

Dedicated to Prof. dr. LJUDEVIT LIJANIĆ on the occasion of his 70<sup>th</sup> birthday.

## Reconsidering endemism in the North-eastern Limestone Alps

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The restricted distribution of endemic plant species in the Northern Limestone Alps is commonly explained by a severe loss of biotypes and genetic plasticity during Pleistocene glaciation. In the present paper we examine the ecological features of the regional endemic species and plant communities to see if they actually support this interpretation. In particular, we focus on (1) species composition and habitat characteristics of endemic plant communities, (2) the frequency of endemic species in different plant communities and habitat types, (3) the correlation between the frequency of endemic species and the density of the vegetation cover and (4) the altitudinal distribution of endemic species.

Concerning endemic plant communities, there is considerable variation in species composition as well as in habitat requirements. Communities of rock, scree and snowbed habitats are characterised by the predominance of endemic or subendemic species, whereas endemic alpine grassland types contain mainly non-endemic plants.

Regarding the distribution of endemic plants, no uniform trend could be detected. The endemic species pool contains plants restricted to azonal stands as well as typical species of climax grasslands and widespread generalists. Some endemics distinctly prefer open vegetation types, others predominantly occur in dense grasslands. The bulk of the species considered performs best in the lower alpine zone, some others are especially common in the subalpine zone, whereas only one species showed an occurrence peak in the upper alpine belt.

In summary, it may be said that the habitat requirements of endemic plants are rather species-specific and that there are only a few general trends. This fact seems to indicate the complex nature of the phenomenon of regional endemism, which is influenced by a range of factors. The prevailing historical explanation may not be appropriate for every species. Hence, the consideration of current ecological conditions in addition to historical factors may provide a more comprehensive explanation of regional endemism.

**Key words:** Limestone, Alps, endemic, plant, communities

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## Introduction

The flora and vegetation of the North-eastern Limestone Alps are characterised by some peculiarities. The comparatively high percentage of endemic species in the flora is a well-known fact (PAWŁOWSKI 1970, FAVARGER 1972). This unusual accumulation of endemic plants (and animals, see HOLDHAUS 1954) has commonly been explained historically since MERXMÜLLER (1952–1954) published his comprehensive studies on species-distribution and speciation in the Alps. MERXMÜLLER (1952–1954) observed a distinct correspondence between the distribution of many endemic plant species and the patterns of Pleistocene glaciation, especially during the last glacial period (Würm). In fact, endemics are obviously restricted to those peripheral areas of the Alps that were free of ice or only locally glaciated, serving as »massifs de refuge« for the bulk of the alpine species (see Fig. 1). According to MERXMÜLLER (1952–1954), this fact clearly indicates the relict nature of alpine endemism. Endemic plants are simply that part of the old, preglacial mountain flora that survived glaciation but was not able to recolonise the former glaciated areas when the glaciers retreated. Redispersal might have been prevented by a lack of genetic plasticity caused by a severe loss of biotypes during glaciation (EHRENDORFER 1965, NIKLFELD 1972).

This explanation of alpine endemism clustered at the north-eastern as well as at the south-eastern and south-western fringes of the Alps has been »state of the art« for a few decades. But ZIMMERMANN (1972) called for a more comprehensive view and, more recently, PILS (1988, 1995) severely criticised the historical approach, privileging current ecological conditions as primary reasons for the restricted distribution of endemic plants at least in the north-eastern part of the Alps. He particularly stresses the special climatic features of this region and the frequent phenomenon of vicariism among endemic species and widespread ecological equivalents missing exactly in the »massifs de refuge«.

However, the region's peculiarities are not restricted to endemic species. There are some special features at the community level, too. The recently published review of Austrian plant communities (MUCINA et al. 1993 a,b, GRABHERR and MUCINA 1993) lists a couple of endemic associations and geographically restricted assemblages lacking explicit syntaxonomic description. There is, of course, a close connection between species and community endemism. But the existence of endemic species does not provide a sufficient explanation for the occurrence of endemic syntaxa, since endemic plant communities are only partially dominated or characterised by endemic plant species. The existence of these special vegetation types indicates some distinct ecological features of the region beyond the fact of not having been glaciated during the Pleistocene.

Any attempt to explore the reasons for regional endemism presupposes sufficient knowledge on the distribution and ecology of the species and communities in question. The present study is primarily meant to contribute to this latter issue. It is based upon a set of vegetation samples from a couple of mountain ranges in the extreme northeast of the Alps (Schneeberg, Raxalpe, Zeller Staritzen and Hochschwab). This area represents the catchment area for the water supply of Vienna and is the subject of an interdisciplinary long-term research-initiative that includes large-scale vegetation mapping above the tree line. Syntaxonomic units,

mainly associations, served as mapping units. They were derived from relevés done by the authors during the last six years. This dataset was subject to statistical analysis with special reference to the ecology of endemic species and communities. Besides a survey of the species composition and the habitat requirements of endemic communities, we especially focus on the syntaxonomic distribution of endemic species and their relation to altitude. Correlations with overall plant species diversity and the density of the vegetation cover were analysed, supposing that especially the latter issue may provide an indicator of their competitive ability.

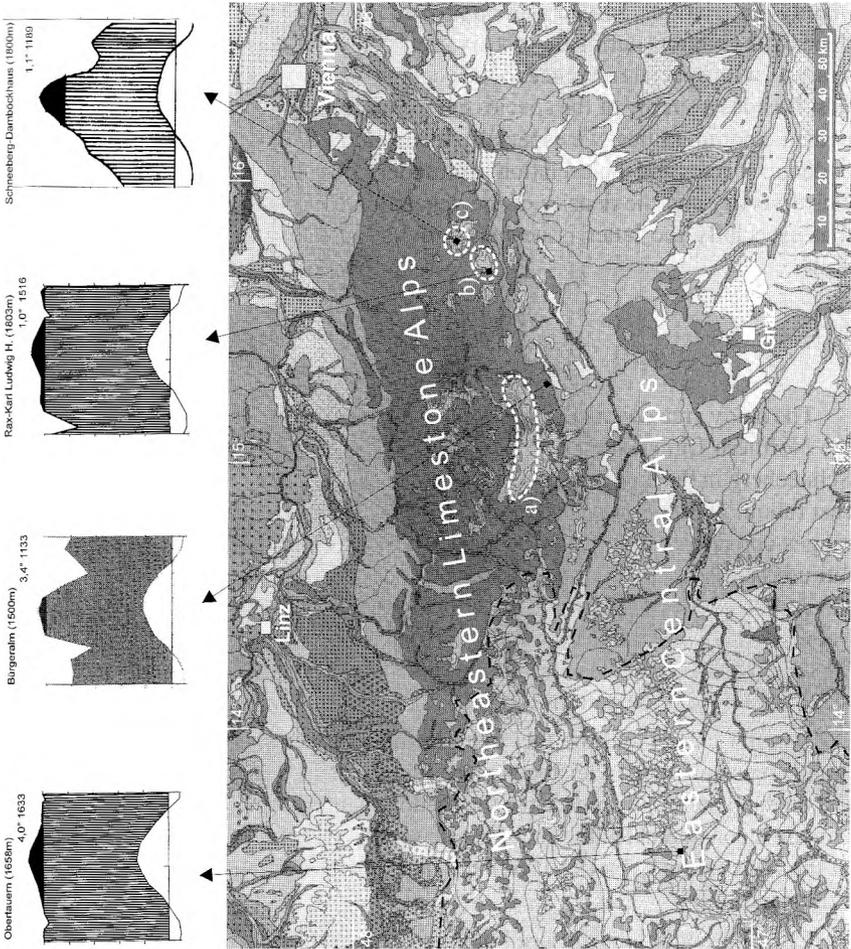
### Study area

The study area covers the subalpine and alpine belt of the easternmost part of the Northern Limestone Alps from Mount Hochschwab in the west to Mount Schneeberg in the east (see Fig. 1). Summit altitudes continuously increase from east (about 2000 m) to west (about 2300 m). Geomorphologically, all mountain ranges considered may be called table mountains forming vast plateaus at high altitudes with steep slopes down to the valley bottoms marking their boundaries. Geologically, they are built up foremost of different kinds of limestone. Consequently, meso- and micro topography are characterised by a variety of karst landforms like poljes, dolines and karren, essentially determinants of microclimate and hence vegetation patterns.

The flat terrain and the fact that glaciation was restricted to comparatively small areas during the Pleistocene (see Fig. 1), caused tertiary sediments to persist on the plateaus. In contrast to the predominant, shallow postglacial soils they contain a considerable amount of aeolic sediments from adjacent siliceous parts of the Alps (see e.g. FRANZ 1960) and therefore form deep, loamy, more or less acid soils.

Climatic conditions are not homogeneous even within the limited range of the study area. The proximity of continental climatic conditions bordering the eastern edge of the study area is responsible for a distinct decrease of precipitation from west to east (see Fig. 1). Moreover there is a significant decrease of precipitation from north to south due to frequent dynamic air pressure at the northern border of the Alps. Taking Mt. Schneeberg as an example, the altitudinal increase of precipitation accounts for approximately 18 mm/100 m during the vegetation growth period and the altitudinal decrease in temperature for 0.6 °C/100 m (DIRNBÖCK and GRABHERR 2000). Temperature inversion with high summit temperatures and low valley temperatures frequently occurs in autumn and early winter.

Along the altitudinal gradient, the following vegetation belts are established: At the tree line, currently around 1500 m and about 200 metres below the natural one due to a long history of human land use, pure spruce forests (*Picea abies*) are dominant. Primarily on north facing slopes, they are regularly intermixed with larch (*Larix decidua*). The adjacent krummholz-zone is, in fact, a mosaic of prostrate pine forests (*Pinus mugo*) and different types of alpine pastures, mainly dominated by *Nardus stricta*, *Deschampsia cespitosa* or *Festuca nigrescens*, to-



**Fig. 1.** Map of the eastern part of the Alps with study areas a) Hochschwab, b) Raxalpe and c) Schneeberg. Pale shades within the Northern Limestone and Central Alps indicate late Pleistocene glaciers diminishing eastwards, and dark shades indicate ice-free regions (after FINK and NAGL 1979). A broken black line indicates the border. Additionally, four climate plots (WALTER and LIETH 1960 and own data) are given along a west-east gradient. Taking into account the altitudinal differences of these four stations, a clear decrease in precipitation can be seen.

gether with some perennial herbs (*Leontodon hispidus*, *Crepis aurea* etc.). Less frequent, tall herb communities (*Adenostyles alliaria*, *Aconitum napellus*) and fens (*Carex nigra*, *C. rostrata*) are found. Between 1700 and 1800 m there is a gradual transition to the alpine belt in the strict sense. Natural alpine grasslands, predominated mainly by *Carex sempervirens* and *Sesleria albicans* or by *Carex firma*, are to be regarded as the zonal vegetation type there. However, azonal habitats, especially rock faces, screes and snowbeds are widespread from the valley bottoms up to the summit area.

For more details on the physical geography and vegetation of the study area see GREIMLER and DIRNBOCK (1996), DIRNBOCK and GREIMLER (1997), DIRNBOCK et al. (1998, 1999).

## Methods

### Data-collection

Data collection was aimed at the acquisition of a complete inventory of all plant communities present in the research area, including the very rare ones, to create a reference data set for large scale vegetation maps. In other conditions, this requirement would have necessitated a large amount of random sampling points, many of which would have been inaccessible due to the rugged mountainous terrain. Thus, no special sampling design was applied, and sampling points were chosen arbitrarily. Requirements to be met were accessibility, homogeneity of species composition as well as of habitat quality, an even distribution of sampling plots over the whole research area and a coarse quantitative representativeness of relevé-counts and the area covered by each community. Relevé plots were 4x4 m in size, except for krummholz and forests (20x20 m). Data were collected according to BRAUN-BLANQUET (1964) with seven cover-abundance values (r, +, 1, 2, 3, 4, 5). Moreover total vegetation cover, slope, aspect, altitude, soil type and-as far as possible-soil depth and soil horizon formation were recorded for each site.

### Data-analysis

The survey of Austrian plant communities (MUCINA et al. 1993a, b, GRABHERR and MUCINA 1993) served as the basis for defining the units of the vegetation maps. Relevés were assigned to this classification as far as possible. Dominance of species, presence of floristic indicators and habitat-quality were used as criteria for identification of syntaxa. We used TWINSPLAN (HILL 1979), a divisive hierarchical classification technique, for structuring the dataset.

Endemics and subendemics to be considered were selected with respect to ADLER et al. (1994). From the whole set of 19 selected species, 14 are decisively restricted to the North-eastern Limestone Alps. Two of them may also be found on calcareous stands in the easternmost siliceous Alps (eastern parts of Niedere Tauern Mts.: *Draba stellata*, *Pedicularis portenschlagii*) and another two in parts of the Bavarian Alps (Berchtesgadener Alpen Mts.: *Draba sauteri*, *Primula clusiana*). *Viola alpina* is not an endemic or subendemic species in the strict sense but is disjunctly distributed in the Alps and the Carpathian mountains. It was taken into account because within the Alps it is restricted to the same regions as the real endemic species.

Generally, only communities represented by at least five records, and only species recorded in at least ten relevés, were included into statistical calculations.

To achieve constancy-tables, we calculated the percentage of relevés of a community, within which any one species was recorded. These constancies were summarized in five classes according to BRAUN-BLANQUET (1964).

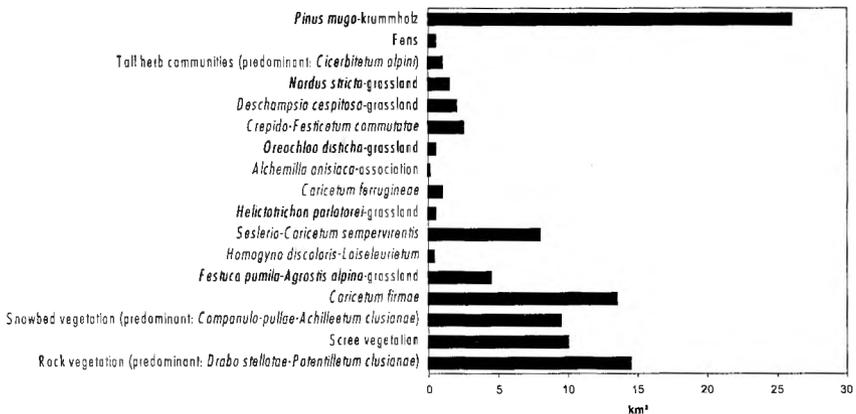
Regarding the syntaxonomic distribution of endemic species, we calculated their different performance in different communities by weighting their summarized constancies by their respective mean cover-abundance values giving *r* and + a weight of 1, 1 and 2 a weight of 2 and 3, 4 and 5 a weight of 3. The total range of values characterising the frequency of a species in a community therefore lies between 0 and 15.

To analyse the distribution of species along the altitudinal gradient we first assigned all relevés to distinct altitudinal belts of 50 m each beginning with 1400–1450 m up to 2150 to 2200 m. The overall abundance of each species in each altitudinal belt was then calculated. Overall abundance represents the summed abundance of a species in all relevés after transformation of the Braun-Blanquet-values into numerical ones (*r* = 1, + = 2, 1 = 3 etc.). To avoid bias of data due to different relevé-counts, overall abundance of each species was divided by the sum of relevés per altitudinal belt.

$$A_i^{b*} = \Sigma a_{ir} / \Sigma r^b * 100$$

with  $A_i^{b*}$  = relative overall abundance of species *i* in altitudinal belt *b* and *a<sub>ir</sub>* abundance of species *i* in relevé *r*.

Regression analysis was applied to detect associations between these relative overall abundances and altitude. We compared linear and second order polynomial regression to assess if a species performs best within or without the altitudinal range considered in this study. Thus we tried to circumvent the problem that the study area extends neither into the montane nor the upper alpine or nival belt.



**Fig. 2.** Area covered by the most important vegetation types. Areas are calculated on the basis of the digital vegetation maps of Mt. Schneeberg, Mt. Rax, Mt. Zeller Staritzen and Mt. Hochschwab (see GREIMLER and DIRNBÖCK 1996, DIRNBÖCK and GREIMLER 1998, DIRNBÖCK et al. 1999). Forests were not considered. Communities of rock, scree and snowbed habitats were summed, because the different associations were not mapped separately.

To examine how altitude effects the contribution of endemic species to the overall species pool, the count of species and the count of endemics recorded in all relevés were calculated for the same altitudinal belts of 50 m.

In a similar way, the total set of relevés was subdivided with respect to total vegetation cover per plot. Five classes were arbitrarily selected (0–20%, 20–40%, 40–60%, 50–80%, 80–100% total vegetation cover) and each relevé was assigned to the appropriate class. The count of species and the count of endemics recorded in all relevés of the respective classes were calculated.

Regression analysis was performed with SPSS 7.5.

Nomenclature follows ADLER et al. (1994) for flowering plants, FRAHM and FREY (1992) for bryophytes, WIRTH (1980) for lichens, MUCINA et al. (1993 a, b) and GRABHERR and MUCINA (1993) for syntaxa.

## Results

### Endemic communities

Syntaxonomic analysis of the complete data set (964 relevés) revealed 73 plant communities. Details on their flora, ecology and distribution are given elsewhere (GREIMLER and DIRNBÖCK 1996, DIRNBÖCK and GREIMLER 1997, DIRNBÖCK et al. 1998, 1999).

This total of 73 associations contains nine endemic plant communities. Their contributions to the overall vegetation cover differ considerably. Whereas the *Drabo stellatae-Potentilletum clusianae* or the *Campanulo pullae-Achilleetum clusianae* cover large areas, the *Alchemilla anisiaca*-community and the *Oreochloa disticha*-grasslands are restricted to small parts of the investigation area with a highly scattered distribution of these communities even within these regions (see Fig. 2).

To characterise these nine plant communities in some detail, Table 1 provides a survey of their species composition and Table 2 summarises some important ecological features.

### *Drabo stellatae-Potentilletum clusianae*

The *Drabo stellatae-Potentilletum clusianae* is the predominating vegetation type of alpine rock-faces. Like any other type of alpine rock vegetation it is characterised by a very low total vegetation cover. Soils are poorly developed and cushion plants, being able to accumulate detritus and aerosols (see e.g. KÖRNER 1999), are the dominating life-form. The community is dominated by *Potentilla clusiana* and *Draba stellata* is its character species. Unlike *Draba stellata*, *Potentilla clusiana*, though mainly distributed in the North-eastern Limestone Alps, is not an endemic or subendemic in the strict sense, because it occurs regularly in some parts of the Southeastern Calcareous Alps, too (MERXMÜLLER 1954: Steiner Alpen Mts., Karnische Alpen Mts.). Moreover *Carex firma* and *Festuca versicolor* subsp. *brachystachys*, another endemic species of the region, are frequent in this community. Average plant species diversity is quite low (see Tab. 1 and 2).

**Tab. 1.** Constancies of species in the endemic plant communities of the North-eastern Limestone Alps. Constancies are calculated as percentage of all relevés of a plant community, within which a species was recorded. These percentages were then summarized in five classes according to BRAUN-BLANQUET (1964). Assignment of species to syntaxonomic blocks follows MUCINA et al. (1993a, b) and GRABHERR and MUCINA (1993) or their relative constancies in the dataset. Mean abundance of each species is given in brackets. Endemic and subendemic species of the region are given in bold italic. Character species are indicated by the following abbreviations: AS—association, AL—alliance, OR—order, CL—class.

Species	Number of samples	<i>Draba stellatae-Potentilletum clusianae</i>	<i>Campanulo pullae-Achilleetum clusianae</i>	<i>Campanulo pullae-Achilleetum atratae</i>	<i>Athamanto-Festuceetum pallidulae</i>	<i>Helictotrichon parlatorei-grassland</i>	<i>Alchemilla anisiaca-association</i>	<i>Homogyna discoloris-Loiseleurietum</i>	<i>Festuca-Agrostis-grassland</i>	<i>Juncion trifidi</i>
<b><i>Draba stellatae-Potentilletum clusianae</i></b>										
AS <i>Draba stellata</i>		IV(+)								
OR <i>Potentilla clusiana</i>		V(1)	I(+)		III(+)					
<b><i>Potentillion caulescentis</i></b>										
AL <i>Petrocallis pyrenaica</i>		I(+)			I(+)					I(1)
AL <i>Hieracium humile</i>		I(+)								
AL <i>Campanula praesignis</i>		I(+)			I(+)					
AL <i>Androsace lactea</i>					III(+)					I(+)
AL <i>Draba sauteri</i>		I(+)								
AL <i>Draba aizoides</i>		I(+)		I(+)	II(1)					
AL <i>Arabis stellulata</i>		I(+)	I(+)	I(+)						
<i>Valeriana elongata</i>		II(+)	I(+)							
<b><i>Potentilletalia caulescentis</i></b>										
OR <i>Primula auricula</i>		III(+)	I(+)		V(1)		I(r)	I(+)	II(+)	
OR <i>Trisetum alpestre</i>		III(+)			V(1)		I(1)		I(+)	
OR <i>Asplenium viride</i>		II(+)	I(+)				I(r)		I(+)	
OR <i>Kernera saxatilis</i>		I(+)			V(+)					
OR <i>Campanula cespitosa</i>		I(+)								
OR <i>Festuca alpina</i>		I(+)								
OR <i>Minuartia cherlerioides</i>		I(1)								
OR <i>Valeriana saxatilis</i>		II(+)			I(+)					I(+)
<b><i>Asplenietaea trichomanis</i></b>										
CL <i>Asplenium ruta-muraria</i>		I(+)			II(+)					
<i>Festuca versicolor subsp. brachystachys</i>		IV(+)	I(1)	I(1)	II(1)		I(1)	II(+)	II(1)	II(1)
<b><i>Campanulo pullae-Achilleetum clusianae</i></b>										
AS <i>Achillea clusiana</i>		I(+)	V(2)	I(1)			I(2)		I(1)	I(+)
AS <i>Thlaspi alpestre</i>			III(+)	II(1)	I(+)	I(+)	IV(1)	II(+)	II(+)	II(+)
<b><i>Campanulo pullae-Achilleetum atratae</i></b>										
AS <i>Achillea atrata</i>		I(+)	II(1)	V(2)			I(1)		I(+)	
<b><i>Arabidetalia caeruleae</i></b>										
OR <i>Campanula pulla</i>		I(+)	V(2)	V(2)			II(+)		I(+)	
OR <i>Ranunculus alpestris</i>		III(+)	IV(1)	V(1)			I(1)	II(+)	II(+)	I(+)
OR <i>Galium noricum</i>			III(+)	III(1)			II(+)	II(+)	III(+)	I(+)

Tab. 1. – continued

Species	Number of samples	24	41	8	6	11	10	14	66	16
OR <i>Carex parviflora</i>			II(+)	IV(+)			I(+)		I(+)	I(+)
OR <i>Soldanella austriaca</i>		I(+)	III(1)	III(+)			II(1)	I(+)	I(1)	
OR <i>Gnaphalium hoppeanum</i>			II(+)	I(+)					I(+)	I(1)
OR <i>Saxifraga androsacea</i>			II(1)	IV(+)						
OR <i>Potentilla brauneana</i>			II(1)	I(+)			I(+)			
OR <i>Arabis caerulea</i>			I(+)	III(+)						
OR <i>Leontodon montaniformis</i>			I(1)	II(1)					I(2)	
OR <i>Rumex nivalis</i>			I(1)	II(1)			I(+)			
<i>Veronica alpina</i>		I(+)	IV(1)	V(1)			II(+)		I(+)	I(+)
<i>Saxifraga stellaris</i>		I(+)	IV(1)	V(1)			I(+)			I(+)
<i>Myosotis alpestris</i>		I(r)	III(+)	II(+)		I(+)	I(+)		I(+)	I(+)
<i>Pritzelago alpina</i>		I(+)	III(1)	V(1)				II(+)	I(1)	
<i>Saxifraga sedoides</i>		II(1)	III(1)	IV(1)			I(+)			
<i>Sedum atratum</i>		I(+)	III(+)	II(+)	I(+)				I(+)	
<i>Taraxacum</i> sp.			II(1)	IV(+)			I(+)		I(+)	
<i>Gentiana bavarica</i> subsp. <i>bavarica</i>			I(+)	II(+)			II(+)		I(+)	
<b><i>Thlaspietea rotundifolii</i></b>										
CL <i>Moehringia ciliata</i>			IV(1)	IV(1)			I(+)			
CL <i>Poa minor</i>			III(1)	V(1)						
CL <i>Arabis alpina</i>			III(+)	I(+)			I(+)			
CL <i>Campanula cochlearifolia</i>		IV(+)	I(+)		III(+)					
CL <i>Arabis bellidifolia</i>			II(+)	II(1)			II(+)			
CL <i>Linaria alpina</i>			I(1)							
<i>Cerastium carinthiacum</i> subsp. <i>carinthiacum</i>		I(1)	II(1)	II(1)	I(+)		I(+)			
<b><i>Athamanto-Festucetum pallidulae</i></b>										
AS <i>Festuca versicolor</i> subsp. <i>pallidula</i>		I(r)			V(3)					
<i>Athamanta cretensis</i>		I(+)			IV(1)	I(+)				
<i>Carex mucronata</i>		II(1)			IV(1)					
<i>Galium meliodorum</i>		I(+)			IV(1)	I(1)		I(2)		
<i>Oxytropis montana</i>		I(+)			III(+)				I(1)	
<b><i>Helictotrichon parlatorei</i>-grassland</b>										
OR <i>Helictotrichon parlatorei</i>			I(+)		I(+)	V(4)		II(3)		
<i>Lotus corniculatus</i>			I(+)			V(1)	III(+)	II(+)	I(+)	
<i>Buphthalmum salicifolium</i>						IV(1)		I(+)	I(+)	
<i>Carlina acaulis</i>			I(+)			IV(1)		I(1)	I(+)	
<i>Scabiosa lucida</i>			I(1)			IV(+)	III(+)	II(1)	I(+)	
<i>Hippocrepis comosa</i>						III(1)			I(+)	
<i>Pimpinella major</i>						III(+)	i(+)	i(+)		
<i>Ranunculus nemorosus</i>						III(1)	I(+)	II(1)		
<b><i>Seslerion caeruleae</i></b>										
AL <i>Dianthus alpinus</i>					I(+)	I(+)	I(+)	II(+)	II(+)	
AL <i>Arabis ciliata</i>						I(+)		I(+)	I(+)	
<i>Carex sempervirens</i>		I(+)	II(+)	I(+)	III(+)	V(2)	IV(1)	II(3)	IV(1)	II(+)
<b><i>Alchemilla anisiaca</i>-Ass.</b>										
AL <i>Alchemilla anisiaca</i>			II(1)			III(1)	V(4)		I(+)	
<i>Soldanella alpina</i>			I(+)	I(+)		II(+)	IV(+)	II(+)	I(1)	I(+)
<i>Primula elatior</i>			I(+)	I(2)		I(+)	III(+)	II(1)		
<b><i>Caricion ferrugineae</i></b>										
AL <i>Phleum hirsutum</i>						V(1)		II(1)	I(+)	
AL <i>Luzula glabrata</i>			I(+)				IV(1)	II(+)	I(+)	II(1)
AL <i>Carex ferruginea</i>			I(+)			II(2)	III(2)	I(2)	I(2)	
AL <i>Crepis mollis</i>						I(1)		I(1)		

Tab. 1. – continued

Species	Number of samples	24	41	8	6	11	10	14	66	16
AL <i>Festuca pulchella</i> subsp. <i>pulchella</i>							I(+)			
<b>Festuca pumila-Agrostis alpina-grassland</b>										
<i>Agrostis alpina</i>		I(+)	I(+)		I(+)	I(+)	II(1)	III(2)	V(3)	III(1)
OR <i>Festuca pumila</i>		II(+)	III(+)	II(+)			III(+)	IV(2)	V(2)	III(1)
<i>Potentilla crantzii</i>			I(+)					I(+)	III(1)	I(+)
<b>Homogyna discoloris-Loiseleurietum</b>										
<i>Loiseleuria procumbens</i>								IV(3)	I(+)	I(+)
<i>Empetrum nigrum</i>								III(2)	I(+)	
<i>Hedysarum hedysaroides</i>								III(1)	I(+)	I(+)
<b>Caricion firmæ</b>										
AL <i>Carex firma</i>		V(1)	I(+)	II(+)	IV(1)		I(1)	III(1)	IV(1)	II(+)
AL <i>Helianthemum alpestre</i>		II(+)	I(+)		V(1)		I(1)	III(+)	IV(+)	I(+)
AL <i>Androsace chamaejasme</i>		I(+)	I(+)		I(1)		I(+)	IV(1)	III(1)	II(+)
AL <i>Primula clusiana</i>		I(+)	I(+)		I(+)		II(+)	II(1)	III(1)	I(+)
AL <i>Minuartia gerardii</i>		I(+)	I(1)		I(+)			II(+)	II(+)	I(+)
AL <i>Pedicularis portenschlagii</i>									II(+)	I(+)
AL <i>Saxifraga caesia</i>		III(+)	I(r)						I(+)	
AL <i>Crepis jacquinii</i>		I(+)			I(+)		I(+)		I(2)	
AL <i>Pedicularis rosea</i>		I(+)		I(+)				I(+)		
AL <i>Saussurea pygmaea</i>		I(+)							I(+)	
AL <i>Chamorchis alpina</i>								I(+)	I(+)	
<i>Carex capillaris</i>		I(+)					I(1)	III(1)	IV(1)	I(+)
<i>Minuartia sedoides</i>		I(+)	I(+)	II(+)			I(+)	II(1)	IV(1)	II(1)
<i>Dryas octopetala</i>		II(+)			I(+)			II(1)	IV(1)	II(+)
<i>Carex atrata</i>		I(+)	I(+)				I(+)	III(1)	IV(1)	IV(+)
<b>Seslerietalia coeruleae</b>										
OR <i>Linum alpinum</i>		I(+)			IV(1)	I(1)				
OR <i>Leucanthemum atratum</i>		I(+)	I(+)	I(+)		V(+)	I(+)	II(+)	I(+)	
OR <i>Carduus defloratus</i>		I(+)	II(+)			V(1)	I(1)		I(1)	
OR <i>Helianthemum glabrum</i>		I(+)	I(+)			V(2)	IV(1)		I(1)	
OR <i>Betonica alopecurus</i>			I(+)		I(+)	V(1)		I(1)	I(1)	
OR <i>Acinas alpinus</i>		I(+)	I(+)			IV(+)	II(+)	I(+)		
OR <i>Achillea clavennae</i>		II(+)	I(+)		III(+)	III(+)	II(+)		I(+)	
OR <i>Aster bellidiastrum</i>		II(+)	II(+)			III(+)	IV(+)	II(+)	I(+)	I(+)
OR <i>Phyteuma orbiculare</i>			I(+)		I(+)	III(1)	II(+)	II(1)	II(+)	
OR <i>Anthyllis vulneraria</i> subsp. <i>alpestris</i>					I(+)	III(+)	I(1)	II(+)	II(+)	
OR <i>Ranunculus hybridus</i>					II(+)	I(1)				
OR <i>Rhinanthus glacialis</i>					I(+)	III(+)			I(1)	
OR <i>Homogyne discolor</i>			I(+)	I(+)		II(+)	IV(1)	II(1)	III(1)	I(+)
OR <i>Heracleum austriacum</i>						V(1)	I(+)	II(1)	I(+)	
OR <i>Pedicularis rostratocapitata</i>		I(+)	I(r)	II(+)	II(+)			II(+)	II(+)	I(+)
<b>Seslerietea albicantis</b>										
CL <i>Euphrasia salisburgensis</i>		I(+)	II(+)	I(+)	V(+)	I(+)	I(+)	I(1)	II(+)	I(+)
CL <i>Galium anisophyllum</i>		I(+)	II(+)	I(+)	V(+)	V(1)	III(1)	III(+)	III(+)	I(+)
CL <i>Biscutella laevigata</i> subsp. <i>austriaca</i>		I(+)	I(+)			I(1)	I(+)	I(+)	II(+)	I(+)
CL <i>Globularia cordifolia</i>		I(+)			III(1)				I(1)	
CL <i>Sesleria albicans</i>		II(+)			III(1)	III(1)	II(+)	IV(1)	II(1)	I(+)
CL <i>Thesium alpinum</i>			I(1)		II(+)	I(+)		I(+)	I(+)	
CL <i>Selaginella selaginoides</i>			I(+)			I(+)	IV(+)	II(+)	IV(+)	III(+)
<b>Oreochloa disticha-Agrostis rupestris-grassland</b>										
<i>Oreochloa disticha</i>									I(+)	IV(3)

Tab. 1. – continued

Species	Number of samples	24	41	8	6	11	10	14	66	16
<i>Agrostis rupestris</i>			I(+)	I(+)			I(+)	II(2)	II(1)	IV(2)
<i>Juncion trifidi</i>										
AL <i>Hieracium alpinum</i>									II(+)	III(+)
<i>Caricetalia curvulae</i>										
OR <i>Campanula alpina</i>			I(1)					IV(+)	IV(+)	III(+)
OR <i>Valeriana celtica</i>									I(2)	IV(2)
<i>Caricetea curvulae</i>										
CL <i>Leontodon helveticus</i>							I(+)		I(1)	IV(1)
CL <i>Potentilla aurea</i>			I(1)	I(+)		I(+)	IV(+)	III(1)	IV(1)	V(1)
<i>Homogyne alpina</i>								II(1)	II(1)	V(1)
<i>Deschampsia cespitosa</i>			I(+)			I(+)	III(+)		I(1)	IV(1)
<i>Geum montanum</i>							III(+)	I(+)	II(1)	IV(1)
<i>Luzula multiflora</i>								I(1)	II(+)	III(+)
<i>Moreover</i>										
<i>Viola alpina</i>		I(+)	I(2)		I(+)			I(+)	I(+)	
<i>Poa alpina</i>		II(+)	IV(1)	V(1)	I(+)	I(1)	V(1)	III(1)	IV(1)	IV(+)
<i>Viola biflora</i>		II(+)	IV(1)	II(1)	I(1)	III(+)	III(1)	III(+)	II(1)	I(+)
<i>Persicaria vivipara</i>		II(+)	III(1)	III(1)		II(+)	V(1)	V(1)	V(1)	IV(+)
<i>Silene acaulis</i>		III(+)	II(+)	II(+)			I(+)	IV(1)	V(1)	IV(1)
<i>Salix reticulata</i>		I(+)	I(+)	II(1)			II(+)	III(+)	II(+)	I(+)
<i>Salix retusa</i>		I(+)	II(+)	II(+)			II(+)	III(2)	III(1)	IV(1)
<i>Salix alpina</i>		I(+)	I(1)					III(1)	II(+)	I(2)
<i>Armeria alpina</i>		I(+)	I(+)	II(+)			I(+)	II(1)	III(+)	III(+)
<i>Pedicularis verticillata</i>			I(+)	II(+)			II(+)	I(+)	II(+)	
<i>Festuca rupicaprina</i>		II(+)	IV(+)			I(1)	III(1)	II(1)	I(1)	I(+)
<i>Campanula scheuchzeri</i>		III(+)	II(+)			III(+)	V(+)	IV(+)	V(1)	IV(+)
<i>Ranunculus montanus</i> agg.		III(+)	I(+)			III(1)	V(+)	III(+)	III(1)	I(+)
<i>Trifolium pratense</i>		I(+)				III(+)	II(2)	II(+)	I(1)	
<i>Leontodon hispidus</i>		I(+)				I(1)	III(1)	II(1)	I(1)	
<i>Cerastium arvense</i> subsp. <i>strictum</i>		I(+)	I(+)			I(1)	III(1)	II(+)	II(1)	I(+)
<i>Euphrasia picta</i>		I(+)	I(+)			I(+)	III(1)	I(+)	II(1)	I(1)
<i>Gentiana pumila</i>		I(+)	II(+)				II(+)	II(+)	III(+)	I(+)
<i>Ligusticum mutellina</i>			I(1)	I(+)			IV(1)	II(1)	II(1)	IV(1)
<i>Anemone narcissiflora</i>			I(+)			I(+)	I(+)	III(+)	II(+)	I(+)
<i>Anthoxanthum alpinum</i>						II(+)	II(1)	IV(1)	IV(1)	V(1)
<i>Vaccinium vitis-idaea</i>								III(1)	III(1)	II(1)
<i>Vaccinium gaultherioides</i>								II(1)	II(1)	I(3)
<i>Euphrasia minima</i>				I(+)				I(1)	II(1)	II(1)

***Campanulo pullae-Achilleetum clusianae***

The *Campanulo pullae-Achilleetum clusianae* association is the predominant type of calcareous snowbed-vegetation. The canopy covers usually less than 50% (see Tab. 2). The community grows on debris, typical of snowbed-associations of calcareous mountain ranges. Soils are poorly developed. Perennial herbs are the most important, among them *Achillea clusiana* and *Campanula pulla*, both endemics, are dominant. Some other typical plants of moist scree vegetation like *Saxifraga stellaris*, *Ranunculus alpestris*, *Moehringia ciliata*, or the endemic *Soldanella austriaca*, are the most frequent accompanying species (see Tab. 1).

**Tab. 2.** Main topographical variables, overall vegetation cover, plant species diversity and predominant soil type of the endemic plant communities of the North-eastern Limestone Alps. Aspect, measured in degrees, is transformed to orientation to south (north = 0, west and east = 90 and south = 180) and orientation to east (west = 0, north and south = 90 and east = 180) to obtain ecologically meaningful gradients.

Variable	<i>Drabo stellatae-Potentillatum clustanae</i>	<i>Campanulo pullae-Achilleetum clustanae</i>	<i>Campanulo pullae-Achilleetum atraiae</i>	<i>Athamanto- Festucetum pallidum</i>	<i>Helictitrichon potantoretgrassland</i>	<i>Alchemilla anisica-association</i>	<i>Homogyne discoloris- Loiseleurietum</i>	<i>Festuca- Agrostisgrassland</i>	<i>Juncion trifidi</i>
Number of samples	24	41	8	6	11	10	14	66	16
Altitude (m)	1773	1858	1893	1589	1614	1846	1816	1861	1959
Standard Deviation	208	126	151	135	153	132	114	127	93
Inclination (°)	70	28	23	42	34	19	16	12	3
Standard Deviation	14	18	9	13	3	12	12	9	4
Average	89	111	115	150	145	90	61	75	44
Standard Deviation	68	51	65	23	37	57	61	61	62
Average	76	96	98	105	104	81	90	60	44
Standard Deviation	38	60	45	37	50	56	52	57	60
Vegetation cover (%)	11	47	42	48	93	95	99	96	94
Standard Deviation	8	23	19	13	8	7	3	7	6
Average	17	27	26	24	38	37	36	38	28
Standard Deviation	5	9	6	9	11	8	9	8	12
Predominante soil-type	none to initial soil	initial soil	initial soil	initial Rendosina	typical grassland Rendosina	mixed soil of Rendosina and brown earth	Rendosina with high organic matter or brown earth	brown earth	deep brown earth

***Campanulo pullae-Achilleetum atratae***

The *Campanulo pullae-Achilleetum atratae*, another snowbed-community, is distinctly less frequent than the *Campanulo pullae-Achilleetum clusianae*. Habitat qualities of both communities are quite similar (see Tab. 2). However, the *Campanulo pullae-Achilleetum atratae* prefers higher altitudes, whereas the *Campanulo pullae-Achilleetum clusianae* is found down to the tree line. The species composition of both communities does not differ very much except for the fact that *Achillea clusiana* is replaced by *Achillea atrata* and *Arabis caerulea* is nearly restricted to the *Campanulo pullae-Achilleetum atratae* (see Tab. 1). Both associations may occasionally intermix. The syntaxonomic rank of their distinction may therefore be put up for discussion.

***Athamanto-Festucetum pallidulae***

Initial grassland vegetation of steep and rocky slopes facing south. Total vegetation cover usually amounts to about 50% (see Tab. 2). The community takes an intermediate position between rock- and grassland vegetation. *Festuca versicolor* subsp. *pallidula* predominates, and most of the accompanying species belong to the typical flora of rock faces (*Kernera saxatilis*, *Primula auricula*, *Trisetum alpestre*, *Carex mucronata*) and debris (*Athamanta cretensis* and the endemic *Galium meliodorum*) (see Tab. 1). In fact, the community is distributed mainly below the tree line (GREIMLER and MUCINA 1992, GRABHERR et al. 1993). Hence, the sites recorded may not provide typical examples but are representing the upper fringes of the association.

***Helictotrichon parlatoarei-grasslands***

Typical grassland vegetation of south facing avalanche paths and other habitats characterised by a similar combination of high radiation income and moisture. Moisture is caused mainly by specific soil properties. Soils of *Helictotrichon*-grasslands are often patchy, combining situations with dry and shallow soils and others with comparatively deep and loamy ones. This causes less drainage and improved water storage compared to typical rendsina soils of the related *Seslerio-Caricetum sempervirentis*.

The community is mainly distributed around the tree line. It rarely establishes in the alpine zone itself and may thus be a typical subalpine vegetation type. Its ecological and floristic position is exactly in between the well-known grassland communities *Seslerio-Caricetum sempervirentis*, preferring similarly warm but drier habitats, and *Caricetum ferrugineae*, also bound to comparatively moist but usually less insolated stands. The predominance of *Helictotrichon parlatoarei*, a large tussock graminoid, characterises not only the species composition but also the structure of the community (see Tab. 1).

***Alchemilla anisiaca-community***

A vegetation type predominated by *Alchemilla anisiaca*, another endemic species of the most northeastern Alps. The community is frequent in the western parts of Mount Hochschwab and was also reported from Gesäuse-Mts. (GREIMLER 1997), but it is missing on Mt. Rax, Mt. Schneeberg and Mt. Schneecalpe. It usu-

ally covers only small areas, forming typical patchy mosaics with grasslands, especially with the *Seslerio-Caricetum sempervirentis*. Those vegetation patterns are controlled by microscale variation in relief and soil properties. The *Alchemilla*-community grows on deeper, partly loamy soils in flat depressions and shallow drains, where snow may accumulate, snow-melt is delayed, water storage is improved and a certain impact of nutrients may be expected due to microscale flow accumulation. There is some ecological resemblance to the patchy mosaics of *Caricetum curvulae* and *Salicetum herbacea* in siliceous mountains but the overall species composition of the *Alchemilla anisiaca*-community with *Carex ferruginea*, *C. sempervirens*, *Luzula glabrata*, *Poa alpina*, *Soldanella alpina*, *Primula elatior*, *Homogyne discolor*, *Potentilla aurea*, *Campanula scheuchzeri* and *Helianthemum glabrum* as the most important accompanying species indicates an assignment to the *Caricion ferrugineae* alliance. Besides the predominating *Alchemilla anisiaca* and a moderate constancy of *Soldanella austriaca*, endemic species are rare in this community (see Tab. 1).

*Alchemilla anisiaca* was also reported to characterise nutrient poor pastures in the region of Mt. Dachstein (PIGNATTI-WIKUS 1959).

### ***Festuca pumila-Agrostis alpina*-grassland**

Grasslands predominated by the small tussocks of *Agrostis alpina* and *Festuca pumila* are frequent on flat slopes above the tree line up to 2000 m. Stands are moderately windy but the community does not grow on extremely exposed sites. Species composition and habitat requirements indicate close relationships to the *Caricetum firmae*. Most important for an ecological differentiation of both these communities are soil properties. Relict brown, loamy soils with a high silt fraction facilitate the establishment of *Festuca-Agrostis*-grassland. Hence there is a typical accumulation of moderately acidophilous species in this community (e.g. *Potentilla crantzii*, *Carex capillaris*, *C. atrata*, *Vaccinium vitis-idaea*) and the only acidophilous (sub-) endemic of the most north easterly Alps, *Pedicularis portenschlagii*, occurs mainly in this community. From the pool of endemics *Primula clusiana* and *Festuca versicolor* subsp. *brachystachys*, especially frequent in the *Caricetum firmae*, are also moderately constant in this community (see Tab. 1).

### ***Homogyno discoloris-Loiseleurietum***

In alpine habitats where pronounced humus accumulation enhances soil acidification-or acidity is due to relictic loams-a specific plant community of the *Caricion firmae* alliance appears. This community is dominated by dwarf shrubs (*Loiseleuria procumbens*, *Arctostaphylos alpina*, *Vaccinium vitis-idaea*), graminoids (*Agrostis rupestris*, *Festuca pumila*, *Carex capillaris*) and lichens (*Cetaria islandica*, *C. nivalis*, *C. cucullata*). Herbs are less frequent and those that occur indicate acidic soil properties (e.g. *Campanula alpina*, *Potentilla aurea*). Typically, a mixture of acidophilous and calciphilous plant species is established, reflecting different contact to the calcareous bedrock. The area of the *Homogyno discoloris-Loiseleurietum* as well as of the *Festuca pumila-Agrostis alpina*-grasslands respectively may have been extended by former krummholz cutting.

The *Homogyno discoloris-Loiseleurietum* is a subendemic community of the North-eastern Limestone Alps. It also occurs on isolated stands in other parts of the Northern and Southern Alps.

### *Juncion trifidi*

Grasslands usually dominated by *Oreochloa disticha* or, sometimes, by *Agrostis rupestris* or even *Carex curvula* are grouped into the *Juncion trifidi* alliance. They have a highly scattered distribution and are restricted to deep loamy soils on tertiary sediments, accumulated in flat depressions on the plateaus. The communities are exclusively developed in the alpine belt above 1800 m. Average species diversity is low in *Juncion trifidi* grasslands (see Tab. 2). Besides the small tussock-graminoids, which determine vegetation structure, *Leontodon helveticus*, *Homogyne alpina*, *Valeriana celtica*, *Potentilla aurea*, *Geum montanum* and *Anthoxanthum alpinum* are the most important accompanying species. The community is especially poor in endemics. Except for *Festuca versicolor* subsp. *brachystachys*, which is not an endemic species in the strict sense, none of them is present in more than 20% of the relevés (see Tab. 1).

In summary, it may be said that there is a considerable heterogeneity among the endemic plant communities of the Northeastern Alps (see Tab. 1, Tab. 2). Communities generally forming dense canopies (e.g. *Homogyno discoloris-Loiseleurietum*) are represented as well as particularly open vegetation types (*Drabo stellatae-Potentilletum clusianae*). Mean plant species diversity varies between 17 and 38 per relevé. Floristic differences are quite pronounced; *Drabo stellatae-Potentilletum clusianae* and *Juncion trifidi*-grasslands have only few species in common. There are pioneer communities growing on initial soils (e.g. *Campanulo pullae-Achilleetum clusianae*), on rendsina (*Helictotrichon parlatoarei*-grasslands) and on brown earth (*Juncion trifidi*). Some are restricted to steep slopes (*Helictotrichon parlatoarei*-grasslands), while others occur only on flat terrain (*Juncion trifidi*). Some communities are concentrated at the lower (*Athamanto-Festucetum pallidulae*), while others are restricted to the upper end (*Juncion trifidi*) of the altitudinal range considered. Common features of all communities are that they are free of woody plants and that they are part of the natural vegetation cover, i.e. none of them has developed under the influence of human land-use. There are no endemic forest nor krummholz types nor alpine pastures.

## Endemic species

### *Relation to syntaxa*

The brief outline of endemic plant communities demonstrates that endemic plant species are, not surprisingly, prominent and even take the part of keystone species in the bulk of endemic plant communities. However, endemic species are not at all restricted to endemic vegetation types. Table 3 summarises the weighted constancies of endemic species in the total set of plant communities present in the study area. The distribution of endemic plants confirms the trend already mentioned. Like endemic communities, endemic species occur predominantly on natural alpine stands and decrease rapidly in seminatural pastures, fens,



krummholz and forests. But regarding natural alpine vegetation only, endemic species are considerably widespread. There is no species restricted to just one plant community and very few to just one habitat type. On the contrary, many of them are distributed over a wide range of plant communities and stands.

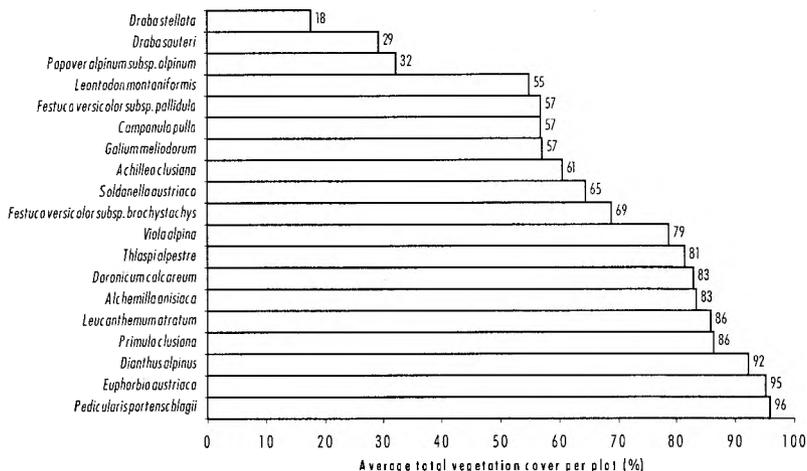
The most important habitat type for endemic species is natural alpine grassland. 10 out of 19 species are most frequent in grasslands. Among them the climax communities of the alpine belt, *Seslerio-Caricetum sempervirentis* and *Caricetum firmae* (see GRABHERR 1997), are especially rich in endemics. The frequency of endemics distinctly decreases with increasing soil acidity. Whereas *Festuca pumila-Agrostis alpina*-grassland, representing an intermediate position on the pH-gradient, is still rich in endemics, they become rare in the *Homogyno discoloris-Loiseleurietum* and especially in the *Juncion trifidi*-grasslands. Many of the species concentrated in grassland communities are more or less frequent in rock, scree and snowbed vegetation, too. Especially, *Festuca versicolor* subsp. *brachystachys* and *Alchemilla anisiaca* are considerably widespread. Only a few species of natural alpine grasslands also occur with some constancy in pastures, fens, krummholz and forests. *Euphorbia austriaca* is the only endemic species that is as frequent in these latter habitats as in natural alpine vegetation types.

The other half of the endemic species pool (8 out of 19) focuses on so-called azonal communities, i.e. rock, scree and snowbed vegetation. Most of these species are characterised by rather specific habitat requirements (*Draba stellata* on rocks, *Papaver alpinum* subsp. *alpinum* on scree, *Achillea clusiana*, *Soldanella austriaca* in snowbeds) and only *Campanula pulla* is frequent on different stands, though it has a distinct peak in snowbed vegetation. Generally, frequency and abundance of endemics are lowest on rocks and highest in snowbeds, with scree vegetation taking an intermediate position. All of the endemic species of azonal stands also occur in grasslands, some of them infrequently (e.g. *Draba stellata*, *Papaver alpinum* subsp. *alpinum*) others more regularly (*Campanula pulla*, *Soldanella austriaca*). Remarkably, only snowbed species may invade alpine pastures, fens, krummholz and forests. Species of scree- and rock habitats were hardly ever found in these vegetation types.

### **Relation to total vegetation cover**

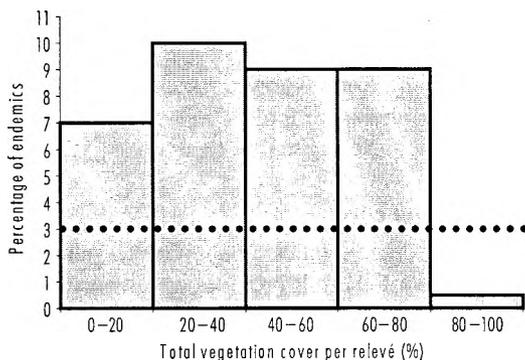
Figure 3 shows the average total cover abundance-values of all plots the respective species were recorded on. It provides a confirmation of the dichotomy just demonstrated. There is a group of species preferring azonal habitats, characterised by the lack of a closed vegetation cover, and a second one, that performs well even in closed vegetation canopies and that is therefore able to invade climax-communities, too.

**Tab. 3.** Constancies of endemic plant species, weighted by their respective average cover abundance values, in the different plant communities of the investigation area. Constancies are calculated as percentage of all relevés of a plant community, within which a species was recorded. These percentages were then summarized in five classes according to BRAUN-BLANQUET (1964).



**Fig. 3.** Average total vegetation cover per relevé for the endemic plant species considered. For details see text.

However, in general, endemic species are over-represented in open vegetation types. The contribution of endemic species to the total species pool amounts to about 3%. But there is obviously a negative, although not linear, correlation of this figure with total vegetation cover. Whereas the species pool of plots without a closed vegetation cover contains about 8-10% endemic species, the contribution of endemics drops drastically in densely vegetated areas (see Fig. 4).



**Fig. 4.** Contribution of endemic species to the total species pool of plots with different total vegetation cover. On average the group of endemic species contributes about 3% to the total species pool of all plots recorded (dashed line).

### Relation to altitude

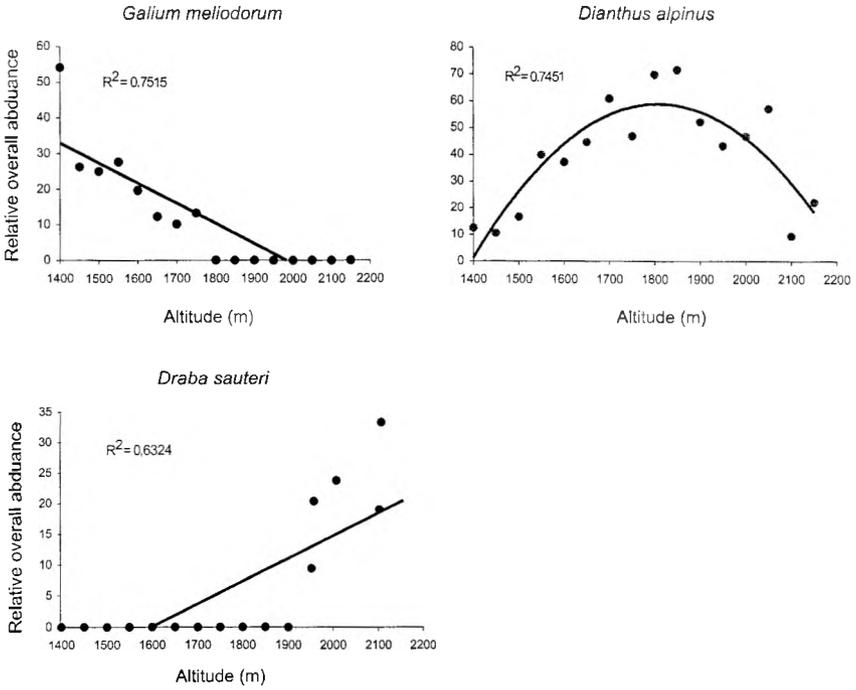
The distribution of nearly all endemic species is significantly associated with altitude (see Tab. 4). Three different types of response models may be distinguished. A negative linear response to the altitudinal gradient, indicating optimal performance of the species below the lower boundaries of the investigation area,

characterises a rather small group of endemics, namely *Papaver alpinum* subsp. *alpinum*, *Galium meliodorum*, *Festuca versicolor* subsp. *pallidula*, *Euphorbia austriaca* and *Leucanthemum atratum* (see Tab. 4 and Fig. 5). *Draba sauteri* on the other hand is the only species showing a pronounced linear increase of its abundance with altitude up to the summit areas (Fig. 5). However, the bulk of the endemic flora is not linearly dependent on altitude, whereas fitting a parabola to the data provides significant results. Peaks of the regression curves lie between 1750 and 1900 m (Tab. 4 and Fig. 5).

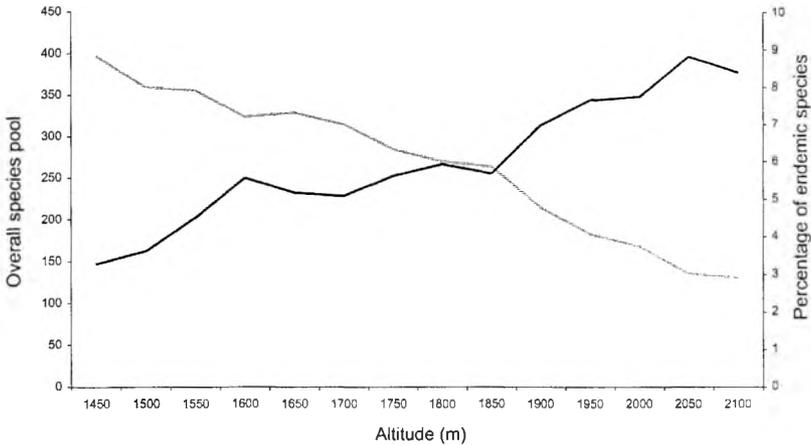
**Tab. 4.** Relative overall abundances of endemic plant species in successive altitudinal belts of 50 metres. The altitude indicated represents the lower boundary of each altitudinal step. Coefficients of determination of both linear and 2<sup>nd</sup>-order polynomial regression are given together with significance values of the regression coefficients.  $b_1$  represents the regression coefficient of the linear regression model,  $b_2$  the coefficient of the additional quadratic term in the 2<sup>nd</sup>-order polynomial regres-

Species	1400	1450	1500	1550	1600	1650	1700	1750	1800	1850	1900	1950	2000	2050	2100	2150	R <sup>2</sup> - linear	Significance of $b_1$	R <sup>2</sup> - polynomial	Significance of $b_2$
<i>Euphorbia austriaca</i>	0	11	23	6	0	0	0	0	0	0	0	0	0	0	0	0	0.24	0.05	0.31	0.10
<i>Papaver alpinum</i> subsp. <i>alpinum</i>	8	12	0	12	6	11	0	0	3	3	7	0	0	0	0	0	0.42	0.01	0.42	0.03
<i>Galium meliodorum</i>	54	26	25	28	20	12	10	13	0	0	0	0	0	0	0	0	0.75	0.00	0.91	0.00
<i>Festuca versicolor</i> subsp. <i>pallidula</i>	21	9	10	17	12	8	17	13	0	2	0	0	0	0	0	0	0.67	0.00	0.67	0.00
<i>Leucanthemum atratum</i>	54	74	60	62	63	71	80	50	36	51	14	25	10	0	0	0	0.77	0.00	0.85	0.00
<i>Leontodon montaniformis</i>	0	0	0	0	6	0	10	6	3	8	8	4	0	0	0	0	0.00	0.90	0.48	0.02
<i>Doronicum calcareum</i>	0	0	0	0	4	6	0	18	29	0	13	25	10	19	10	0	0.20	0.09	0.36	0.05
<i>Alchemilla anisiaca</i>	0	32	48	12	20	51	92	66	20	67	60	38	0	0	33	0	0.02	0.60	0.41	0.03
<i>Viola alpina</i>	0	0	0	0	0	3	7	21	17	13	31	19	18	38	0	0	0.24	0.05	0.42	0.03
<i>Pedicularis portenschlagii</i>	0	0	0	0	0	5	3	18	10	7	21	32	18	10	0	0	0.17	0.11	0.41	0.03
<i>Dianthus alpinus</i>	13	11	17	40	37	45	61	47	70	72	52	43	47	57	10	22	0.07	0.32	0.75	0.00
<i>Thlaspi alpestre</i>	8	39	40	20	47	40	63	50	70	67	76	72	37	81	57	0	0.10	0.22	0.51	0.01
<i>Primula clusiana</i>	8	12	37	54	45	55	54	75	99	99	123	147	90	57	52	44	0.28	0.04	0.69	0.00
<i>Festuca versicolor</i> subsp. <i>brachystachys</i>	21	7	23	17	33	63	88	124	104	116	65	104	108	148	71	33	0.36	0.01	0.64	0.00
<i>Draba stellata</i>	0	0	3	3	12	9	3	6	6	5	8	0	29	10	19	0	0.18	0.11	0.19	0.25
<i>Achillea clusiana</i>	0	14	0	6	14	20	47	62	14	46	63	43	16	67	57	0	0.25	0.05	0.42	0.03
<i>Soldanella austriaca</i>	17	7	13	9	16	32	17	18	24	27	62	38	37	24	62	0	0.21	0.07	0.28	0.12
<i>Campanula pulla</i>	0	19	30	12	22	57	61	91	61	42	82	60	63	67	100	0	0.25	0.05	0.51	0.01
<i>Draba sauteri</i>	0	0	0	0	0	0	0	0	0	0	0	9	20	24	19	33	0.63	0.00	0.90	0.00

Whereas plant species diversity steadily decreases with altitude from the sub-alpine zone up to the summit area, the number of endemics reaches its maximum between 1600 and 1750 m (see Tab. 4). Above 1750 m the number of endemics decreases again, but this decrease is less pronounced than the decrease in the overall species diversity. Thus the percentage of endemics of the overall species pool per altitudinal belt is steadily on the increase up to 2100 m (see Fig. 6).



**Fig. 5.** Regression plots of three species representing the three different response models of endemic plant species to the altitudinal gradient. For details see text.



**Fig. 6.** Changes in the total number of species in successive altitudinal belts of 50 m and in the respective percentage of endemic species. Only 50 m steps containing more than 10 relevés were considered. The altitude indicated means the lower boundary of each altitudinal step.

## Discussion

### Endemic plant communities

The formation of endemic plant communities in the north-eastern calcareous Alps can be explained first by the occurrence of endemic plant species and, secondly, through the geomorphologic peculiarities of the region. Whereas most of the endemic communities of rock, scree and snowbed habitats owe their specific character to the fact that they are predominated by species restricted to the North-eastern Limestone Alps, most of the endemic grassland-communities, being much closer to the climax vegetation of the alpine belt, lack such endemic keystone species (for the term keystone species see below and GRABHERR 1989). These plant communities consist mainly of widespread taxa. This is especially true for the predominating graminoids. *Festuca pumila*, *Agrostis alpina*, *Agrostis rupestris* and *Oreochloa disticha* occur frequently in different grassland communities throughout the Alps especially in climax communities like the *Caricetum curvulae*, the *Caricetum firmae* or the *Seslerio-Caricetum sempervirentis* (see e.g. GRABHERR and MUCINA 1993, ELLENBERG 1996, OZENDA 1988). They normally do not dominate these climax communities but they apparently replace the regular keystone species, i.e. *Carex curvula*, *Carex firma*, *Carex sempervirens* or *Sesleria albicans*, if habitat qualities deviate from the prevailing environmental conditions of climax stands. This replacement seems to be due to a significant loss of competitive abilities among the regular keystone species. Strong competitors with rather specific habitat requirements are replaced by species acting more like generalists with a somewhat ruderal strategy (GRIME 1979, GRABHERR 1989). Patches with acidic soils in the midst of a calcareous environment provide typical examples of such deviations. Consequently, these more or less isolated acidic patches are the prevailing stands of *Festuca pumila*-*Agrostis alpina* and *Juncion trifidi*-grasslands as well as of *Homogyno discoloris*-*Loiseleurietum*. Their occurrence is primarily due to the persistence of tertiary sediments on the vast plateau areas that are found mainly in these most north easterly parts of the calcareous Alps.

Within an extensive and geologically quite homogeneous calcareous landscape, like the North-eastern Limestone Alps, the regional species pool for acidophilous plant communities is rather small. As regional species pool and per-community-species diversity are closely correlated (PÄRTEL et al. 1996, ZOBEL 1997), it is not surprising that average plant species diversity of the *Juncion trifidi*-grasslands is rather low and that most of the accompanying species are not typically acidophilous, but are rather unspecific in their habitat requirements (like e.g. *Poa alpina*, *Persicaria vivipara* or *Campanula scheuchzeri*). Communities indicating only moderate acidification like *Festuca pumila*-*Agrostis alpina*-grasslands or *Homogyno alpini*-*Loiseleurietum* may, on the other hand, combine a considerable part of both the calcicolous and the acidophilous species pool. The result is a rather high average plant species diversity and a very characteristic intermixture of plants usually growing on different stands (e.g. *Carex firma* and *Loisleuria procumbens*, *Campanula alpina* and *Helianthemum alpestre*, *Potentilla aurea* and *Androsace chamaejasme*). In contrast, *Festuca pumila* and *Oreochloa disticha* grasslands reported from other parts of the Alps

are mainly initial vegetation types of either silicious or calcareous rock habitats and therefore characterised by a rather homogenous acidophilous or calciphilous flora (see e.g. SMETTAN 1981, GRABHERR and MUCINA 1993, PAULI et al. 1999).

As the *Athamanto-Festucetum pallidulae* may be rather seen as part of the rock vegetation, the only endemic grassland-community growing mainly on typical calcareous soils is the *Helictotrichon parlatorei*-grassland. However, *Helictotrichon parlatorei* was reported to predominate in grassland vegetation in other parts of the Alps, too (e.g. GRABNER 1997, RÖSLER 1997). But there seems to be general agreement among the authors from outside the most North-eastern Limestone Alps, that these *Helictotrichon*-grasslands are simply a variant of the *Seslerio-Caricetum sempervirentis* or the *Caricetum ferrugineae*, whereas we consider this vegetation type rather to be an association of its own.

As already mentioned, the endemic vegetation of rock, scree and snowbed habitats owes its specific character mainly to the predominance of (sub)endemic species. The remaining flora of these communities resembles the species composition of related vegetation types on similar stands outside the calcareous Alps (GRABHERR and MUCINA 1993, ENGLISCH 1999). We may therefore conclude that the formation of these endemic communities is primarily due to the existence of the respective endemic plants.

## Endemic species

Generally, endemic species, and in particular those of the Alps, are supposed to be specifically adapted to extreme environments, where stable conditions and low competition enables long lasting survival (see for example PAWŁOWSKI 1969, 1970, OZENDA 1988). PAWŁOWSKI (1970) estimated that around 40% of the total endemic flora of the Alps (including species of all altitudinal belts from the valley bottoms to the summit areas) are distinctly restricted to rock and debris habitats.

If we focus on endemic plant communities this trend is confirmed. None of them represents a climax community; they are in fact exclusively established in azonal habitats. However, with endemic species the situation differs. Endemic plants are very frequent in the climax communities of the alpine belt. This may be partially due to spatial autocorrelation, because these communities constitute the majority of the overall alpine grassland vegetation (see Figure 2). The low constancies of many species support this interpretation. Species concentrated in azonal habitat types, like *Draba stellata* (rocks), *Papaver alpinum* subsp. *alpinum* (scree) or *Campanula pulla* (snowbeds), occasionally occur in the *Caricetum firmae* or *Seslerio-Caricetum sempervirentis*, presumably due to proximity effects. But there is no general association between the frequency of endemics and the area covered by a specific plant community. Rare and patchily distributed associations like *Athamanto-Festucetum pallidulae* and *Alchemilla anisica*-ass. may be very rich in endemics, whereas endemics are, in turn, rare in *Pinus mugo*-krummholz, predominating in more than 25% of the total area mapped.

The frequency of endemics in climax-grasslands of the alpine belt is surely facilitated by the spatially and temporally patchy structure of these grasslands (see e.g. PACHERNEGG 1973), providing canopy gaps and micro terraces with

habitat conditions similar to those of rock, scree or snowbed stands. But, besides endemic species that occasionally invade from azonal habitats and occupy these gaps, there are others that distinctly prefer climax grasslands or vegetation types closely resembling them like *Primula clusiana*, *Pedicularis portenschlagii*, *Dianthus alpinus*, *Alchemilla anisiaca* and *Leucanthemum atratum* or species with a similar frequency in both zonal and azonal habitats like *Thlaspi alpestre*, *Doronicum calcareum*, *Viola alpina* *Festuca versicolor* subsp. *brachystachys* or *Alchemilla anisiaca* (for the latter see also PIGNATTI-WIKUS 1959). Neither spatial autocorrelation nor microhabitat diversity may therefore provide a sufficient explanation for the frequency of endemic plants in climax communities.

Competition has been demonstrated to be of major importance even in alpine grasslands (see e.g. GIGON 1971, THEODOSE and BOWMAN 1997). Such grasslands are generally structured by only a few species, mostly long-living graminoids forming dense canopies and acting as strong competitors. They were thus termed keystone species by GRABHERR (1989). The bulk of the endemic plants of the North-eastern Alps is obviously able to deal with the presence of such competitors and to survive in vegetation types predominated by them. Moreover, some of them seem to act as keystone species themselves. *Festuca versicolor* subsp. *pallidula* and subsp. *brachystachys*, *Alchemilla anisiaca*, *Achillea clusiana* and *Campanula pulla* may be called keystone species in their respective communities. Indeed, all these communities are restricted to azonal stands, but the habitats they are established in are in no way unusual in mountainous terrain. On the contrary, rock and snowbed vegetation cover vast areas especially in the alpine belt of calcareous mountains, where the distinction between zonal and azonal stands becomes more and more difficult to make.

The altitudinal distribution of endemic plants does not seem to correspond with the theory of endemics being restricted to the most extreme habitats, either. The bulk of them obviously perform best in the lower alpine belt, and the summit areas are rather poor in endemics, although the mountain ranges considered hardly extend into the upper alpine zone. This concentration of endemic species in the lower alpine belt is no peculiarity of the North-eastern Limestone Alps but was also reported from other mountain ranges (see AGAKHANYANZ and BRECKLE 1995). Extreme altitudes seem to be generally dominated by widespread species (KÖRNER 1999).

Hence it may be concluded that the concept of endemics being generally weak competitors and restricted to azonal stands does not hold true. On the other hand, the frequency of endemic plants in plots lacking a closed vegetation cover and the fact that the percentage of endemics of the overall species pool increases with altitude, apparently indicate that endemics profit from decreasing interspecific competition. But these figures are, at least in part, caused by the fact that there are two different groups of species: one that apparently avoids competition (e.g. *Draba stellata*, *Draba sauteri*, *Papaver alpinum* subsp. *alpinum*), and another one that grows well in dense grasslands. Thus, the competitive abilities of endemic plant species obviously vary considerably.

It has already been pointed out that many of the endemic plant species are not restricted to one plant community or even one habitat type. Recent studies on the distribution of relict species in the easternmost silicious Alps have provided sim-

ilar results (SCHNEEWEISS and SCHÖNSWETTER 1999). This fact seems to be inconsistent with one of the standard explanations of the regional endemism in the Alps, which is that reduced genetic plasticity prevented the redispersal of endemics when the glaciers retreated (see EHRENDORFER 1965, NIKLFELD 1972). Even if large parts of the North-eastern Alps were not glaciated, landscapes may be assumed to have changed significantly with climatic change during the Holocene. Nevertheless, endemic species were, at least partly, capable of reinvading most of these changing habitats. Species that had suffered a severe loss of genotypes should not be expected to do so. It is hardly plausible that species as widespread within their area of distribution as *Leucanthemum atratum*, *Primula clusiana*, *Dianthus alpinus* or *Thlaspi alpestre*, should be characterised by a particular lack of biotypes.

We therefore agree with PILS (1988, 1995), that the prevailing historical explanation of endemism in the most north-eastern calcareous Alps is in need of revision and that the importance of current ecological conditions requires reconsideration (see also ZIMMERMANN 1972, SCHNEEWEISS and SCHÖNSWETTER 1999). The climatic peculiarities of this region (BAUMGARTNER et al. 1983) may significantly influence plant distribution. Indeed, climatic conditions change gradually from east to west and this has often been interpreted to be inconsistent with abrupt plant distribution limits (MERXMÜLLER 1952, NIKLFELD 1967, 1972). However, this combination is a common phenomenon, for which population theory provides some possible explanations (e.g. metapopulation dynamics: SILVERTOWN and LOVETT DOUST 1995, »geographical selection gradient model«: FISCHER 1950, SLATKIN 1973, 1975, MAY et al. 1975, »tension zone model«: BARTON and HEWITT 1989). The specific climatic conditions may contribute to the competitive ability of regional endemics especially in relation to closely related vicariants growing in similar habitats outside the North-eastern Alps (e.g. *Dianthus alpinus*-*Dianthus glacialis*, *Leucanthemum atratum*-*Leucanthemum halleri*, *Festuca versicolor*-*Festuca varia*). However, it is unlikely that mechanisms of competitive exclusion should be restricted to pairs of closely related taxa. Such mechanisms normally operate within groups of species with similar habitat requirements and resource utilization (see e.g. NEWMAN 1982, WILSON and TILMAN 1991) that need not be taxonomically related.

## Conclusion

With regard to syntaxonomic distribution, habitat requirements and competitive abilities, the endemic plant species of the Northeastern Limestone Alps are not a homogenous group. There are species more or less restricted to one single habitat type as well as generalists growing in nearly every alpine plant community. Hence, any single-factor explanation of regional endemism is bound to be an oversimplification. Without denying the important contribution of the specific history to the accumulation of endemic species in this part of the Alps, we do not consider the theory of biotype reduction and poor dispersal capacity to be an adequate explanation for the restricted distribution of any particular endemic species. The role of current ecological conditions, especially climatic gradients, re-

quires integration into a more comprehensive explanation of the distributional patterns of endemic species.

Plant community endemism of the North-eastern Limestone Alps illustrates the fact that local and regional endemism may be due to different causal factors. Whatever determinants may be responsible for the occurrence of endemic taxa, the existence of an endemic flora does not provide a sufficient explanation for the existence of all endemic syntaxa present in the North-eastern Limestone Alps. The peculiar geomorphology of the region is responsible for the formation of at least a third of the endemic plant communities. Hence, we should be aware of the fact that regional endemism, though seeming homogeneous in a geographic perspective, may be due to complex ecological as well as historical reasons.

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