

Predictive mapping of alpine grasslands in Switzerland: Species versus community approach

Zimmermann, Niklaus E.* & Kienast, Felix

Swiss Federal Institute of Forest, Snow and Landscape Research, CH-8903 Birmensdorf, Switzerland;

*Corresponding author; Fax +4117392215; E-mail niklaus.zimmermann@wsl.ch

Abstract. Separate logistic regression models were developed to predict the distribution and large-scale spatial patterns of dominant graminoid species and communities in alpine grasslands. The models are driven by four bioclimatic parameters: degree-days of growing season (basis 0 °C), a moisture index for July, potential direct solar radiation for March, and a continentality index. Geology and slope angle were used as a surrogate for nutrient availability and soil water capacity. The bioclimatic parameters were derived from monthly mean temperature, precipitation, cloudiness and potential direct solar radiation. The environmental parameters were interpolated using a digital elevation model with a resolution of 50 m. The vegetation data for model calibration originate from field surveys and literature. An independent test data set with samples from three different climatic zones was used to test the model.

The degree of coincidence between simulated and observed patterns was similar for species and communities, but the κ -values for communities were generally higher ($\kappa = 0.539$) than for species (mean individual $\kappa = 0.201$). Information on land use was detected as a major factor that could significantly improve both the species and the community model. Nevertheless, the climatic factors used to drive the model explained a major part of the observed patterns.

Keywords: Logistic regression; Model comparison; Niche; Species distribution modelling; Vegetation classification; Vegetation modelling.

Abbreviations: DEM = Digital Elevation Model; *GDD* = Degree-Days of Growing Season.

Nomenclature: Binz & Heitz (1990) for taxa; Zimmermann (1996) for syntaxa.

Introduction

The procedures for assessing potential impacts of climate change on terrestrial ecosystems call for proper, spatially-explicit estimates of vegetation patterns. Thus, there is increasing need for climatically sensitive modelling tools to predict the spatial and temporal patterns of species or community types at different scales (Hunsaker et al. 1990; Graham et al. 1991; Silbergeld 1993; Kienast et al. 1996). In this study we present models to predict the spatial distribution of dominant

alpine graminoid species and the species assemblages.

Various mathematical models are in use to simulate either the spatial distribution of species (e.g. Huntley et al. 1989, 1995; Prentice et al. 1992; Leathwick & Mitchell 1992; Lenihan 1993; Leathwick 1995, 1998; Austin et al. 1994; Guisan et al. 1998) and of communities (Fischer 1990, 1994; Brzeziecki et al. 1993, 1995) or the temporal patterns of vegetation (Kienast 1991; Solomon & Shugart 1993; Bugmann 1996; Roberts 1996a, b). Although the models differ in many aspects, they can be divided into two basic types, (1) static equilibrium models for spatially-explicit analysis and (2) dynamic, process-oriented models for temporal prediction of species composition (Loehle & LeBlanc 1996; Korzukhin et al. 1996). Up to the present large-scale spatial predictions rely upon static equilibrium approaches since the spatially explicit information on driving forces is usually not detailed enough to be used in process-oriented models (e.g. Box 1981; Prentice et al. 1992; Brzeziecki et al. 1995; Tchebakova et al. 1993; Neilson & Marks 1994; but see also Steffen et al. 1996). Due to a high level of detail of the input parameters used, dynamic models are usually computed for specific localities and spatial extrapolation is often difficult (e.g. Bugmann & Solomon 1995; Lasch & Lindner 1995).

In this study a static equilibrium approach was chosen for the following reasons: 1. Alpine vegetation is heterogeneous on small spatial scales. To account for this heterogeneity the resolution of a realistic model should not be coarser than 50 - 100 m. This results in up to 1.75 million grid cells for the study area considered. 2. The life history traits of alpine grassland species are often unknown. Therefore, general models for simulating population dynamics are difficult to develop and are restricted to smaller, well-investigated areas and to a limited number of taxa (see Humphries et al. 1996).

Species, though behaving individualistically (Gleason 1926), form communities as a result of: (1) overlapping resource requirements and ecological tolerances, (2) of historical events like disturbance, and (3) of local interaction processes such as competition among species. Species assemblages vary continuously along ecological gradients (e.g. Goodall 1963; Austin 1990), although

there is evidence that vegetation can switch sharply where there is no corresponding sharp change in the underlying environment (Agnew et al. 1993; Collins et al. 1993). These continuous shifts in species composition are due to the individual life history traits like migration rate, plasticity, adaptation potential or competitive ability. These individual characteristics result in individual dynamic behaviour of different species. Consequently, one should use individual species as modelling entities instead of communities, as is often stated (e.g. Lenihan 1993). Another main argument is that there is no formal logic in formulating communities, but rather a practical reasoning. Especially in the case of predicting 'species composition' under altered site conditions (e.g. climate change), it is expected that species assemblages will not move as an entity, as they did not do so in the past (Birks 1986).

Although simulation of individual species behaviour is favoured from a theoretical point of view, it is – from the practical point of view – impossible to fully integrate the species' 'individualistic' characteristics into static equilibrium models. Moreover, the observed presence of a species on a specific site is always an expression of its realized niche (Ellenberg 1953; Hutchinson 1957) and the species response curves are context-sensitive and vary depending on other species present (Austin et al. 1994). Simulating the distribution patterns of individual species rather than those of communities is therefore more likely a formal than a logical consequence of the general acceptance of the continuum concept of vegetation and of Gleason's individualistic concept of the plant association.

It should be stressed that election of either the species or the community approach depends heavily on the aim of the study. The focus on communities is related to the emphasis on concrete landscape patterns while the focus on individual species is rather related to exploring their realized niche and, thus, is related to the emphasis on abstract environmental gradients (Austin & Smith 1989). The present study aims at comparing the two approaches. The major hypothesis is that community patterns are easier to simulate, because of their more uniform response to environmental gradients. Thus, communities reflect small-scale topographic differences in vegetation. Contrarily, species have more complex realized niches that are more difficult to interpret in terms of (DEM-) topography. Thus, it can be expected that small-scale patterns of species are predicted with a lower accuracy.

Study area

The study area covers the mountainous part of Switzerland above the timberline, and has an area of ca. 17 500 km² (Fig. 1, below). The northern zone is generally under maritime influence, with annual precipitation sums > 1500 mm. The intermediate intra-alpine zone has a more continental climate and the annual precipitation sum is well below 1200 mm. The southern zone is influenced by a submediterranean climate, with mild winter temperatures and high summer precipitation (annual precipitation sum > 1200 mm). Nevertheless there is a certain risk of drought especially in spring and summer.

The study area is characterized by strong altitudinal temperature gradients and a moderate precipitation gradient. Although there are significant differences in temperature between the climatic zones, a mean July temperature of ca. 10 °C is rarely exceeded. The 10 °C isoline for July is also highly correlated with the timberline (Brockmann-Jerosch 1919; Köppen 1919). The latter is as low as 1800 m in the northern and southern zone and increases up to > 2400 m in the intra-alpine zone (Brockmann-Jerosch 1919; Landolt 1984; Theurillat 1991; Eggenberg 1995). These environmental changes can occur within a horizontal distance of ca. 40 km.

The rugged topography combined with the high elevation climate generates an active natural disturbance regime. Snow, rock and debris avalanches, mud flows, talus accumulations, water and glacier erosion and periglacial activities are frequent above the timberline and inhibit the development of soils. Therefore bedrock type has a relatively strong influence on nutrient availability and soil water capacity compared to lowland areas. Approximately 50 % of the study area is underlain with siliceous rock whereas the rest is sedimentary rock with various amounts of carbonates. Only minor areas contain ophiolitic bedrock.

In areas with mainly siliceous rocks, the dominant graminoids in the lower alpine zone are *Agrostis tenuis*, *Festuca varia* s.l. and *Nardus stricta*, whereas *Carex curvula*, *Festuca halleri* and *Luzula alpino-pilosa* are dominant in the upper alpine zone. On calcareous rocks *Carex ferruginea*, *Festuca rubra* and *Sesleria albicans* are abundant in the lower alpine zone, whereas in the upper alpine zone *Elyna myosuroides*, *Festuca quadriflora* and *F. violacea* are generally dominant. Grazing and mowing has a long history in the lower alpine zone and has regionally altered the vegetation types significantly. However, the upper alpine zone is more or less undisturbed. In the southern part of the study area, grazing and mowing activities have been abandoned for ca. 50 yr. Secondary succession of old-fields and reforestation has taken place.

Material and Methods

Climate data

Climatic variables are usually considered the major environmental factors to explain large-scale patterns of species and communities (cf. Box 1981; Woodward 1987). In addition to climate, 'disturbance' and 'edaphic' factors have been proposed (Hall et al. 1992). Whereas meteorological parameters can easily be included into static equilibrium models, disturbance is rather difficult to integrate (Brown 1994).

Concerning meteorological data, we generated maps by using data from meteorological recordings and a digital terrain model to spatially interpolate the climate data (Zimmermann 1996). The digital elevation model (DEM) with a 50-m resolution originated from satellite data (TYDAC Inc., Bern). It was tested in several areas against a 25-m DEM based on maps at scale 1 : 25 000 (available only for parts of the study area). The 50-m DEM is generally in good agreement with the 25-m DEM, with a mean absolute error of less than 10 m. However, in the vicinity of flat glaciated terrain the remotely sensed elevation model differed up to 200 m.

Meteorological data were derived from the national network with recording stations at different altitudes. We used long-term monthly means for average temperature (°C), precipitation (mm), and cloudiness (%) for the period 1961-1990. For precipitation, 365 stations were available (31 of which situated near, 11 above timberline), for average temperature 158 (22 near, 9 above timberline), and for cloudiness 95 (18 near, 8 above timberline). A linear regression model was used to calculate the lapse rates for the whole study area for temperature. In order to enable the spatial interpolation of average temperature, all station values were standardized to sea level using the regression lapse rates to separate regional trends from elevation. We then used local thin-plate SPLINE-functions (Franke 1982; Mitas & Mitasova 1988) to interpolate the long-term monthly values at sea-level to the whole study area. The regression parameters were then used to re-project the values to actual elevation using the DEM. Similar techniques were applied by Hutchinson & Bischof (1983), Mitchell (1991), Daly et al. (1994), Lennon & Turner (1995) and Thornton et al. (1997). Monthly values of the lapse rate differed from 0.38 °C/100 m (December) to 0.61 °C/100 m (April). Cloudiness was calculated likewise using a second-order polynomial regression model.

A regionalized linear regression model was employed to calculate the relationships between precipitation and elevation. We distinguished five different climatic zones (e.g. northern extra-alpine, western intra-alpine, eastern intra-alpine, southern extra-alpine and a transition-zone between extra- and intra-alpine). Regional intercepts and

lapse rates were spatially interpolated between adjacent climatic zones using a buffer of 12 km.

Potential direct solar radiation was calculated for spring and summer months by using the empirical formula of Müller (1984) which is valid between 1500 m and 4000 m and with which radiation can be calculated for given sun positions (azimuth and zenith angle) from latitude and elevation. We calculated hourly values of radiation for level surfaces and corrected values for topographic overshadowing, actual slope, and aspect values from the DEM. We then calculated daily values by integrating the hourly intervals using the Simpson-integral (Press et al. 1989). Because these calculations are very time consuming, we derived monthly totals from a linear interpolation of 10-day intervals. For similar techniques, see Dubayah & Rich (1995) and Kumar et al. (1997).

For modelling purposes three derivative climate parameters were generated from the basic climate: (1) degree-days of growing season (*GDD*), (2) a continentality index and (3) a moisture index. *GDD* was calculated on the basis of interpolated daily mean temperatures by using formula (1):

$$GDD = \sum_{i=1}^{365} \max[0, (T_i - T_0)] \quad (1)$$

where T_i = daily mean temperature, T_0 = threshold value, summed up over time for $T_i > T_0$ (Tuhkanen 1980). T_0 is the minimum temperature for plant growth. For trees of cold environments it is set to 5.56 °C (Prentice et al. 1992), for alpine grasslands it is assumed to be lower (Larcher 1994). Here we used a basis of 0 °C, which is used in high altitude/latitude modelling (Lenihan 1993). The isoline of $GDD = 0$ proved to be correlated well with the upper distribution limit of both individual species and plant communities. However, on especially favoured sites individual plants may occur at much higher altitudes (Grabherr et al. 1994).

A continentality index was derived from annual precipitation and mean annual temperature, using Eq. (2) (Gams 1932, 1935):

$$CIg = \arctan\left(\frac{T_a}{P}\right) \quad (2)$$

where P is annual precipitation, and T_a is a value derived from the mean annual temperature using Eq. (3). Gams (1932) originally used altitude instead of temperature. T_a is an equivalent of altitude in m:

$$T_a = \left[100 \times \frac{(T_0 - T_y)}{a} \right] \quad (3)$$

where T_0 = average mean annual temperature at sea-level, T_y = actual mean annual temperature, and a is the mean annual lapse rate of temperature (0.52 °C/100 m).

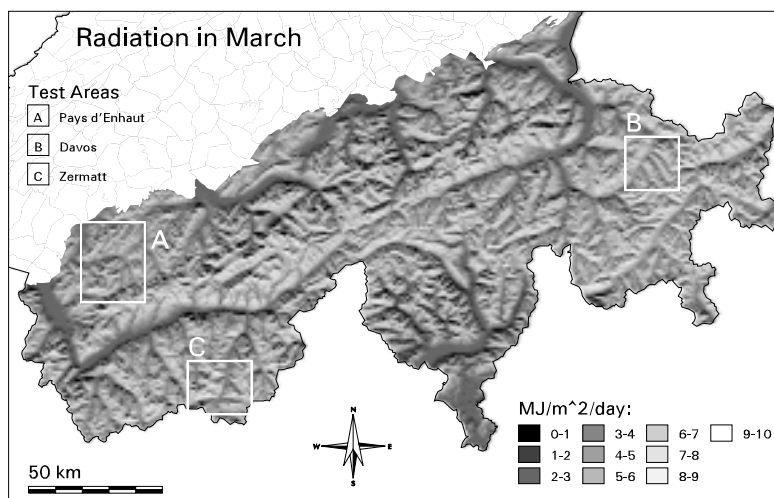


Fig. 1. The study area and daily potential direct solar radiation in March. The map gives values in a 50-m grid for the study area within Switzerland. Boxes indicate the location of the three test areas.

The Gams-index gives a general estimate of large-scale weather patterns. It is not sensitive to variation in topography, only to regional differences in precipitation and temperature at given elevations. In contrast, the moisture index – the difference between precipitation and potential evapotranspiration (*PET*), which is driven by topography-induced variability in radiation – gives an estimate of small-scale water availability. Monthly *PET* is calculated with the formula of Turc (1961):

$$PET = \left[0.4 \times \frac{T}{(T+15)} \times (R_s + 50) \right] \quad (4)$$

where T = monthly mean temperature (°C) and R_s = mean global radiation (cal/cm²). In our study we calculate mean global radiation from direct solar radiation:

$$R_s = \left[\frac{100 - C}{100} \times R_d \right] \quad (5)$$

where C = monthly cloudiness (%) and R_d = potential direct solar radiation (cal/cm²). The Turc formula proved to yield a reliable estimate in temperate, relatively humid regions (Schrödter 1985; Müller 1989).

Four climatic parameters were selected as predictors for species and communities in the 'climatic' space. *GDD* with a 0 °C threshold was used to assign topography-independent thermal energy. Direct solar radiation during March (Fig. 1) was chosen to integrate radiation energy which is strongly dependent on topography. The period of March was chosen *a priori* because of its significance for early spring spatial differentiation of snow melting and because of its strong correlation with annual total solar radiation (Fischer 1994). Potentially available soil water is approximated by the moisture index for July (Fig. 2), which is usually the driest and of greatest significance for species occurrence. Finally, general seasonality of climate is expressed with the continentality index of Gams.

Edaphic data

No detailed information is available on soil texture or nutrient availability for the whole study area. Instead we used the digital map of geotechnical information (Anon. 1990) as a rough estimate for soil type, nutrient availability and soil water capacity. The map has a spatial accuracy of +/- 100 m; 18 bedrock types are distinguished.

Disturbance data

We only included slope angle, which is not a primary factor governing species distribution, but an explanatory variable, which is not correlated with the climatic factors and a surrogate for gravitation processes operating with increasing steepness. Both geotechnical information and slope were used only as presence/absence-filters (Box 1981; Brzeziecki et al. 1993).

Vegetation data

The vegetation data originate from different sources, namely from a 2-yr field survey (largest part), literature analysis and unpublished Ph.D. and M.Sc. theses. Data were sampled in 16 biogeographically defined regions (see Zimmermann 1996 for details). In each region a representative subregion was selected. Vegetation was then sampled along altitudinal transects crossing different geological formations. At each location along the transects a vegetation type was assigned by using a key for alpine vegetation. This key was developed on the basis of a hierarchically-grouped overview of phytosociologically defined vegetation types (Theurillat 1995; Zimmermann 1996). The key is based on dominance and species composition. If the species' composition and/or dominance deviated from the units in the mapping key,

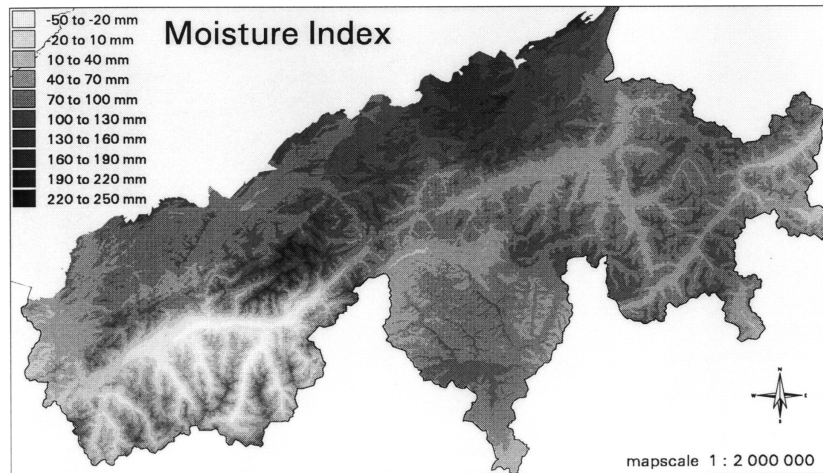


Fig. 2. Moisture Index for July. The map gives values in a 50-m grid for the study area within Switzerland.

new types were described. The database contains ca. 10 000 spatially-explicit records for ca. 280 alpine community types. Site variables were added to the data set by map-overlay of the point data set with climatic, topographic and soil maps. The observed attributes for altitude, aspect and slope were then used to test the agreement between observed and digital topography. All observations where the difference between 'real' and 'digital' topography exceeded 30 m in altitude, 50° in aspect and 20° in slope were re-examined and excluded from the analysis if the deviation was due to errors in the DEM.

The high floristic resolution of the community data allowed to derive presence/absence of dominant graminoid species from community types by using the mapping key and the descriptions of the newly defined types. A similar approach was applied by Lenihan (1993). Graminoid species were chosen because of their biogeographical robustness. Non-graminoid species are often used to define regional (endemic) phytosociological units which do not differ significantly in site conditions and in the presence of dominant graminoids from other similar units. Therefore, the focus on dominant graminoid species leads to ecologically more meaningful units. We recognized 51 dominant graminoid species out of which 15 species had too few observations (< 25) and were therefore omitted from the analysis. 34 graminoids remained in this species data set.

In order to generate ecologically more meaningful and better differentiated community types, we classified the whole data set based on the dominant graminoid species. The analysis was performed using the chord metric and the minimum variance cluster algorithm. This step reduced the ca. 170 alpine grassland communities of the original field data set to 34 synthetic graminoid communities (Table 1), which represent the community data set.

The statistical model

Both species and communities are dependent variables of the presented models. They represent nominal data; thus traditional linear regression techniques cannot be applied. Instead, we used logistic regression (Hosmer & Lemeshow 1989) to predict the probability of community and species occurrence as a function of four climatic parameters. Slope and bedrock were used as potential presence/absence filters only. The maximum likelihood estimates of the regression parameters enabled us to calculate the probability of the dependent variable for different combinations of the predictor variables. Probabilities can be mapped in space if the predictor variables are available in a spatially-explicit form or along theoretical gradients (Wrigley 1977; Hengeveld 1990). For each dependent entity there is an optimum in site conditions where probabilities are highest.

When modelling individual species occurrence this optimum reflects areas in the geographical and theoretical space where specific species might achieve dominance. Low probabilities point to unsuitable sites where the species are usually not dominant. This rule does not apply for locations where very specific site conditions (gullies, avalanche channels, extreme shelter, etc.) enable species to dominate and grow far outside their expected range (Bonan & Sirois 1992; Neilson et al. 1992; Loehle & LeBlanc 1996). These situations cannot be simulated in the present study due to the limited resolution of the input data used. When modelling community occurrence, the optimum depicts situations where a given species combination is most likely. Decreasing probabilities indicate that a given species combination is likely to be altered, forming another community.

Response surfaces were calculated for each of the 34 dominant graminoid species and the 34 synthetic community types. We applied stepwise logistic regression

probability of $\geq 75\%$ of the taxon. Model performance for the communities was tested as follows: If the observed unit is among the three most probable units and has a minimum probability of 25% the simulation is considered as correct on a specific point. Test points are selected according to the following criterion: (1) higher than timberline minus 200 m; (2) located on grassland (talus slopes, dwarf-scrub- and forest sites were excluded); (3) > 30 test points per community or > 100 test points per species. The independent data allowed to test the models of 25 communities and of 26 graminoids.

In addition to the coincidence tables the κ -statistic (Cohen 1960; Cliff & Ord 1981) was calculated to express the model performance. It is frequently used to calculate the similarity between maps (Monserud & Leemans 1992; Prentice et al. 1992; Lenihan 1993; Brown 1994; Goodchild 1994; Huntley et al. 1995). Interpretation of κ -values follows Monserud & Leemans (1992).

Table 2. Comparison between actual and simulated community patterns for the total of three test areas. κ -values are differentiated for three altitudinal zones. Lower boundaries of the zones are 1600 m / 1900 m / 2200 m in *Pays d'Enhaut*; 1800 m / 2100 m / 2400 m in *Davos*; 2000 m / 2300 m / 2600 m in *Zermatt*. The zones represent the upper subalpine, the lower, and the upper alpine zone, respectively. Communities are ranked according to decreasing κ -values and grouped according to Monserud & Leemans (1992). (See Table 1 for community numbers and text for further information).

Comm.	Number of pixels				Individual κ			
	Whole area	Sub-alpine	Low alpine	High alpine	Whole area	Sub-alpine	Low alpine	High alpine
30	267	-	33	234	0.905	-	0.841	0.907
19	49	3	38	8	0.785	0	0.792	0.888
41	266	92	123	51	0.736	0.864	0.776	0.109
6	97	14	33	50	0.728	0.558	0.568	0.990
25	611	2	234	375	0.713	0.024	0.619	0.772
27	453	-	108	345	0.651	-	0.541	0.640
3	3099	2424	665	10	0.600	0.528	0.389	0
33	221	142	72	7	0.557	0.613	0.421	0
36	145	23	99	23	0.551	0.638	0.608	0
7	729	231	442	56	0.540	0.365	0.608	0.557
21	97	9	74	14	0.526	0.714	0.524	0.351
23	902	17	397	488	0.508	0.614	0.594	0.379
18	194	-	79	115	0.502	-	0.500	0.474
12	514	347	157	10	0.501	0.533	0.424	0.181
14	277	192	85	-	0.476	0.505	0.424	-
24	87	-	36	51	0.446	-	0.532	0.349
17	294	233	61	-	0.425	0.405	0.411	-
8	107	72	27	8	0.415	0.434	0.340	0
26	62	1	25	36	0.361	0	0.076	0.484
32	154	22	103	29	0.341	0	0.333	0.472
4	150	27	93	30	0.278	0	0.313	0.341
11	110	1	19	90	0.273	0.012	0.136	0.710
28	36	-	15	21	0.129	-	0.116	0.174
35	63	56	7	-	0.043	0.045	-0.001	-
34	42	27	15	-	0.009	0.006	0	-
Σ	9026	3935	3040	2051	0.539	0.461	0.486	0.590

Results and Discussion

The models generated an overall satisfactory agreement between 'expected' and 'observed' patterns. Coincidence for 25 communities amounts to 58% (Table 2) and for 26 species to 55% (Table 3) in the three test regions considered. The overall κ for the comparison between observed and simulated community patterns reached 0.539 ± 0.019 (Table 2). This value is significant at the 1% level. It represents fair agreement considering the relatively large number of simulated species and communities, and the topographic and climatic complexity and the size of the study area (17 500 km²). Fig. 3 gives a visual comparison of simulated and mapped community patterns for the MaB test area of Davos. Simulated species patterns on the other hand produced only a mean individual κ -value of 0.201.

Simulation studies on similar spatial scales are usually performed for smaller numbers of modelling units (Lenihan 1993; Brown 1994) or they are tested on the level of vegetation belts that are combinations of simulated units rather than on the level of single units (Brzeziecki et al. 1993). Better agreement between 'expected' and 'observed' patterns in alpine simulation studies were achieved by Fischer (1994) and by Guisan et al. (1998). They developed spatial models for relatively small areas only. However, Fischer's most important explanatory variable to predict community distributions was land use, a variable that is not available for the whole of our study area. Several modelling studies found that land use is an important explanatory variable for predicting small scale vegetation pattern while it is mostly unimportant to predict large scale patterns in coarse resolution (Prentice et al. 1992; Lenihan 1993; Huntley et al. 1995).

The discussion of land use is important in assessing the model performance. Generally, anthropogenic-zoogenic influences on alpine ecosystems is greatest at sites with highest productivity and ease to reach. It decreases with decreasing soil depth and soil water availability and with increasing slope angle and elevation. Grasslands that are affected most by anthropogenic-zoogenic activities include No. 3 (*Crepido-Festucetum rubrae*), No. 4 (*Trifolio-Festucetum violaceae*), Nos. 12 - 14 (*Caricetum ferrugineae* with subass.), and No. 40 (*Polygalo-Poetum violaceae*), respectively. High grazing and mowing pressure impoverishes such grasslands and favours more resistant graminoids like *Nardus stricta* (Ellenberg 1988). If such activities last over decades it results in a major change in species composition and converts such grasslands to communities Nos. 32 - 36 (*Nardetum strictae* with subass.). Thus, *Nardus*-dominated communities occur both on sites that are naturally poor in nutrients as well as on secondarily impoverished

sites and the distribution of some communities and species are not only and primarily driven by climate and geology, but also by land use and its history.

Community patterns

Although the overall agreement is satisfactory, there are considerable differences in the performance of the individual community models (Table 2). We discuss the performance of the model in the order of decreasing individual κ :

1. Very good to excellent agreement between observed and simulated distribution was achieved for five communities. A common characteristic of these five units is the absolute lack of anthropogenic-zoogenic disturbance. Climatic predictors are sufficient to explain the large-scale and the local distribution of these communities. Four community types have their highest performance in the upper alpine zone where they cover ridges: *Arenario-Salicetum reticulatae* (Comm. 19) and *Caricetum curvulae* (25), stony slopes on shallow soils: *Caricetum firmae* (6), or sheltered sites with a long snow cover duration: *Hygro-Caricetum curvulae* (30). The fifth: *Sempervivo-Pulsatilletum* (41), is found on very xeric sites in the lower alpine and subalpine belt on rocky slopes in the inner-alpine continental zone. Comm. 25 belongs to the most abundant communities in the upper alpine belt.

2. Good agreement between observed and simulated distribution was achieved for another four communities. Three can be found on in the subalpine and lower alpine belt, where they cover well developed rich soils: *Crepidofestucetum rubrae* (3), or poor soil: *Geo-Nardetum strictae typicum* (33), *Festucetum variae* (36). Comm. 36 is found on steep, strongly insolated, dry and shallow sites, whereas the *Festucetum halleri elynetosum* (27) is found at similar sites in the upper alpine zone. Comm. 3 and 33 belong to the most common in the lower alpine belt throughout the whole study area. The selected climatic predictors are thus sufficient in predicting the large-scale and local distribution. Better information on land use would certainly improve the performance of Comm. 3 and 33, since they are partly dependent on anthropogenic-zoogenic disturbance.

3. Fair agreement between observed and simulated distribution was achieved for another five communities. Three of them mainly occur in the upper and lower alpine belt, where they are found on sheltered sites with long snow cover duration and low insolation: *Salicetum herbaceae* (23), on sharp ridges with strong frost and wind disturbance: *Elynetum myosuroidis* (18), and on xeric, rocky slopes with high insolation: *Seslerio-Caricetum sempervirentis* (7). None of them is associated with distinct anthropogenic-zoogenic disturbance.

Table 3. Comparison between actual and simulated species patterns for the total of three test regions. Species are ordered by decreasing κ -values and grouped according to Monsrud & Leemans (1992). Bold-faced values indicate that more than 50% of the simulated occurrence is identical with mapped occurrence (see text and Table 2 for further information).

Species	No. of pixels	%	Individual κ
<i>Agrostis rupestris</i>	2273	87	0.553 *
<i>Carex curvula s.str.</i>	2537	72	0.551 *
<i>Luzula alpino-pilosa</i>	2024	63	0.537 *
<i>Carex firma</i>	452	30	0.417 *
<i>Nardus stricta</i>	2398	74	0.406 *
<i>Carex ferruginea</i>	1474	49	0.372 *
<i>Festuca varia s.l.</i>	175	56	0.339 *
<i>Luzula multiflora</i>	1278	65	0.331 *
<i>Anthoxanthum alpinum s.l.</i>	1172	66	0.311 *
<i>Elyna myosuroides</i>	972	76	0.288 *
<i>Avenula versicolor</i>	1501	48	0.284 *
<i>Sesleria albicans</i>	2549	65	0.247 *
<i>Festuca rubra s.lat.</i>	4346	91	0.242 *
<i>Calamagrostis varia</i>	812	27	0.207 *
<i>Carex ericetorum</i>	256	82	0.192 *
<i>Phleum alpinum s.l.</i>	3845	69	0.118 *
<i>Festuca curvula s.l.</i>	419	85	0.086 *
<i>Agrostis alpina</i>	1173	96	0.079 *
<i>Koeleria pyramidata s.l.</i>	276	51	0.079 *
<i>Festuca quadriflora</i>	2481	19	0.067 *
<i>Poa alpina</i>	6093	80	0.048 *
<i>Festuca violacea s.l.</i>	505	51	0.048 *
<i>Carex parviflora</i>	327	7	0.028
<i>Carex sempervirens</i>	4305	75	0.016
<i>Festuca pulchella s.l.</i>	670	1	0.006
<i>Avenella flexuosa</i>	1121	0	-0.072
Summary:	1960	55	0.216

* $p < 0.001$

Differences in the performance can be best explained with the generally small spatial extent of these types. Thus, they are often systematically neglected in vegetation mapping. Comm. 7 is limited not only by climatic, but also by pedological factors. Under similar climatic conditions but on better developed soils, other communities occur: the *Crepidofestucetum rubrae* (3) and the *Caricetum ferrugineae* (12). Since this information is not available for the whole of the study area, there is a relatively great amount of unpredictable variance. Comm. 12 and 21, *Salicetum retuso-reticulatae*, occur optimally in the upper subalpine belt. Both are generally found on shady, relatively steep slopes with a low risk of drought. They differ in mineral content of the soils and in snow cover duration. If precipitation is high and/or soil water holding capacity is large, i.e. when there is no severe drought, Comm. 12, *Caricetum ferrugineae*, is also found in sites with high insolation. These sites are of highest productivity and are therefore often used and influenced by mowing and grazing.

4. Poor agreement between observed and simulated distribution was observed for eight communities. Three

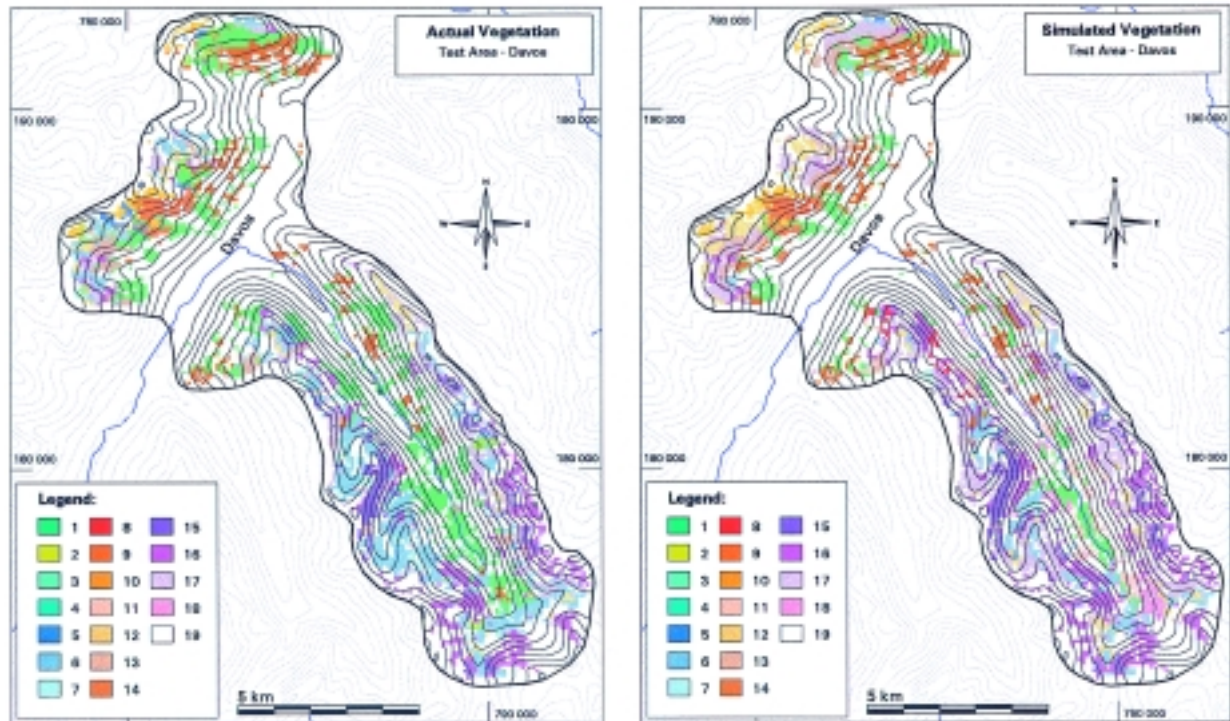


Fig. 3. Mapped and simulated community patterns for the test area in Davos. The corresponding communities of the legend numbers are as follows: 1: *Crepido-Festucetum rubrae*; 2: *Trifolio-Festucetum violaceae*; 3: *Caricetum ferrugineae calamagrostietosum varia*; 4: *Caricetum ferrugineae* and *Caricetum ferrugineae festucetosum pulchellae*; 5: *Arenario-Salicetum reticulatae* and *Salicetum retuso-reticulatae*; 6: *Salicetum herbaceae*; 7: *Luzuletum alpino-pilosae*; 8: *Festucetum varia*; 9: *Seslerio-Caricetum sempervirentis* and *Astragalo-Seslerietum varia*; 10: *Caricetum firmae*; 11: *Artemisio-Festucetum quadriflorae*; 12: *Elynetum myosuroidis*; 13: *Avenulo-Nardetum strictae*; 14: *Geo-Nardetum strictae typicum*, with *Avenella flexuosa*, and with *Carex sempervirens*; 15: *Hygro-Caricetum curvulae*; 16: *Caricetum curvulae*; 17: *Festucetum halleri typicum* and *elynetosum*; 18: *Elyno-Caricetum rosae*; 19: other than alpine grasslands. Contour interval is 100 m.

occur in strongly disturbed sites: *Trifolio-Festucetum violaceae* (4), *Caricetum ferrugineae calamagrostietosum varia* (14), *Avenulo-Nardetum strictae* (32), and two in moderately disturbed sites: *Astragalo-Seslerietum varia* (8) and *Serratulo-Caricetum sempervirentis* (17). These communities require similar ecological conditions as other ones which are not disturbed by human activities, but the model cannot distinguish between them (see Table 4). Thus, further information of land use would improve the simulation of these communities. Another reason for the poor model performance for some communities is the limited biogeographic distribution of dominating species such as for example *Artemisia glacialis*, which is a key species for the *Artemisio-Festucetum quadriflorae* (11), or *Serratula tinctoria* for the *Serratulo-Caricetum sempervirentis* (17).

5. Very poor agreement between observed and simulated distribution was achieved for three uncommon communities. The low number of test points prevents a sound assessment. Strong anthropogenic-zoogenic disturbance might be a major source in the lack of climatic predictability of the *Geo-Nardetum strictae* with *Avenella*

flexuosa (34), and the *Geo-Nardetum strictae* with *Carex sempervirens* (35). The *Elyno-Caricetum rosae* (28) has a high value in the cross-validation (Table 4) but is largely overestimated in the simulated distribution, mainly in the test area of Davos.

Species patterns

Cross-validation of observed and mapped species distribution is very similar to communities. Individual κ 's, however, are much lower for all individual species models (Table 3). This shows that species are generally overestimated as to their spatial distribution. This is mainly due to the broad amplitude of species compared with communities; it can be related to the problem of calibrating realized species niche. Species' realized niches are generally more complex and can probably not be fitted sufficiently with polynomial regression (Austin et al. 1994; Bio et al. 1998). Nevertheless the simulated large- and meso-scale spatial distribution of species is satisfactory (see e.g. Fig. 4: *Festuca halleri* in Davos). Model performance will now be discussed in

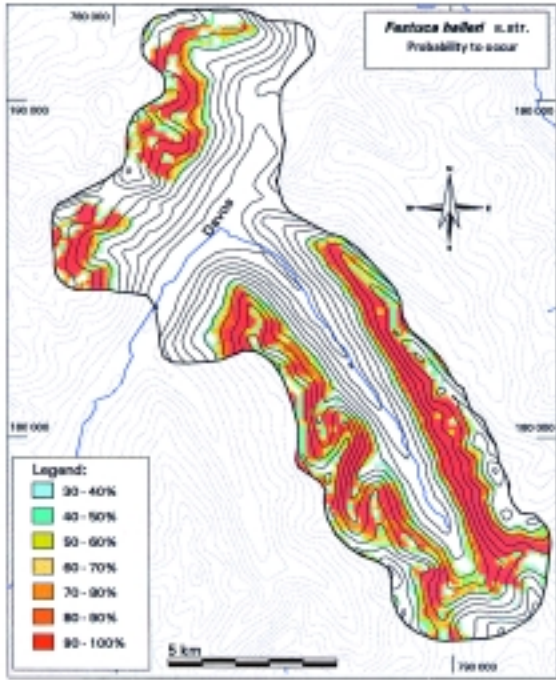


Fig. 4. Probability of occurrence for species No. 21 (*Festuca halleri*). Probabilities below 30% represent areas where the species is unlikely to occur for (1) climatic reasons or (2) for pedological and/or topographical reasons (see text for further explanation).

order of decreasing individual κ (Table 3).

1. Good agreement between simulated and mapped patterns of dominant graminoid species was achieved for *Agrostis rupestris* and *Carex curvula*. Both species are (sub-)dominant in high-alpine communities without anthropozoogenic influence. *Agrostis rupestris* prefers sites with long snow cover duration, whereas *Carex curvula* is found on less sheltered sites on granitic bedrock with higher exposure to wind and frost and a short lasting snow coverage.

2. Simulations of *Carex firma*, *Luzula alpino-pilosa*, and *Nardus stricta* were reasonable. *Carex firma* is mainly found on exposed ridges and slopes on limestone, while *Luzula alpino-pilosa* prefers sheltered sites with a long snow cover duration. *Nardus stricta* is widely distributed in the upper subalpine and lower alpine belt. Its sites are usually poor in nutrients and the species is affected in its geographical distribution by land use activities.

3. Nine species show a poor performance even though their large scale patterns are predicted reasonably well. A majority of them has an agreement of more than 50 % between measured and simulated occurrence. This indicates an overestimation in micro-scale distribution, since the lower κ -values are due to errors in correctly simulating the local absence of the species occurrence. Most of the species grow on sites that are altered easily by human activity. Especially *Carex ferruginea*, *Luzula multiflora*, *Anthoxanthum alpinum*, *Sesleria albicans*,

Table 4. Comparison between field mapping and simulated vegetation (Sim. veg.) for the total of three test regions. For community numbers see Table 1. Bold-faced figures show the numbers of points that are identical in the simulated and in the mapped vegetation.

Sim. veg. \	Mapped vegetation																				Σ					
	3	4	6	7	8	11	12	14	17	18	19	21	23	24	25	26	27	28	30	32		33	34	35	36	41
3	1715	2	.	19	.	.	43	3	2	.	12	.	.	
4	2	27	.	10	.	.	1	.	1	
6	.	39	94	20	.	.	4	1	1	.	1	
7	.	2	.	298	.	.	18	1	7	.	.	2	1	
8	44	.	.	34	63	.	24	17	6	1	.	1	.	.	
11	198	.	.	.	36	88	.	.	.	4	9	4	12	.	16	15	1	7	.	11	26	.	.	48	27	
12	3	6	.	29	.	.	196	5	2	
14	86	1	.	183	3	.	95	219	15	.	.	
17	391	7	.	51	2	.	80	29	262	.	.	.	1	1	2	2	2	33	.	
18	6	15	2	1	.	6	.	.	.	184	3	35	110	4	49	21	2	3	17	1	18	.	.	29	11	
19	4	1	35	
21	.	.	.	11	40	3	
23	12	.	.	1	1	336	1	1	
24	1	12	29	
25	94	3	.	36	.	.	16	.	1	.	.	84	7	506	2	18	
26	16	1	9
27	45	34	.	7	10	.	.	5	247	43	2	.	450	.	3	21	1	3	.	1	10	
28	115	2	.	.	1	16	.	.	.	5	.	2	78	.	29	10	.	26	21	17	4	.	.	3	19	
30	222
32	93	8	.	8	4	1	.	3	12	.	2	64	6	7	.	.	.	
33	89	1	1	15	.	.	13	2	1	.	.	1	1	18	156	28	.	.	.	
34	179	.	.	3	.	.	12	4	2	.	.	.	
35	4	2	.	3	.	.	12	2	.	.	
36	2	60	8	
41	18	1	.	5	4	6	2	3	.	.	3	182	
Σ	3099	150	97	729	107	110	514	277	294	194	49	97	902	87	611	62	453	36	267	154	221	42	63	145	266	5272
%	55	18	97	41	59	80	38	79	89	95	71	41	37	33	83	26	99	72	83	42	71	5	3	41	68	58

Festuca rubra and *Calamagrostis varia* often do not occur throughout their potential climatic space. *Festuca varia* and *Elyna myosuroides* on the other hand grow on patches with limited spatial extent. Thus, the corresponding communities are often systematically neglected in vegetation mapping.

4. A very poor agreement is achieved for six species. *Carex ericetorum*, *Festuca curvula* and *Koeleria pyramidata* occur generally in the subalpine zone, and have been mapped only on a relatively small number of pixels and are thus tested insufficiently. They all grow on xeric sites with high insolation and a more or less continental climate. *Agrostis alpina* and *Festuca quadriflora* have a wide climatic range where they are able to (co-)dominate, generally limited by shallow, stony soils with a high risk of drought. Consequently, they cannot be simulated successfully with climatic factors alone. *Phleum alpinum* co-dominates with *Nardus stricta* and *Poa alpina* on sites with anthropogenic-zoogenic disturbance.

5. For six species no agreement was found. Although their simulated biogeographical distribution is generally sufficient, their simulated small-scale, local prediction is unsatisfactory and generally overestimated (*Poa alpina*, *Carex sempervirens*). Four species are tested on a relatively small number of pixels only (Table 3). The majority of these species is not primarily limited in their spatial distribution by climatic factors – *Avenella flexuosa*, *Carex sempervirens*, *Festuca pulchella*, *F. violacea* and *Poa alpina*.

As with the community models, the lack of detailed land use information is apparently responsible for the failures in the species models. Additional problems arise in calibrating the more complex ecological niches of individual species.

Naturally, only the presence of species points to a suitable environment, whereas its absence provides no information on the suitability of the site. The fact that biological patterns are simulated where there is no corresponding observation does not necessarily imply that the general relationship between vegetation and site is calibrated incorrectly. Often, a species is missing because of historical reasons (Leathwick 1998), or because vegetation is not in the appropriate successional stage. This can be due to long-term (e.g. climate change) or due to short-term shifts (e.g. land abandonment) in the driving variables. Since predictive modelling is based on the equilibrium paradigm, there is no solution to that problem except to evaluate and interpret the model output and performance carefully.

Conclusions

The two types of models (species- and community models) presented in this paper both yield vegetation patterns that are significantly correlated with real patterns observed in field. We conclude that the climatic factors used to drive the model explain a major part of the observed patterns. However, fitting a model for the realized niche of individual species needs more sophisticated and probably more ‘individual’ statistical fitting than for communities. This is due to the fact that species are ‘evolutionary individuals’ with specific physiology, plasticity and potential to adapt and to migrate (Gleason 1926). In contrast, communities are not evolutionary units but rather assemblages of species with overlapping resource requirements and ecological tolerances that emerge from competitive processes, and historical and stochastic events. It thus can be argued that communities generally have a narrower realized (and no fundamental) niche as compared to species. Consequently, the probability to occur in the multidimensional ecological space is more uniform for communities. All these community properties are an advantage if real landscape patterns have to be simulated. In contrast, the fitted model for a species is more ‘biological’ and thus more realistic in predicting large-scale patterns for geographic areas that have not been used for model calibration. Nevertheless, we found that most of the characteristics that can be attributed as ‘individualistic’ to species (e.g. plasticity, adaptation, migration), usually cannot be integrated into static distribution models. Moreover we have to be aware that individual species responses – the standard input for static model calibration – are generally context-sensitive and vary depending on the presence of other species (Austin 1982; Austin et al. 1985; Austin & Smith 1989). Predicting future behaviour of species is – by definition – based on the observation of today’s jointly present species. Thus, future predictions are not independent of the initial context. There is only one (rather theoretical) solution to that problem, i.e. to calibrate the fundamental niche for species, a task that cannot be performed with comparative studies. As a consequence, predictions for the future have to be interpreted with care for both species and communities. The selection of biologically relevant (climatic) parameters is probably the most sensitive part of model development and should be performed with care (Woodward 1987; Prentice et al. 1992; Lenihan 1993). This is (1) to increase the probability to simulate realistic patterns and (2) to address biogeographically important information for the ‘spatial part’ in process models (Loehle & LeBlanc 1996; Korzukhin et al. 1996).

Besides these theoretical conclusions we would like to draw the attention to the following aspects.

Model improvement

The models presented may be improved on several levels. First, adding new explanatory variables will improve the models significantly. In the present study major problems arose from the lack of spatially-explicit information on land use (-history) and the associated influence on soil development and secondary succession. Still, such information is very difficult to obtain for such large areas. Second, the calibration data set on community or species occurrence can be improved, namely with a more effective climatically stratified sampling to avoid under-representation of combinations of climatic variables in the calibration data set. Finally, we believe that comparing different statistical models to simulate either species or communities would be highly desirable, a task that has not been performed thoroughly for predictive models, so far.

Model assessment

A sound assessment of the model performance must be based on reliable, independent test data. Large-scale sampled vegetation maps tend to smooth out or suppress small-scale patterns of vegetation. Especially in topographically heterogeneous regions, field maps often have a low level of detail. As a result, several mapping units are combined, because their localities are inaccessible. This produces low model performance in cases where the model is better than the test map and might underestimate the ability of the model to generate correct patterns. Ca. 70 % of the simulated species and communities could be evaluated from the independent test data.

Model applicability

Both types of models yielded satisfactory results, with the community models performing more precisely for actual climatic conditions. This means that actual patterns in an alpine landscape are better predicted from community models than from dominant graminoid species. On the other hand, predictions for areas outside of the calibration area, or for changed climatic conditions bear a higher risk for communities than for species. Theoretically, this is due to the fact that species adapt and migrate individualistically. Both aspects, as well as competition, are not represented in a static equilibrium model. Practically, however, we conclude that simulating species for altered site conditions is preferable, since this approach does not predict vegetation structure and community composition. Rather, the potential of single species to grow and reproduce in a modified landscape is predicted. This is in better accordance with the concepts of multiple steady-states

and multiple successional pathways (Allen & Hoekstra 1992; Tausch et al. 1993) for vegetation development and composition. Finally, we repeat that predictions for changed climatic conditions cannot be executed beyond the range of currently calibrated climatic variables (Prentice et al. 1991; Lenihan 1993).

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