Remote sensing versus field survey for vegetation mapping – a contradiction?



MASTER THESIS IN ECOLOGY BY STEFANIE CALIARO

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Abstract

A major topic in biology and environmental science is to describe and understand the patterns of the distribution and abundance of organisms. Remote sensing techniques can help to make such patterns visible. In this study, I used such techniques combined with various GIS layers of environmental factors to search for vegetation patterns in the alpine landscape of the Swiss National Park. GIS based stratification of the study area was examined with vegetation surveys of plant species composition in 26 selected strata and estimations of aboveground net primary production (ANPP) in nine strata. The analysis of the vegetation surveys revealed highly significant differences between the strata in terms of plant species and composition and the GIS based stratification corresponded generally well with differences in the vegetation composition. However, stratification failed sometimes in geological transition zones or in areas with small-scale changes in vegetation cover. The strata were also well discriminated with ANPP. However, discriminating power was smaller than that of the vegetation composition. This pattern was probably caused by high precipitation during my study in the summer 2008, which resulted in low variation of ANPP between the strata. Overall, the combination of remote sensing with GIS techniques proved to be successful in detecting vegetation patterns in the study area. These techniques might be helpful for future studies in this high alpine landscape, where access is partly difficult and disturbance should be restricted to a minimum.

Zusammenfassung

Es ist ein Hauptanliegen der Biologie und der Umweltwissenschaften, die Verteilungs- und Häufigkeitsmuster der Organismen zu beschreiben und zu verstehen. Diverse Fernerkundungstechniken ermöglichen die Visualisierung solcher Muster. In dieser Studie versuchte ich, mit Hilfe solcher Fernerkundungstechniken in Kombination mit GIS Layern von Umweltfaktoren, die Vegetationsmuster der alpinen Landschaft im Schweizerischen evaluieren. Die HABITALP wurde Nationalpark zu Stratifizierung mittels Vegetationsaufnahmen in 26 Straten und durch Messungen der oberirdischen Biomasse in neun Straten überprüft. Die Analyse der Vegetationsaufnahmen zeigte deutliche Unterschiede zwischen den Straten, sowohl in Bezug auf die Pflanzenarten, als auch auf deren Zusammensetzung. Des Weiteren zeigte die Untersuchung auch, dass die GIS basierte Stratifizierung in geologischen Übergangszonen, sowie auch in Gebieten mit kleinräumigen Vegetationsänderungen limitiert ist. Die Straten unterscheiden sich in Bezug auf die oberirdische Biomasse, dennoch sind die Unterschiede geringer als jene der Vegetationszusammensetzung. Die geringen Differenzen beruhen wahrscheinlich auf erhöhten Niederschlagseinträgen im Sommer 2008, welche zu einer kleineren Variation in der Biomassenproduktivität zwischen den Straten führte. Zusammenfassend konnte also gezeigt werden, dass die Kombination von Fernerkundung und GIS-Techniken zu einer guten Erfassung von Vegetationsmustern führt. Diese Techniken könnten hilfreich sein für zukünftige Studien in schwer zugänglichen alpinen Regionen, oder in Gebieten, in welchen die anthropogenen Störungen auf einem Minimum gehalten werden müssen.

Introduction

"Ecology is defined as a scientific investigation of the distribution and abundance of organisms and the interaction that affects the distribution and the abundance" (Townsend et al. 2003). Today, conservation and preservation of biodiversity is a major topic in biology and environmental science, thus, it is important to describe and understand the patterns of the distribution and abundance of organisms. With the availability of remote sensing techniques, it is possible to make such patterns visible. According to Gould (2000) "remote sensing provides the best tool for looking at large areas of the earth's surface to analyze, map, and monitor ecosystem patterns and processes". The most frequently used parameters to delineate, characterize or rate vegetation patterns in landscapes, are the reflection pulses of electromagnetic waves (visible, infrared, microwave). Their strengths and timings have been used as indicators for physical vegetation characteristics (Turner et al. 2003) like aboveground standing crop, plant cover as well as species composition and richness and the spectral heterogeneity represents the spatial heterogeneity, thus allows us to predict vegetation properties at larger spatial scales (Palmer et al. 2002; Rocchini 2007).

Site-related (biotic and abiotic) environmental factors define where certain plants grow and how the vegetation is composed (Staffelbach 2008). The interpretation of aerial photographs can be markedly improved when such factors are considered. The study of Gould and Walker (1997) in an arctic river watershed showed, for example, that substrate, slope, drainage regime and pH of the bedrock are important factors explaining vegetation patterns at the landscape-scale (Townsend et al. 2003). Like arctic river watersheds, alpine habitats are characterized by small-scale changes of the environment resulting in a high spatial heterogeneity. For Körner (1999) alpine plant life mainly depends on the following environmental components: solar radiation, slope, exposition and plant stature. Sebastià (2004) added topography and various soil properties to Körner's components.

Since alpine habitats are difficult to access, remote sensing techniques are advantageous to survey such areas (Levin et al. 2007). In this context the HABITALP project was launched by several National Parks in the European Alps. HABITALP combines remote sensing (infrared aerial photographs) with GIS models of various environmental factors to identify vegetation patterns. One of the Parks that founded and promoted HABITALP was the Swiss National Park (SNP) in which my study area is located. In the SNP, HABITALP should help to detect and monitor both vegetation patterns and long-term vegetation changes, since vegetation is an important resource for consumers such as large herbivores (red deer, roe deer, chamois and ibex) that inhabit the Park. In this thesis, patterns delineated with HABITALP were tested for their suitability to describe qualitative as well as quantitative vegetation patterns adequately, i.e., forage supply patterns for large herbivores in the Park.

More specifically, the goal of the study was to (1) underlay the HABITALP strata with field surveys to characterize the plant communities, i.e., the plant species composition, (2) measure the aboveground net primary production (ANPP) in selected strata, and (3) relate the detected vegetation patterns to various environmental factors potentially explaining the patterns. I hypothesize that the HABITALP stratification is appropriate to describe vegetation patterns, since it combines remote sensing information with environmental factors gained from mapping or modeling such as geology, topography, solar radiation or slope.

Materials and methods

Study area

The study area, the two valleys Val Trupchun and Val Müschauns, are part of the SNP. The SNP is located in the southeastern part of Switzerland in the lower Engladina (Fig.1a). The study area covers 1804.4 ha and an altitudinal range of 1823 to 2776 m above sea level (a.s.l.). The area is characterized by a continental climate, with long-term average annual precipitation of 868.76 \pm 155.9 mm and average annual temperature of 0.57 \pm 0.59 °C (mean \pm St. Dev.) measured at the meteorological station in Buffalora (1977 m a.s.l.) between 1959 and 2007 (Swiss Meteorological Institute 2007).



Stratification of the study area

The study area was chosen, since a lot of relevant data is available for this area. In the project HABITALP remote sensing information and models of various environmental factors were combined in ArcGIS 9.2 to develop a habitat model (Fig.2, Lotz 2006). The layers of the HABITALP stratification were taken for the two valleys Val Trupchun and Val Müschauns. Delineation of infrared aerial photographs formed the basis of the habitat model and was combined with the following ArcGIS model layers: habitat [(grassland, immature soils with 0% vegetation cover (gh_0), immature soils with 1 - 40% vegetation cover (gh_40), forest)], curvature (basin, planar, summit), solar radiation (high, low), geology (dolomite, limestone, silicate, debris), aspect (north, south, east, and west), slope (13 classes from 5% - 65%), and elevation (grades: 5 m).

Selection of strata and sampling design for field survey

The HABITALP stratification generated 153 different habitat types (four-digit code: 1110-8235), a number far too complex to survey in the field. Consequently, I selected 26 strata according to the following rules: i) all strata, which only differed in curvature, and ii) all strata that covered less than 2.2% of the study area were omitted. The 26 strata selected for this study as well as the original four-digit HABITALP codes are shown in Table 1.

In a second step I examined vegetation survey data from former studies (Madl 1991; Camenisch 1997), which consisted of vegetation relevés sampled according to the method of Braun-Blanquet (1964). I entered their coordinates into ArcGIS and assigned them to one of the 26 selected strata (Table 1). This resulted in an extremely skewed distribution of surveyed area. 13 strata were not represented, while other strata were represented by up to 54 relevés. I decided to conduct more relevés to have at least ten for each stratum (Table 1). Since the study area is difficult to access and the animals in the SNP should not be disturbed too much, I generated a buffer zone in GIS that covered 100 meters on both side of hiking trails. In this buffer zone I randomly selected as many survey sites as necessary (up to ten survey points per stratum, 167 in total). In the field I located the 167 survey sites with the aid of the stratification map that was created in GIS and a GPS. The fieldwork was conducted between June and August 2008. The same buffer zone was used to randomly select ten sampling sites in nine different strata (strata 1, 3, 8, 12, 15, 22, 30, 31, 33) for measuring ANPP. For logistic reasons, all the ANPP sampling sites were located in the Val Müschauns.



Fig. 2: HABITALP model of the study area Val Trupchun and Val Müschauns in the SNP.

Tab. 1: Strata selection based on HABITALP (Lotz 2006) and number of relevés from Madl (1991) and Camenisch (1997) assigned to one of the 26 strata. HABITALP types code explanation: 2xxx = grassland, 3xxx = immature soils with 0% vegetation cover, 4xxx = Immature soils with 1 - 40% vegetation cover, 8xxx = forest.

Strata in this study		н	ABITALP type	es		Number of surveys						
number	size (ha)		Code		Madl	Camenisch	- This study					
1	154.7	2112	2122	2132	4	9	-					
2	91.8	2115	2125	2135	5	2	3					
3	48.5	2215	2225	2235	17	4	-					
4	76.9	3111	3121	3131	-	-	10					
5	114	3115	3125	3135	-	-	10					
6	62.8	3215	3225	3235	-	-	10					
7	57.8	4111	4121	4131	-	-	10					
8	93.9	4112	4122	4132	-	-	10					
9	29.4	4115	4125	4135	-	-	10					
10	108.9	4211	4221	4231	-	-	10					
11	26.8	4215	4225	4235	-	-	10					
12	36.1	8212	8222	8232	-	14	-					
13	26.9	8213	8223	8233	1	15	-					
14	249.5	3211	3221	3231	-	-	10					
15	10.7	8215	8225	8235	-	-	10					
16	36.2	2211	2221	2231	-	-	21					
17	80.8	3112	3122	3132	-	1	9					
18	22.3	2111	2121	2131	-	-	10					
22	18.9	2213	2223	2233	-	-	10					
23	16.2	3212	3222	3232	1	-	10					
26	12.8	8115	8125	8135	-	6	4					
30	84.4	4212	4222	4232	20	-	-					
31	96.5	2212	2222	2232	54	-	-					
32	79.5	8113	8123	8133	-	53	-					
33	52.6	8112	8122	8132	-	29	-					
34	65	2113	2123	2133	-	18	-					

Vegetation composition

The vegetation composition was determined at 167 survey sites selected to complement the 253 sites already surveyed by Madl (1991) and Camenisch (1997). Vegetation relevés were sampled according to Braun-Blanquet (1964). The plot sizes of the quadrates for the relevés differed between vegetation types to match the plot sizes chosen by Madl (1991) and Camenisch (1997) as good as possible. Pasture and forest plots measured 7 × 7 m (49 m²), and meadow plots 3 × 3 m (9 m²). The abundance of plant species was estimated with seven cover classes suggested by Braun-Blanquet (1964): r = one individual, + = more than one individual and cover < 1%, 1 = cover 1% - 5%, 2 = cover 5% - 25%, 3 = cover 25% - 50%, 4 = cover 50% - 75%, 5 = cover 75% - 100%.

Aboveground net primary production (ANPP)

ANPP was estimated on ten different plots in nine selected strata (90 plots). All ninety plots were protected with baskets covering an area of 1260 cm² to prevent grazing. The baskets were set up immediately after the snow melt in spring 2008 and fixed to the ground with long nails. At the beginning of autumn in late August I revisited the plots and I clipped the vegetation to a level of 2 cm above the soil surface (excluding dead biomass). In the lab, the biomass was dried at 60 °C for 48 hours. I then allowed the dried biomass to stand for one hour in the lab to guarantee same conditions for all the samples and then weighted the samples to the nearest milligram (Mettler Toledo Excellence XS 400 2S Delta Range, Greifensee, Switzerland).

Data analysis

To characterize the differences between the strata and to describe the strata in terms of plant species composition, I entered the vegetation data of the 420 relevés available into MULVA-5.1, a multivariate statistical program for analyzing plant data (Wildi and Orlòci 1996). I transformed the cover data (Braun-Blanquet code) of the relevés as follows: r = 1, + = 2, 1 = 3, 2 = 4, 3 = 5, 4 = 6 and 5 = 7. To search for differences between the strata I calculated a resemblance matrix using the following similarity measurement:

$$S_{x,y} = \frac{\sum x_i y_i}{\sum x_i^2 + \sum y_i^2 - \sum x_i y_i} (i = 1, ..., n)$$
(1)

where x_i and y_i represent the scores of species i in the relevés x and y and n is the number of species.

I conducted a principal component analysis (PCA) and the PCA coordinates of the relevés were used to i) draw an ordination diagram and ii) for statistical analysis. Before analysis, I transformed the coordinates to assure a normal distribution of the residuals as follows: axis 1: arc-sin (axis 1+0.7); axis 2: arc-sin (axis 2+0.5). Differences between strata and between the PCA coordinates of the relevés, respectively, were tested with one-way ANOVA followed by t-tests for pairwise comparisons. To characterize the strata in terms of species composition, I conducted a discriminance analysis with Jancey's ranking upon F-values (Jancey 1979). This method allows to rank species in a vegetation table and to select species with high differentiating power (Wildi 1995). I selected the fifty plant species with the highest discriminating power. Out of these fifty species I removed those that occurred in less than three strata, which resulted in 47 remaining species.

The differences in ANPP among strata were evaluated with an ANOVA followed by pairwise comparisons with two sample t-tests. To guarantee a normal distribution I used the transformation:

$$x' = x^{0.25}$$
 (2)

where x represents dry biomass of ANPP.

I correlated ANPP with the environmental factors used in HABITALP and tested the differences of ANPP subject to several environmental factors with ANOVA for significance. To characterize the significant environmental factors in terms of species composition, I conducted a discriminance analysis with Jancey's ranking upon F-values (Jancey 1979).

Results

The HABITALP stratification proofed to be suitable for describing vegetation patterns in my study area, the valleys of Trupchun and Müschauns in the SNP. The 26 selected strata were significantly different with respect to both vegetation composition and ANPP.

Strata characterization by vegetation composition

The PCA ordination shows that the 26 selected strata form a vegetation gradient from stratum 18 to stratum 32 (Fig. 3). With exception of strata 9 and 26, the strata were well defined, i.e., the variability in species composition within specific strata was restricted, while differences between strata were distinct (Fig. 3). In general, strata were significantly different and separated by PCA axis 1 and 2, i.e., by their species composition (axis 1: F_{25, 388} = 71.59, p < 0.001; axis 2: $F_{25, 388}$ = 66.13, p < 0.001, Fig. 4). Six distinctive clusters of strata were distinguishable in the PCA ordination (Fig. 3). Strata 18, 4, 7 and 16 formed cluster 1 with negative scores of PCA axis 1 (Fig. 3, Fig. 4). This cluster was characterized by the predominant plant species Carex firma, Saxifraga caesia, Dryas octopetala, Bartisa alpina and Hieracium staticifolium (Table 2). Within the cluster, strata 18, 4 and 7 are further characterized by Rhododendron hirsutum, which discriminates them positively to stratum 16. Cluster 2 (strata 10 and 14) showed similarities to several other habitat clusters on the second axis, but discrimination to all the other clusters was significant on PCA axis 1 (Fig. 3, Fig. 4). The relevés were characterized by occurrences of Sedum atratum, Thlaspi rotundifolium, Arabis caerulea, Saxifraga oppositifolia and Minuartia recurva. Trisetum distichophyllum connects cluster 2 with cluster 3 and Saxifraga caesia as well as Ranunculus alpestris with cluster 1 (Table 2). The habitat cluster 3 (strata 5, 17, 23, 11 and 6) showed higher variation in species composition within the strata compared to cluster 1 and 2 and thus also a larger overlap with other clusters. The coordinate scores of the second PCA axis evidenced differences between strata 17/5 and the strata 23/11, where Larix decidua was recorded. Stratum 6 linked those two groups (Fig. 4). Cluster 3 is characterized by high abundance of Saxifraga aizoides (Table 2) and by Arabis alpina which was exclusively found in this cluster. Cluster 4 (8, 30 and 31) was located in the upper part of the positive area of the coordinate system of the PCA ordination (Fig. 3). The cluster shows a differentiation from all the other clusters (except of stratum 11) on the second axis and partly on the first axis (Fig. 4). However, the cluster is difficult to describe since there were no species growing exclusively in this cluster (Table 2). However, many species were missing that were abundant in all the other clusters. Cluster 4 was linked to both cluster 3 and 5 by Carduus defloratus, Senecio doronicum, Ranunculus montanus, Helianthemum grandiflorum, Galium anisophyllon and Euphorbia cyparissias (Table 2). Cluster 5 was formed by the strata 3, 12, 2, 1, 15, 22 and 13 (Fig. 3), with the dominating species *Phyteuma orbiculare* and *Polygala* chamaebuxus (Table 2). It was separated from clusters 1 to 4 by *Geranium sylvaticum*, *Homogyne alpina*, *Anthoxanthum odoratum*, *Alchemilla vulgaris*, *Luzula sieberi* and *Potentilla* aurea and from cluster 6 (strata 32, 33, 34) by *Rhododendron ferrugineum* (Table 2). Other predominant species in cluster 6 include *Homogyne alpina*, *Anthoxanthum odoratum*, *Alchemilla vulgaris*, *Luzula sieberi*, *Potentilla aurea*, *Calamagrostis villosa*, *Vaccinium vitisidaea*, *Vaccinium myrtillus*, *Veratrum album*, *Oxalis acetosella* and *Rhododendron* ferrugineum. Hieracium sylvaticum and Ranunculus montanus were linking this cluster to cluster 5.



Fig. 3: PCA of the relevés from the 26 selected HABITALP strata (mean and standard deviation). The graph in the top left hand corner shows the explanatory power of the axis 1 (7.87%) to axis 6 (1.66%).



Fig. 4: Coordinate scores (mean and standard error) of the relevés from the 26 selected HABITALP strata of PCA axis 1(a) and 2 (b). Different letters indicate significant differences between means at p < 0.05 (t-test).

Tab. 2: Species composition of the 26 HABITALP strata. The boxes highlight differentiating species between the strata (F-values: I)f = 25,
388). Species abundance corresponds to the system of Braun-Blanquet (1964): r = one individual, + = more than one individual an	d cover
< 1%, 1 = cover 1% - 5%, 2 = cover 5% - 25%, 3 = cover 25% - 50%, 4 = cover 50% - 75%, 5 = cover 75% - 100%.	

Snecies	1												St	ratun	n											
Opecies	18	7	4	16	10	14	5	17	9	23	11	6	30	8	31	15	22	12	3	13	2	1	26	34	33	32
Rhododendron hirsutum	3	+	1						+						•.					r	-		+	• ·		r
Carex firma	3	3	3	3	1 +				+										r	r.			+			•
Saxifraga caesia	2	3	3	3	r	r			+	l r			r							r			r			
Ranunculus alpestris	+	1	+	2	2	1	r	r					•			r				•						
Sedum atratum	r	r	r	1	2	3	1	+			r	r							r			r				
Hieracium staticifolium	2	2	' 2	1	2	2	1	2	+	+	2	' r		r									+			
Theracium staticionum	2	2	2	, ,	1			2			 r												•			
Arabis caerulea					1	1	r																			
Savifraga oppositifolia				+	2	3	+											r								
Trisotum distichonbullum		+	r		2	3		3	1	2	2	٦.	1	1	-	r						r				r
Savifraga aizoidos			, ,	1		5	2	3	' +	2 ب	2	Ľ	'	'		1										1
Minuartia regultices			'		2	2	2	-			2		-													
Coractium latifolium				r	0 1	3 1	2	- -	I	I	I		1		ſ											
Arabis serovilifolio				י ר	י ד	י ז	2 r	I	r		r															
Pritzelago alnino e etr				' -	1	2	1	1	י ד		I			'												
Arabia alpina s.su.					I	5	1	1	-			-														
niavis alpilla s.sll.	2	0	0	0			<u> </u>	-	r	4	1	Ŧ								-	_	0	,			
Dryas ociopeiaia	3	3	3	3 -	+		+	г -	+	1	2	2	2	+	2	2	+	2	r	r ₄	r	2	+	+	+	r
Carduus denoratus s.str.	2	2	r	r Q	r	+	+	r	I		I	3	Z	3	2	3	I	3	2	1	+	+	r	r	r	r
Barisia alpina	3	2	+	2	r		_	r Q	_	r	4	_	_	2	r	4	_	2	ŗ	2	г	+	+ 0	r Q	r 2	r o
Aleracium sylvalicum		ſ	ſ	r			Г.	2	1	+	1		1 0	2	r	1	r	2	+	2	+	2	2	Z	3	ა
Gypsopnila repens							+	1	1	2	3	+	3	2	1		r	r	r	r		r				
Hieracium villosum							r	+		r	3			+	r	•	r		r			r				
Carlina acaulis				r			+	+	+	r	3		r	2	1	3	2	1	3	+	1	+				r
Thymus polytrichus							1	1	1	1	2	+	3	3	2	1	+	2	1	1	+	+				
Senecio doronicum										+	r	r	1	3	2	3	r	+	2	r	+	+				
Aster bellidiastrum	r		r				+			r	r		r	r	r	r	+		r	r	r	1	1	3	1	2
Ranunculus montanus agg.				r			1	1	+	+	3	r	2	3	2	3	3	3	3	2	3	3	1	3	3	3
Helianthemum grandiflorum							1	1	1	1	3	+	3	3	3	3	2	1	3	+	1	2	+	+	r	r
Galium anisophyllon							1	+	1	2	2	2	2	2	3	3	3	3	3	3	2	2	r	3	2	2
Euphorbia cyparissias								r	+	1	2	+	1	2	2	3	2	3	2	1	1	+	r		r	r
Viola biflora							r	+	+	r				r		r	r	r		r	r	r	+	2	1	2
Phyteuma orbiculare										r			r	2	1	2	2	+	3	+	1	2	r		r	r
Polygala chamaebuxus												r	r	r	+	3	+	1	3	2	1	+	r		r	
Larix decidua										+	r	1		1		3		+	r	+	+	+	+	2	1	2
Festuca violacea agg.										1			+	r	2	r		r	2		2	2	+	3	1	1
Geranium sylvaticum							r					+		r		r	r	+	r	+	r	+	1	2	2	3
Homogyne alpina		r											r		+			r	1	+	r	1	1	3	3	3
Anthoxanthum odoratum								r					r				r	+	r	r	r	+	r	2	2	2
Alchemilla vulgaris agg.															r	r	r	+	r	r	+	r	+	3	+	2
Luzula sieberi							r									r		r	r	r	r	+	1	3	3	3
Potentilla aurea																	r	r	r	r	r	r	r	2	1	2
Calamagrostis villosa							r											+	r	r		r	+	+	2	2
Vaccinium vitis-idaea															r			+		r	r	+	1	1	2	2
Vaccinium myrtillus																		r	r	r	r	r	+	1	2	2
Veratrum album s.str.																				r	r		r	+	+	2
Oxalis acetosella																				r		1	+	r	1	1
Rhododendron ferrugineum																						+	+	1	2	1

Strata characterization by ANPP

ANPP was significantly different between the nine selected HABITALP strata ($F_{8,80}$ = 6.197, p < 0.001). However, the discriminating power of ANPP was smaller than that of vegetation composition. Pairwise comparisons showed that ANPP was very similar in strata 33/8, strata 30/12/31/15 as well as strata 22/3/1 (Fig. 5). The mean range of ANPP that I measured was between 68.30 g m⁻² (stratum 12) and 194.36 g m⁻² (stratum 22).



Fig. 5: Aboveground net primary productivity (ANPP) of nine selected HABITALP strata (mean and standard error). Different letters indicate significant differences between means at p < 0.05.

ANPP of the different strata seemed to be strongly influenced by the environmental factors geology ($F_{2, 86}$ = 10.851, p < 0.001) and slightly by the slope ($F_{9, 79}$ = 1.861, p = 0.07). Strata 22, 3 and 1 showed high productivities at rather low mean slope gradients of 24.5% to 35%. In contrast, the strata 8 to 12 indicated steeper hillsides from 35% to 44.5% with lower ANPP than the strata before. In contrast, neither curvature ($F_{2, 86}$ = 1.021, p = 0.365) nor aspect ($F_{3, 85}$ = 0.451, p = 0.717), solar radiation (t = 1.172, df = 79.89, p = 0.245) nor altitude ($F_{1, 87}$ = 0.008, p = 0.930) explained differences in ANPP.

Effects of environmental factors on vegetation composition

The environmental factors, geology and slope seemed to affect the plant species composition in the study area. The vegetation composition varied strongly between different bedrock types. The vegetation on limestone and on debris was guite similar, whereas differences between silicate and dolomite were very large (Table 3). I detected many species that not only occurred on both limestone and on debris, but also were found with the same abundance on both bedrock types. This includes species that were usually found as single individuals such as Viola biflora, Alchemilla vulgaris, Potentilla aurea, Trollius europaeus, Calamagrostis villosa, Bartsia alpina, Salix retusa, Saxifraga oppositifolia, Ranunculus alpestris, Sedum atratum and Saxifraga caesia. However, also predominant species such as Galium anisophyllon, Helianthemum grandiflorum, Thymus polytrichus and Ranunculus montanus were abundant on both bedrock types (Table 3). The only differences in plant species composition I could detect between limestone and debris concerned Hieracium staticifolium and Dryas octopetala, which were more abundant on debris and Geranium sylvaticum and Luzula sieberi, which were more abundant on limestone. The vegetation on silicate differed mainly in the abundance of several species that only occurred sporadically on limestone and debris, but grew well on silicate: Alchemilla vulgaris, Calamagrostis villosa, Geranium sylvaticum, Luzula sieberi, Potentilla aurea, Trollius europaeus and Viola biflora (Table 3). In contrast, many species that grew well on limestone and debris were absent on silicate: Hieracium staticifolium, Ranunculus alpestris, Saxifraga oppositifolia, Sedum atratum and Saxifraga caesia. The vegetation on dolomite also differed from limestone and debris as well as from silicate vegetation (Table 3). Predominant species on dolomite included Hieracium staticifolium. Saxifraga caesia, Carex firma, Ranunculus alpestris and Sedum atratum.

Bartsia alpina, Dryas octopetala and *Salix retusa* seemed to grow preferably on dolomite. However, these species were also found on all the other bedrock types, but in lower abundance. **Tab. 3**: Abundance of selected species in dependence of geology. Species abundance corresponds to the system of Braun-Blanquet (1964): r = one individual, + = more than one individual and cover < 1%, 1 = cover 1% - 5%, 2 = cover 5% - 25%, 3 = cover 25% - 50%, 4 = cover 50% - 75%, 5 = cover 75% - 100%.

Species		F-Value			
	Silicate	Limestone	Debris	Dolomite	Df = 3, 410
Geranium sylvaticum	2	+	r		52.058
Luzula sieberi	2	+	r		58.753
Viola biflora	1	r	r		38.181
Alchemilla vulgaris agg.	1	r	r		43.636
Potentilla aurea	1	r	r		39.881
Trollius europaeus	1	r	r		36.578
Calamagrostis villosa	1	r	r		36.204
Galium anisophyllon	2	2	2		59.659
Helianthemum grandiflorum	+	2	2		42.993
Thymus polytrichus	r	1	1		42.411
Ranunculus montanus agg.	3	2	2	r	69.876
Bartsia alpina	r	r	r	1	39.124
Salix retusa	r	r	r	1	48.101
Dryas octopetala	r	r	+	2	48.377
Saxifraga oppositifolia		r	r	+	41.812
Ranunculus alpestris		r	r	1	118.77
Sedum atratum		r	r	1	42.817
Hieracium staticifolium		r	+	2	69.195
Saxifraga caesia		r	r	2	127.73
Carex firma			r	2	130.39

Slope seemed to be another important environmental factor that explained the species patterns found in the study area. The steepest hillsides in the study area were characterized by *Oxytropis jacquinii, Saxifraga paniculata and Gypsophila repens.* Also *Trisetum distichophyllum* and *Minuartia recurva* predominated on these steeper slopes. Slopes of 30% - 50% were dominated mostly by *Homogyne alpina* and *Festuca violacea*. Many species such as *Hieracium staticifolium, Trifolium repens, Saxifraga aizoides, Saxifraga oppositifolia* and *Sedum atratum* were found the most often at inclinations of 10% to 25%. Slopes of 5% were characterized by plant species such as *Salix purpurea, Lamium album, Epilobium fleischeri, Chenopodium bonus-henricus, Gnaphalium hoppeanum, Petasites paradoxus, Arabis hirsuta* and *Dactylis glomerata* (Table 4).

Tab. 4: Abundance of selected species in dependence of slope gradient. Species abundance corresponds to the system of Braun-Blanquet (1964): r = one individual, + = more than one individual and cover < 1%, 1 = cover 1 - 5%, 2 = cover 5% - 25%, 3 = cover 25% - 50%, 4 = cover 50% - 75%, 5 = cover 75% - 100%.

Species						s	lope (%	6)						F-Value
	65	60	55	50	45	40	35	30	25	20	15	10	5	Df = 12, 401
Viola pinnata		1		r	r									6.316
Androsace helvetica		1	r		r	r								4.134
Carex rupestris		1				r								4.944
Oxytropis jacquinii	3	3	+	+	+	r	r			r				5.202
Minuartia rupestris	1		r			r	r							9.998
Saxifraga paniculata	3	1	+	r	+	r	r	r	r	+	r			4.112
Festuca violacea agg.		1	r	1	1	+	1	+	r		r		+	3.412
Trisetum distichophyllum	3	1	1	+	r	r	r	r	+	2	+	+	+	4.885
Gypsophila repens	3	3	2	1	+	r	r	r	+	+	r	r	2	7.296
Knautia dipsacifolia					r	r	+	r	r					3.841
Homogyne alpina				+	+	1	1	+	r	r	r			3.597
Anthoxanthum odoratum				r	r	+	+	r	r		r	r		3.418
Arabis hirsuta					r	r	r	r		r			1	5.386
Hieracium staticifolium			+	r	r	r	r	+	1	1	1	1	1	5.531
Trifolium repens				r	r	r	r	r	+	r	+	r		3.592
Saxifraga aizoides			r	r	r	r	r	r	+	1	+	r	+	8.09
Saxifraga oppositifolia					r	r	r	r	r	+	+	+		4.431
Sedum atratum				r		r	r	r	r	+	+	1		7.312
Cerastium latifolium						r	r	r	r	+	r	r		3.307
Arabis serpyllifolia						r	r	r	r	r	+	+		4.187
Petasites paradoxus			r		r	r		r	r	r	r	r	2	4.722
Epilobium fleischeri				r			r					r	+	3.326
Dactylis glomerata					r	r	r		r	r	r	r	1	4.028
Chenopodium bonus-henricus							r						+	4.806
Gnaphalium hoppeanum						r				r	r		+	3.74
Salix purpurea s.str.										r		r	1	6.269
Lamium album											r		+	5.707

Discussion

The goals of this study were to test the suitability of remote sensing techniques for detecting and describing vegetation patterns in an alpine region. The delineation of vegetation patterns by interpreting infrared aerial photographs proves to result in strata that are well separated in terms of vegetation composition. Especially, strata with rather homogenous vegetation cover could be well distinguished from one another at larger scales as my field surveys demonstrate. The strata cluster 6 consisting of 3 delineated strata clearly differed from all other clusters and strata by the predominance of forest dwarf shrubs such as *Rhododendron* ferrugineum, Vaccinium myrtillus or Vaccinium vitis-idaea. These three particular species indicate that the forest communities of strata cluster 6 most likely grow on siliceous substrate (Ellenberg 1963). Consequently, also differences in geology were well detectable at larger scale. In general, the vegetation seems to reflect geological pattern very well (see also Ellenberg 1963; Pausas and Carreras 1995). The geology determines soil chemical, physical or biological properties such as nutrient cycling, water availability, pH, bulk density, or microbial biomass (Klink 1998; Schulze et al. 2002). The siliceous and calcareous bedrocks that are found in the study area differ strongly in most of those properties and so does. consequently, the composition of the vegetation. Frey and Löscher (1998), for example, distinguished between characteristic plant species growing on siliceous bedrock like Rhododendron ferrugineum and on calcareous bedrock like Ranunculus alpestris. Calcareous substrate in the study area consists of both, dolomite and limestone. These two substrates differ again in many chemical and physical properties. Dolomite is, for example, less reactive compared to limestone, finer grained and contains more magnesium (Markl 2004; Staffelbach 2008), which was again reflected in the composition of the vegetation. The evaluation of the field surveyed vegetation composition revealed on the one hand the similarity of the calcareous characteristic of the two bedrocks with the occurrence of calciphiles like Saxifraga caesia (Lauber and Wagner 2007) and on the other hand the dissimilarity with the absence of certain plants like Alchemilla vulgaris. Luzula sieberi and Trollius europaeus from dolomite. It is likely that the absence of certain plant species from dolomite, which grow well on limestone, can be attributed to "the dolomite phenomenon". Thereby it is expected that the oversupply of magnesium deactivates phosphor within the plants and, as a consequence, nitrogen cycling would change and result in physiological stress (Glatzel 1968; Baier 2004). Remote sensing with aerial photography facilitates landscape mapping at a high resolution (approximately 0.25 m; Lotz 2006). However, it does not solve the problem of identifying plant species composition accurately especially in the alpine vegetation belt, where i) small-scale variability of environmental factors results in small-scale variability in vegetation composition, and ii) due to the short growing season and

high radiation plants are generally small growing (Körner 1999). Consequently, the remote sensing stratification, generally predicted the vegetation composition quite well in our study area, failed sometimes. For example, the strata cluster 1 contained four strata with very similar vegetation composition. According to the stratification these strata varied from grassland with high vegetation cover, strata with 40% vegetation to strata with almost no vegetation cover. However, the vegetation survey revealed low vegetation cover for all the strata: they were all located in an area close to the climatic snow line in the high alpine to subnival vegetation belt where Dryas octopetala acts as a pioneer and dense tussocks of Carex firma predominated (Ellenberg 1963). In general, the remote sensing techniques used had more problems in predicting vegetation patterns in transition zones e.g., open habitats such as rocky areas/scree slopes to grasslands or grasslands to forests as well as in transition zones of changing geology. Good examples are the two strata 9 and 26, which have shown to be very heterogeneous in respect to vegetation composition. In stratum 26, species of the subnivale belt (Carex firma) are, for example, combined with species from forests of both calcareous (Rhododendron hirsutum) and siliceous soils (Rhododendron ferrugineum). These problems concerning the identification of vegetation patterns with different species composition on various bedrock types in transition zones seemed to be the result of the coarse resolution. This aspect will be discussed later. Overall, my results were in a line with several former studies, which proved that patterns created by remote sensing techniques correspond well with field surveys (Lauver 1997; Fuller et al. 1998 a, b; Nagendra and Gadgil 1999 a, b; Shuman and Ambrose 2003; Foody and Cutler 2006; Groom et al. 2006; Hernandez-Stefanoni et al. 2006) and that vegetation patterns are well detectable with environmental factors (Noss 1990; Bunce et al. 1996; Bunce et al. 2008). Especially remote sensing techniques based on aerial photography proved to be efficient in the detection and identification of vegetation patterns at the level of plant communities and species in the past (Shuman and Ambrose 2003).

It was stated that vegetation patterns delineated from hyperspectral or multispectral remote sensing data correlated with productivity patterns (Hansen et al. 2000; Zeng et al. 2007; Luus and Kelly 2008). Since the infrared aerial photography reflects activity of the plant tissue, delineated strata should differ in aboveground net primary production (ANPP). The analysis of my field data showed that the differences were much less obvious compared with differences in vegetation composition. These difficulties could be a result of the 2008 weather conditions compared to longtime averages. Pursuant to the records of the Swiss Meteorological Institute at Buffalora, precipitation was well above average in 2008. Precipitation events were both more frequent and more intense, especially in spring and summer. Heisler-White et al. (2008) mentioned in their study that the inter-annual variability in winter/early spring precipitation might affect annual ANPP patterns, since larger rain

events enable the water to penetrate to greater depths were it is conserved over longer time periods (Parton et al. 1981; Sala et al. 1992) and therefore the water supply for plants improved. Improved water availability correlates with enhanced nutrient flow and, consequently, in an increase in biomass. Several studies evidenced the importance of rainfall quantity and timing with regard to ANPP (Harper et al. 2005; Chou et al. 2008). They showed that ANPP and soil CO₂ fluxes increased with more intense rainfall events and with higher soil temperature. Similar processes might have affected ANPP, mainly in the poor grassland habitats, in the study area in 2008, resulting in lower variation in ANPP between the strata. Productivity monitoring data from the SNP seems to confirm this potential explanation. Compared to 2007, ANPP was more than 10 times higher in the most unproductive grassland types in 2008 (5.7 vs. 62.8 g dry biomass m⁻²). In the most productive tall-herb communities, however, ANPP increased from 255.3 g in 2007 to only 278.2 g m⁻² in 2008 (unpublished data). Another factor that influences ANPP was the slope gradient. The inclination directly affects the degree of mechanical disturbance. Indirectly, also water holding capacity is affected, since the disturbance regime determines grain size as well as humus accumulation. All these relations result in higher ANPP in flat areas were solifluctuation events are rare, ground grain size small, and water and nutrients accumulate in contrast to steep hillsides. However, the resulting differences may be suppressed when the micro-relief is too heterogeneous at small scale. Thus, for example, in our heterogeneous alpine study area, it is possible that the inclination at a steep hillside seemed to be relatively homogeneous at the remote sensing scale, but finer resolution would have shown differences in the slope gradient, i.e., a mosaic of flat as well as steep patches at a small scale. Such small-scale variability could have resulted in a balanced ANPP between different strata in our study and to a reduced differentiation power of ANPP.

The spatial resolution might also have played an important role in relation concerning the vegetation composition in the various strata. The remote sensing stratification was made at a resolution of 20 m × 20 m. This resolution seems to be too coarse, especially when an alpine landscape is concerned where environmental factors may change almost in square meter intervals, for example in the transition zones of geology (Körner 1999). It is possible that vegetation patterns of the inhomogeneous strata 9 and 26 were more consistent at a finer spatial, i.e., the strata would be divided into several substrata. However, such studies bring the dilemma of losing information for the gain of efficiency and predictability (Levin 1992).

Conclusion

The results of this study play a decisive role with regard to future conservation, preservation and monitoring efforts in the SNP. The HABITALP stratification in combination with field surveys enables, for example, to characterize habitat types with high biodiversity as well as habitat types with rare, valuable species. This knowledge permits to protect, conserve and monitor the alpine landscape also in inaccessible locations. Furthermore, such studies will also help to visualize changes of the vegetation in the Alps due to the global change in the future.

The distribution of the vegetation patterns, their quality as well as their quantity affects the abundance and distribution of other organisms, particularly herbivores. The use of different habitats by herbivores is not random, but rather an answer to different environmental conditions like habitat use by other animals (inter- and intra-specific competition), habitat structure and food supply (Bergerud 1974; Crawley 1983). These factors define the suitability of certain habitat types for certain herbivores and they influence directly or indirectly the physical conditions of the herbivores and drive their population growth. Forage strategies of large herbivores like ungulates include habitat selection on various spatial scales (Senft et al. 1987; Turner et al. 1997). Ungulates have to make a decision between the demand for important but rare nutrients and the maximization of energy intake (Sinclair et al. 2006). Thus, the HABITALP stratification could prove an insight into the interaction between vegetation and large herbivores that inhabit the SNP in terms of, for example, habitat selection and habitat use. Further, the costs and benefits for herbivores to frequent a habitat type changes with the emergence of a predator. Some studies showed changes in the habitat selection of herbivores with the interaction of wolves and changes of the vegetation composition in wolf preferred habitat types (Mao et al. 2005; Frank 2008; Halofsky and Ripple 2008; Halofsky et al. 2008). The re-immigration of predators like wolves and bears can be expected in the next few years in the SNP. Consequently, we will have the chance to investigate the changes in habitat use due to predator activities using HABITALP. Furthermore, the combination of ongoing studies on the diet compositions of alpine chamois and alpine ibex on the basis of feces analysis (Trutmann 2009; Zingg 2009) with this study

may help to clarify forage preferences and availability of these two ungulate species, which both inhabit the study area. In addition, the combination of these studies enables to analyze possible interactions such as competition between the two species.

The habitat classification by HABITALP is especially valuable for alpine landscapes like the study area, where accessibility is restricted. The results evidence, that remote sensing in combination with environmental factors are suitable tools to detect vegetation patterns and processes in the study area.

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Appendix A

Tab. 1 A: field measurements of the productivity and additional information about the environmental factors of the several survey locations.

stratum/number	aeoloay	solar	curvature	aspect	slope (%)	contour (a.s.l.)	biomass (g m ⁻²)
Str1 1	limestone	low	hasin	east	40	1994	180.63
Str1.2	limestone	low	basin	oast	-0	1003	152.06
Str1 3	limestone	low	basin	north	30	2009	253.97
Str1.0	limestone	low	basin	north	30	2003	205.6
Str1 5	limestone	high	basin	north	25	2004	288.02
Str1.6	limestone	low	planar	east	50	1986	54.44
Str1.0	limestone	low	basin	east	50	1984	45.16
Str1.8	limestone	low	basin	east	45	1942	91 75
Str1 9	limestone	low	basin	north	20	1993	62.78
Str1 10	limestone	low	basin	east	40	1944	75
Str3 1	debris	high	planar	east	25	1968	239 13
Str3 2	debris	high	hasin	east	20	1966	265.32
Str3.3	debris	high	planar	east	30	1977	209.6
Str3 4	debris	high	basin	east	25	1976	251 43
Str3.5	debris	high	basin	east	30	1989	143.1
Str3.6	debris	high	basin	east	35	1991	132.3
Str3.7	debris	high	summit	south	25	1983	93.5
Str3.8	debris	high	planar	east	25	1995	170.4
Str3.9	debris	hiah	summit	east	20	1998	303.02
Str3.10	debris	high	basin	north	30	1987	43.5
Str8.1	limestone	low	summit	east	40	2123	123.89
Str8.2	limestone	low	planar	east	45	2066	55.24
Str8.3	limestone	low	planar	east	45	2077	83.17
Str8.4	limestone	low	planar	east	45	2073	102.86
Str8.5	limestone	low	summit	east	40	2141	144.13
Str8.6	limestone	low	summit	north	55	2109	83.17
Str8.7	limestone	low	summit	north	50	2124	173.97
Str8.8	limestone	low	basin	north	45	2133	106.83
Str8.9	limestone	high	planar	east	30	1904	105.16
Str8.10	limestone	high	planar	east	25	1904	65.79
Str12.1	limestone	high	summit	east	45	2027	54.21
Str12.2	limestone	high	summit	east	35	2044	54.84
Str12.3	limestone	high	summit	east	55	2059	92.14
Str12.4	limestone	high	planar	east	45	2031	69.68
Str12.5	limestone	high	planar	east	50	2061	76.59
Str12.6	limestone	low	summit	south	55	2046	57.86
Str12.7	limestone	high	planar	east	40	2054	48.17
Str12.8	limestone	high	summit	east	35	2061	86.51
Str12.9	limestone	high	basin	east	45	2065	110.95
Str12.10	limestone	high	summit	east	40	2078	32.06
Str15.1	debris	high	basin	east	30	1972	104.37
Str15.2	debris	high	basin	south	30	1976	38.81
Str15.3	debris	high	basin	east	30	1987	130.79
Str15.4	debris	high	summit	south	30	2003	40.24
Str15.5	debris	high	planar	east	50	2014	40.24
Str15.6	debris	high	planar	east	30	2014	135.79
Str15.7	debris	high	summit	east	35	2026	120.56
Str15.8	debris	high	basin	east	40	2013	98.17
Str15.9	debris	high	planar	east	45	2023	87.94
Str15.10	debris	low	planar	east	35	2026	142.14

Tab. 2 A: Continuation of the table 1A: field measurements of the productivity and additional information about the environmental factors of the several survey locations.

stratum/number	geology	solar	curvature	aspect	slope (%)	contour (a.s.l.)	biomass (g m ⁻²)
Str22.1	silicate	high	summit	east	30	1997	301.19
Str22.2	silicate	high	summit	east	20	1997	195.08
Str22.3	silicate	high	summit	east	30	1976	183.97
Str22.4	silicate	high	summit	east	30	1975	99.92
Str22.5	silicate	high	planar	east	20	1960	105
Str22.6	silicate	high	basin	east	20	1958	93.65
Str22.7	silicate	high	summit	south	20	1917	230.56
Str22.8	silicate	high	summit	south	25	1913	206.98
Str22.9	silicate	high	basin	south	15	1909	265.95
Str22.10	silicate	high	basin	east	35	1920	261.27
Str30.1	limestone	low	basin	north	35	2007	24.13
Str30.2	limestone	high	basin	east	40	1984	82.38
Str30.3	limestone	high	basin	east	25	1945	78.1
Str30.4	limestone	high	summit	east	35	1949	192.94
Str30.5	limestone	high	planar	east	35	1981	142.06
Str30.6	limestone	low	basin	east	40	1888	37.54
Str30.7	limestone	low	basin	east	40	1891	22.06
Str30.8	limestone	low	basin	west	35	1883	55.56
Str30.9	limestone	low	basin	west	15	1881	75.32
Str30.10	limestone	high	basin	east	50	2073	69.37
Str31.1	limestone	high	planar	east	45	1948	45.63
Str31.2	limestone	high	summit	east	25	1950	49.37
Str31.3	limestone	high	planar	east	40	1943	50.87
Str31.4	limestone	high	summit	east	40	1944	35.08
Str31.5	limestone	high	basin	east	35	1959	122.94
Str31.6	limestone	high	planar	east	35	1962	49.6
Str31.7	limestone	high	planar	east	40	1962	70.87
Str31.8	limestone	high	basin	east	25	1999	13.81
Str31.9	limestone	high	basin	east	30	2003	85.4
Str31.10	limestone	high	summit	east	35	1962	173.81
Str33.1	limestone	low	planar	east	40	2052	69.21
Str33.2	limestone	low	planar	east	35	2057	96.9
Str33.3	limestone	low	planar	east	30	2067	70.95
Str33.4	limestone	low	summit	east	50	2037	84.76
Str33.5	limestone	low	planar	east	40	2090	96.98
Str33.6	limestone	low	basin	east	60	2079	90.32
Str33.7	limestone	low	basin	east	55	2165	153.51
Str33.8	limestone	low	summit	east	30	2145	135.48
Str33.9	limestone	low	basin	east	40	2089	132.54
Str33.10	-	-	-	-	-	-	-