Niche differentiation and distribution of *Carex curvula* along a bioclimatic gradient in the southwestern Alps

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Abstract. *Carex curvula* is a dominant sedge of European alpine tundra, exhibiting two morphological forms: *C. curvula* ssp. *curvula* (*Ccc*) and *C. curvula* ssp. *rosae* (*Ccr*). In this paper, we attempt to explore whether *Ccc* and *Ccr* are ecotypes or vicariant forms and whether between- and within-regional distribution patterns can be explained by variations in the amount of available habitats and/or by changes in niche attributes. The study area covered three bioclimatically distinct regions of the southwestern Alps in which local abundances of *Ccc* and *Ccr* strongly differ.

The realized niche of both forms was investigated by a direct gradient analysis performed on an extensive floristic and environmental data set. We found no evidence of niche overlap between *Ccc* and *Ccr* as their distribution curves differ strongly along disturbance, mesotopography and soil acidity gradients. We investigated the effect of region on the structure of local scale variables tables. Highly concordant patterns among regions were found, except that optimal habitat conditions for *Ccc* were infrequent in the southernmost regions. We compared the ecological behaviour of range centre and range margin populations of each form. We found a narrower ecological amplitude for *Ccr* in the northern part of its range, whereas for *Ccc* the niche breadth of range-margin populations was not reduced compared to range centre populations. At its southern range limit, *Ccc* mostly occupies ecologically marginal habitats.

We conclude that *Ccc* and *Ccr* represent ecotypes, not vicariant forms. Finally, we suggest that habitat availability, resulting from the interplay of regional-scale and local-scale variables, satisfactorily explains the distributional patterns of *Carex curvula* ecotypes in the southwestern Alps.

Keywords: Alpine tundra; Ecotype; Niche theory; Ordination; Outlying Mean Index.

Abbreviations: CCA = Canonical Correspondence Analysis; *Ccc* = *Carex curvula* ssp. *curvula*; *Ccr* = *Carex curvula* ssp. *rosae*; OMI = Outlying Mean Index; PCA = Principal Component Analysis; RDA = Redundancy Analysis.

Nomenclature: Tutin et al. 1964-1980.

Introduction

Two forces, i.e. ecogenesis (adaptation to ecological conditions) and phylogenesis (historical events) interact in a complex manner to shape current species distributions (Thorpe et al. 1994). Taxonomically related species offer opportunities of exploring this intricacy of underlying processes driving distributional variations through time and space. On the one hand, physiological and morphological variations have been related to ecological specialization and closely related taxa constitute ecotypes (Langlet 1971). On the other hand, variation in traits might not be due to environment but to habitat fragmentation causing vicariance (Nelson 1976). These two alternative hypotheses can be tested using species-environment analyses since 'true' ecotypes can be sympatric with different ecological requirements, whereas vicariant forms are expected to be allopatric with similar niche attributes. Such a test then requires partitioning the variance in floristic tables among local-scale and regional-scale sources of variation.

Historically, alpine landscapes have been a favourite place for ecological and evolutionary studies of paired species (Mooney & Billings 1961; McGraw & Antonovics 1983; Galen et al. 1991). In this paper, we focus on the alpine species *Carex curvula*, a dominant sedge of most European alpine tundras which exhibits two closely related morphological forms (Gilomen 1938): *C. curvula* ssp. *curvula* (*Ccc*) and *C. curvula* ssp. *rosae* (*Ccr*). At a local scale, much emphasis has been placed on the ecological specialization of each form, pointing out the calcifuge habit of *Ccc* and the calcicole habit of *Ccr* (Gensac 1977; Erschbamer 1992). At a regional scale, the differential distribution of these two ecotypes across the Alps and especially the decrease in the abundance of *Ccc* in the southwestern Alps (Ozenda 1985) have long been noticed, even though outcrops of siliceous rocks are quite common at high elevations in this area. In contrast, *Ccr* is a common taxon in the southwestern Alps but is infrequent in the central and eastern Alps,

these patterns suggest that the two forms might also constitute geographical vicariant forms.

In this paper, we compare alpine vegetation patterns in three bioclimatically distinct regions of the south-western Alps with large differences between *C. curvula* forms. Direct gradient analysis of an extensive floristic and environmental data sets allowed us to: (1) re-assess the realized niche of *Ccc* and *Ccr*, (2) compare the amount of suitable habitats for each form along the bioclimatic gradient and (3) examine the ecological behaviour of range-margin and range-centre populations of *Ccc* and *Ccr*.

Study sites

Field work was conducted in three regions of the French Alps (See App. 1): (1) the Vanoise massif; (2) the mountainous area of Lautaret-Galibier, the northern part of Oisans and the eastern part of Grandes Rousses; (3) Queyras massif and the northern part of Mercantour.

The selected regions encompass a north-south latitudinal gradient and a west-east longitudinal gradient along which strong distributional variations in *C. curvula* are described (Chas 1994). The southern limit of well-developed *Ccc*-tundra is located between regions 1 and 2, whereas *Ccr* is found more frequently in regions 2 and 3. The three regions were also chosen because of the availability of information from previous phytosociological investigations: Claudin (1970) and Gensac (1977) for region 1; Molinier & Pons (1955) for region 2; Guinochet (1938), Dalmas (1972), Verger (1987) and Reynier (1988) for region 3.

Methods

Climate data

Large-scale climatic patterns in the study area were derived from meteorological recordings of 32 Météo-France climatic stations located inside or in the vicinity of the three selected regions, mainly between 1000 and 1500 m a.s.l. Mean climate variables were calculated over the period 1951-1990 and for a 3-mo summer period (June, July and August) corresponding to the growing season of alpine vegetation. We used minimum temperature (T_{min}), maximum temperature (T_{max}) and precipitation (P). Temperatures were standardized to sea level for comparison among stations. Temperature change gradients per 100-m altitudinal change were adjusted for each region using a larger set of climatic stations (Michalet et al. in press). We calculated a summer continentality index as $C = \arctan (T/P)$ (Zimmermann & Kienast

1999) where T is the monthly mean summer temperature (°C) and P is the monthly mean summer precipitation (mm). Monthly mean solar radiation (SR) was derived from the Meteosat satellite images during 1996 and 1997. We used the monthly mean frequency of sunny sky from June to August derived from the data for western Europe at a resolution of 5 km (http://www.satel-light.com/).

Vegetation sampling

Our data set for gradient and community analyses comprised 920 vegetation relevés of which 48 % were collected for this study. The numbers of relevés for the three regions were 204, 198 and 463 and the proportions of relevés from literature were 63 %, 15 % and 69 % respectively. For each region, we had at least two different sources of data (including our own), this limited the problem of autocorrelation between sampling person and sampling region. Within each region, individual ordinations of floristic data did not reveal different patterns among authors.

The data set contained relevés from herbaceous and heath communities occurring above the treeline and with a vegetation cover exceeding 30 %. Extremely specialized habitats (bogs, screes and cliffs) were not considered. Neither *Ccc* nor *Ccr* occur in these habitats.

The old monographs included in our analysis all aimed to cover the full phytosociological range of alpine vegetation in their sampling area. The location of relevés was entirely dependent on what the investigator considered to be important for this purpose. Accordingly, vegetation sampling was subjective, primarily based on physiognomy types. The multivariate analyses we performed are thus exploratory analyses.

The same sampling strategy was followed for newly collected data. Relevés did not have fixed areas and were conducted by visually estimating the relative abundance of vascular plant species within a contiguous, homogeneous area ranging from 25 to 100 m². To avoid spatial autocorrelation relevés were separated by a minimum of 500 m. We used the standard phytosociological approach (Braun-Blanquet 1932) with a 6-point scale for species cover:

1: < 5%; 2: 5-10%; 3: 10-25%; 4: 25-50%; 5: 50-75%; 6: > 75%.

It appeared that there were 77 relevés with *Ccc* (all from region 1) and 283 relevés with *Ccr* (80 were from region 3) out of a total of 920. An additional sampling effort was then made for range margin populations of *Ccc* in regions 2 and 3; 12 localities were visited in Mercantour (Guinochet 1938), Grandes Rousses, Belledonne and Oisans (reports from Parc National des Ecrins and Conservatoire Botanique National Alpin Gap Charance) and 40 additional relevés were collected.

Sampling of environmental variables

For each relevé, we recorded six local-scale variables: elevation (in m. a.s.l.), slope steepness (°), aspect, mesotopographic position on slope, soil stability and bedrock type (Table 1). Many of the sites for which relevés were from other authors were revisited to check that there were no differences in recording. These variables were transformed for subsequent multivariate analyses. From the elevation of a site (*At*) we estimated the summer mean temperature (*Tm*) using the formula:

$$Tm = Tmr – G*(At – Ar) / 100 \qquad (1)$$

where *Tmr* and *Ar* are respectively the summer mean temperature and the elevation of the closest climatic station which serves as a reference and *G* is the estimated temperature lapse rate for the region (see above). Aspect was coded with a five-level scale, from north to south facing. Hence, east and west exposed slopes were coded identically. Topographic position on slope was coded as either crest, upper- mid, lower-slope and gully or flat. We evaluated the relative area (*D*) of a relevé covered by unvegetated 'frost-churned soil' at the snow melting period (Fox 1981) and related this to the intensity of physical disturbance due to soil instability. Disturbance was then coded as stable: D < 5 %; nearly stable: 5 - 25 %; unstable: 25 - 50 %; very unstable: D > 50 %. For old relevés which were not revisited, we relied on the percentage of bare ground given by the literature. This leads to a weak underestimation of the unvegetated area at the snow-melting period. However, this was not a problem since each disturbance level we used covers a large range of variation. Dominant bedrocks, determined from a geological map on a 1: 200 000 scale, included hard calcareous rocks, calcareous shale and marls, metamorphic rocks and granites were coded from 1 to 4 along a gradient of increasing acidity.

Species-environment relationships and niche analyses

All multivariate analyses were carried out using ADE-4 (Thioulouse et al. 1997). The floristic table contained 920 (or 960) relevés and 204 species. Rare

Table 1. Local-scale environmental variables used.

Relative south aspect:N (1), NE-NW (2), E-W-flat (3), SE-SW (4), S (5)
Slope: <5° (1), 5-15° (2), 15-30° (3), 30-45° (4)
Mesotopography: Crest (1), Upper slope (2)Mid slope (3),
    Lower slope (4), Gully (5)
Bedrock acidity: Calcareous / Dolomites (1), Shales and base-rich flysch (2),
    Siliceous flysch (3) Granites and micashists
Disturbance (soil instability): Stable (1), Nearly stable (2), Unstable (3),
    Stronlgy unstable (4)
Mean summer temperature : Derived from elevation and recordings
    from the closest climatic station.

species (frequency < 2 %) were removed. The local scale environmental table contained 920 (or 960) relevés and six explanatory variables.

Niche attributes of each form of *C. curvula* were investigated by a direct gradient analysis, or co-inertia analysis, between the floristic and environmental tables. Since we do not know species response curves along gradients, ordination techniques with minimum preliminary assumptions are recommended (Austin 1985). We used a new technique of constrained ordination, the Outlying Mean Index (OMI) (Dolédec et al. 2000). OMI addresses different types of species response to the environment, including linear and non-linear. Moreover, OMI weights all relevés equally, contrary to Canonical Correspondence Analysis (CCA) that down-weights species-poor relevés. This is particularly valuable when data sets include species-poor relevés because of strong environmental limiting factors (Dolédec et al. 2000). OMI is a two-table ordination technique in which (1) the table of normalized environmental variables (**X**) is analysed by a PCA and (2) the floristic table (**Y**) is simply transformed into a species' profile table (**F**). The general term of **F** is computed as follows:

$$f_{i/j} = y_{ij} / y_j \qquad (2)$$

where y_{ij} is the general term of **Y** (i.e. the abundance of species *j* in relevé *i*) and y_j is the column total for *j*.

The table **Z = Ft Y** (**Ft** = **F** transposed) contains the mean position (or gravity centre) of each species (rows) on each variable (columns). The distance of the gravity centre of species *j* to the origin is called the marginality of *j*. The origin could be considered as the gravity centre of a theoretical ubiquitous species uniformly distributed among habitat conditions in the data set. OMI is the eigenvalue analysis of table **Z** with the species weights given by y_j. The first OMI axis maximizes the species marginality. The total inertia given by the analysis is a measure of how the environmental variables separate the species' niche. A Monte-Carlo test with 1000 permutations of the rows of table **F** was used to test for the significance of environmental variables on niche separation. Further mathematical details on OMI analysis, including a comparison with other co-inertia techniques, can be found in Dolédec et al. (2000).

The table of local scale environmental variables defines combinations of abiotic conditions where alpine plant communities are established. To compare habitat patterns among regions we performed a within group PCA. The table of environmental variables was divided into three blocks of rows corresponding to the three studied regions. Raw data were centred by block and normalized by columns. The correlation coefficients obtained in the within group PCA are partial correlations after removing the effect of region.

Results

Direct gradient analysis and niche attributes

We ordinated the same data set of 920 relevés by RDA, CCA and OMI analysis and found highly concordant patterns whatever the ordination technique, indicating that our data set was robust. The Monte-Carlo randomization test was significant at $P = 0.001$ for all three analyses. However, having the highest percentage of floristic variance explained by environmental variables along the first two axes (73 %, as compared to 63 % for CCA and 68 % for RDA), OMI appeared as the most powerful technique to investigate species-environment relationships in our data set.

The first two axes of the OMI analysis accounted for 41 % and 32 % of the total marginality respectively (upper insert of Fig. 1). The first axis was primarily related to a temperature gradient separating subalpine or low alpine tall grassland communities from communities of the alpine-nival ecotone (Fig. 1 and Table 2). The second axis was mainly explained by mesotopographic position on slope and disturbance level (Table 2). It showed a contrast between communities of non-disturbed, mostly concave situations and communities of disturbed, upper slopes or crests.

The niche separation between the two forms of *C. curvula* was clearly established by all two table ordination techniques. Both ecotypes are found at high altitudes but the optimal habitat of *Ccc* occurs in weakly disturbed tundra on mid or lower slopes whereas *Ccr* mostly occurs on highly disturbed upper slopes (Fig. 1). *Ccc* is restricted to acidic siliceous rocks whereas *Ccr* exhibits a wider amplitude along this gradient. Hence, our results indicate that niche attributes of the two morphological forms are non-overlapping, suggesting that *Ccc* and *Ccr* should be considered as ecotypes.

Regional-scale vs local-scale patterns of variation

The three studied regions are located along a north to south and a west to east transect which correspond to a strong bioclimatic gradient. Significant differences were found for the summer continentality index and the frequency of clear sky, whereas the mean monthly amplitude in temperature was similar among regions (Table 3). The rain shadow effect, as measured by the continentality index, was most pronounced in region 2 and illustrated one of the most particular climatic features of the inner valleys in the Alps. The increasing frequency of clear sky from region 1 to region 3 reflects the Mediterranean climate influence. Overall, the combined effect of lower precipitation and higher solar radiation during the summer period should strongly enhance evapotranspiration in regions 2 and 3.

We then assessed to what extent the within region patterns of local-scale environmental variables is affected by this macroclimatic gradient. Using a within group PCA, we removed the regional effect and compared the three sets of environmental variables. Projections of each set of relevés in the plane formed by axes 1 and 2 highlighted the infrequency of high elevation, low disturbance and acidic habitats in regions 2 and 3 (Fig. 2). This particular combination of local-scale environmental variables constitutes the most suitable conditions for *Ccc*, suggesting that optimal habitats for *Ccc* are rare in regions 2 and 3. Conversely, there was no indication of a lack of *Ccr* habitat in region 1.

### Niche attributes of range margin populations

Results from the OMI analysis performed on the extended data table of 960 relevés revealed no major differences with the previous analysis. To compare niche attributes along the bioclimatic gradient, the position of range margin and range centre relevés were displayed separately along axes 1 and 2 (Fig. 3).

Ccc relevés from regions 2 and 3 were all located far from the optimal position (or gravity centre) of the species (Fig. 3). Results from a one-way ANOVA indicated that the scores of these relevés differed significantly from range centre relevés along OMI axis 1 ($F_{1, 118} = 10.1$, $P < 0.01$) and OMI axis 2 ($F_{1, 118} = 6.09$, $P < 0.05$). The shifts in ecological behaviour were particu-

Table 2. Pearson correlation coefficients between the local-scale environmental variables and the first two axes of the OMI analysis; $\lambda_1 = 0.42$, $\lambda_2 = 0.32$.

	OMI axis 1		OMI axis 2	
Relative south aspect	– 0.41	**	– 0.01	ns
Slope	– 0.49	**	0.60	**
Mesotopography	– 0.07	*	– 0.79	**
Bedrock acidity	0.67	**	– 0.35	**
Disturbance	– 0.12	**	0.99	**
Mean summer temperature	– 0.82	**	– 0.37	**

** = $p < 0.01$; * = $p < 0.05$; ns = non-significant.

Table 3. Bioclimatic features of the three study regions. Means (+/– s.e.) were calculated for three climatic variables. The regional effect on each variable was tested by a one-way ANOVA. Regions with the same letter did not differ significantly at $P = 0.05$ in a post-hoc Tukey test; n is number of climatic stations used.

	$T_{max} - T_{min}$ (°C)	Continentality index	% of clear skies
Region 1 ($n = 12$)	11.58 (1.13)[a]	0.35 (0.15)[a]	40.01 (2.55)[a]
Region 2 ($n = 9$)	12.62 (2.29)[a]	0.56 (0.11)[b]	47.56 (3.14)[a]
Region 3 ($n = 11$)	12.39 (1.45)[a]	0.5 (0.06)[b]	52.35 (5.33)[a]

Fig.1. Display of 920 alpine relevés along OMI axis-1 and axis-2. Relevés with *Ccr* (●) or *Ccc* (○) are indicated with a symbol size proportional to the abundance of the species in the relevé. Dots are for relevés without *Carex curvula*. Ellipses were drawn to contain 80% of *Ccc*- or *Ccr*-containing relevés. Canonical weights of local-scale environmental variables are indicated in the lower-left insert. Eigenvalues of the OMI analysis are indicated in the upper-right insert.
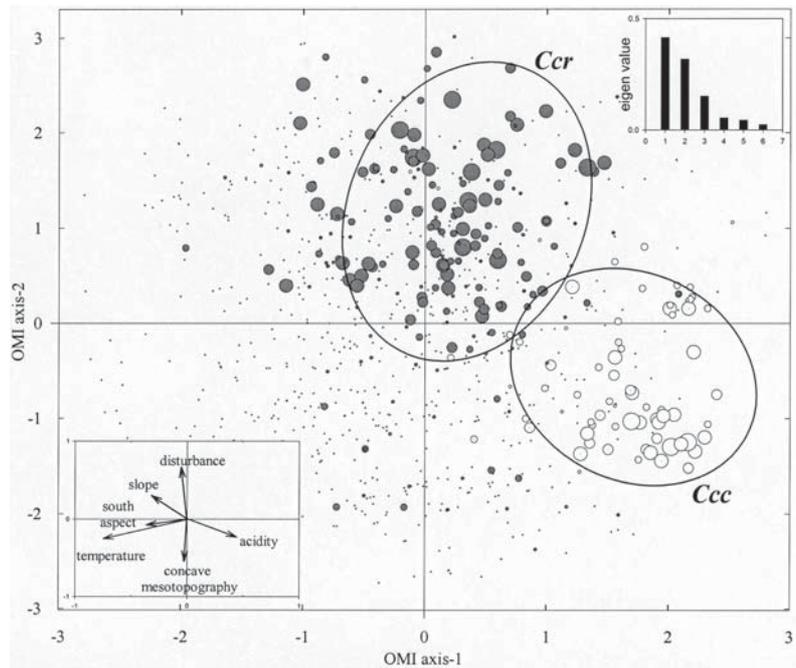
larly obvious with respect to disturbance level and mesotopography. In the south, *Ccc* habitats mainly include upper slopes, disturbed communities floristically related to *Festuca halleri* communities or snowbed communities dominated by *Salix herbacea* or *Alchemilla pentaphyllea* (Fig. 3). Both of these habitats correspond to ecologically marginal situations of the species.

Compared to regions 2 and 3, *Ccr* relevés from region 1 had significantly higher scores along OMI-axis 1 ($F_{1,282} = 17.7, P < 0.001$) which mainly corresponds to a shift towards higher altitude and northerly aspects (Fig. 3). This suggests a niche narrowing along the temperature gradient for *Ccr* in region 1, whereas the niche width along disturbance and mesotopographical gradients remained unchanged across regions.

Fig. 2. Within-group PCA of local-scale environmental variables. Display of relevés from region 1 (○) and regions 2, 3 (●) along axis 1 and axis 2. Scores of variables are indicated in insert. The line points out the infrequency of high-elevation, acidic and low-disturbed habitats in the regions 2 and 3.
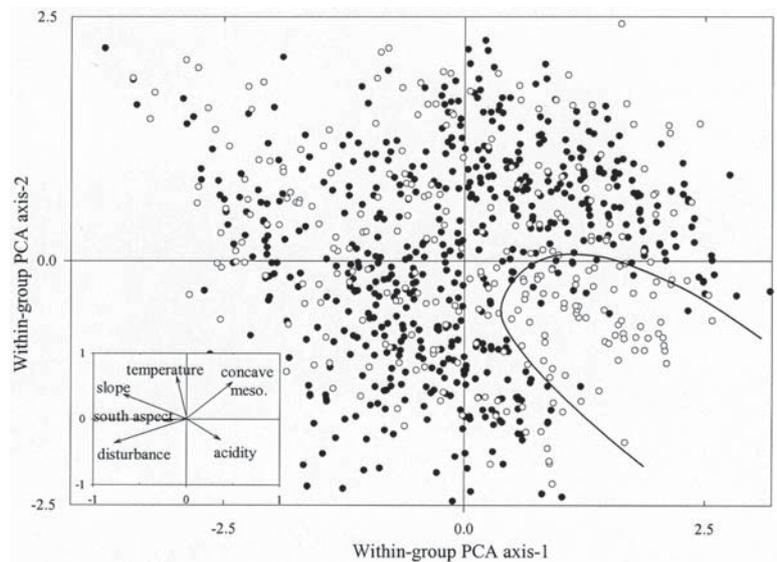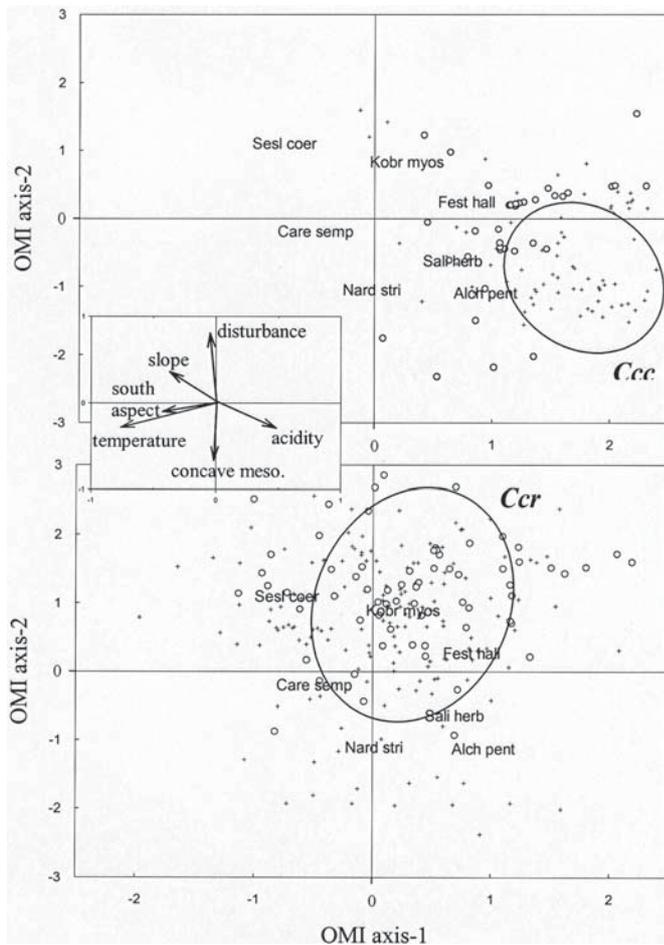
Fig. 3. Display of range-margin (○) and range-centre (.) relevés containing *Ccc* (upper diagram) or *Ccr* (lower diagram) along OMI axis-1 and axis-2. A margin-range location corresponds to regions 2 and 3 for *Ccc* and to region 1 for *Ccr*. Ellipses were drawn to contain 80 % of *Ccc*- or *Ccr*-containing relevés. Canonical weights of local-scale environmental variables are indicated in the insert. Positions of the following dominant species are indicated: *Alchemilla pentaphyllea, Carex sempervirens, Festuca halleri, Kobresia myosuroides, Nardus stricta, Salix herbacea, Sesleria coerulea.*

Discussion

Ecological specialization of Carex curvula forms

The niche attributes of *Carex curvula* ssp. *curvula* and ssp. *rosea* were derived from a comparative study of an extensive data set. We do not know about a similar comprehensive study in the southwestern Alps using direct gradient analysis. We showed that the realized niches of sympatric populations of *Ccc* and *Ccr* do not overlap. The ecological specialization in *C. curvula* is more complex than the substrate type preference on which previous investigations focused (Gensac 1977; Erschbamer 1992). *Ccc* and *Ccr* also differ along meso-topographical and concurrent disturbance gradients. Among local-scale gradients, mesotopographic position on slopes is a complex gradient along which major shifts in floristic assemblages have been described (Billings 1973). Mesotopographical variations and wind control snowpack accumulation. Snow depth and duration are known to influence temperature regime and determine important resource gradients such as nitrogen and water (Billings & Bliss 1959; Isard 1986; Stanton et al. 1994).

Top slopes or crests on which *Ccr* mostly occurs have long snow-free periods and are subject to severe stress and disturbance. Alpine tundra dominated by *Ccc* is traditionally considered climax alpine vegetation on acidic substrates (Grabherr 1989; Theurillat 1996) and *Ccc* tussocks are very sensitive to soil instability driven by repeated freeze-thaw cycles (Baudière et al. 1985).

Between-regional variation in habitat availability and niche attributes

Our study provides strong evidence that between-region variation in habitat availability explains the distributional variation of *C. curvula* forms in the southwestern Alps. Hierarchical analysis of gradients was once proposed as a conceptual and heuristic model to assess large-scale spatial variations of floristic diversity in arctic and alpine ecosystems (Billings 1973). However, there have been few studies examining the interplay of regional and local-scale factors on floristic patterns in alpine landscapes. Kirkpatrick et al. (1998) showed the primacy of large-scale climatic factors vs edaphic local-scale factors to explain floristic differ-

ences between Australian and Tasmanian alpine tundra. Ferreyra et al. (1998) emphasized the strong impact of a rain shadow gradient on alpine community organization in the south Andes. Large-scale shifts in the physiognomy of alpine tundra have also been described in the Alps (Ozenda 1985).

Summer is the wettest season in the central and eastern parts of the range, whereas the Mediterranean influence is responsible for dry summers in the southwestern Alps (Frei & Schär 1998). Lower summer precipitation limits the development of dense vegetation dominated by graminoids. Furthermore, as graminoid tussocks stabilize soils (Heilbronn & Walton 1984; Wilson & Agnew 1992), an increased level of disturbance is to be expected in the southernmost regions. The particular set of abiotic variables realized in *Ccc* optimal habitat is lacking here, probably because of these specific macroclimatic features.

Changes in the nature and strength of plant interactions have long been recognized as important driving forces shaping species' distribution along gradients (Whittaker 1967; Austin 1985; Choler et al. 2001). At a between-regional scale, evidence of niche widening/narrowing due to changes in competitive level have been documented for birds (Blondel et al. 1988) and vascular plants (Diekmann & Lawesson 1999). In contrast, we found no evidences of reduced niche breadth for range margin populations of *Ccc* compared to range centre populations. Our results suggest that changes in habitat availability rather than competitive displacement explain infrequency and low abundance of *Ccc* in the southwestern Alps. The situation might be different for *Ccr* as the species is restricted to very cold sites in region 1, whereas the thermal range of the species is wider in the south.

Ecogenesis vs phylogenesis

Obviously, historical factors warrant consideration when interpreting our results. The impact of past climatic or geological crises in shaping the current distribution of alpine taxa has long been postulated (Taberlet et al. 1998). Unfortunately, the phytogeography of high altitude taxa is still poorly understood (but see Stehlik et al. 2001). It seems unlikely that dispersal limitation *per se* might explain the infrequency of *Ccc* in the southwestern Alps if one remembers that the species is distributed throughout the European mountain ranges from the Pyrenees to the Carpathians.

Over shorter time periods, stochastic processes such as dispersal and recruitment events affect the occupancy level of suitable habitats (Pulliam 2000). It is supposed that permanent occupation of unsuitable or distant sites is dependent on replenishment by successful dispersers.

In the southern part of its range, the fragmented nature of *Ccc* habitats, and the lack of source-sites, might limit these dynamic processes. However, *C. curvula* is a clonal, long-lived perennial species (Steinger et al. 1996) and recruitment by seeds appears very rare in the field (Grabherr 1989). These characteristics should severely slow down the patch dynamics of this species.

In this study, we tried to unravel the features of the ecological specialization in the alpine species, *C. curvula*. The examination of niche attributes leads us to conclude that *Ccr* and *Ccr* are ecotypes, not vicariant forms, and that most of the distributional variation observed in the southwestern Alps is primarily explained by differences in habitat availability along the bioclimatic gradient. We believe that this ecological analysis provides a relevant framework for examining other causes – mainly historical – of the current geographical distribution.

References

Austin, M.P. 1985. Continuum concept, ordination methods, and niche theory. *Annu. Rev. Ecol. Syst.* 16: 39-61.

Baudière, A., Gauquelin, T. & Serve, L. 1985. La régression des pelouses culminales et les facteurs de la géomorphologie sur les hautes surfaces planes oriento-pyrénéennes. *Coll. Phytosociol.* 13: 149-171.

Billings, W.D. 1973. Arctic and alpine vegetations: similarities, differences, and susceptibility to disturbance. *BioScience* 23: 697-704.

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

Blondel, J., Chessel, D. & Frochot, B. 1988. Bird species impoverishment, niche expansion and density inflation in mediterranean habitats. *Ecology* 69: 1899-1917.

Braun-Blanquet, J. 1932. *Plant sociology*. McGraw-Hill, New York, NY.

Chas, E. 1994. *Atlas de la flore des Hautes-Alpes*. Conservatoire des Espaces Naturels de Provence et des Alpes du Sud - Parc National des Ecrins, FR.

Choler, P., Michalet, R. & Callaway, R.M. 2001. Facilitation and competition on gradients in alpine plant communities.

Ecology 82: 3295-3308.

Claudin, J. 1970. *Sol et végétation de l'étage alpin sur roche mère acide dans la région du col de Chavière*. Thèse de Spécialité, Université de Grenoble, CH.

Dalmas, J.-P. 1972. *Etude phytosociologique et écologique de l'étage alpin des Alpes sud-occidentales françaises et plus particulièrement de la région de Vars (Hautes-Alpes)*. Ph.D Thesis, Université Aix-Marseille III, FR.

Diekmann, M. & Lawesson, J.E. 1999. Shifts in ecological behaviour of herbaceous forest species along a transect from northern Central to North Europe. *Folia Geobot. Phytotax.* 34: 127-141.

Dolédec, S., Chessel, D. & Gimaret-Carpentier, C. 2000. Niche separation in community analysis: a new method. *Ecology* 81: 2914-2927.

Erschbamer, B. 1992. Zwei neue Gesellschaften mit Krumm-seggen (*Carex curvula* ssp. *rosae*, *Carex curvula* ssp. *curvula*) aus den Alpen: ein Beitrag zur Klärung eines alten ökologischen Rätsels. *Phytocoenologia* 21: 91-116.

Ferreyra, M., Cingolani, A., Ezcurra, C. & Bran, D. 1998. High-andean vegetation and environmental gradients in northwestern Patagonia, Argentina. *J. Veg. Sci.* 9: 307-316.

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

Frei, C. & Schär, C. 1998. A precipitation climatology of the Alps from high-resolution rain-gauge observations. *Int. J. Clim.* 18: 873-900.

Galen, C., Shore, J. S. & Deyoe, H. 1991. Ecotypic divergence in alpine *Polemonium viscosum*: genetic structure, quantitative variation, and local adaptation. *Evolution* 45: 1218-1228.

Gensac, P. 1977. Les groupements végétaux à *Carex curvula* All. dans le massif de la Vanoise. *Trav. Sci. Parc Vanoise* 8: 67-94.

Gilomen, H. 1938. *Carex curvula* All. sp. nov. *rosae* (Kalk-Krummsegge). *Ber. Geobot. Inst. Eidg. Tech. Hochsch. Stift. Rübel*: 77-104.

Grabherr, G. 1989. On community structure in high alpine grasslands. *Vegetatio* 83: 241-250.

Guinochet, M. 1938. *Etudes sur la végétation de l'étage alpin dans le bassin supérieur de la Tinée*, Université de Grenoble, CH.

Heilbronn, T.D. & Walton, W.H. 1984. Plant colonisation of actively sorted stone stripes in the subantarctic. *Arct. Alp. Res.* 16: 161-172.

Isard, S.A. 1986. Factors influencing soil moisture and plant community distribution on Niwot Ridge, Front Range, Colorado, U.S.A. *Arct. Alp. Res.* 18: 295-304.

Kirkpatrick, J.B. & Bridle, K.L. 1998. Environmental relationships of floristic variation in the alpine vegetation of southeast Australia. *J. Veg. Sci.* 9: 251-260.

Langlet, O. 1971. Two hundred years genecology. *Taxon* 20: 653-722.

McGraw, J.B. & Antonovics, J. 1983. Experimental ecology of *Dryas octopetala* ecotypes. I. Ecotypic differentiation and life-cycle stages of selection. *J. Ecol.* 71: 117-124.

Michalet, R., Rolland, C., Joud, D., Gafta, D. & Callaway, R.M. In press. Associations between canopy and understory species increase along a rainshadow gradient in the Alps: habitat heterogeneity or facilitation? *Plant Ecol.*

Molinier, R. & Pons, A. 1955. Contribution à l'étude des groupements végétaux du Lautaret et du versant sud du Galibier. *Bull. Soc. Sci. Dauphiné* 69.

Mooney, H.A. & Billings, W.D. 1961. Comparative physiological ecology of arctic and alpine populations of Oxyria digyna. *Ecol. Monogr.* 31: 1-29.

Nelson, G. 1976. Biogeography, the vicariance paradigm, and continental drift. *Syst. Zool.* 24: 490-504.

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

Pulliam, H.R. 2000. On the relationship between niche and distribution. *Ecol. Lett.* 3: 349-361.

Reynier, P. 1988. *Etude phytoécologique, pédologique et statistique de stations sur schistes lustrés en haute Ubaye et régions avoisinantes, aux étages alpins et subalpins supérieur d'adret*. Ph.D Thesis, Université de Grenoble, CH.

Stanton, M.L., Rejmánek, M. & Galen, C. 1994. Changes in vegetation and soil fertility along a predictable snowmelt gradient in the Mosquito range, Colorado U.S.A. *Arct. Alp. Res.* 26: 193-200.

Stehlik, I., Schneller, J. J. & Bachmann, K. 2001. Resistance or emigration: response of the high-alpine plant *Eritrichium nanum* (L.) Gaudin to the ice age within the Central Alps. *Mol. Ecol.* 10: 357-370.

Steinger, T., Körner, C. & Schmid, B. 1996. Long-term persistence in a changing climate: DNA analysis suggests very old ages of clones of alpine *Carex curvula*. *Oecologia* 105: 307-324.

Taberlet, P., Fumagalli, L., Wust-Saucy, A.-G. & Cosson, J.-F. 1998. Comparative phylogeography and postglacial colonization routes in Europe. *Mol. Ecol.* 7: 453-464.

Theurillat, J.-P. 1996. Les pelouses à *Carex curvula* subsp. *curvula* (*Caricion curvulae*) dans les Alpes. *Diss. Bot.* 258: 267-294.

Thioulouse, J., Chessel, D., Dolédec, S. & Olivier, J. M. 1997. ADE-4: a multivariate analysis and graphical display software. *Stat. Comput.* 7: 75-83.

Thorpe, R.S., Brown, R.P., Day, M., Malhotra, A., McGregor, D.P. & Wüster, W. 1994. Testing ecological and phylogenetic hypotheses in microevolutionnary studies. In: Eggleton, P. & Vane-Wright, R.I. (eds.) *Phylogenetics and ecology*, pp. 189-206. Academic Press, London, UK.

Verger, J.-P. 1987. *Végétation et pédogenèse sur roches vertes et gneiss acide dans une séquence altitudinale montagnard-alpin en Val d'Aoste (Italie)*. Ph.D. Thesis, Université de Grenoble, Grenoble, CH.

Whittaker, R.H. 1967. Gradient analysis of vegetation. *Biol. Rev.* 42: 207-264.

Wilson, J.B. & Agnew, A.D.Q. 1992. Positive switches in plant communities. *Adv. Ecol. Res.* 23: 263-336.

Zimmermann, N.E. & Kienast, F. 1999. Predictive mapping of alpine grasslands in Switzerland: Species versus community approach. *J. Veg. Sci.* 10: 469-482.

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www.opuluspress.se/pub/archives/index.htm