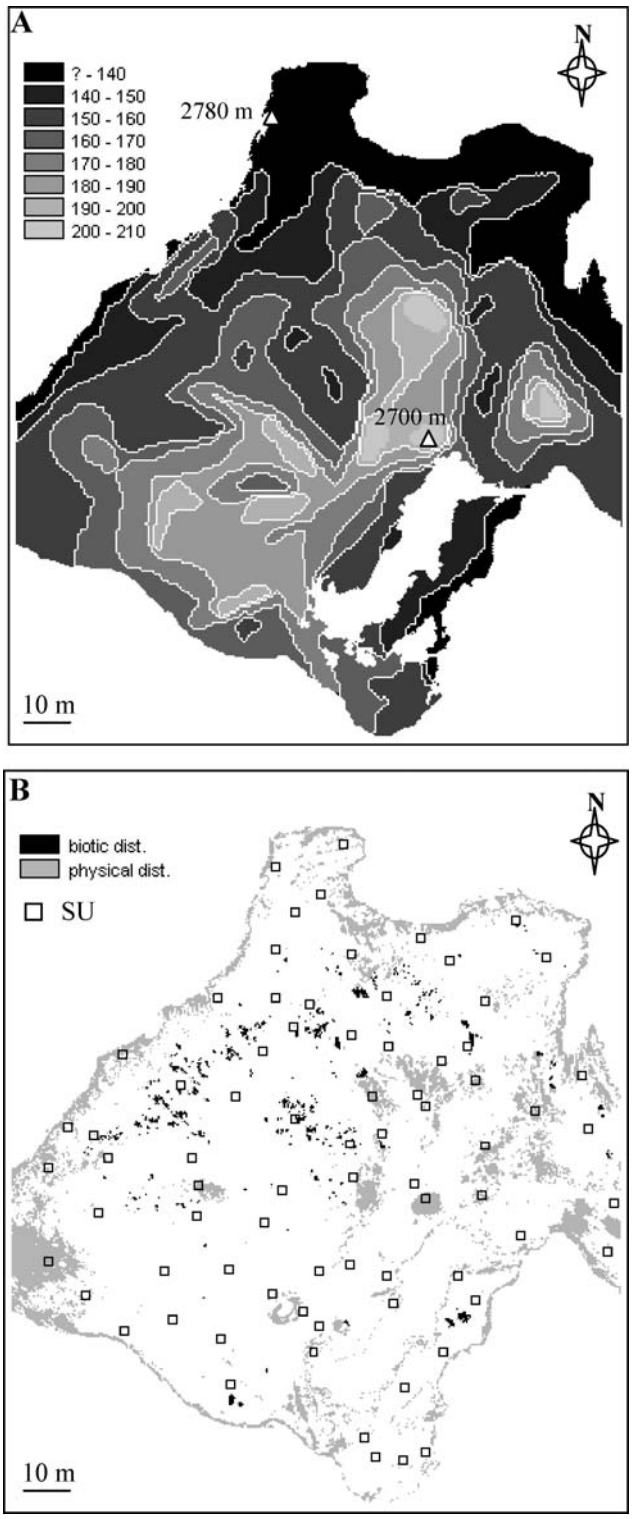


FIGURE 1. (A) Mean snowmelt isoclines in Julian days of the study site. Snow-melting dates were documented from a weekly survey during the years 1997–1999. (B) Distribution of zoogenic (black) and physical (gray) disturbance (dist.) patches. Disturbed patches were mapped from a 1990 aerial photograph and assigned to zoogenic or physical processes by field inspection. The squares indicate the location of the 75 sampling units (SUs).

fundamental processes of plant life, i.e., dispersal, establishment, and persistence (Westoby, 1998; Weiher et al., 1999). Large-scale comparisons among biomes including temperate Alpine meadows give evidence that these traits may be viewed as relevant functional markers particularly suitable for predicting species performance along gradients (Reich et al., 1997).

The aim of the present work is thus to test for a significant relationship between this set of key traits and mesotopographical heterogeneity in Alpine plant communities. More specifically, the attempt is to determine which particular combination of trait attributes are to be expected depending on the particular position along the mesotopographical gradient. The study is also intended to provide an insightful framework for further discussion of the adaptive value of variations in plant traits along a gradient in growing-season length in temperate Alpine grasslands.

Materials and Methods

STUDY SITE

Our research site is located in the Grand Galibier massif, which is part of the southwestern Alps (Lieu-dit Aravo, Commune de Valloire, France, 45°7′N, 6°5′E). The site was chosen in 1997 while conducting a large-scale study of relationships between species and environment (Bounemoura et al., 1998). The site looks like an inclined depression of ~2 ha, located on a mostly south-facing slope between 2700 and 2750 m. The vegetation is composed of truly Alpine grasslands, so interpreted because the potential treeline is thought to occur at ~2300–2400 m in the area (Ozenda, 1985). The bedrock is uniformly calcareous shales. Soils are generally deep (as much as 1 m in the most concave parts). Since 1960, the site has been moderately grazed by sheep at the end of the growing season (generally between the end of August and mid-September). The herd never rests on the site during the night.

FLORISTIC DATA

In July 2000, we established a temporary grid by marking points at each 10-m interval. For each of the 445 grid points, we noted the occurrence and abundance of the 10 dominant plants on a surface of 5×5 m centered around each marked position. Twelve main plant communities were sorted by a cluster analysis. On the basis of this preliminary work, 75 of the 5×5 m square plots, thereafter referred as sampling units (SUs), were chosen for a complete vegetation survey during summer 2001. SUs were chosen so as to sample in each community type and to cover the whole area of the study site (Fig. 1B). We left a distance of at least 10 m between each plot. The floristic composition of each plot was determined by visually estimating the percentage cover of each vascular plant species. A six-level scale was used: 1: <5%; 2: 5–10%; 3: 10–25%; 4: 25–50%; 5: 50–75%; 6: >75%. In total, 130 species of vascular plants were recorded. Rare species occurring in less than four floristic surveys were removed before statistical analysis, and the floristic table (table L) finally contained 75 rows (sites or SUs) and 82 columns (species).

ENVIRONMENTAL VARIABLES

The mesotopography of the study area causes a strong gradient of snow-cover duration. For three years (1997–1999), snowmelt isoclines were recorded every 2 wk on a map derived from an aerial photograph (Fig. 1A). Because of the winter closure of the Galibier Pass road, it was not possible to visit the site before mid-May. The mean elapsed time between the earliest and the latest melting sites—around two months—is hence underestimated. However, erratic records during winter indicated that the snow cover on windy ridges and upper most slopes was exceptionally variable and snow-free periods were observed even in midwinter. The last spots of snow usually disappear around mid-July.

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TABLE 1

Environmental variables of table R.

Abbreviation	Comments
Aspect	Relative south aspect (opposite of the sine of aspect with flat coded 0)
Slope	Slope inclination in degrees
Form	Microtopographic landform index: 1 = convexity, 2 = convex slope, 3 = right slope, 4 = concave slope, 5 = concavity
Snow	Mean snowmelt date (Julian day) averaged over 1997–1999
PhysD	Physical disturbance, i.e., percentage of unvegetated soil due to physical processes
ZoogD	Zoogenic disturbance, i.e., % of unvegetated soil due to marmot activity

TABLE 2

Plant traits of table Q.

Abbreviation	Comments
Height	Vegetative height in centimeters
Spread	Maximum lateral spread of clonal plants in centimeters
Angle	Leaf elevation angle estimated at the middle of the lamina
Area	Area of a single leaf
Thick	Maximum thickness of a leaf cross section (avoiding the midrib)
SLA	Specific leaf area
N_{mass}	Mass-based leaf nitrogen content
Seed	Seed mass

For each of the 75 SUs, we documented the following six environmental variables (see Table 1): the mean snowmelt date (as a Julian day) from the 1997–1999 survey, the slope inclination (in degrees), the aspect, the microscale landform, and the disturbance level. Disturbance was quantified as the relative area (%) of the plot covered by unvegetated "frost-churned soil" during the snow-melting period (Fox, 1981). We distinguished two main sources of disturbance (Fig. 1B): a physical disturbance driven by periglacial processes (cryoturbation and solifluction) and a zoogenic disturbance due to the trampling and burrowing activities of the Alpine marmot, *Marmota marmota* L. Bare-ground patches due to marmot activity were mostly concentrated on the steeper south-facing slopes with intermediate time of snow melting (Fig. 1B).

For three SUs of each community, we harvested the peak standing biomass in a 50×50 cm quadrat at the end of July. Material was dried at 85°C for 24 h and weighed. In addition, we collected a soil sample 5–10 cm deep. Soil was air dried and sieved to retain the <2-mm fraction. The pH was measured in H_2O in a 1:2.5 (g:g) soil/solution suspension. Total carbon and nitrogen were determined in ground samples with a CHONS microanalyzer.

TRAITS MEASUREMENTS

Plant traits (Table 2) measurements were taken in July or August 2001. All field measurements or leaf sampling were done between 10:00 a.m. and 3:00 p.m. All the investigated species exhibit deciduous leaves except some rosette forbs with overwintering leaves (*Geum montanum*, for example). No evergreen shrubs were observed in our study site. Several species of graminoids exhibit a particular leaf habit; late-season–initiated leaves keep a basal green part during the winter and resume growth the next year.

Vegetative height, lateral spread, and leaf angle were measured in situ. Leaf thickness, leaf surface, and specific leaf area (SLA) were determined on samples collected from the study site and transported in a wet and cool container to the nearby Alpine field station of Lautaret. Leaf angle was measured with a protractor. Plants with upright leaves were assigned an angle of 90°, and those with leaves parallel to the ground surface were assigned an angle of 0°. Measurements were made on fully expanded leaves located in the middle of the stem. When both upright and horizontal leaves occurred on the same plant (some rosette species with cauline leaves), we set a value of 45°.

Because many species exhibit some level of phenotypic plasticity along the toposequence, we managed to choose individuals in the sites of their highest abundance, which represented what we assumed to be their optimal habitat. For leaf traits, we sampled 5–10 leaves from different individuals, and measurements were made in the hour after sampling on fresh material. For leaf thickness, we performed 5–10 transverse sections. Measurements were done to the nearest 0.01 mm by using a binocular lens. To determine SLA, we isolated 10–15 discs from the lamina of fresh leaves (one to two discs from each sampled leaf) by using a punch. Disc diameter varied from 4 mm to 10 mm. Discs were pooled, dried at 85°C for 24 h, and weighed. Leaf surface was estimated indirectly by a making proportion between the weight of fresh discs and that of fresh leaves, excluding the petiole. For very tiny or narrow leaves, surface was estimated by approximating a geometric shape. Total carbon and nitrogen in leaf tissues were determined with a CHONS microanalyzer.

Seeds were collected in the study site, but also in nearby Alpine meadows of Grand Galibier massif. A total of 30–50 mature seeds from different ramets were pooled and dried at 85°C for 24 h and weighed. Seeds were not cleaned of their accessories prior to weighting.

STATISTICAL ANALYSES

To relate the floristic diversity of the 75 SUs of our study area to the diversity assessed at the regional scale, we relied on a data set comprising 960 floristic surveys of Alpine grasslands in the southwestern Alps. These 960 floristic surveys were collected so that different mountain ranges, altitudes, topographic positions, and substrates were sampled in a roughly stratified approach. Further details on this data set are given in Choler and Michalet (2002). Floristic gradients were extracted by a correspondence analysis (CA), and the rows of table L were projected as supplementary individuals in the CA ordination space.

The RLQ co-inertia analysis has been extensively described in Dolédec et al. (1996), and the reader is referred to this paper for further details on the mathematical model. The main objective is to relate a plot-by-environmental-variable table (R) to a species-by-traits table (Q), with a plot-by-species table (L) serving as a link between R and Q (Fig. 2). It is thus assumed that the table L measures the intensity of the relationships between R and Q. The first step consisted of three separate ordinations. The ordination for table L was done by a correspondence analysis (CA). The CA of table L gives the optimal correlation between SUs and species scores. The ordination for table R was done by a principal component analysis (PCA) with row weights as in table L. The ordination of table Q was done by a PCA with the column weights of table L (Fig. 2).

The RLQ analysis is a three-tables co-inertia analysis that tends to maximize the covariance between the SU scores constrained by the environmental variables of table R and the species scores constrained by the traits of table Q. A fourth-corner table containing the covariance between SU and species is calculated. The axis that maximizes covariance between species and SU is obtained by the eigenvalue decomposition of this fourth table. This axis is the RLQ axis 1. Because of the constraints imposed by tables R and Q, the correlation between SU scores and species scores given by the RLQ analysis cannot exceed the correlation obtained by the CA, which is given by the square root of the first eigenvalue.

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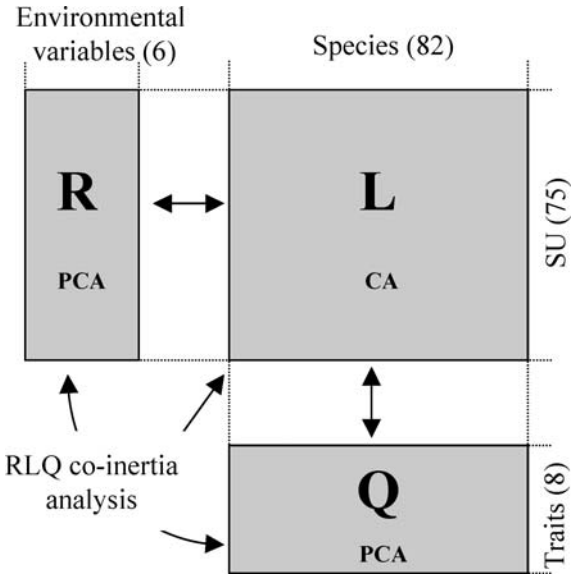


FIGURE 2. Data arrangement and principle of the RLQ analysis. Modified from Dolédec et al. (1996). The aim of the RLQ is to explore the co-structure between the two marginal tables R and Q, by using the central table L as a link. Number of rows and columns of each table are indicated in parentheses. The ordinations of R and Q were performed by principal component analyses, and the ordination of L by a correspondence analysis.

The total co-inertia of the RLQ analysis, given by the trace of the fourth table, measures the linkage between R and Q (Kazi-Aoual et al., 1995). This trace was used as a statistic to test for the significance of the co-structure between R and Q. Rows and columns of the table L were left fixed while rows of the tables R and Q were permuted. Trace values obtained from 1000 permutations were compared with the observed value. It can be considered that the co-structure between R and Q is significant when the number of trace values exceeding the observed value is <50 (i.e., a frequency of $50/1000 = 0.05$). Reciprocally, if this number exceeds 50, it is assumed that the total inertia of the RLQ analysis does not significantly differ from the null hypothesis, i.e., the independence between the two tables R and Q.

Species of table Q can be pooled into three life-form groups (graminoids, forbs, and legumes). Each life-form exhibits particular developmental constraints that might affect values of traits (Garnier, 1991). To take this possibility into account, we also conducted three separate RLQ analyses with data subsets including species from one life-form only.

We related the scores of each species along RLQ axes 1 and 2 with its mean elevation range in this part of the southwestern Alps. These data were derived from an exhaustive floristic survey conducted in the nearby mountain ranges by Chas (1994).

All statistical analyses were carried out by using the ADE-4 software package (Thioulouse et al., 1997).

Results

MESOTOPOGRAPHICAL GRADIENT

The indirect gradient analysis of the regional data set revealed two main floristic gradients (Fig. 3). Along the CA axis 1, the gradient ranged from sub-Alpine grasslands to Alpine communities and is clearly attributable to elevation. The CA axis 2 set snowbed communities in opposition to fell-field communities and is, thus, understandable in terms of mesotopographical variations (Fig. 3). Projection of the SU floristic surveys indicated that the floristic turnover along the mesotopographical gradient encompassed the floristic gradient documented at the regional scale. Except for sub-Alpine grasslands, most of

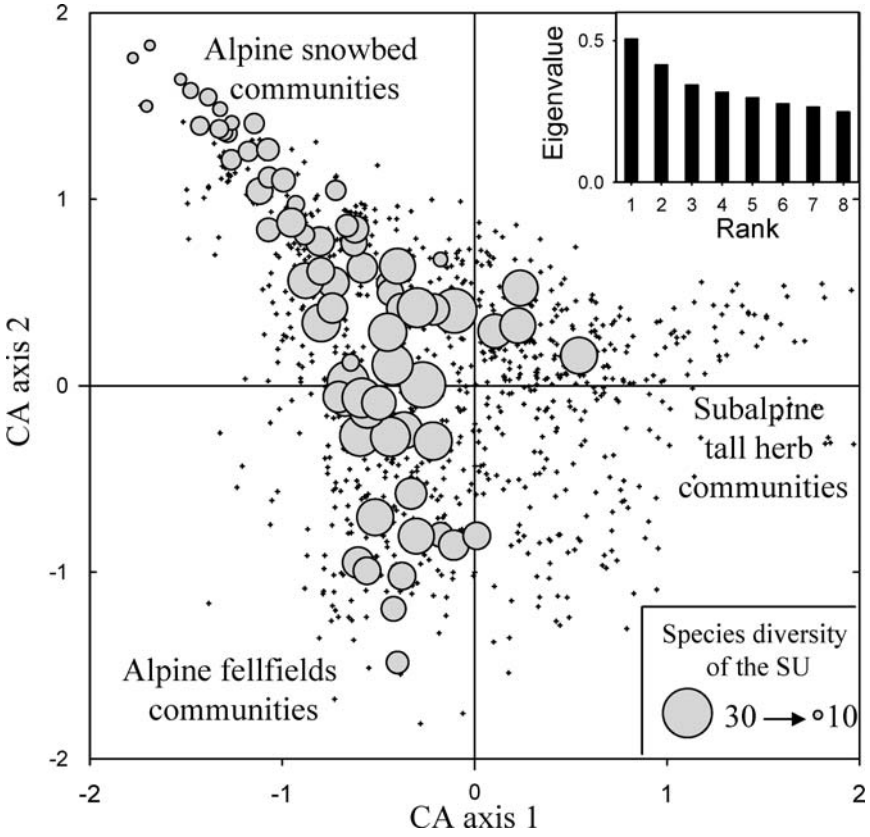


FIGURE 3. Floristic diversity of the study site. The 75 surveyed plots were projected as supplementary individuals (gray circles) onto the first two axes of a correspondence analysis (CA) performed on 960 surveyed plots of sub-Alpine and Alpine communities from the southwestern Alps, as described in Choler and Michalet (2002). Eigenvalues of the CA are indicated in the upper-right insert. Each SU is represented with a gray circle, the size of which is proportional to the SU's species diversity as indicated in the lower-right insert.

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TABLE 3

Main features of the plant communities distributed along the mesotopographical gradient divided as follows: US = upper slope, MS = middle slope, LS = lower slope, *N* is the number of SUs for each community. Snow-melting date range is derived from a weekly survey during the years 1997–1999 (see Fig. 1). Species diversity and percentage cover by mosses and lichens were recorded in each SU in summer 2001. Aboveground phytomass and soil parameters were estimated for only three different SUs and hence are not included in the R table of the RLQ analysis. Means (±1 SE) are given for each variable.

Abbreviation	Dominant species	Mesotopographical position	*N*	Snow melting date range (Julian day)	Species richness in the 5 × 5 m plot	Lichens & mosses (% cover)	Aboveground phytomass (g m^{-2})	Soil pH (5–10 cm)	Soil organic matter (%)	C/N
CR	*Carex rosae* & *lichens*	US	7	<140	21.9 (3.6)	43 (23)	435 (154)	6.5 (0.6)	24.8 (0.3)	14.3 (0.2)
KM	*Kobresia myosuroides*	US	9	<140	27 (3.9)	30 (21)	486 (65)	5.9 (0.7)	22.6 (0.4)	13.1 (1.7)
AR	*Agrostis rupestris*	MS	7	150–160	26.6 (3.6)	45 (21)	250 (43)	4.9 (0.3)	17.3 (1.4)	12.5 (3.4)
SH	*Salix herbacea*	MS	9	160–180	22.1 (4.7)	35 (15)	367 (11)	3.7 (0.3)	10.7 (0.6)	14.3 (0.9)
PA	*Plantago alpina* and *Ranunculus kuepferi*	MS	10	160–180	19.5 (3.6)	17 (11)	456 (31)	4.8 (1.2)	12.8 (1.2)	10.7 (1.7)
FV	*Festuca violacea*	MS	6	140–160	30 (4.2)	<5	443 (89)	5.5 (0.7)	20.1 (1.8)	10.8 (2.5)
TS	*Trifolium* spp.	MS	4	150–160	27.7 (3.2)	<5	352 (77)	5.7 (0.3)	15.1 (2.2)	10.3 (2.8)
CA	*Cirsium acaule*	MS	5	160–180	13 (1.7)	<5	412 (112)	5.9 (0.4)	no data	no data
PS	*Poa supina*	LS	3	200–210	10.3 (3.2)	16 (15)	140 (27)	4 (0.1)	21 (0.4)	11.4 (1.7)
AP	*Alchemilla pentaphyllea*	LS	8	170–200	11.9 (0.5)	<5	370 (36)	4.2 (0.8)	11.9 (1.1)	10.6 (1.9)
CF	*Carex foetida*	LS	4	180–200	14.2 (0.6)	<5	398 (67)	3.9 (0.2)	16.1 (1.5)	15.3 (2.3)
GS	*Gnaphalium supinum*	LS	3	180–210	16.3 (3.2)	46 (7)	200 (63)	4.2 (0.2)	14.8 (0.6)	12.8 (0.6)

the beta diversity of Alpine meadows of the southwestern Alps was thus investigated in our work (Choler and Michalet, 2002).

Species richness tended to be highest in the middle part of the mesotopographic gradient (Fig. 3). The number of vascular species strongly decreased with increasing snow cover and declined to a lesser extent in the most exposed sites.

Table 3 shows the main features of the 12 plant communities sorted by the cluster analysis. Vegetation units of upper slopes (CR, KM) were turf meadows dominated by dense tussocks of graminoids (*Kobresia myosuroides*, *Carex rosae*) and lichens. Tall grasslands characterized by *Festuca violacea* (FV) or *Trifolium* spp. (TS) occurred on mid-slopes and corresponded to the richest plant communities of our study site. Lower slopes were occupied by short-herb meadows dominated by *Plantago alpina* (PA), *Agrostis rupestris* (AR), or dwarf shrubs communities dominated by *Salix herbacea* (SH) in the northern-exposed slopes. The most chionophilous vegetation units were species poor and consisted of four distinct communities (PS, AP, GS, and CF). Overall, the aboveground biomass tended to decrease with snow-cover duration (Table 3). Leaves of cespitose graminoids accounted for most of the biomass in CR and KM communities. Because the leaf life span of these species is several years long (Erschbamer et al., 1998; and personal observation), productivity is expected to be higher in mid-slope than in upper-slope communities. Most soil characteristics exhibited changes along the mesopographical gradient (Table 3). Soils from late-melting sites were more acidic and contained less organic matter compared to soils from early-melting sites. Conversely, available nitrogen slightly increased from late- to early-melting sites. However, the PS community departed from this trend, maybe because of increased feces deposition by sheep or lower nitrogen uptake due to sparse vegetation. The soil C/N ratio strongly depended on the dominant plant; soils under Cyperaceae (CR, KM, CF) or low shrubs (SH) exhibit the highest ratio whatever the position along the mesotopographical gradient.

RLQ ANALYSIS AND COVARIATION BETWEEN TRAITS AND HABITAT

The Monte-Carlo permutation test indicated that the co-structure between R and Q was significant at $P < 0.001$. The tests performed with the three data subsets corresponding to the three life-form groups were also significant at $P < 0.001$. There was thus clear evidence for a strong link between traits and environmental variables in the data set.

The results of the RLQ analysis performed with the full data set are summarized in Table 4. The main part of the co-structure between

TABLE 4

Results of the multivariate analyses. (A) Separate analyses: eigenvalues and percentages of the total inertia accounted for by axis 1 and axis 2. Ordinations were a principal component analysis (PCA) of R and Q and a correspondence analysis (CA) of L. (B) Summary of RLQ analysis: eigenvalues (λ) and percentages of the total co-inertia accounted for by RLQ axis 1 and axis 2, covariance and correlation between the SU scores constrained by the environmental variables in R and species' scores constrained by the traits in Q, projected intertia of table R and Q onto the first two RLQ axes, and percentage of the inertia obtained in the separate analysis of R and Q along the same axes. For example, the RLQ axis 1 accounts for 94.8% of the projected inertia of R along PCA axis 1 [(100 × 1.81)/1.91 = 94.8].

A. Separate analyses			B. RLQ analysis		
	Axis 1	Axis 2		Axis 1	Axis 2
R/PCA	1.91 (31.8%)	1.52 (25.4%)		λ = 1.12 (87.4%)	λ = 0.13 (10.5%)
L/CA	0.66 (15.7%)	0.42 (10%)	Covariance	1.06	0.37
Q/PCA	2.41 (30.1%)	1.49 (18.7%)	Correlation	0.51	0.28
			Projected inertia of		
			table R	1.81 (94.8%)	1.34 (88.2%)
			table Q	2.34 (97.1%)	1.31 (87.9%)

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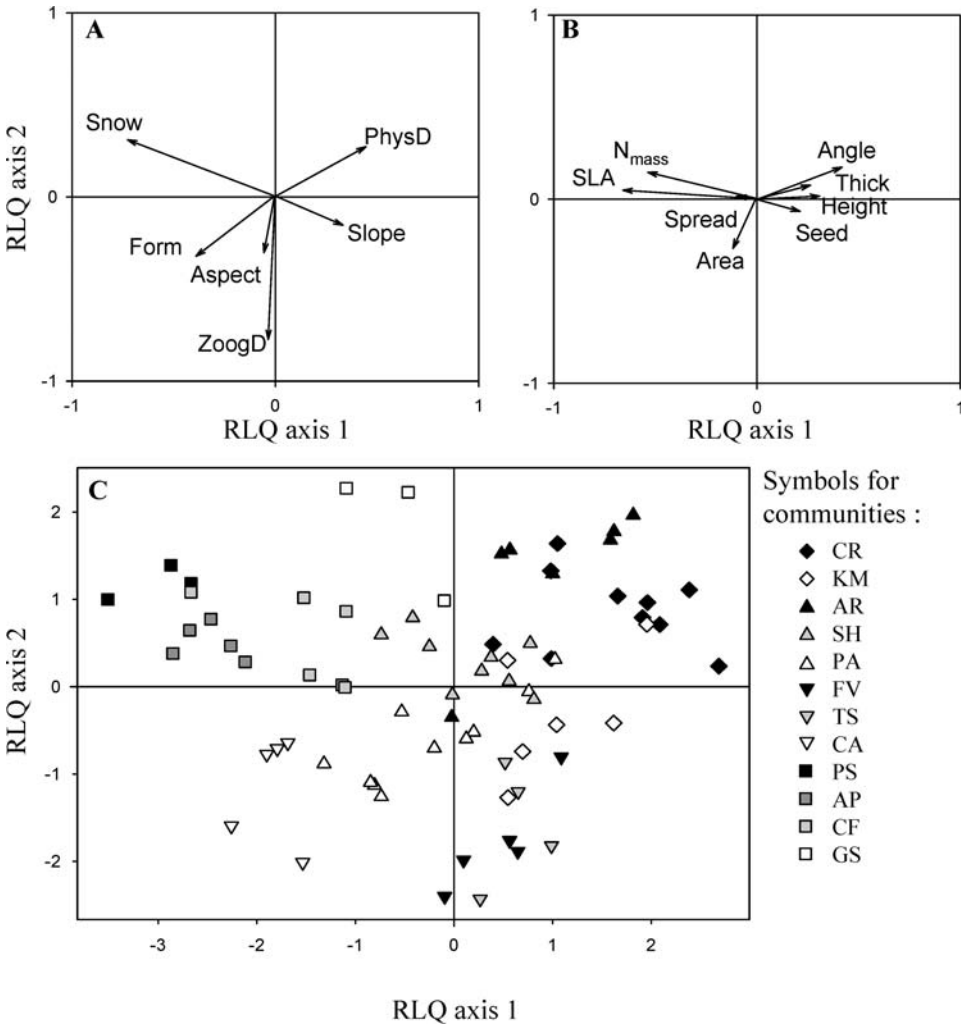


FIGURE 4. Display of environmental variables (A; abbreviations explained in Table 1), plant traits (B; abbreviations explained in Table 2), and SUs (C) along the first two RLQ axes. Each SU is represented by a symbol corresponding to a community type (abbreviations explained in Table 3) sorted by a cluster analysis. In C, SUs are located at the weighted average of environmental variables. In B, traits are positioned at the weighted average of the species.

R and Q was represented by the first RLQ axis; the percentage of the total inertia extracted by this axis equals 87.4%, whereas the value is 10.5% for the second axis. The RLQ analysis optimized the covariance between the new SU scores—constrained by environmental variables—and the new species scores—constrained by traits. The covariance was 1.06 along the first axis but only 0.37 along the second axis. The correlation between the SU scores and the species scores along RLQ axis 1 equaled 0.51 (Table 4). By comparison, the separate ordination of table L gave a first eigenvalue of 0.66, which corresponded to a maximal correlation between SUs and species scores of 0.81. The RLQ axis 1 took into account 94.8% and 97.1% of the first-axis inertia given by the separate ordination of tables R and Q, respectively. Overall, these results showed that the structure of tables R and Q were strongly related to the floristic gradients contained in L.

To allow a detailed examination of covariations, the environmental variables, the traits, and the SUs were graphically displayed along the first two RLQ axes (Fig. 4). The left part of the RLQ axis 1 is indicative of a higher SLA, a higher nitrogen content on a mass basis (N_{mass}), a lower height, and a reduced seed mass in late-melting habitats. This trend was exemplified by snow-bed specialists such as *Poa supina* Schrader, *Carex foetida* All., or *Alchemilla pentaphyllea* L. (Fig. 4).

The right part of the RLQ axis 1 outlined trait attributes associated with convex, disturbed, and mostly early-melting sites. Diagnostic traits included upright and thick leaves. Corresponding species were mostly dominant turf graminoids, such as *Carex rosae* (All.) Gilomen and *Kobresia myosuroides* (Vill.) Fiori, occurring in upper-slope communities (Fig. 4).

Finally, the second RLQ axis mostly underscored a zoogenic disturbance gradient; an increased leaf area was the common trait attribute in the habitats intensively affected by the trampling and burrowing activities of the Alpine marmots. Zoogenic disturbance was preferentially located on southern-exposed mid-slopes with intermediate snow-melting dates. There, plant communities were dominated by *Festuca violacea* Gaudin and several species of *Trifolium* (Fig. 4). Large-leaved rosette species (*Geum montanum* L., *Alchemilla glaucescens* Wallr., *Arnica montana* L.) and tall forbs (*Alchemilla vulgaris* Wallr., *Cirsium acaule* Scop.) were among the characteristics species of these communities.

We found a positive correlation between species scores along the RLQ second axis and species' mean-elevation distribution (Fig. 5). No such relationship was observed along the RLQ first axis (Fig. 5). This finding seems to indicate that plant communities with the lowest RLQ scores along axis 2—noticeably FV and TS communities—comprised many species whose mean-elevation distribution is located below the elevation of the study site.

Discussion

DIVERSITY PATTERNS ALONG THE MESOTOPOGRAPHICAL GRADIENT

At the latitudinal and altitudinal scales, it is widely accepted that species diversity declines in concert with shortening of the growing

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season (Huston, 1999). The mesoscale pattern of species diversity reported in this study is congruent with what is documented at these two global scales. Indeed, the highest species richness was found on the southern-exposed habitats located in the middle of the toposequence where the plots richest in species contained many sub-Alpine species (Figs. 3 and 4). Onipchenko et al. (1998) reported similar patterns in Alpine plant communities of the Caucasus Mountains. Intermediate snow cover might efficiently preclude freezing of the soil during winter while allowing a sufficient growing-season length. Therefore, corresponding habitats are expected to have the yearly optimal temperature regime, and the increased plant-growth period might favor less cold-tolerant species (Epstein et al., 2000).

In addition, we found that thermally optimal habitats are also the most highly disturbed by marmots. Burrowing mammals have the potential to affect floristic composition of Arctic and Alpine meadows essentially through two mechanisms. First, they modify microtopography and soil properties. Compared to undisturbed patches, mounds differ in soil texture and commonly exhibit higher nitrogen levels, though this feature may be transitory (Semenov et al., 2001; Sherrod and Seastedt, 2001). These differences could favor several nutrient-demanding sub-Alpine species. Second, marmot-induced vegetation gaps may locally reduce the dominance of tall graminoids and create favorable patches for new recruitments (Chambers, 1995a, 1995b). Grasses are generally positively affected by elevated temperature and nitrogen inputs (Dormann and Woodin, 2002), and the highest cover of tall grasses (for example *Festuca violacea*) occurs in the middle of the gradient. Much evidence supports the concept that competition is particularly intense in these grasslands (Choler et al., 2001; Callaway et al., 2002). In the study site, marmot-induced patches could notably benefit light-demanding rosette forbs such as *Geum montanum*, *Alchemilla glaucescens*, or *Arnica montana*. The fact that the maintenance of subordinate forbs may strongly depend upon zoogenic disturbance has been primarily described for lowland herbaceous communities (Grubb, 1977; Bonis et al., 1997); subsequently, zoogenic disturbance has been advocated as an important mechanism for the maintenance of species diversity in sub-Alpine and Alpine meadows as well (Chambers et al., 1990; Chambers, 1995a). In summary, it is hypothesized that the interplay of zoogenic disturbance and milder habitat conditions explains the richest species diversity in the middle of the mesotopographical gradient.

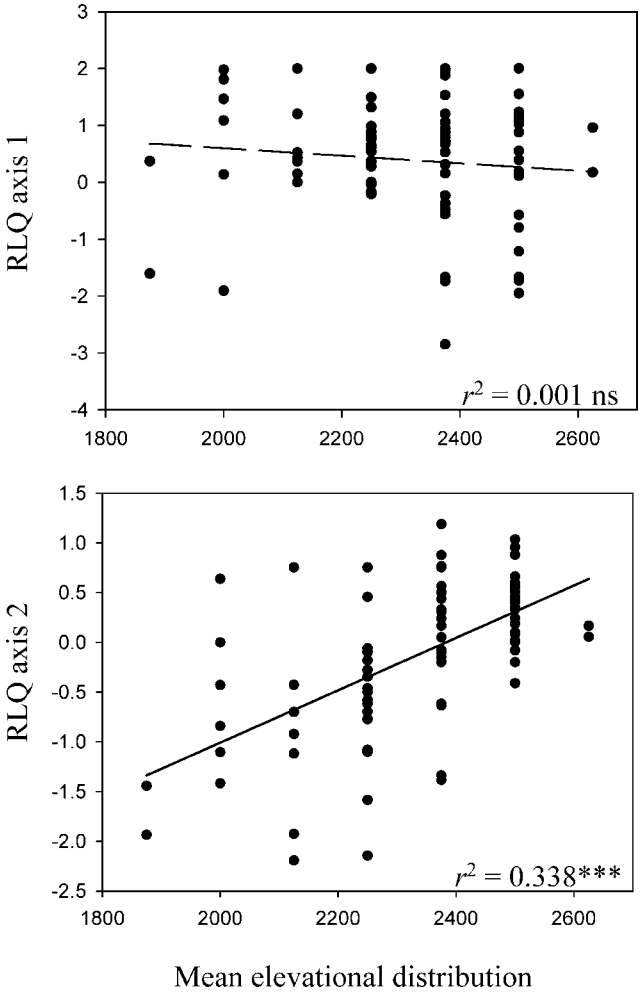


FIGURE 5. Relationships between species' scores along RLQ axis 1 (A; ns = not significant) and along RLQ axis 2 (B; ***$P < 0.001$) and the mean-elevation range of the same species in the southwestern Alps, as given in Chas (1994).

PLANT TRAITS IN RELATIONSHIP TO HABITAT CONSTRAINTS

Our exploratory analysis provided evidence that consistent changes in functional traits could be documented on a quantitative basis along an Alpine mesotopographical gradient (Fig. 4). It is thus reasonable to infer that somehow these traits mediated the ecological sorting of Alpine species, possibly during the recolonization of high-elevation habitats after ice retreat.

Upright and thick leaves exhibiting low SLA are the key features of plants growing on wind-exposed, early-melting sites. This result is in agreement with a pioneer study of Alpine meadows' canopy architectures (Caldwell et al., 1974). It has long been claimed that increased leaf thickness along with reduced surfaces of Alpine plants might protect tissues from being abraded by wind-transported particles (Tranquillini, 1964; Hadley and Smith, 1986). More recent investigations also highlighted the impact of leaf orientation on the temperature actually experienced by tissues, especially at night (Germino and Smith, 2000a, 2001). A steep inclination of leaves reduces sky exposure of photosynthetic surfaces and thereby limits night-time radiation loss. Milder leaf temperature during cold nights should be particularly advantageous for species without snow-cover protection in the very early growing season. Moreover, it is likely that resistance to very low temperatures is more at stake in the inner part of the Alps where prolonged clear sky periods and low relative humidity enhance the frequency of freezing nights (Ozenda, 1985).

Another specific constraint of early-melting sites is the combination of high light intensity and low temperatures that regularly occurs early in spring at the time of leaf initiation. This combination severely damages photosynthetic membranes of nonadapted plants (Öquist et al., 1987; Long et al., 1994). It is likely that the combination of high leaf angle and reduced leaf area in early-melting site species might ensure structural photoprotection against photoinhibition (Valladares and Pugnaire, 1999; Germino and Smith, 2000b).

At the other part of the snow-melting gradient, the most striking relationship was found between high SLA and short growing season, a trend that has also been reported at the intraspecific level for several deciduous Arctic plants (Kudo et al., 1999). It has commonly been considered that low SLA was a key feature of high-elevation species (Körner, 1989). Clearly, snowbed species depart from this trend. Actually, SLA exhibits as much variation along mesotopographical gradients as along elevation gradients. Large-scale interspecific comparisons strengthened the idea that SLA is related negatively with leaf life span and positively with relative growth rate (Reich et al., 1999; Wright et al., 2004). Growth in snowbed habitats is "time-limited", and the persistence of deciduous species in late-melting sites

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might be achieved by the fast production of horizontal, low-cost leaves with short life span and high SLA (Kudo et al., 2001). It is hypothesized these particular trait attributes should permit snowbed specialists to optimize carbon gain and thus overcome the constraint of a shortened growing season.

ALPINE HABITAT TEMPLATE AND PLANT STRATEGIES

By using a bottom-up approach, a particular combination of traits might help defining tactics and strategy that are supposed to match the habitat-specific constraints (Southwood, 1988). In the last quarter of the twentieth century, plant ecologists mainly considered two axes as structuring the habitat template, namely, a gradient of "habitat quality" or resource availability for plant growth and a gradient of disturbance or habitat stability (Grime, 1977; Huston, 1979; Tilman, 1988). Snow has the potential to affect both resource availability and disturbance regime. Snow enhances soil resource availability either directly, through nitrogen storage in snowpacks (Bowman, 1992), or indirectly, via snow's effects on temperature and soil water content, which in turn determine microbial activity and mineralization rates (Chapin, 1983; Isard, 1986; Fisk et al., 1998). In addition, physical disturbance especially due to freeze-thaw cycles is more severe when snow cover disappears early in the season (French, 1996).

An overall habitat deterioration is thus expected in the early-melting sites. A high level of physical disturbance and low fertility drives a decline in vascular plant diversity. "Gaps" between graminoids are commonly colonized by mosses or lichens with very low growth rates (Onipchenko et al., 1998; Cornelissen et al., 2001). Vascular plants of early-melting sites exhibit a combination of trait attributes, including low SLA, which has been recurrently associated with stress tolerance and an efficient strategy for nutrient conservation (Chapin et al., 1993; Westoby, 1998; Wright et al., 2004).

Setting plant strategies for chionophilous species is more problematic. Short available time for growth has been generally associated with resource-rich soils and severe disturbance regime in previous classification schemes (Grime, 1977): the so-called ruderal strategy. In the Alpine landscape, the attendant habitat amelioration with increasing snow cover is counterbalanced by the reduction of the growing-season length. Part of the snowy habitats investigated in this study show an only low amount of disturbance and exhibit a dense matrix of a few clonal species, i.e., *Carex foetida* and *Alchemilla pentaphyllea*. Trait attributes of these species, such as high SLA and high N_{mass}, are indicative of a high capacity of resource acquisition, often documented for species of fertile habitats (Aerts and van der Peijl, 1993; Schlapfer and Ryser, 1996). However, low-recruitment and low-dispersal ability of these dominant species are among traits that do not match with the ruderal syndrome. Indeed, convergence toward the ruderal syndrome is more likely to be found for species growing on disturbed microhabitats such as the small convexities occurring in flat snowy habitats (Mark, 1994). For example *Gnaphalium supinum* (L.) DC., one of the most abundant species of these microhabitats, exhibits both a high seed production and a high seed dispersal ability (personal observation, and Onipchenko et al., 1998) as described for ruderals.

It is concluded that the trade-off between an efficient strategy for nutrient conservation and the high capacity of resource acquisition is probably a fundamental clue to understanding the consistent shift in plant traits along the investigated mesotopographical gradient. It has been claimed that key ecosystem characteristics such as decomposition rates (Cornelissen et al., 1999) or productivity (Chapin et al., 1993) may be predicted from the traits of the dominants (Lavorel and Garnier, 2002). Further investigations are now required to assess how these shifts in plant traits are related to the functional properties of the Alpine grasslands.

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References Cited

Aerts, R., and van der Peijl, M. J., 1993: A simple model to explain the dominance of low-productive perennials in nutrient poor habitats. *Oikos,* 66: 144–147.

Barbaro, L., Corcket, E., Dutoit, T., and Peltier, J.-P., 2000: Réponses fonctionnelles des communautés de pelouses calcicoles aux facteurs agro-écologiques dans les Préalpes. *Canadian Journal of Botany,* 78: 1010–1020.

Billings, W. D., 1974: Adaptations and origins of alpine plants. *Arctic and Alpine Research,* 6: 129–142.

Billings, W. D., and Bliss, L. C., 1959: An alpine snowbank environment and its effect on vegetation, plant development and productivity. *Ecology,* 40: 388–397.

Bonis, A., Grubb, P. J., and Coomes, D. A., 1997: Requirements of gap-demanding species in chalk grassland: Reduction of root competition versus nutrient-enrichment by animals. *Journal of Ecology,* 85: 625–633.

Bounemoura, Z., Lambert, K., Cadel, G., Choler, P., Manneville, O., and Michalet, R., 1998: Influence des facteurs édapho-climatiques sur la distribution des pelouses alpines dans le massif du Galibier (Alpes Françaises). *Ecologie,* 29: 53–58.

Bowman, W. D., 1992: Inputs and storage of nitrogen in winter snowpack in an alpine ecosystem. *Arctic and Alpine Research,* 24: 211–215.

Caldwell, M. M., Tieszen, L. L., and Fareed, M., 1974: The canopy structure of tundra plant communities at Barrow, Alaska, and Niwot Ridge, Colorado. *Arctic and Alpine Research,* 6: 151–159.

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire, F. I., Newingham, B., Cook, B. J., and Aschehoug, E. T., 2002: Positive interactions among alpine plants increase with stress. *Nature,* 417: 812–820.

Cernusca, A., 1976: Bestandesstuktur, Bioklima und Energiehaushalt von alpinen Zwergstrauchbeständen. *Acta Oecologica, Oecologia Plantarum,* 11: 71–102.

Chambers, J. C., 1995a: Disturbance, life history strategies, and seed fates in alpine herbfield communities. *American Journal of Botany,* 82: 421–433.

Chambers, J. C., 1995b: Relationships between seed fates and seedling establishment in an alpine ecosystem. *Ecology,* 76: 2124–2133.

Chambers, J. C., Mcmahon, J. A., and Brown, R. W., 1990: Alpine seedling establishment: The influence of disturbance type. *Ecology,* 71: 553–563.

Chapin, F. S., III, 1983: Direct and indirect effects of temperature on Arctic plants. *Polar Biology,* 2: 47–52.

Chapin, F. S., III, Autumn, K., and Pugnaire, F., 1993: Evolution of suites of traits in response to environmental stress. *American Naturalist,* 142: 578–592.

Chas, E., 1994: *Atlas de la flore des Hautes-Alpes.* Gap, France: Conservatoire Botanique National de Gap-Charance—Conservatoire des Espaces Naturels de Provence et des Alpes du Sud—Parc National des Ecrins, 816 pp.

Choler, P., and Michalet, R., 2002: Niche differentiation and distribution of *Carex curvula* along a bioclimatic gradient in the southwestern Alps. *Journal of Vegetation Science,* 13: 851–858.

Choler, P., Michalet, R., and Callaway, R. M., 2001: Facilitation and competition on gradients in alpine plant communities. *Ecology,* 82: 3295–3308.

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Cornelissen, J. H. C., Perez Harguindeguy, N., Diaz, S., Grime, J. P., Marzano, B., Cabido, M., Vendramini, F., and Cerabolini, B., 1999: Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytologist,* 143: 191–200.

Cornelissen, J. H. C., Callaghan, T. V., Alatalo, J. M., Michelsen, A., Graglia, E., Hartley, A. E., Hik, D. S., Hobbie, S. E., Press, M. C., Robinson, C. H., Henry, G. H. R., Shaver, G. R., Phoenix, G. K., Jones, D. G., Jonasson, S., Chapin, F. S., Molau, U., Neill, C., Lee, J. A., Melillo, J. M., Sveinbjornsson, B., and Aerts, R., 2001: Global change and Arctic ecosystems: Is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology,* 89: 984–994.

Diaz, S., Cabido, M., Zak, M., Carretero, E. M., and Aranibar, J., 1999: Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. *Journal of Vegetation Science,* 10: 651–660.

Dolédec, S., Chessel, D., Ter Braak, C. J. F., and Champely, S., 1996: Matching species traits to environmental variables: A new three-table ordination method. *Environmental and Ecological Statistics,* 3: 143–166.

Dormann, C. F., and Woodin, S. J., 2002: Climate change in the Arctic: Using plant functional types in a meta-analysis of field experiments. *Functional Ecology,* 16: 4–17.

Epstein, H. E., Walker, M. D., Chapin, F. S., and Starfield, A. M., 2000: A transient nutrient-based model of Arctic plant community response to climatic warming. *Ecological Applications,* 10: 824–841.

Erschbamer, B., Buratti, U., and Winkler, J., 1998: Long-term population dynamics of two *Carex curvula* species in the central Alps on native and alien soils. *Oecologia,* 115: 114–119.

Fisk, M. C., Schmidt, S. K., and Seastedt, T. R., 1998: Topographic patterns of above- and belowground production and nitrogen cycling in Alpine tundra. *Ecology,* 79: 2253–2266.

Fox, J. F., 1981: Intermediate levels of soil disturbance maximize alpine plant diversity. *Nature,* 293: 59–124.

French, H. M., 1996: *The periglacial environment.* Harlow, U.K.: Longman, 341 pp.

Frenzel, B., Pécsi, M., and Velichlko, A. A., 1992: *Atlas of paleoclimates and paleoenvironments of the Northern Hemisphere. Late Pleistocene-Holocene.* Budapest: Gustav Fisher, 153 pp.

Friend, A. D., and Woodward, F. I., 1990: Evolutionary and eco-physiological responses of mountain plants to the growing-season environment. *Advances in Ecological Research,* 20: 978–988.

Garnier, E., 1991: Resource capture, biomass allocation and growth in herbaceous plants. *Trends in Ecology and Evolution,* 6: 126–131.

Germino, M. J., and Smith, W. K., 2000a: Differences in microsite, plant form, and low-temperature photoinhibition in alpine plants. *Arctic, Antarctic, and Alpine Research,* 32: 388–396.

Germino, M. J., and Smith, W. K., 2000b: High resistance to low-temperature photoinhibition in two alpine, snowbank species. *Physiologia Plantarum,* 110: 89–95.

Germino, M. J., and Smith, W. K., 2001: Relative importance of microhabitat, plant form and photosynthetic physiology to carbon gain in two alpine herbs. *Functional Ecology,* 15: 243–251.

Grime, J. P., 1977: Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist,* 111: 1169–1194.

Grubb, P. J., 1977: The maintenance of species richness in plant communities: The importance of the regeneration niche. *Biological Review,* 52: 107–145.

Hadley, J. L., and Smith, W. K., 1986: Wind effects on needles of sub-alpine conifers: Seasonal influence on mortality. *Ecology,* 67: 12–19.

Hausner, V. H., Yoccoz, N. G., and Ims, R. A., 2003: Selecting indicator traits for monitoring land use impacts: Birds in northern coastal birch forests. *Ecological Applications,* 13: 999–1012.

Huston, M. A., 1979: A general hypothesis of species diversity. *American Naturalist,* 113: 81–101.

Huston, M. A., 1999: Local processes and regional patterns: Appropriate scales for understanding variation in the diversity of plants and animals. *Oikos,* 86: 393–401.

Isard, S. A., 1986: Factors influencing soil moisture and plant community distribution on Niwot Ridge, Front Range, Colorado, U.S.A. *Arctic and Alpine Research,* 18: 295–304.

Kazi-Aoual, F., Hitier, S., Sabatier, R., and Lebreton, J. D., 1995: Refined approximations to permutation tests for multivariate inference. *Computational Statistics and Data Analysis,* 20: 643–656.

Keddy, P. A., 1992: Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science,* 3: 157–164.

Komarkova, V., 1993: Vegetation type hierarchies and landform disturbance in Arctic Alaska and alpine Colorado with emphasis on snowpatches. *Vegetatio,* 106: 109–120.

Körner, C., 1989: The nutritional status of plants from high altitudes. *Oecologia,* 81: 623–632.

Körner, C., 1999: *Alpine plant life.* Berlin: Springer-Verlag, 338 pp.

Kudo, G., 1992: Performance and phenology of alpine herbs along a snow-melting gradient. *Ecological Research,* 7: 299–316.

Kudo, G., 1996: Intraspecific variation of leaf traits in several deciduous species in relation to length of growing season. *Ecoscience,* 3: 483–489.

Kudo, G., and Ito, K., 1992: Plant distribution in relation to the length of the growing season in a snow-bed in the Taisetsu Mountains, northern Japan. *Vegetatio,* 98: 319–328.

Kudo, G., Nordenhall, U., and Molau, U., 1999: Effects of snowmelt timing on leaf traits, leaf production, and shoot growth of alpine plants: Comparisons along a snowmelt gradient in northern Sweden. *Ecoscience,* 6: 439–450.

Kudo, G., Molau, U., and Wada, N., 2001: Leaf-trait variation of tundra plants along a climatic gradient: An integration of responses in evergreen and deciduous species. *Arctic, Antarctic, and Alpine Research,* 33: 181–190.

Lavorel, S., and Garnier, E., 2002: Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology,* 16: 545–556.

Legendre, P., Galzin, R., and Harmelin-Vivien, M. L., 1997: Relating behavior to habitat: Solutions to the fourth-corner problem. *Ecology,* 78: 547–562.

Long, S. P., Humphries, S., and Falkowski, P. G., 1994: Photo-inhibition of photosynthesis in nature. *Annual Review of Plant Physiology and Plant Molecular Biology,* 45: 633–662.

Mark, A. F., 1994: Patterned ground activity in a southern New Zealand high-alpine cushionfield. *Arctic and Alpine Research,* 26: 270–280.

Michalet, R., Gandoy, C., Joud, D., Pagès, J.-P., and Choler, P., 2002: Plant community composition and biomass on calcareous and siliceous substrates in the northern French Alps: Comparative effects of soil chemistry and water status. *Arctic, Antarctic, and Alpine Research,* 34: 102–113.

Onipchenko, V. G., Semenova, G. V., and Van Der Maarel, E., 1998: Population strategies in severe environments: Alpine plants in the northwestern Caucasus. *Journal of Vegetation Science,* 9: 341–352.

Öquist, G., Greer, D. H., and Ögren, E., 1987: Light stress at low temperature. *In* Kyle, D. J., Osmond, C. B., and Arntzen, C. J. (eds.), *Photoinhibition.* Amsterdam: Elsevier Science, 67–87.

Ozenda, P., 1985: *La végétation de la chaîne alpine dans l'espace montagnard européen.* Paris: Masson, 331 pp.

Reich, P. B., Walters, M. B., and Ellsworth, D. S., 1997: From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America,* 94: 13,730–13,734.

Reich, P. B., Ellsworth, D. S., Walters, M. B., Vose, J. M., Gresham, C., Volin, J. C., and Bowman, W. D., 1999: Generality of leaf trait relationships: A test across six biomes. *Ecology,* 80: 1955–1969.

Ribera, I., Dolédec, S., Downie, I. S., and Foster, G. N., 2001: Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology,* 82: 1112–1129.

Schlapfer, B., and Ryser, P., 1996: Leaf and root turnover of three ecologically contrasting grass species in relation to their performance along a productivity gradient. *Oikos,* 75: 398–406.

Semenov, Y., Ramousse, R., Le Berre, M., and Tutukarov, Y., 2001: Impact of the black-capped marmot (*Marmota camtschatica* bungei)

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on floristic diversity of Arctic tundra in northern Siberia. *Arctic, Antarctic, and Alpine Research,* 33: 204–210.

Sherrod, S. K., and Seastedt, T. R., 2001: Effects of the northern pocket gopher (*Thomomys talpoides*) on alpine soil characteristics, Niwot Ridge, Colorado. *Biogeochemistry,* 55: 195–218.

Southwood, T. R. E., 1988: Tactics, strategy and templets. *Oikos,* 52: 3–18.

Stanton, M. L., Rejmanek, M., and Galen, C., 1994: Changes in vegetation and soil fertility along a predictable snowmelt gradient in the Mosquito Range, Colorado, U.S.A. *Arctic and Alpine Research,* 26: 193–200.

Stearns, S. C., 1989: Trade-offs in life-history evolution. *Functional Ecology,* 3: 259–268.

Thioulouse, J., Chessel, D., Dolédec, S., and Olivier, J. M., 1997: ADE-4: A multivariate analysis and graphical display software. *Statistics and Computing,* 7: 75–83.

Tilman, D., 1988: *Plant strategies and the dynamics and structure of plants communities.* Princeton, New Jersey: Princeton University Press, 376 pp.

Tranquillini, W., 1964: The physiology of plants at high altitude. *Annual Review of Plant Physiology and Plant Molecular Biology,* 15: 121–128.

Valladares, F., and Pugnaire, F. I., 1999: Tradeoffs between irradiance capture and avoidance in semi-arid environments assessed with a crown architecture model. *Annals of Botany,* 83: 459–469.

Walker, D. A., Halfpenny, J. C., Walker, M. D., and Wessman, C. A., 1993: Long-term studies of snow-vegetation interactions. *BioScience,* 43: 471–480.

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E., and Eriksson, O., 1999: Challenging Theophrastus: A common core list of plant traits for functional ecology. *Journal of Vegetation Science,* 10: 609–620. *Plant and Soil,* 199: 213–227.

Westoby, M., 1998:A leaf-height-seed (LHS) plant ecology strategy scheme.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M. L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J., and Villar, R., 2004: The worldwide leaf economics spectrum. *Nature,* 428: 821–827.

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