Alpine plant species richness in the Swiss Alps : diversity hot spots reconsidered

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Abstract

WOHLGEMUTH, T. (2002). Alpine plant species richness in the Swiss Alps : diversity hot spots reconsidered. *Mém. Soc. Bot. Genève*, 3, p. 63 - 74.

A paradigm in the debate on the origin of Alpine plants is the correspondence between present-day hot spots of plant species and presumed nunatak or peripheral refugial regions. In order to question this correspondence, I analyzed numbers of plant species in the Alps with respect to different species groups. Distribution patterns were compared to the only existing map of Alpine hot spots early proposed by Christ (1879). Often cited hot spots such as the Monte Rosa region and the Upper Engadine could be confirmed to be rich in alpine plants. A large region encompassing the Glarner Alps and the Alps of the Rhine valleys proofed to be extraordinary species-rich, too. The importance of substrate to explain old and new richness features was highlighted by analyzing Alpine endemics grouped into calcifuges and calcicoles. Results open new questions on generalities of alpine plant diversity and the threat of climate warming.

Résumé

WOHLGEMUTH, T. (2002). Richesse spécifique des plantes alpines dans les Alpes Suisses : hauts lieux de diversité reconsidérés. *Mém. Soc. Bot. Genève*, 3, p. 63 - 74.

Les débats sur l'origine des plantes alpines sont axés sur la correspondance entre les actuels "hot spots" des espèces végétales et les nunataks présumés ou les régions-refuges périphériques. Pour étudier cette correspondance, j'ai analysé de nombreuses espèces végétales présentes dans les Alpes en considérant les différents groupes spécifiques. Les actuels schémas de distribution ont été comparés à la seule carte existante établie jadis par Christ (1879). Les "hot spots" fréquemment cités, comme les régions du Mont Rose et de la Haute Engadine, présentent en effet une grande diversité de plantes alpines. Une vaste région, comprenant les Alpes glaronnaises et les montagnes des vallées du Rhin, a également prouvé qu'elle est extrêmement riche en espèces. Les variations dans la diversité ont été expliquées par les différences entre les substrats, c'est-à-dire les différences dans la distribution des calcifuges et des calcicoles. Les résultats posent de nouvelles questions d'ordre général sur la diversité des plantes alpines et la crainte du réchauffement climatique.

MOTS-CLÉS
Alpes
calcicoles
calcifuges
Christ
inventaire floristique
"hot spots"
plantes des Alpes et de montagne
diversité spécifique
Suisse

KEYWORDS
Alps
calcicoles
calcifuges
Christ
floristic inventory
hot spots
mountain and Alpine plants
plant species richness,
Switzerland

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ISSN : 0250-166

1. Introduction

In two recent publications the debate on the correspondence between patterns of actual distribution of plant species and the last maximum glaciation in the Alps has been warmed up (Stehlik, 2000; Stehlik et al., 2000). In summary, the general assumption has been adopted that proposed nunatak regions (nunatak hypothesis) or peripheral refugia (tabula rasa hypothesis) during the last maximum glaciation are still species-rich in present days (Christ, 1879; Chodat & Pampanini, 1902; Briquet, 1906; Jerosch, 1903; Braun-Blanquet, 1923; Brockmann-Jerosch & Brockmann-Jerosch, 1926; Becherer, 1972). Beyond the pro and contra arguments for these hypotheses, a few basic questions have not been satisfactorily answered: where are the present-day hot spots of plant species richness in the Swiss Alps, and which species groups contribute to the large number of species in these regions?

The first and to my knowledge unique map of alpine plant species richness was designed by Christ (1879). Accordingly, Christ considered the Matterhorn region, the Upper Engadine and parts of the Lower Engadine as large hot spot regions in the Swiss Alps. Smaller and partly isolated hot spot regions concerned western and southern parts of the Wildhorn region, southern parts of the Finsteraarhorn range, summit regions of the Saane/Simme and Emme ranges, northern parts of the Maggia range, parts of the Damma, Sardona and Thur ranges, and the Rhätikon range (Fig. 1; circles in Fig. 2). The map also contains large regions with poor Alpine flora i.e. cold spots, such as the Berner Oberland, the Glarner Alps, the Thur and the Adula ranges. Because both none of the later publications mentioned above has more precisely described hot spot regions for the Swiss Alps, and generally were in keeping with the large hot spots regions, this map served as an orientation in the following analyses. At the beginning of the 20th century, the principal arguments on the origin of Alpine plant life as well as on the locations of plant diversity and their causes were already at hand (e.g. Jerosch, 1903; Schröter, 1908). Nevertheless, Jerosch (1903) asked for data to test the hypotheses on species-rich areas in the alpine zone of the Alps.

Eighty years later, good data on the distribution of Alpine plants have been compiled at local and regional scales by Welten & Sutter (1982), the following supplementary publications by Welten & Sutter (1984), Wagner (1995) and the periodical publications of the Center of the Swiss Floristic Network (Palese & Moser, 1995). Within the frame of this Swiss Floristic Inventory, plant species lists in contiguous mapping areas below and above the timberline have been updated. On the basis of actual regional species lists, I compared present-day hot spots with Christ's early map in order to question the long-standing paradigm of diversity hot spots in the Swiss Alps.

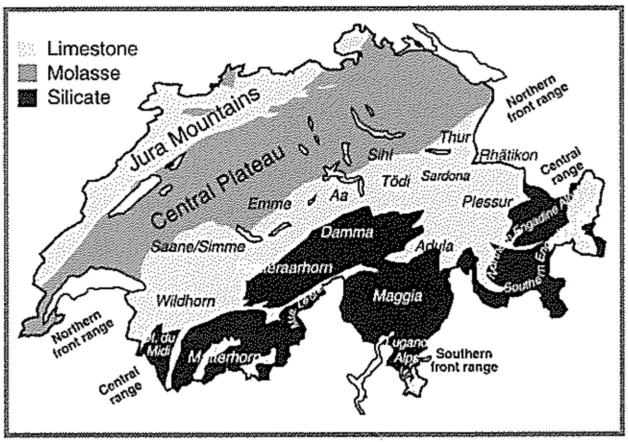

Figure 1. Limestone and silicate in Switzerland after Labhart (1987). In the category limestone, calcareous substrates such as schists and Flysch are included as well. Large mountain areas/ranges within the Swiss Alps are given according to Knapp et al. (1902).

2. Materials and methods

Species data

The system of 593 contiguous mapping areas drawn in the distribution atlas of pteridophytes and phanerogams of Switzerland (Welten & Sutter, 1982) served as reference system for the floristic data (Wohlgemuth, 1993). Accordingly, 350 lowland mapping areas below the timberline are distinguished from 215 mountain mapping areas above the timberline. In the Jura Mountains, 17 mapping areas were defined mountainous, in contrast to 198 mountain areas in the Swiss Alpine Arc. Because of their low elevation, the mountain mapping areas "Napf" and "La Berra" were excluded from parts of the analyses, resulting in 196 mountain mapping areas (9620 km^2) in the Swiss Alps. The 28 lake areas were not treated in the analyses.

Species lists, i.e. presence/absence data, were composed by the original atlas signatures on rare or common species' occurrence, as well as by supplementary species records published by Welten & Sutter (1984), Wagner (1995), Moser & Palese (1995 - 1999), Bäumler & Palese (1996 - 1998), Moser et al. (1999 - 2000). All data are available on the Internet (www.webflora.ch). Four variables of species richness per mapping area were distinguished according to Table 1: the total number of species (SRt), the number of species with subalpine and alpine altitudinal distribution (SRm), the number of species with limited distribution range in the European mountain system and in the Arctic, based on SRm (SRmeu) and the number of species that are endemic to the Alpine Arc, based on SRm (SRmend). Species of the latter variable are listed in the Appendix. Only species with well-known distribution areas in Switzerland were considered (published maps in Lauber & Wagner, 1998; www.webflora.ch). Therefore, many subspecies or varieties were not considered. With respect to species' reaction to substrate, I additionally used Landolt's indicator values to characterize corresponding diversity patterns (Landolt, 1977). The original five categories of the reaction gradient were merged into the three categories "calcifuges" (Landolt's indicator values 1 and 2), "calcicoles" (4 and 5) and "neutrals" (3). Calcifuges indicate acidic substrate or silicate, calcicoles indicate high-base status of soils or of bedrock i.e. calcareous substrate (Grime, 1979). Neutrals are those species with a main distribution on slight acidic, neutral or slight basic substrate. The geographical distribution of substrate classes in Switzerland is given in Figure 1. Results for variables defined in Table 1 are distinguished by the categories calcifuges, calcicoles and neutrals. All figures were produced with GIS-facilities of ARCINFO© and with the software ADOBE ILLUSTRATOR ® 8.0.

3. Results and discussion

A total of 1295 plant species resulted from 196 mountain mapping areas in the Swiss Alpine Arc. 8.5 % (n = 109) of them are endemic to the Alps (SRmend), 17 % (n = 221) can be found in the European mountain system and/or in the Arctic (SRmeu), and 35 % (n = 452) have a narrow subalpine/alpine altitudinal distribution (SRm; Tab. 1). 24 % of the latter species group are endemic to the Alps. In order to locate regions of high and low regional species richness, numbers of species are displayed geographically (Figs. 2-6). Mountain mapping areas that fitted Christ's proposed regions of rich Alpine flora (Christ, 1879), are indicated (circles). Numbers of subalpine/alpine species SRm

Variable	Indication	N	Source
SRt	Total number of species	1 295	Welten & Sutter (1982) and all supplementary records until 2000 (www.webflora.ch)
SRm	Number of species with narrow subalpine and/or alpine altitudinal distribution range; "subalpine" corresponds to the coniferous bel; 'alpine' corresponds to above the timberline (Landolt 1983)	454	According to Lauber & Wagner (1998)
SRmeu	Number of species with (a) limited distribution range in the Alps and in other European mountain ranges such as the Pyrenees, the Apennin, the Carpathians and the Arctic and (b) with narrow subalpine and/or alpine altitudinal distribution range	221 (291)	According to Lauber & Wagner (1998)
SRmend	Number of species with (a) limited distribution range within the Alpine Arc, i.e. endemic plant species, to the Alps (excluding endemics to the Jura Mountains see Appendix), and (b) with narrow subalpine and/or alpine altitudinal distribution range	109 (151)	According to Lauber & Wagner (1998)

Table 1. Definition of variables of species richness per mapping area. N: total number of species; for SRmeu and SRmend, the total numbers of species without altitudinal distribution constraints are put in brackets.

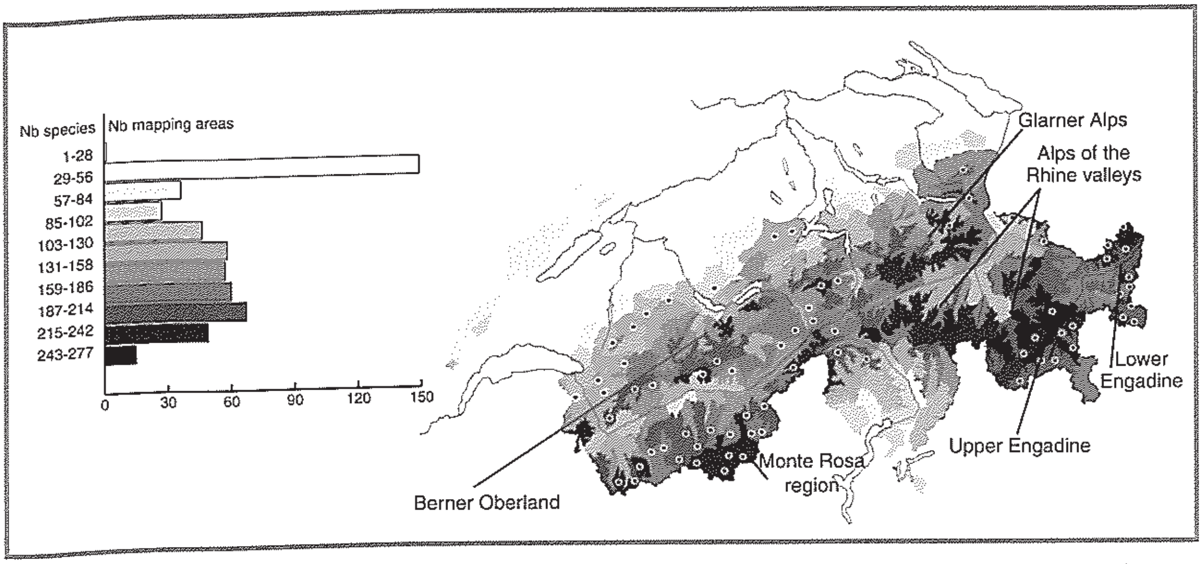

Figure 2. Number of species with a narrow subalpine and/or alpine altitudinal distribution (SRm) in lowland and mountain mapping areas of Switzerland. Circles refer to mapping areas, which fully or partly correspond to Christ's hot spot regions of alpine species diversity (Christ 1879).

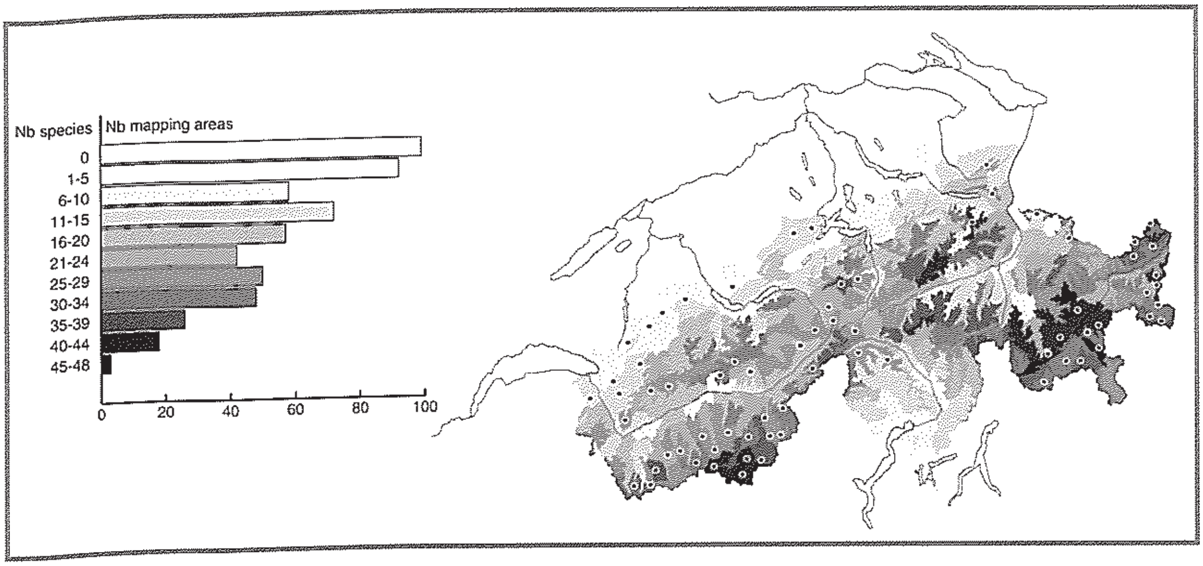

Figure 3. Number of species that are endemic to the Alps (SRmend) in lowland and mountain mapping areas of Switzerland. Species and their mapping area frequencies are listed in the Appendix. For further explanations see Figure 2.

(Fig. 2), as well as numbers of endemics to the Alps SRmend (Fig. 3) are displayed for the whole of Switzerland. Total numbers of species (Fig. 4), numbers of endemic calcifuges (Fig. 5), and numbers of endemic calcicoles (Fig. 6) are displayed for the 196 mountain mapping areas of the Swiss Alps, i.e. alpine regions above the timberline.

Figure 7 displays the numbers of species reported from all 196 mountain mapping areas of the Swiss Alps in four species groups (SRt, SRm, SRmeu, SRmend) and three substrate classes. For the same substrate classes, nationwide frequencies of Alpine endemics (SRmend) are displayed in Figure 8.

3.1. Scale, species-area relationship, and collecting effort

Species richness is a scale-dependent measure. In this paper, numbers of species refer to local or regional scales between 0.1 and 135 km². At smaller scales, Virtanen et al. (in press) compared species richness of ecosystems of various European mountain ranges including the Alps. There is a large body of literature referring to Alpine species distribution and biodiversity, but most publications treat distributions of single taxa, species within a genus or other groups of taxa (e.g. Merxmüller, 1952-1954; Favarger & Galland, 1996; Stehlik et al., 2000). Quantitative comparisons of systematically collected species data in mountain systems over broader scales are rare (Birks, 1996).

The relationship between species richness and area is one of the most studied relationships in ecology (Palmer & White, 1994). With increasing area size, numbers of species increase as well. Various functional forms have been formulated to fit the curve slopes (e.g. Arrhenius, 1921; Gleason, 1922; Williamson, 1981; Crawley & Harral, 2001). In the Swiss Floristic Inventory, mapping areas were defined by topography and hence they are of different sizes (Welten, 1971). Considerations on species richness per mapping have been affected by this fact (Wohlgemuth, 1993, 1998). The advantage of the then chosen mapping areas is the precise localization of species occurrences. Because of the mountain mass elevation effect ("Massenerhebungseffekt"; Körner, 1999), mountain mapping areas at the front ranges of the Alps are small in size and less elevated, in contrast to those of the central ranges having larger area sizes and higher elevations. Wohlgemuth (1993) found no correlation between area size and species richness for lowland mapping areas despite the wide range of area sizes ranging from 9 to 175 km². In contrast, for mountain mapping areas, the correlation for mapping areas ranging from 0.1 to 20 km² was positive, but mapping areas larger than 20 km² and up to 135 km² showed no further increase in species richness with increasing area sizes. As a consequence, species richness of small mapping areas along the front ranges needs to be interpreted with caution (Wohlgemuth, 2002).

Another bias relates to the varying collecting efforts that are typically encountered in large-scale inventories with many collaborators involved (Connor & Simberloff, 1978; Prendergast et al., 1993; Wohlgemuth, 1998). Collecting efforts in touristic regions such as the Upper Engadine or in parts of the Valais are presumably larger than in remote or less attractive regions with limited access. Evidence for considerable differences was given by Wohlgemuth (1993). Conservative estimations of collecting efforts for lowland mapping improved the explained variability in a multiple regression model by an amount of 5 % (Wohlgemuth, 1998). Unequal mapping areas and variable collecting efforts hence limit the interpretation of the presented analyses on plant species richness.

3.2. Areas "rich in alpine species" or with "rich alpine flora"

The locations of diversity hot spots of plant species in the Swiss Alps vary, to a considerable extent, depending on the species groups considered. To test proposed hot spots also implies to identify the meaning of terms such as "rich alpine flora" or "rich in alpine species" in former and present-day publications (Christ, 1879; Chodat & Pampanini, 1902; Briquet, 1906; Jerosch, 1903; Brockmann-Jerosch & Brockmann-Jerosch, 1926; Becherer, 1972; Stehlik, 2000). Despite the fact that, in most cases, the presence of many rare or biogeographically remarkable species coincided with the definition of hot spots (e.g. Furrer, 1923; Becherer, 1972; Stehlik, 2000), the reason to name a region species-rich may be based on more integral impressions on richness. Terms such as "alpine flora" or "alpine species" are ambivalent because of difficulties in the definition of distribution ranges (Körner, 1999). To disentangle the connected vague richness definitions, I analyzed richness patterns of different species groups. The nationwide pattern of SRm (Fig. 2) resulted in a particularly clear distinction between the Alps and the rest of Switzerland, namely the Jura Mountains and the Central Plateau. Also,

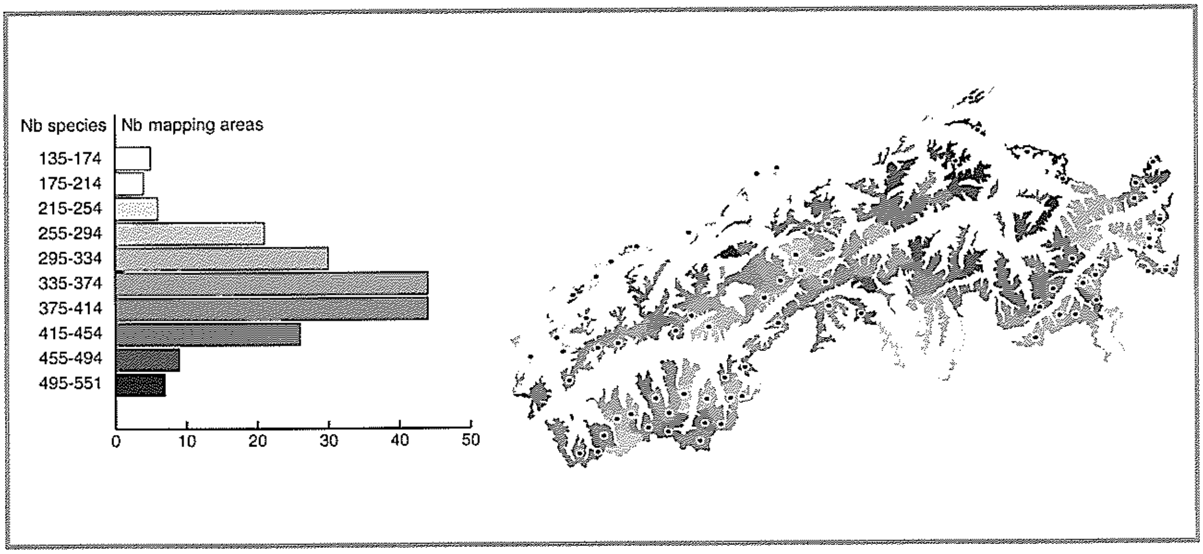

Figure 4. Total number of species (SRt), in 196 mountain mapping areas of the Swiss Alps. For further explanations see Figure 2.

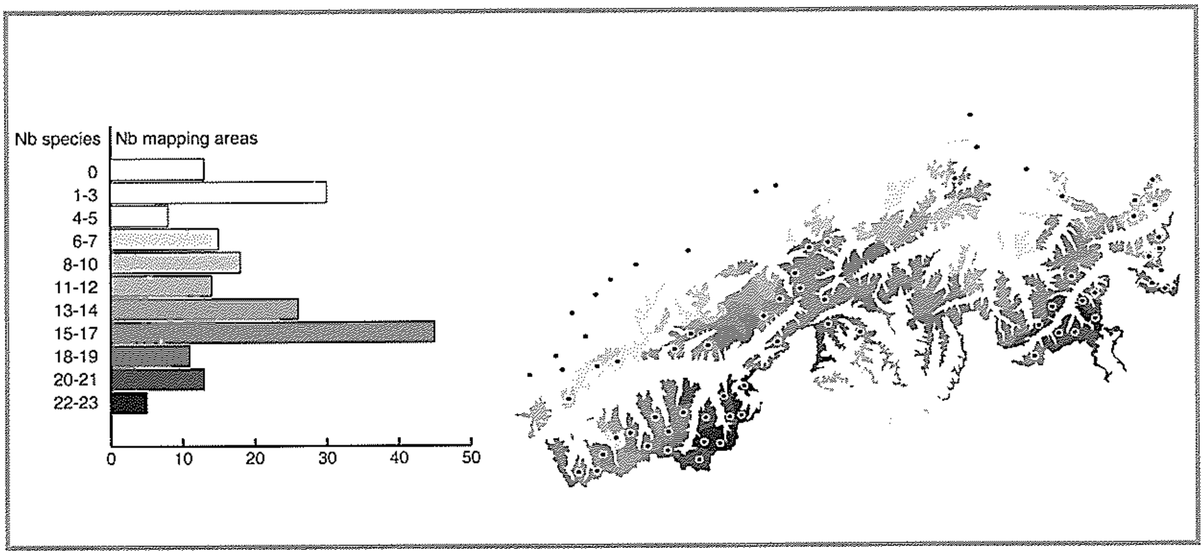

Figure 5. Number of endemic calcifuges (SRmend), in 196 mountain mapping areas of the Swiss Alps. For further explanations see Figure 2.

most of the highly elevated areas of the central ranges of the Alps had large numbers of species in both mountain and adjacent lowland mapping areas. From 454 subalpine/alpine species, only 24 grow exclusively above the timberline, and 15 of the latter are endemics to the Alps (Appendix). Many of Christ's proposed hot spot regions corresponded with increased SRm-values (subalpine/alpine species). In addition, the Glarner Alps (Tödi and Sardona ranges) and the Alps of the Rhine valleys (Adula and Plessur ranges) were conspicuous hot spot regions. In the map of SRmend (species endemic to the Alps; Fig. 3), most noticeable hot spot regions were (1) the Monte Rosa region including the valleys of Zermatt and Saas, (2) an extended Upper Engadine region encompassing the western parts of the Northern Engadine Alps, (3) the Lower Engadine, (4) the Glarner Alps (Tödi and Sardona ranges), and (5) the Adula range. Christ's hot spot regions resembled best the regions with silicate substrate and the eastern parts of the Swiss Alps. Dissimilarities were conspicuous along the western parts of the northern front range (Wildhorn and Saane-/Simme ranges), the Glarner Alps, and the Adula range.

The map of SRt (total species number) in mountain mapping areas (Fig. 4) showed, in general, increased numbers of species in the eastern parts of the Swiss Alps, namely in the Glarner Alps and in the Alps of the Rhine valleys (Rhätikon, Plessur, and Adula ranges). Surprisingly, the Matterhorn range in the Valais was not as rich in species as the latter region. In contrast to Figures 2 and 3, the small and low elevated mapping areas of the northern front range of the Alps partly showed as many species as much larger mapping areas of the central range had (Saane/Simme and Thur range). In this context, Christ's propositions in that region are plausible.

Extensive rock outcrops of different substrates distinguish the alpine zone (Fig. 1). Depending on the substrate, species compositions vary fundamentally under otherwise similar climate (e.g. Landolt, 1992). A conspicuous life history trait of plants is the response to substrate - be it directly by the tolerance or the incompatibility of substrate related to nutrient uptake, be it indirectly by competitive exclusion. Thus, a majority of plants indicate acidic and silicate or basic and calcareous substrate. By displaying the number of plant species endemic to the Alps (SRmend) into the two categories calcifuges and calcicoles, differences in species richness emerged (Figs 5 and 6). Both features reflect the limestone and silicate distribution in Fig. 1. Hot spots of endemic calcifuges in the extended region of Monte Rosa and the Upper Engadine confirmed the assumption of many botanists. In addition, between these two hot spots the Damma and the northern Maggia ranges (Gotthard massif) showed large numbers of calcifuges endemic to the Alps, too. The distribution pattern of endemic calcicoles was virtually the negative of that of endemic calcifuges, with clear hot spot regions of the Glarner Alps (Damma, Tödi, and Sardona ranges), the Thur range, the Alps of the Rhine valleys (Rhätikon and Plessur ranges) and parts of the Engadine (Northern Engadine Alps, Lower Engadine). The concerning regions are characterized by a multitude of different and often calcareous bedrock, e.g. Bündner schist or Flysch. Only to a small degree, Christ's hot spots corresponded with these calcicoles hot spot regions.

3.3. Diversity and rarity

Figures 2-6 displayed the regional richness of different groups of plant species. In all species groups analyzed, numbers of calcicoles were larger than those for calcifuges (Fig. 7). 23 % (n = 299) of all plants reported in 196 mountain mapping areas in the Swiss Alpine Arc were calcifuges and 36 % (n = 464) were calcicoles. 34 % (n = 37) of the Alpine endemics were calcifuges and 45 % (n = 49) were calcicoles. For subalpine/alpine species, the respective numbers were 40 % (n = 156) and 52 % (n = 184). A reason for larger numbers of calcicoles may be both their evolution during the evolution of the Alps when limestone substrate covered larger areas than today (Merxmüller, 1952-1954; Wohlgemuth, 2002), and differences in the survival of the glaciation or the post-glacial re-immigration (sect. 3.4). From the total number of calcifuges (n = 299), 12.4 % were Alpine endemics. In comparison, from 454 calcicoles, 10.6 % were endemic to the Alps. Figure 8 revealed differences in the frequency structure with respect to the substrate classes calcifuges, neutrals, and calcicoles. There were only few endemic calcifuges of extreme rarity (ten species in less than ten mapping areas; 13 species in less than 25 mapping areas; Appendix). In contrast, there were more rare endemic calcicoles (13 and 21 species, respectively). Whereas rare endemic calcifuges were aggregated in the two centers of the Alpine "Massenerhebung", i.e. the Monte Rosa region and the Upper Engadine, rare endemic calcicoles were more evenly distributed along the

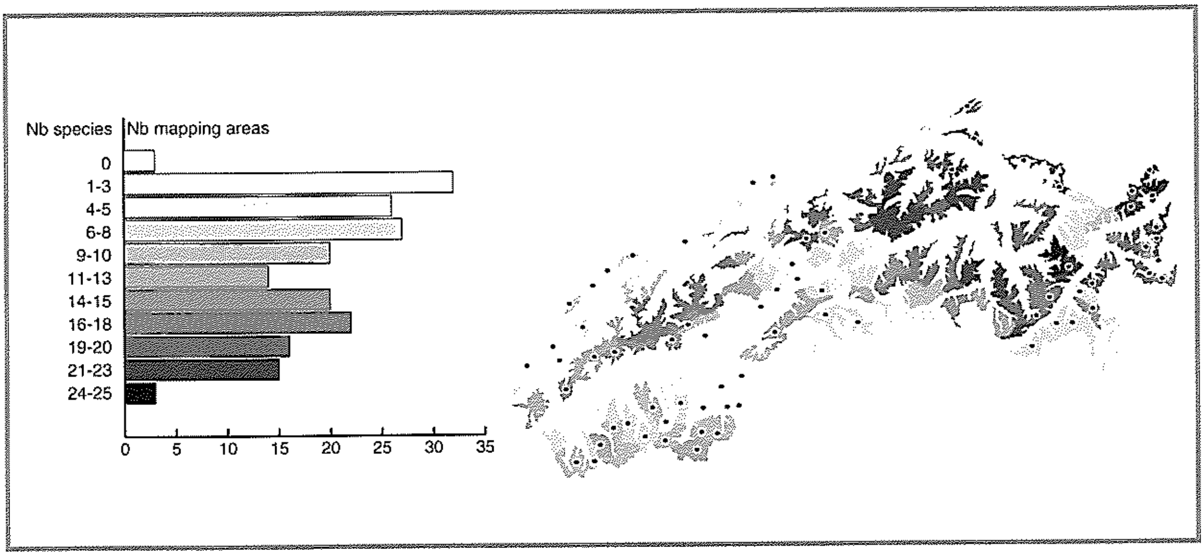

Figure 6. Numbers of endemic calcicoles (SRmend), in 196 mountain mapping areas of the Swiss Alps. For further explanations see Figure 2.

limestone Alps and, to some degree, aggregated in the large hot spot region of the Glarner Alps and the Alps of the Rhine valleys (Figs 5 and 6).

Presumably, it was not the absolute number of subalpine/alpine species within a restricted area that forced botanists to define hot spot regions in the Alps. It may have been the considerable aggregation of rare calcifuges endemic to the Alps, together with a large number of subalpine/alpine species, and, possibly, coupled with the touristic accessibility, e.g. in Zermatt and St. Moritz. In contrast, statements on the richness of the large region of the Glarner Alps and the Alps of the Rhine valleys have not been put forward. Christ defined most of his hot spots in the Silicate Alps. It seems as if he and many of his successors overlooked the large limestone region of the eastern Swiss Alps. The result of diversity hot spots in the Swiss Alps also holds for larger scales: species numbers increase more rapidly with increasing area sizes in the Northern Limestone Alps than in the Silicate Alps of the Valais (Wohlgemuth, 2002).

3.4. Diversity and historical explanations

Is there a correlation between large numbers of species and nunatak or peripheral refugial areas during quarternary glaciation? Results of this paper can support both hypotheses mentioned in the introduction (Stehlik, 2000). This holds also true for hot spot regions of the alpine flora that were determined for the first time in the present paper, i.e. the Glarner Alps and the Alps of the Rhine valleys. For endemic calcifuges, centers of richness coincide with the largest elevations within the Alps on silicate substrate and confirm the nunatak hypothesis (Brockmann-Jerosch & Brockmann-Jerosch, 1926; Landolt, 1992). For the endemic calcicoles, the tabula rasa hypothesis as well as the nunatak hypothesis can be applied. Several rare calcicoles occur on the smaller summit areas along the calcareous northern front range (Seitter & Hantke, 1988; Landolt, 1992; Hantke et al., 2000). Distribution patterns of the following species support the hypothesis on the survival on northern peripheral refugials: *Papaver sendtneri* Hayek, *Papaver occidentale* (Markgr.) H. E. Hess & Landolt, *Alchemilla splendens* aggr., *Viola cenisia* L., *Crepis terglouensis* (Hacq.) A. Kern. (all endemic to the Alps); *Ranunculus carinthiacus* Hoppe, *Ranunculus seguieri* Vill., *Draba incana* L., *Petrocallis pyrenaica* (L.) R. Br., *Viola lutea* Huds., *Androsace lactea* L., *Gentiana aspera* Hegetschw., *Tephroseris capitata* (Wahlenb.) Griseb. & Schenk, *Serratula tinctoria* subsp. *macrocephala* (Bertol.) Wilczek & Schinz.

A reason for the large hot spot region of the Glarner Alps and the Alps of the Rhine valleys may be the survival of many calcicoles on nunataks. So far, this region has not been mentioned as outstanding nunatak region. It may be of concern for modern molecular phylogeography that has not yet accumulated enough data to formulate general principles of the history of the Alpine flora. Nevertheless, the new discipline already confirmed east-west differentiations and refugial patterns in alpine mountain systems for many plant species (Stehlik et al., 2001).

New patterns and open questions

The presented results raise questions on the search for generalities of plant diversity in the Alps and on the processes that created it, as well as on the threat of the alpine flora by climate warming. Do ecological reasons dominate over historical reasons for present-day hot spots (Birks, 1996; Wohlgemuth, 2002)? Recently, attention has been attracted to the scale-dependence of diversity and the question of community saturation. Are plant communities on comparable substrate, e.g. alpine grasslands, more diverse and/or more saturated in species-rich regions than such in species-poor regions (e.g. Pärtel et al., 1996; Fox et al., 2000; Herben, 2000; Loreau, 2000)? In the field of climate warming and its ecological consequences, questions focus on poleward and upward shifts of species and communities (Grabherr et al., 1994; Parmesan, 1999). Is the alpine plant diversity really affected by increasing mean temperatures (Körner & Spehn, 2002)? The distribution and diversity of alpine plants in relation to ecological and/or historical factors are of growing importance in assessing the possible effects of climate change in alpine regions. Accurate distribution data are basic data to evaluate the corresponding threats to the Alpine flora.

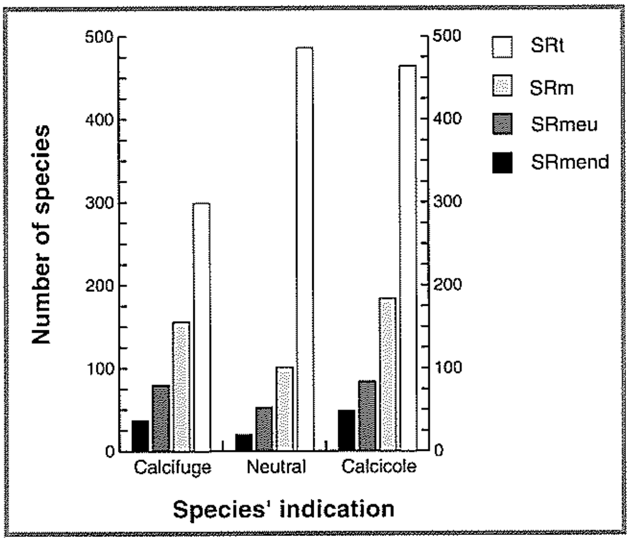

Figure 7. Numbers of species in four species groups and three substrate categories (calcifuge, calcicoles and neutrals) reported from 196 mountain mapping areas in the Alps.

Acknowledgements

I thank Walter Keller and Rolf Holderegger for critical comments on the manuscript.

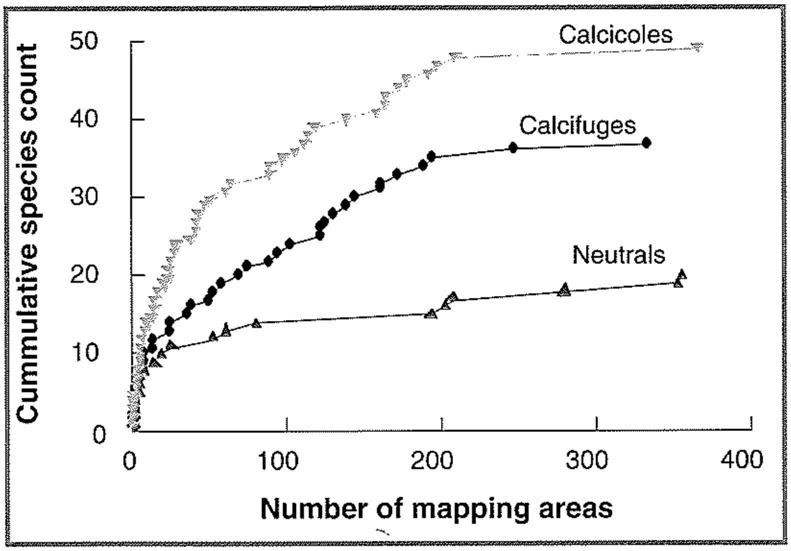

Figure 8. The cumulative number of species endemic to the Alps (SRmend, see Appendix) in Switzerland as a function of frequencies in 565 lowland and mountain mapping areas for three substrate categories (calcifuges, calcicoles and neutrals).

Calcifuges (37 species)

Primula daonensis (Leyb.) Leyb. (2), *Androsace brevis* (Hegetschw.) Ces. (3), ***Primula glutinosa*** **Jacq.** (3), *Valeriana celtica* L. (3), *Phyteuma humile* Gaudin (4), *Sempervivum grandiflorum* Haw. (4), *Potentilla grammopetala* Moretti (5), *Artemisia glacialis* L. (6), ***Minuartia cherlerioides*** **subsp.** ***rionii*** **(Gremli) Friedrich** (8), *Euphrasia christii* Gremli (9), *Senecio halleri* Dandy (14), *Phyteuma hedraianthifolium* Rich. Schulz (15), *Sempervivum wulfenii* Mert. & W. D. J. Koch (24), *Campanula excisa* Murith (26), *Geranium rivulare* Vill. (37), *Koeleria hirsuta* Gaudin (39), *Eritrichium nanum* (L.) Gaudin (49), *Taraxacum cucullatum* aggr. (52), *Erigeron gaudinii* Brügger (59), *Senecio abrotanifolius* L. (68), *Adenostyles leucophylla* (Willd.) Rchb. (74), *Cerastium pedunculatum* Gaudin (88), *Saxifraga muscoides* All. (95), *Bupleurum stellatum* L. (102), *Androsace alpina* (L.) Lam. (121), *Achillea nana* L. (122), *Gentiana ramosa* Hegetschw. (125), *Hieracium angustifolium* Hoppe (129), *Saxifraga seguieri* Spreng. (138), *Hieracium intybaceum* All. (144), *Salix helvetica* Vill. (160), *Alchemilla pentaphyllea* L. (161), *Saxifraga bryoides* L. (172), *Laserpitium halleri* Crantz (189), *Achillea erba-rotta* subsp. *moschata* (Wulfen) A. Vacc. (193), *Ranunculus villarsii* DC. (248), *Phyteuma betonicifolium* Vill. (333)

Neutrals (20 species)

Artemisia nivalis Braun-Blanq. (1), ***Alyssum alpestre*** **L.** (2), *Chaerophyllum elegans* Gaudin (2), *Gentiana pannonica* Scop. (3), *Carex fimbriata* Schkuhr (5), ***Thlaspi lerescheanum*** **(Burnat) A. W. Hill** (6), *Trifolium saxatile* All. (6), *Rhinanthus antiquus* (Sterneck) Schinz & Thell. (7), *Aconitum penninum* (Ser.) Gáyer (15), ***Gentiana schleicheri*** **(A. Vacc.) Kunz** (19), *Salix caesia* Vill. (26), *Geranium phaeum* var. *lividum* (L'Hér.) DC. (52), *Polygala alpina* (DC.) Steud. (61), *Laserpitium gaudinii* Moretti (81), *Aconitum* x *platanifolium* Degen & Gáyer (193), *Viola calcarata* L. (202), *Epilobium fleischeri* Hochst. (207), *Gentiana bavarica* L. (279), *Cirsium spinosissimum* (L.) Scop. (352), *Peucedanum ostruthium* (L.) W. D. J. Koch (355)

Calcicoles (49 species)

Cerastium austroalpinum Kunz (1), *Heracleum austriacum* L. (1), ***Saponaria lutea*** **L.** (1), ***Sesleria sphaerocephala*** **Ard.** (1), *Achillea clavenae* L. (2), ***Draba ladina*** **Braun-Blanq.** (3), ***Pedicularis aspleniifolia*** **Willd.** (4), *Thlaspi sylvium* Gaudin (4), *Papaver sendtneri* Hayek (5), ***Saussurea alpina*** **subsp.** ***depressa*** **(Gren.) Nyman** (5), *Saxifraga diapensioides* Bellardi (5), *Papaver occidentale* (Markgr.) H. E. Hess & Landolt (7), *Festuca norica* (Hack.) K. Richt. (8), ***Taraxacum pacheri*** **Sch. Bip.** (10), *Oxytropis helvetica* Scheele (13), ***Crepis rhaetica*** **Hegetschw.** (15), *Pedicularis rostrato-capitata* Crantz (15), *Valeriana supina* Ard. (18), *Draba stylaris* W. D. J. Koch (21), *Astragalus leontinus* Wulfen (24), *Gentiana aspera* Hegetschw. (24), *Gentiana engadinensis* (Wettst.) Braun-Blanq. & Sam. (25), *Minuartia rupestris* (Scop.) Schinz & Thell. (27), *Pedicularis rostrato-spicata* subsp. *helvetica* (Steininger) O. Schwarz (29), ***Crepis terglouensis*** **(Hacq.) A. Kern.** (38), *Saxifraga biflora* subsp. *macropetala* (Engl.) Rouy & E. G. Camus (42), *Viola cenisia* L. (42), ***Draba hoppeana*** **Rchb.** (43), *Saxifraga aphylla* Sternb. (48), *Rumex nivalis* Hegetschw. (51), *Alchemilla splendens* aggr. (61), *Saxifraga biflora* All. s. str. (64), *Campanula cenisia* L. (90), *Cerastium latifolium* L. (90), *Salix waldsteiniana* Willd. (98), *Thlaspi repens* Maire (106), *Leontodon montanus* Lam. (112), *Festuca rupicaprina* (Hack.) A. Kern. (113), *Arabis caerulea* (All.) Haenke (118), *Daphne striata* Tratt. (139), *Pedicularis recutita* L. (158), *Leucanthemum halleri* (Suter) Ducommun (163), *Festuca pulchella* Schrad. s. str. (164), *Senecio alpinus* (L.) Scop. (172), *Carex parviflora* Host (178), *Achillea atrata* L. (192), *Oxytropis jacquinii* Bunge (197), *Rhododendron hirsutum* L. (209), *Ranunculus montanus* Willd. (365)

No indications (3 species)

Taraxacum fontanum aggr. (6), *Aconitum rostratum* DC. (22), *Euphrasia pulchella* A. Kern. (47)

Appendix: Endemic plant species of the Alps with narrow subalpine and/or alpine altitudinal distribution, arranged according to Landolt's indicator values for reaction (Landolt, 1977) and according to ascending frequency in 565 lowland and mountain mapping areas (in brackets). Only species with mapped distribution were considered (Lauber & Wagner, 1998). Species that have been uniquely reported from above the timberline are written in bold letters (nomenclature after Aeschimann & Heitz, 1996).

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