

# PASSAUER SCHRIFTEN ZUR GEOGRAPHIE

HERAUSGEGEBEN VON

ERNST STRUCK, DIETER ANHUF, WERNER GAMERITH UND KLAUS ROTHER

Schriftleitung: Erwin Vogl



HEFT **21**

Friederike Grüninger

## Scale dependent aspects of plant diversity in semiarid high mountain regions

An exemplary top-down approach for the Great Basin (USA)

With 85 figures, 33 tables, and 30 photos

Selbstverlag Fach GEOGRAPHIE der Universität Passau

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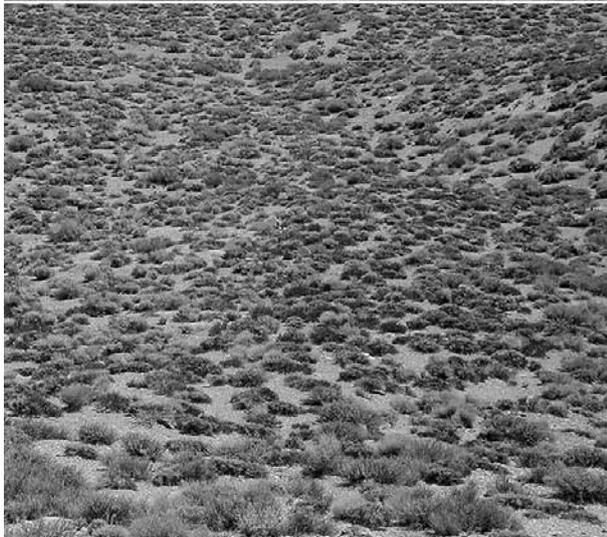
# Scale dependent aspects of plant diversity in semiarid high mountain regions

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## 5 Results White Mountains



### 5.1 Mountain-scale

#### 5.1.1 Plant communities of the White Mountains

The plant communities in the White Mts. are classified from the macro-plot data of A-samples (mature stands, each 2,500 m<sup>2</sup>) along the western flank of the mountain range. A total of 19 samples with 156 species was explored (for location see fig. 12). The result of the clustering procedure is shown in figure 24 as dendrogram. Six discrete plant communities can be distinguished and are named by the two characterizing species:

##### *Psorothamnus arborescens*-*Atriplex confertifolia* semi-desert ( $\leq 1,500$ m a.s.l.):

The basins and lower foothill zones are covered with hygrophilic plants of the desert scrub, dominated by *Atriplex confertifolia* (shadscale) and associated by *Psorothamnus arborescens* var. *minutifolius* and *Ephedra nevadensis*. Annual and perennial forbs (e.g. *Cryptantha* spp., *Chaenactis carphoclinia* var. *carphoclinia*, *Eriogonum nidularium*, *Xylorhiza tortifolia* var. *tortifolia*) and grasses like *Achnatherum speciosum* and *Bromus tectorum* contribute most to the herb layer.

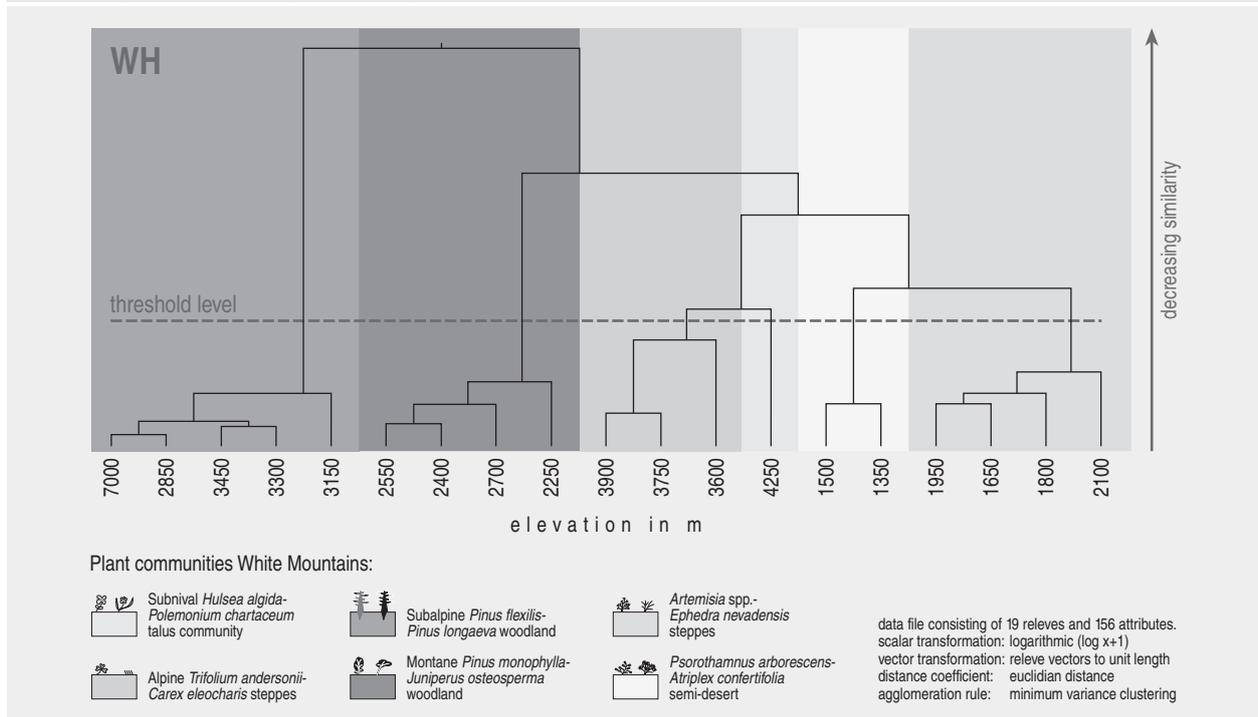
##### *Artemisia* spp.-*Ephedra nevadensis* steppe (1,500 m–2,100 m a.s.l.):

At elevations above 1,500 m a.s.l., the mentioned herbs and shrubs are still present, but several *Artemisia* spp. characterize the higher and less alkaline shrub layer in the foothill zone up to the lower woodland boundary at 2,100 m. *Artemisia arbuscula* ssp. *arbuscula* and *A. tridentata* are important sagebrush shrub species, accompanied by *Menodora spinescens*, *Artemisia spinescens*, *Krascheninikovia lanata* and *Grayia spinosa*. Conspicuous herbs like the endemic *Penstemon monoensis* and *Mirabilis bigelovii* var. *retrorsa* complete the understory vegetation. Structurally, the washes and alluvial fans vary in vegetation due to differences in moisture availability and to the tolerance of disturbances like flash floods. *Populus* spp. and *Salix* spp. line the canyon bottoms with permanent moisture supply (e.g. Silver Canyon, see map in fig. 11), whereas the alluvial fan in front of the Black Canyon is more densely vegetated than its surrounding slopes and features larger amounts of typical ruderal aliens (e.g. *Bromus rubens*, *B. tectorum*).

##### Montane *Pinus monophylla*-*Juniperus osteosperma* woodland (2,250 m–2,800 m a.s.l.):

Different slope aspects and the petrographic variety create a broad ecotonal zone between the before described upper foothill scrub zone and the upward following woodland of *Pinus monophylla* and *Juniperus osteosperma*. It forms the lower tree-line as in many other mountain ranges all over the Great Basin, the Colorado Plateau and towards the southern Rocky Mountains. In the White Mts. as in whole eastern California, this woodland is untypical in its rarity of juniper according to BURWELL (1998), which normally co-dominates with the pinyon throughout the central Great Basin (WEST et al. 1978). Furthermore, BURWELL

**Fig. 24:** Classification of the macro-plot (2,500 m<sup>2</sup>) A-samples (undisturbed zonal vegetation) along the altitudinal gradient of the White Mountains, shown in form of a dendrogram. The plant communities are assigned to the groups of highest similarity (see threshold level) and colored in the background; belt designation according to traditional nomenclature for extra-tropical mountain ranges (see chapter 4.2.6 and also RICHTER 2001).



describes a downward displacement of the lower tree-line (first tree species are found already at 1,900 m a.s.l.) after the beginning of the Anglo-American settlement and the introduction of livestock which diminished the formerly high competitive and fire-fuel providing grasses on mesic soils. This is a widespread phenomenon over the whole Great Basin (see BLACKBURN, TUELLER 1970; VALE 1975).

The *Artemisia* spp. now serve as understory species within the open woodland, associated with *Ephedra viridis*, *Chrysothamnus* spp. and *Purshia tridentata*. Rocky outcrops feature *Cercocarpus ledifolius*, and grasses such as *Elymus elymoides* and *Achnatherum hymenoides* are scattered all-over. Herbs like *Castilleja angustifolia*, *Cryptantha pterocarya* and *Gilia inconspicua* are also widespread but unimportant in regard to absolute ground cover.

#### Subalpine *Pinus flexilis*-*Pinus longaeva* woodland (2,800 m–3,500 m a.s.l.) and the “bald” zone:

Above about 2,800 m a.s.l., the montane woodlands are either directly replaced by a second woodland zone composed of *Pinus flexilis* and/or *Pinus longaeva*, or the vegetation drops back to a sagebrush steppe with *Artemisia arbuscula*, *Eriogonum caespitosum*, *Poa secunda* and smaller amounts of several other grasses and forbs. These treeless areas (see photo 1) are also referred to as “balds” (see BILLINGS 1990 and HÖLLERMANN 1973, who compared these areas with the treeless “upper sagebrush grass zone” of other mountains in Nevada and south-eastern Oregon and the Appalachian grassy balds) and are discussed controversial in literature: MOONEY, WRIGHT (1965) and SPIRA (1991) relate these differences in vegetation to the prevailing substrate, with sandstone and quartzite-rich soils lacking conifers, granite being preferred by limber pine, and limestone supporting bristlecone pine; HETZNER et al. (1997) employ

**Photo 1:** Western flank of the White Mountains and the Silver Canyon, with the Owens Valley in the foreground. Montane and subalpine woodland belt appear generally separated by “balds”, but connect above Silver Canyon.



RICHTER's concept of the “unoccupied niche” (see RICHTER 1996), treating the gap between the woodland belts as a result of the absence of appropriate tree species in these elevations of the mountain range. HÖLLERMANN (1973) states that complex environmental variables (like slope exposure, substrate and topography) create a locally occurring microclimatic-edaphic aridity of the ground, thus preventing conifer growth; mining activity

and fire may also have led to woodland-gaps in these elevations in other ranges, but not in the White Mts.

The (re-)establishment of conifers is being prevented by the narrow seed dispersal ranges of the involved conifers, as all of them apparently reach their ecological limits here. A conclusive proof for one of the theories was not given by any author, and at least in the White Mountains most of them can explain the actual situation in parts, but never completely. As the described treeless areas do not occur continuously between the two woodland zones (see photo 1 and also ARNO, HAMMERLY 1984), these baldy patches are not treated as an independent community but rather as large habitat patches within the woodland community as a result of the above mentioned factors.

Conifer woodland of *Pinus flexilis* and/or *Pinus longaeva* may occur up to 3,500 m, their sparse understory consist mainly of shrubs like *Leptodactylon pungens*, *Ribes cereum*, *Ericameria discoidea* and *Chrysothamnus viscidiflorus*. *Poa secunda*, *Achnatherum pinetorum*, *Elymus elymoides* and *Koeleria macrantha* are the perennial grasses that are likely to occur within the herb layer, together with small amounts of forbs like *Arenaria kingii* var. *glabrescens*, *Penstemon speciosus* and *Senecio multilobatus*. *Pinus longaeva* clearly prefers dolomite substrate in the White Mountains, a fact that HÖLLERMANN (1973) relates to its high light requirement for photosynthesis (high albedo on the white parent material) reproduction and higher soil moisture. As MOONEY, WRIGHT (1965) do point out, the increased reflection of sunlight by the white dolomite leads to lowered summer temperatures of the ground and hence to a decreased evaporation, favoring *P. longaeva* on dolomite in the White Mts. On south and east facing slopes with granite and sandstone as parent material, the elements of the sagebrush steppe may outcompete the conifers and form a dense treeless shrubland.

#### **Alpine *Trifolium andersonii*-*Carex eleocharis* steppes (3,500 m–4,100 m a.s.l.):**

The White Mts. are the only range of the three core mountains where alpine shrub- and graminoid-rich steppes occur (photo 2). The vast terrain above tree-line (~ 3,500 m a.s.l.) with its shallow slopes and depressions together with the petrographic heterogeneity and differences in exposure create a small-scale mosaic of habitats along moisture and temperature gradients.

A fairly dense vegetation cover (described as “Alpine Fell-Field” by SPIRA 1991) can be found on granitic substrate, consisting of *Eriogonum ovalifolium*, *Trifolium andersonii* var. *beatleyae*, *Phlox pulvinata*, *Artemisia rothrockii* and several perennial grasses and sedges (e.g. *Carex eleocharis*). Areas with dolomite are very sparsely vegetated with species like *Castilleja nana*, *Phlox condensata* and *Linum lewsii*. A high moisture supply in depressions and along meltwater courses leads to a dominance of sedges (like *Carex subnigricans* and *Carex helleri*) and grasses like *Deschampsia caespitosa*, while windswept flats or north-facing slopes are sparsely vegetated, with few herbaceous species.

#### **Subnival *Hulsea algida*-*Polemonium chartaceum* talus community (>4,100 m a.s.l.):**

On rocky substrate with poor soil development and high mobility of the coarse debris at the highest elevations above 4,100 m a.s.l. (see WILKERSON 1994; FICKERT, GRÜNINGER 2002), only very few but conspicuous species are present. The hemicryptophytic herbs *Erigeron vagus*, *Polemonium chartaceum* and

**Photo 2:** Dense alpine steppes in the White Mountains at 3,750 m a.s.l.



*Hulsea algida* were found in the samples. MOREFIELD et al. (1988) additionally describe *Anelsonia eurycarpa* and few perennial grasses like *Poa suksdorfii* and *Elymus scribneri* for the flora of these highest elevations.

These classified and described plant communities shall give an overview on the vegetation of the White Mts. and will be used in the following chapter as an aid for further data explorations and identification tool in several figures.

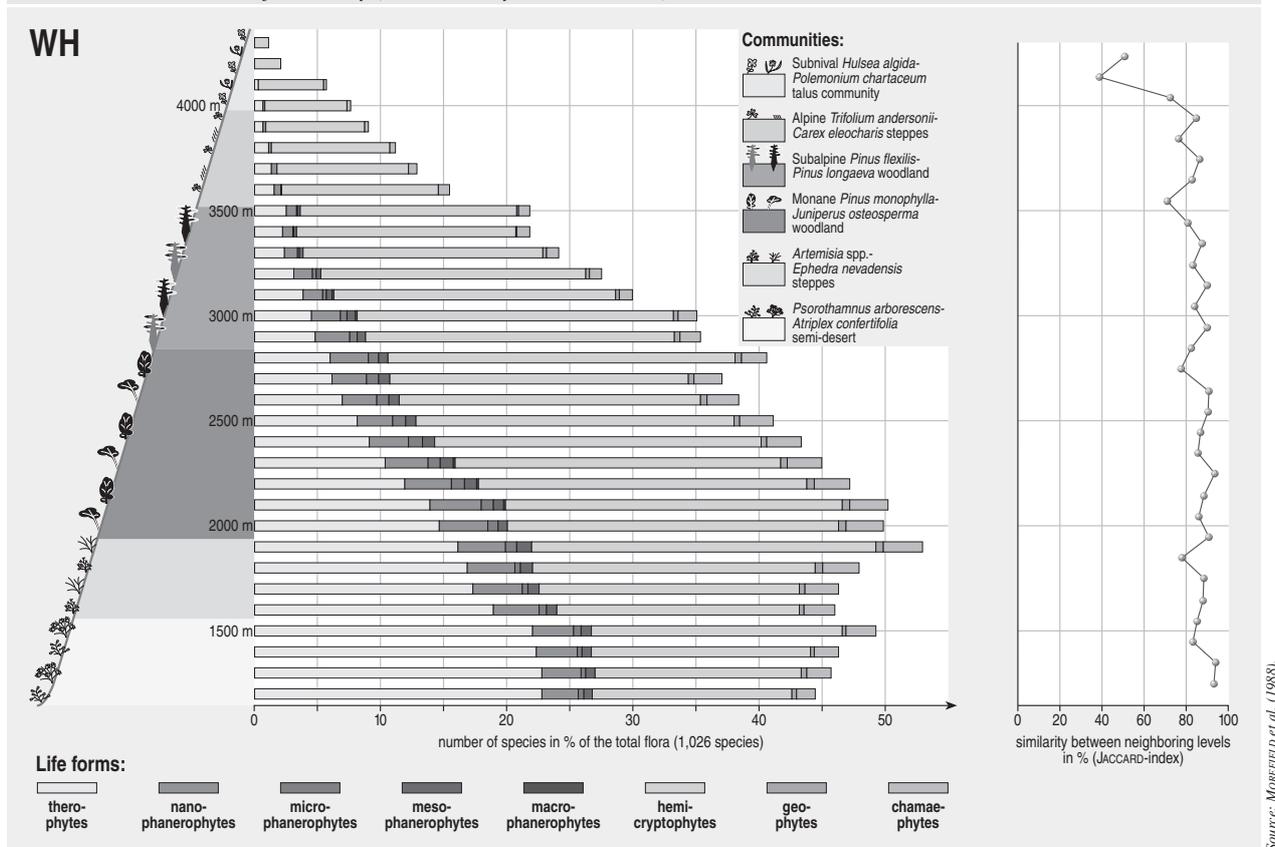
### **5.1.2 Altitudinal gradient of plant and life form diversity in flora**

The flora of the White Mts. consists of 1,026 currently known higher plant species (see MOREFIELD et al. 1988). Their distribution over the elevational gradient result in a quite ideal and “smooth” curve, with maximum values at the ecotone between steppe and montane woodland, where around 50% of the total flora is represented (see fig. 25). Up to 3,600 m a.s.l. the life form diversity per level fluctuates between seven and eight life form classes, while in higher areas it drops steadily to a single life form – the hemicryptophytes – in the subnival peak region. In general, the hemicryptophytic life form shows an overall high contribution to the species diversity in the mountain range.

Basically, the high species richness in the foothill regions is created by the numerous drought adapted therophytes (see light gray bars in fig. 25). Due to their reproductive cycle, they have the ability to cope with the high aridity. Within the montane woodland belt, like in the two other mountain ranges examined, increased plant diversity is furthermore a result of the climate optimum in these elevations: Sufficient precipitation and a moderate temperature regime allows plants the occupation of various niches created by the environmental factors (e.g. topography, petrography, exposure and soil conditions). Above 2,500 m a.s.l., the high species richness of the semi-desert, steppe and montane woodland communities drops continuously towards the peak region. At the species poor high elevations (see also chapter 5.1.1) the similarity drops to only 40%, a figure created by the overall low species numbers present.

Small diversity peaks in the ecotonal zones between the plant communities can be observed in figure 25. This is a result

**Fig. 25:** Number of vascular plant species (in % of total flora) and their life form affiliation in aequidistances of 100 m along the altitudinal gradient in the White Mountains. The graph to the right shows the beta-turnover in flora of neighboring elevation levels in % of similarity (calculated by JACCARD-index).



of the change in floristic composition, which can be also seen in the beta-turnover in flora of the neighboring levels at the right side of the respective figure, where similarity decreases in the transition zones from one community to the next.

### 5.1.3 Altitudinal gradient of plant and life form diversity in mature stands

The own sample data of mature, undisturbed stands presented in figure 26 (same data as in fig. 24 with 19 samples and 156 species) were analyzed to show the species richness and life form affiliation of the taxa along the altitudinal gradient. In the upper foothill regions, the mature vegetation shows the overall highest species richness. A second peak in species richness along the altitudinal gradient is found within the alpine *Trifolium andersonii*-*Carex eleocharis* steppe community which is especially rich in perennial grasses and forbs (see respective bars in fig. 26).

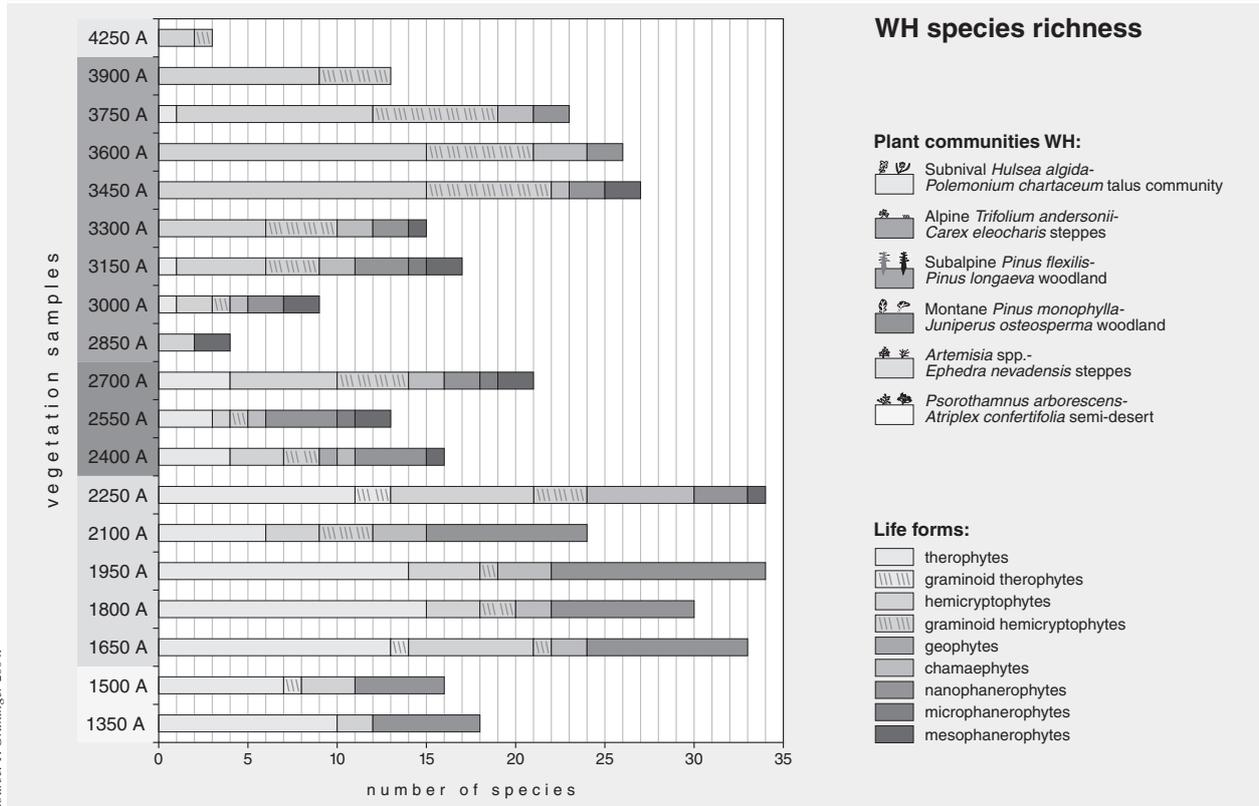
An obvious difference between the data of the flora in figure 25 and the data of the mature stands in figure 26 occurs in the middle elevations of the montane and subalpine woodland zones. Here, the mean alpha-diversity in species decreases to minimum values (mean of 15 species per sample,  $n=8$ ). As stated above, "baldy" treeless patches occur in these elevations mainly on quartzose substrate. As for mature stands the zonal vegetation was sampled, the samples of these elevations were all done in wooded areas on limestone (see also criteria catalogue in chapter 4.1.2). The vegetation is mainly formed by an open cover of *Pinus longaeva* with very species poor understory vegetation, which is typical for this substrate and formation type (see also ARNO, HAMMERLY 1984). The higher species richness

of the flora in these two belts must therefore be caused at least partially by the petrographically induced habitat mosaic, and the chemically and edaphically different soils developing on the respective parent material. This theory will be substantiated in the next paragraphs by using the flora data of MOREFIELD et al. (1988).

According to the flora, nearly 60% of all the species in flora occur between 2,400 m and 3,400 m elevation. Of these species, 32% are chemically facultative, 53% occur only on silicate and quartzose and only 10% are in need of basic or mixed basic substrate (see fig. 27a). The riparian vegetation – which was not sampled during the own field studies – also increases the gamma-diversity of these elevations. The species of these habitats are not included in figure 26, but their percentage in flora is also not very high: Only 33% of all occurring species between 2,400–3,400 m require wet to moist conditions, whereas 67% are found in accumulative to dispersive drainage conditions (MOREFIELD et al. 1988, see also fig. 27b).

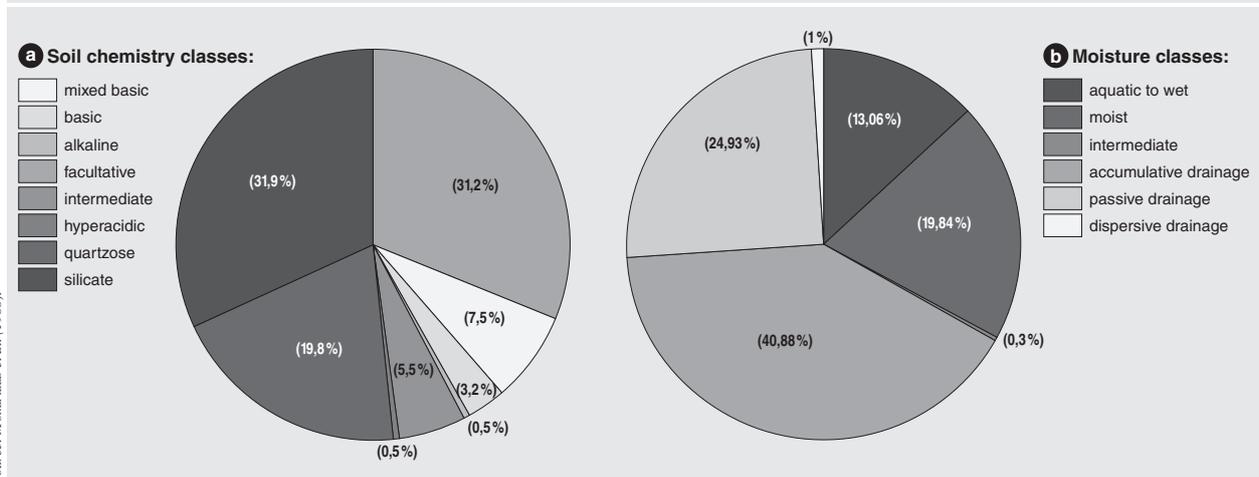
In figure 28, the total ground cover and the contribution of the single life forms to it can be compared with the alpha-diversity of the plots along the altitudinal gradient in figure 26. Of course, highest coverage occurs in the montane and subalpine woodland zones and is induced by the mesophanerophytic conifers of the community, which is nevertheless poor in species diversity. The therophytes, rich in species in the foothill region, are negligible in ground coverage; nanophanerophytic shrubs like *Atriplex confertifolia*, *Psoraleum arborescens* and *Artemisia* spp. dominate instead. The species rich alpine steppe community is also high in ground cover as it is in alpha-diversity, but in contrast to the steppe below the timbered zones, graminoid

Fig. 26: Species richness and life form affiliation of species of undisturbed zonal vegetation samples (macro-plot A-samples, data basis: own relevés) along the altitudinal gradient in the White Mountains.



Source: F. Crittinger, 2004.

Fig. 27: Soil chemistry requirements (a) and moisture requirements (b) of species (in %) in the White Mountains flora, 2,400 m–3,400 m a.s.l.



Source: MOREFIELD et al. (1988).

hemicryptophytes and herbal perennials contribute most to the coverage here.

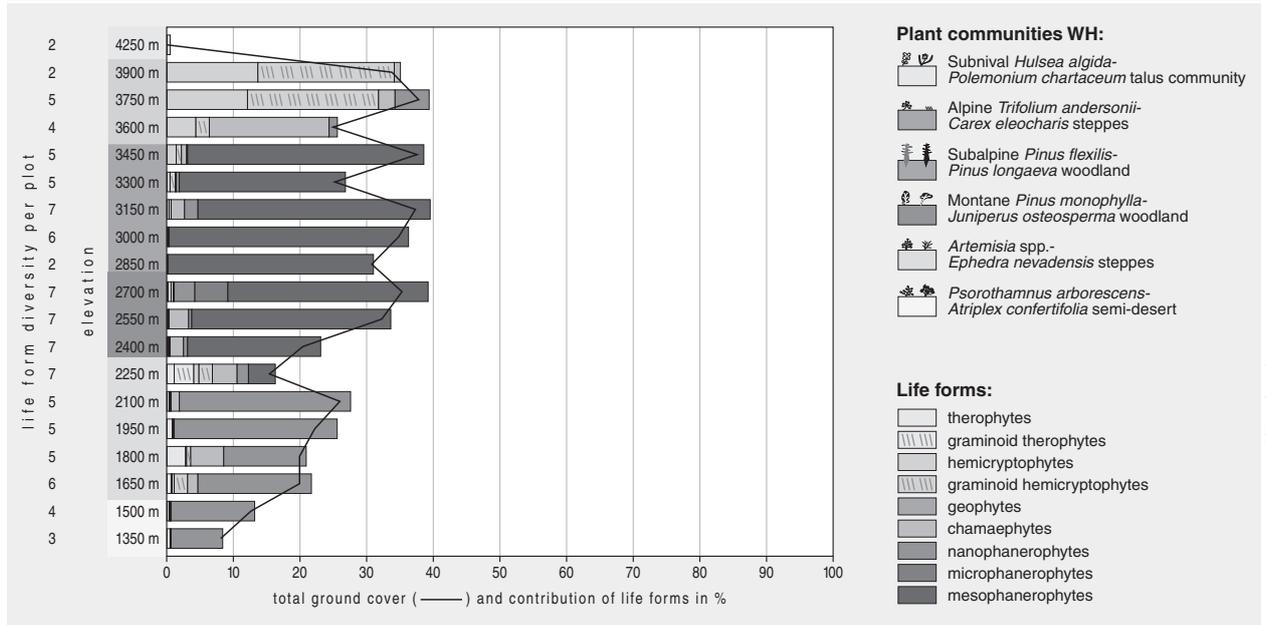
### 5.1.4 Species-area relations along the altitudinal gradient

The species-area relations in the White Mountains in figure 29 resemble those of the other two mountain ranges (see chapters 6.1.4 and 7.1.4) principally. The salt tolerant lowest community just above the valley floor takes an intermediate position with a moderate increase in species richness with sample area. In the structurally uniform *Artemisia* spp.-*Ehedra nevadensis* scrub, where the salt tolerance is no longer a limiting factor for many of the lowland species, the highest increase in species richness with

sampled terrain occurs. This fact is surely related to the high chance of sampling more of the diverse therophytes with increasing area. The two woodland areas take an intermediate position. At the highest elevations, which are poor in species and poor in increase of diversity with sampling area, the existence of plants is restricted by many limiting environmental variables (poor soil development, snow cover, low temperatures, etc.).

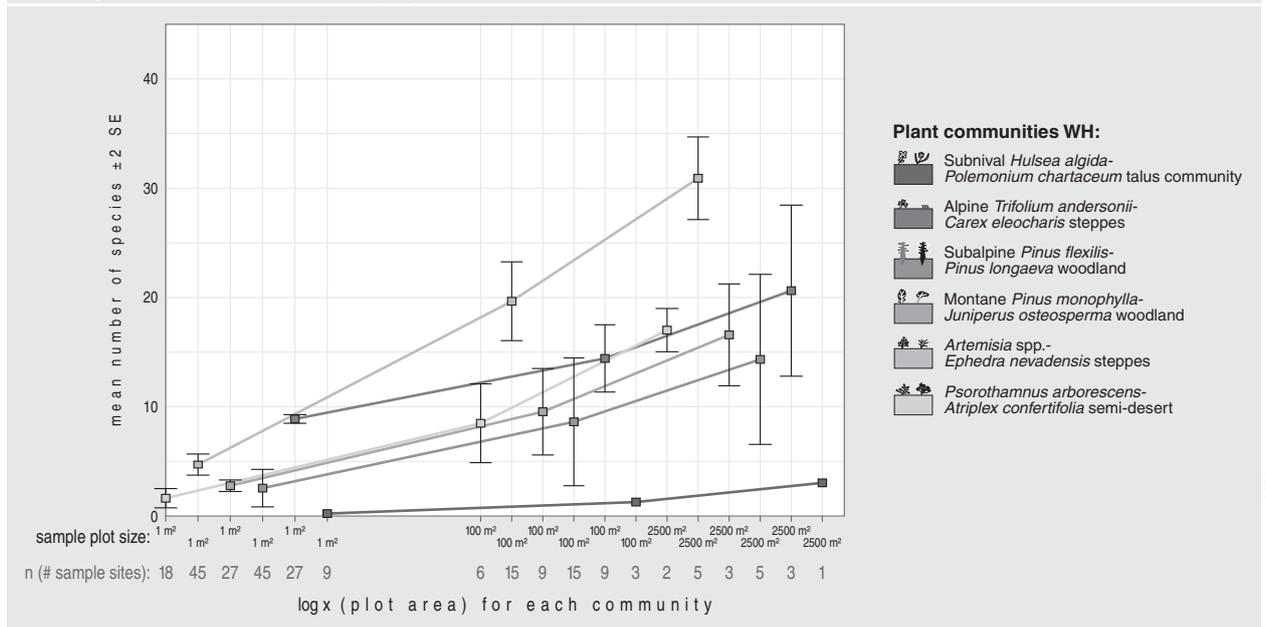
The picture only varies for the *Trifolium andersonii*-*Carex eleocharis* meadow community. Unlike the species poor talus communities, a fairly dense vegetation covers the fine grained granitic substrate sampled, and in places shallow sloping terrain, moisture collecting as well as wind protected depressions and exposed rocky outcrops create a high niche diversity for many

**Fig. 28:** Ground cover of aggregated life forms and their contribution to total ground cover (in %, without dead wood) of macro-plot A-samples along the altitudinal gradient in the White Mountains.



Source: GRUNINGER, FICKER (2003), adapted.

**Fig. 29:** Species-area relations (expressed as semi-log relation), drawn for the mean species numbers of micro-, meso- and macro-plots in each zonal community of the White Mountains.



Source: F. Grubinger 2004.

different species to coexist. Furthermore, the individual shrubs occurring are of a smaller size, and the concurrence in the root-horizon is less pronounced as in the shrub steppes of the lower elevations and “balds”. Thus, species richness is already very high in the micro-plots and increases further with plot size.

The special position and shape of the alpine steppe curve will be presented and discussed once more in the comparative discussion of chapter 8.2.3.

**5.1.5 Relations between the sampled vegetation units**

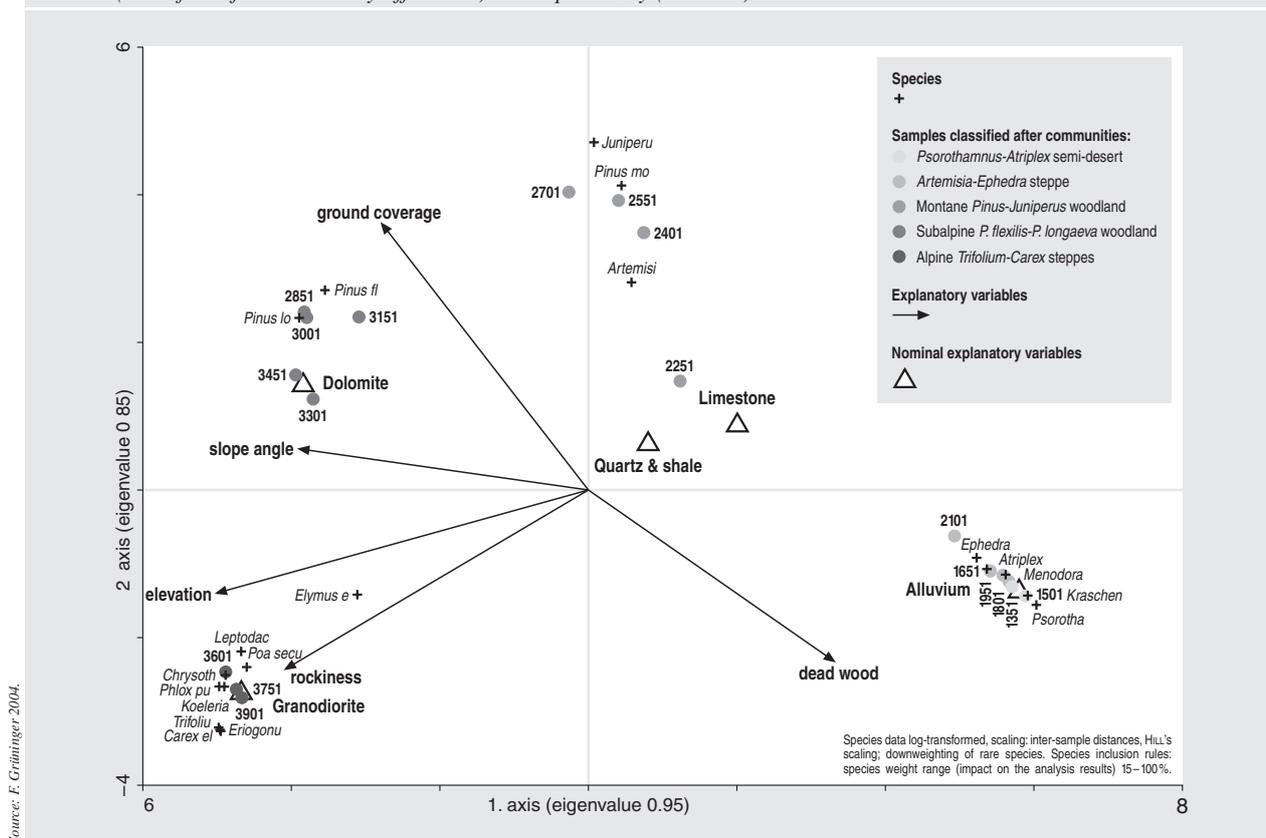
The previous chapters had the intention to give an impression on the zonal distribution of species, life forms and their ground cover within the flora and the sampled mature stands, as well as on the similarity in flora of neighboring elevation levels. For an

interpretation of the relations between the sampled vegetation units, the following chapters will use ordination methods.

In figure 30, the vegetation data of the macroscale A-samples are shown in a CA ordination triplot (1<sup>st</sup> and 2<sup>nd</sup> species axis), together with important species scores and the available explanatory variables (and nominal group variables). The highest sample at 4,250 m a.s.l. was excluded from the ordination, as its low ground cover and its completely distinctive composition produce failures in the analysis matrix. As a result, a total of 18 samples and 153 species were used in the ordination.

The samples are classified after their community affiliation, as displayed in figure 24 and chapter 5.1.1. Table 1 presents the weighted correlation matrix for the first four species axes with the explanatory variables, with values above 0.4 or -0.4 high-

Fig. 30: CA triplot for the White Mountains macro-plot A-samples (sample 4250 excluded, see text), showing species, samples (classified after community affiliation) and explanatory (nominal) variables.



Source: F. Grilinger 2004.

Tab. 1: Weighted correlation matrix of species axis and explanatory variables, eigenvalues of axis, species-environment correlations and explained variance for the CA in figure 30.

	SPEC			
	AX1	AX2	AX3	AX4
Elevation	<b>-0.9633</b>	-0.1625	-0.0779	-0.0510
Slope angle	<b>-0.7434</b>	0.0656	0.0281	-0.2098
Alluvium*	0.3413	-0.1494	0.0919	0.0405
Quartzite & shale*	0.1615	0.2341	-0.1946	<b>0.4088</b>
Limestone*	0.2627	0.2143	0.1793	-0.0324
Dolomite*	-0.2605	0.1795	<b>0.4447</b>	0.0195
Granodiorite*	<b>-0.5224</b>	<b>-0.5653</b>	-0.3144	<b>-0.5214</b>
Vegetation cover	<b>-0.5335</b>	<b>0.4213</b>	0.1236	-0.0746
Dead wood	<b>0.6322</b>	-0.2685	0.2801	0.0964
Rockiness	<b>-0.7832</b>	-0.2821	-0.1481	-0.2081
Eigenvalues:	0.949	0.845	0.816	0.489
Species-environment correlations:	0.989	0.894	0.737	0.888
Cumulative percentage variance				
of species data:	16.8	31.7	46.1	54.8
of species-environment relation:	24.5	42.4	54.2	64.4

Source: F. Grilinger 2004.

lighted (the nominal explanatory group variables are indicated by asterisks). Highest correlation on the 1<sup>st</sup> axis (eigenvalue 0.95) occurs with elevation (-0.96), rockiness (-0.78) and slope angle (-0.74). The 2<sup>nd</sup> species axis (eigenvalue 0.85) is moderately correlated with only one variable, the ground coverage (0.42), leaving the group variables aside. The two other axes show only moderate correlation, and only with group variables. In figure 30, the samples are arranged in elevational order and bend along the 1<sup>st</sup> axis from the lowest (lower right quadrant) to the highest elevations (lower left quadrant). The two lowest foothill communities on the alluvial fans are obviously close in composition and structure. Both woodlands are separately occurring in the upper two quadrants, being dominated by *Juniperus osteosperma*, *Pinus monophylla* and their high ground cover (see arrow), as well as by the high coverage of *P. flexilis* and *P. longaeva* in the adjacent woodland, which is generally restricted to dolomite and higher slope angles. The *Trifolium-Carex* meadow community of the highest elevations is on rocky slopes composed of granodiorite.

Table 2 gives the weighted correlation matrix between the explanatory variables. As visible in the ordination, high positive correlation is found between the elevation and slope angle (0.7), rockiness (0.82) as well as ground cover (0.54). Alluvial fans occur of course at low elevations, whereas the higher elevations in the White Mountains are often built up by granodiorite. Steep slope angles correlate positive with the rockiness of the samples (0.82) and were more often found in mature stands on dolomite (0.43).

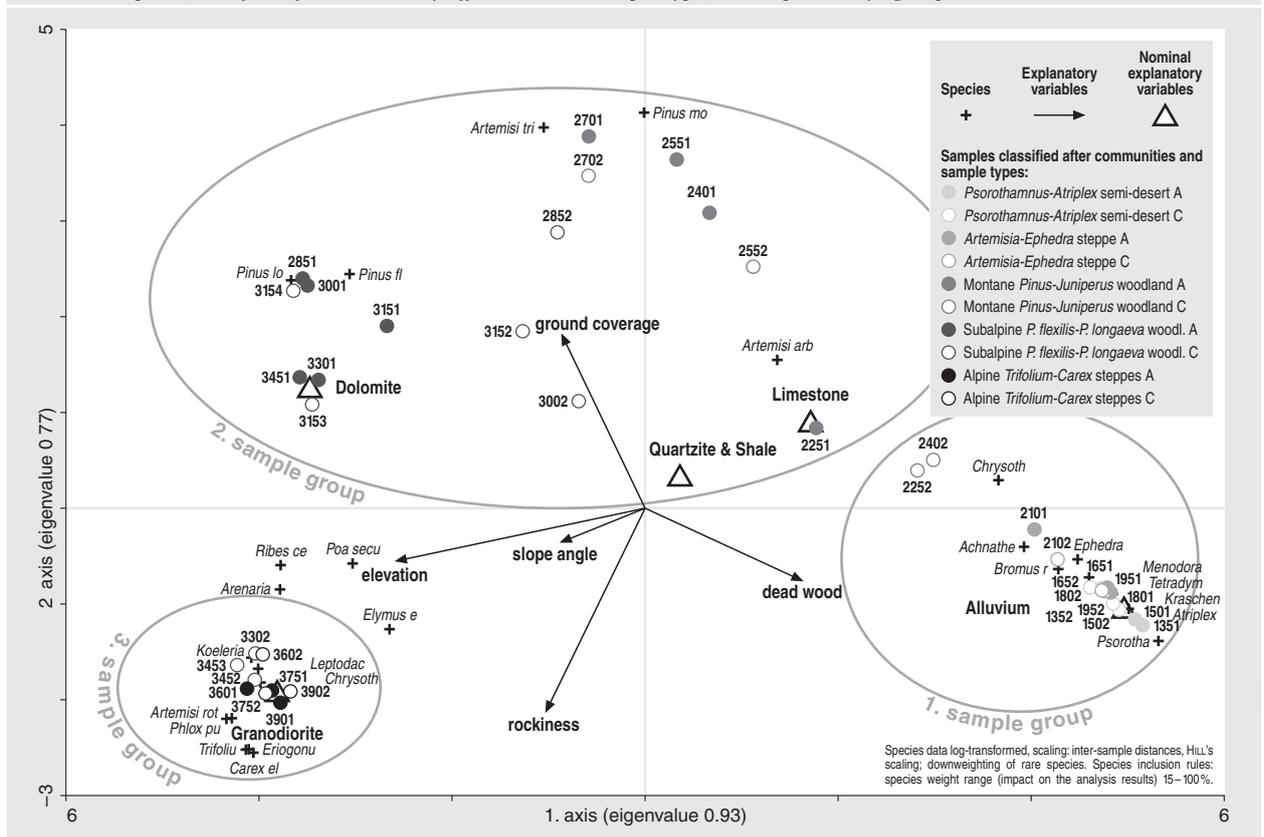
If the C-samples are added in the ordination in figure 31, the picture is generally comparable, but the single sample groups are not as discrete as before. In a total of 39 samples (again without

Tab. 2: Weighted correlation matrix between explanatory variables of CA in figure 30.

Elevation	1									
Slope angle	<b>0.6985</b>	1								
Alluvium*	<b>-0.0421</b>	-0.3195	1							
Quartzite & shale*	-0.1724	-0.1162	-0.2210	1						
Limestone*	-0.3217	-0.2896	-0.1441	<b>-0.4917</b>	1					
Dolomite*	0.2422	<b>0.4272</b>	-0.0747	-0.2547	-0.1661	1				
Granodiorite*	<b>0.6510</b>	0.3657	-0.1222	<b>-0.4168</b>	-0.2718	-0.1408	1			
Vegetation cover	<b>0.5390</b>	0.3186	<b>-0.4770</b>	-0.0573	0.1281	0.2371	0.0600	1		
Dead wood	<b>-0.5730</b>	<b>-0.4432</b>	<b>0.4527</b>	0.3011	-0.3181	0.0014	-0.3107	<b>-0.4732</b>	1	
Rockiness	<b>0.8222</b>	<b>0.8204</b>	-0.2554	-0.1220	<b>-0.5158</b>	0.3130	<b>0.6615</b>	0.1771	<b>-0.4329</b>	1
<b>Explanatory variables</b>	Elevation	Slope angle	Alluvium*	Quartzite & shale*	Limestone*	Dolomite*	Granodiorite*	Vegetation cover	Dead wood	Rockiness

Source: F. Grilinger 2004.

Fig. 31: CA triplot for the White Mountains macro-plot A- and C-sample types (sample 4250 excluded, see text), showing species, samples (classified after community affiliation and sample type) and explanatory (group) variables.



Source: F. Grilinger 2004.

the highest sample 4250), 206 species were encountered. Still high eigenvalues of the first two species axes have dropped slightly to 0.93 (1<sup>st</sup> axis) and 0.77 (2<sup>nd</sup> axis) and less explanatory factors correlate with them (see tab. 3 and 4). The negative correlation between the elevation and the 1<sup>st</sup> species axis is as high as in figure 30 (–0.96), but otherwise there remains only a moderate correlation with the amount of dead wood (0.59). Rockiness now correlates negatively with the 2<sup>nd</sup> species axis (–0.47). The samples are again classified according to their community type and their sample type additionally. As already mentioned, many of the C-samples appear transitionally between the formerly discrete groups of mature stands. Whereas the lowest two com-

munities are still very close in composition and structure, the samples of the Pinyon-Juniper woodland are widely distributed in the upper center area of the graph and are partially linked to the adjacent lower community (2402, 2252). The same happens with the samples 2852 and 3152 of the *P. flexilis-P. longaeva* community and the adjacent Pinyon-Juniper woodland (see right half of upper left quadrant). The sample 3002 appears almost isolated near the center of the graph, still containing a small amount of *Pinus monophylla*. The high meadow community in the lower left quadrant is now mixed with three C-samples of the lower *P. flexilis-P. longaeva* woodland (3302, 3452, 3453), which are treeless, on granodioritic material, and resemble the

Tab. 3: Weighted correlation matrix between explanatory variables of CA in figure 31.

Elevation	1									
Slope angle	0.2984	1								
Alluvium*	<b>-0.4544</b>	-0.1956	1							
Quartzite & shale*	-0.1136	<b>0.0534</b>	-0.3025	1						
Limestone*	-0.2388	-0.0982	-0.1289	<b>-0.4719</b>	1					
Dolomite*	0.1866	0.0976	-0.0788	-0.2887	-0.1230	1				
Granodiorite*	<b>0.5960</b>	0.1008	-0.1258	<b>-0.4606</b>	-0.1962	-0.1200	1			
Vegetation cover	0.3039	-0.2831	-0.1464	0.0692	-0.0849	0.1552	-0.0098	1		
Dead wood	<b>-0.5573</b>	-0.3130	0.3820	0.1456	-0.1598	-0.0091	-0.3054	-0.1841	1	
Rockiness	<b>0.4383</b>	<b>0.6500</b>	0.0653	-0.2170	-0.2445	0.0349	<b>0.4721</b>	-0.2674	-0.3129	1
<b>Explanatory variables</b>	Elevation	Slope angle	Alluvium*	Quartzite & shale*	Limestone*	Dolomite*	Granodiorite*	Vegetation cover	Dead wood	Rockiness

Source: F. Grüniger 2004.

Tab. 4: Weighted correlation matrix of species axis and explanatory variables, eigenvalues of axis, species-environment correlations and explained variance for the CA in figure 31.

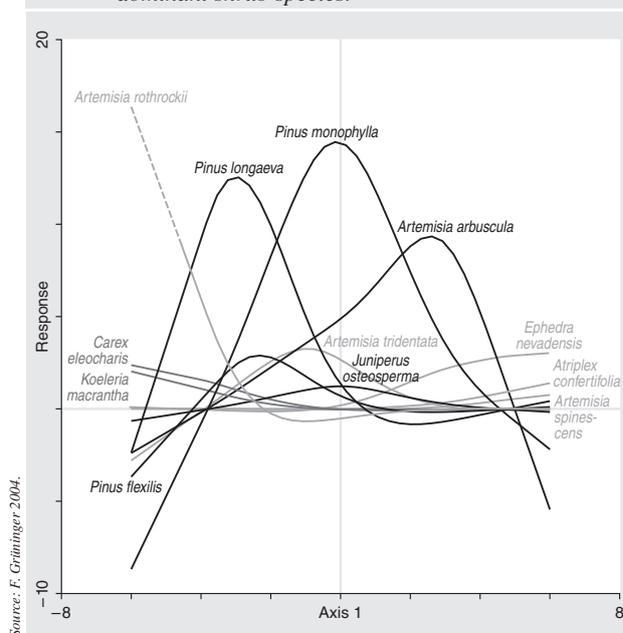
	SPEC			
	AX1	AX2	AX3	AX4
Elevation	<b>-0.9584</b>	-0.1221	-0.1136	0.0952
Slope angle	-0.3003	-0.0729	0.1401	-0.0272
Alluvium*	0.3867	-0.1704	0.0934	-0.3478
Quartzite & shale*	0.1031	0.1791	-0.2197	0.1844
Limestone*	0.2086	0.2165	0.2302	0.2286
Dolomite*	-0.2583	0.1866	<b>0.4504</b>	-0.1044
Granodiorite*	<b>-0.4522</b>	<b>-0.4699</b>	-0.3157	-0.1592
Vegetation cover	-0.3164	0.3966	0.0246	-0.0996
Dead wood	<b>0.5930</b>	-0.1644	0.2064	0.0987
Rockiness	-0.3798	<b>-0.4685</b>	-0.1018	-0.0045
Eigenvalues:	0.932	0.766	0.753	0.538
Species-environment correlations:	0.980	0.743	0.680	0.672
Cumulative percentage variance				
of species data:	11.0	20.1	29.0	35.4
of species-environment relation:	26.0	38.2	48.3	55.4

Source: F. Grüniger 2004.

open and petrography-bound structure of the vegetation in these elevations.

The response of the strongest species along the first species axis is plotted in figure 32, using a GAM model (General Additive Model, see chapter 4.2.3.4). It illustrates the overlap in species response for the classified communities and the replacement of species along the 1<sup>st</sup> axis, which in this case closely resembles the elevational gradient (corr. coeff. -0.96). Well marked is the overall presence of *Artemisia* spp., neither of them showing strong response apart from *A. rothrockii* (see left side of the graph – the shrub shows high coverage in C-samples that were taken within the subalpine *P. flexilis*-*P. longaeva* belt), but

Fig. 32: Species response curves (GAM model) along the first species axis for A- and C-samples of the White Mountains. Species shown include most tree species and dominant shrub species.



Source: F. Grüniger 2004.

obviously filling in the gaps between timbered areas. Below the lower tree-line, *A. arbuscula* has a high response in figure 32, which stretches further towards higher elevations (negative end of the 1<sup>st</sup> axis). *A. tridentata* shows the highest response at the transition zone in-between the vertexes of the *Pinus monophylla* and *P. longaeva* curves (see also “*Artemisi tri*” in fig. 31). And, as already mentioned above, *A. rothrockii* is highly present in the ecotonal zone, covering the treeless areas between the highest woodland patches and the adjacent meadow community. Its species response curve wrongfully opens up widely to the left side of the graph (a model based error); like visible in the species list in supplement I, it was only found as high as 3,750 m a.s.l. with weak ground cover.

This distribution pattern fits quite well to the soil chemistry necessities of the sagebrush and pine species: After MOREFIELD et al. (1988), *A. tridentata* and *A. spinescens* grow facultative on basic or non-basic material, but *A. arbuscula* and *A. rothrockii* are

both restricted to quartzose substrate. This explains why these two species fill the treeless gaps in their altitudinal distribution range, which occur mostly on non-basic material. *Pinus longaeva* and *P. flexilis*, both growing in theory on both basic and non-basic material (see also MOREFIELD et al. 1988), are generally outcompeted on non-basic material by the sagebrush shrubs and their associates.

### 5.2 Belt-scale

On the belt-scale, three sample groups will be observed separately that can be extracted from figure 31: The first group contains all the samples of the two foothill communities plus the still treeless ecotonal samples 2252 and 2402 from the *Pinus-Juniperus* woodland, that appear close to this complex (see right side of the graph); the second group comprises all samples from the montane and subalpine woodland belt except the samples 3302, 3452 and 3453; due to their affinity to the alpine meadow community, these samples are treated in the third sample group (see lower left quadrant in fig. 31).

#### 5.2.1 Foothill communities (1,350 m–2,400 m a.s.l.)

In the foothill communities below the lower tree line (see 1<sup>st</sup> sample group in fig. 31), site differences are mainly caused by the elevation above the basin floor (salinity), the petrographic and topographic differences as well as by variations in plant available water. The present allochthonous material of the alluvial fans and autochthonous rock layers of the mountain base form the differently angled slopes. These slopes are dissected by bigger canyon mouths like that one of the Coldwater, Silver, Poleta Mine or Black Canyon (see map in fig. 12), which are characterized by seasonally active fluvial processes.

Figure 33 displays the analyses of the 14 vegetation macroplot A- and C-samples (composed of 97 species) in the foothill communities. In figure 33a and 33b, the involved samples are classified according to their community and sample type and are shown together with the important species and the explanatory variables (including the nominal explanatory variables of petrographic situation) on the 1<sup>st</sup> and 2<sup>nd</sup> species axis. Like over the whole elevational gradient in figure 31, the samples are distributed in an arch shape over the plot, with low elevation samples to the right and high elevation samples to the left side of the graph. The A-samples were taken on undissected alluvial fans (1351, 1501), quartzite & shale (1801, 1951) or limestone (1651, 2101) slopes of low angles and low debris cover. The C-samples were

either taken on active alluvial fans in front of a canyon mouth (see sample 1352), or on steep slopes with high debris cover (1802 on alluvium; 1502, 1652, 1952, 2252, 2402 on quartzite & shale; 2102 on limestone). The samples 2252 and 2402 are located in treeless areas within the zonal *Pinus-Juniperus* woodland.

The 1<sup>st</sup> species axis (eigenvalue 0.59) is strongly correlated with elevation (–0.92) and weakly with rockiness (see tab. 5). The 2<sup>nd</sup> species axis (eigenvalue 0.42) is only weak correlated with the species ground cover in the samples. Higher correlations between the explanatory variables (see tab. 6) occur between the petrographic units (as they replace each other), but also between slope angle and rockiness and slope angle and ground cover. The negative correlation between elevation and alluvium is also not surprising.

Highest differences in species composition and structure between the A- and C-samples can be detected within the *Pso-rothamnus-Atriplex* scrub. Whereas the two old growth stands

**Tab. 5:** Weighted correlation matrix of species axis and explanatory variables, eigenvalues of axis, species-environment correlations and explained variance for the CA in figure 33.

	SPEC			
	AX1	AX2	AX3	AX4
Elevation	<b>–0.9207</b>	0.1401	0.1002	–0.0893
Slope angle	0.1122	–0.0409	<b>0.5397</b>	–0.3401
Alluvium*	<b>0.6160</b>	0.0238	–0.6001	–0.0417
Quartzite & shale*	–0.2542	0.1621	<b>0.4329</b>	0.0630
Limestone*	–0.2813	–0.2069	0.0628	–0.0332
Vegetation cover	–0.3384	<b>0.5706</b>	<b>–0.5788</b>	0.1377
Dead wood	0.1072	–0.2951	–0.0571	<b>0.4837</b>
Rockiness	<b>0.4567</b>	0.1296	0.0972	–0.3162
Eigenvalues:	0.586	0.424	0.367	0.267
Species-environment correlations:	0.977	0.697	0.905	0.653
Cumulative percentage variance				
of species data:	22.2	38.3	52.2	62.3
of species-environment relation:	33.2	45.5	63.4	70.1

Source: F. Grubinger 2004.

**Tab. 6:** Weighted correlation matrix between explanatory variables of CA in figure 33.

Elevation	1							
Slope angle	0.1434	1						
Alluvium*	<b>–0.6183</b>	–0.1376	1					
Quartzite & shale*	0.3554	0.2988	<b>–0.5486</b>	1				
Limestone*	0.1681	–0.2131	–0.3017	<b>–0.6316</b>	1			
Vegetation cover	0.3520	<b>–0.4686</b>	–0.0437	0.0728	–0.0424	1		
Dead wood	–0.1574	–0.2237	0.2241	0.2299	<b>–0.4699</b>	–0.1487	1	
Rockiness	–0.1776	<b>0.6995</b>	0.3380	–0.1998	–0.0856	–0.1802	–0.2878	1
<b>Explanatory variables</b>	Elevation	Slope angle	Alluvium*	Quartzite & shale*	Limestone*	Vegetation cover	Dead wood	Rockiness

Source: F. Grubinger 2004.

# PASSAUER SCHRIFTEN ZUR GEOGRAPHIE

## Summary

HERAUSGEGEBEN VON

ERSTAUSSGABE DIETER ANLEITER, WERNER GAMERTH UND KAI POTTER

High mountains of the world possess an outstanding biodiversity compared to their surrounding lowlands and are thus considered as "hotspots" of plant diversity. Especially the factorial complex of altitude is supposed to be an important trigger: Abiotic and biotic environmental factors change along the elevational gradient, accompanied by different disturbance regimes and dynamic processes. The thereof resulting patterns in floristic and structural diversity successively change through time and with the scale of observation employed. Factors with a certain spatial or temporal extension create different sized habitat types with different diversity patterns. Mechanisms that affect the diversity on one scale might not be effective on an other, and hence a functional interpretation always has to be orientated on the different spheres of influence.

Furthermore, possible interrelations between significant factors are highly complex and often not to be elucidated. General models result in excellent schematic approaches but may fail to present satisfying hard-facts on diversity-related patterns and processes within an area of interest. Detailed investigations produce excellent data and results within narrow spatial and ecological limits, but are hardly adaptable to larger areas. The research work presented in this thesis focuses on the both of these aspects: A standardized sampling design is employed to create an useful data basis which is used to verify general theoretical statements derived from the observed patterns and processes in plant diversity of high mountain regions.

The semiarid part of the Great Basin Region with its numerous north-south trending mountain ranges was chosen as investigation area. It is located between the Sierra Nevada-Cascade Range axis to the west and the Rocky Mountains to the east. Within three exemplary "core" mountain ranges (the White Mountains in eastern California, the Spring Mountains in southern Nevada and the Snake Range in eastern Nevada) vegetation was sampled using transect studies along the altitudinal gradient. The samples were placed in vertical steps of 150 m in zonal old growth stands, in habitats with varying environmental conditions, in different successional stages and exemplary in unique habitat units. The sampling design employed uses three nested plot sizes with 1 m<sup>2</sup> (micro-plot), 100 m<sup>2</sup> (meso-plot) and 2,500 m<sup>2</sup> (macro-plot). Altogether, almost 1,400 samples are included in the analyzed data sets. Next to floristic aspects, life form spectra and formation characteristics of the sampled vegetation are considered, and the data are accomplished and verified by regional floras and transect studies of other authors.

To take the scale dependent aspect of diversity into account, four different observation scales are employed for the analysis procedure:

- The *landscape-scale* covers the whole region of the Great Basin with its single mountain ranges as a physiographical unit. Next to the own samples, adapted vegetation data are employed to elucidate the influence of large-scale environmental factor-complexes on floristic and structural plant diversity. The vegetation history and petrographic heterogeneity of the Great Basin have an obvious influence on the species diversity

of the mountain ranges. Latitudinal, longitudinal and altitudinal changes of major climate patterns, the mass elevation and absolute vertical gradient of the respective mountain ranges as well as human impact have a considerable impact on the floristic and structural diversity patterns in the mountainous Great Basin region.

- The *mountain-scale* considers one particular mountain range with its vertical zonation of climate-dependent altitudinal belts. Floristic and structural diversity patterns are shown exemplary for the three core mountain ranges, specified by the help of species-area curves and compared in relation to similar or dissimilar patterns for each range. Next to the floristic history and the major climate patterns, the influence of heterogeneous petrographic conditions increases in importance. Natural disturbances and human impact may modify the vegetation structure and hence its diversity in the core mountain ranges.
- The *belt-scale* is employed to describe similarities and differences of diversity patterns within climate induced altitudinal vegetation belts for all three core mountains. Species composition, dominance structures and life form spectra are therefore analyzed and compared within and between corresponding vegetation belts. Whereas the influence of large-scale factorial complexes (like mass elevation effects, vegetation history of the whole region, etc.) is weakened, present petrographic and topographic differences constantly gain importance. Natural disturbances and stress determine the occurrence of short- to medium-term diversity patterns; destructive human impact is able to cause ongoing degradation processes and a loss of floristic and structural plant diversity. The intermingling of adjoining vegetation belts strongly increases the diversity within the ecotonal zones in parts. Natural disturbances and azonal and extrazonal habitats which link vegetation belts along the altitudinal gradient also enrich species composition and the vegetation structure locally.
- The *patch-scale* regards examples of different environmental units formed by small-scale dynamic processes, disturbances or dominant environmental gradients within the essential communities of the various belts. An evaluation of important factors on this smallest observation scale is not transferable to larger patches, as floristic and structural diversity patterns can vary broadly between these smallest environmental units.

Of course, the scales of observation and the data sampled do not allow revealing all the diversity patterns inherent to the mountainous environments. Nevertheless, the developed method seems suitable to compare the still quite natural, relatively stable ecosystems occurring in the Great Basin ranges. Triggers of plant diversity on the four different observation scales are well elucidated, and their influences can be recognized and evaluated faster in future analyses on the plant diversity in semiarid high mountains of southwestern North America, and probably beyond (whether the results are transferable to other, climatically comparable regions, remains to be tested). Furthermore, the gained knowledge helps to understand the fundamental eco-

# PASSALIER SCHRIFTEN ZUR GEOGRAPHIE

logical principles of the area. It is thus a valuable contribution to a basic concept for sustainable development, and helps to protect and preserve the surprisingly high and endangered phyto-diversity of the Great Basin region.

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ERNST STRUCK, DIETER ANHUF, WERNER GAMERITH UND KLAUS ROTHER  
Schriftleitung: Erwin Vogl



HEFT 21

Friederike Grüninger

## Scale dependent aspects of plant diversity in semiarid high mountain regions

An exemplary top-down approach for the Great Basin (USA)

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Selbstverlag Fach GEOGRAPHIE der Universität Passau

# PASSAUER SCHRIFTEN ZUR GEOGRAPHIE

## Zusammenfassung

HERAUSGEGEBEN VON

Die Hochgebirge der Erde zeichnen sich generell durch eine erhöhte Artenvielfalt gegenüber ihrem Umland aus und werden aufgrund dessen seit geraumer Zeit als „Hotspots“ der Phyto-diversität angesehen. Vor allem dem Faktorenkomplex „Höhe“ kommt hierbei eine besondere Bedeutung zu: Mit zunehmender Höhe ändern sich nicht nur abiotische und biotische Standortparameter, es ergibt sich außerdem auch eine charakteristische Abfolge und Durchdringung von zonalen Störungsregimen und dynamischen Prozessen. Daraus resultierende Diversitätsmuster sind von immenser Vielfalt, da sie natürlich nicht nur räumlichen sondern auch zeitlichen Sukzessionszyklen oder -reihen unterworfen sind und sich mit dem Maßstab der Betrachtung ändern. Als logische Konsequenz daraus können wichtige Steuergrößen der Vielfaltsmuster durch eine veränderte Auflösung in den Hintergrund treten oder erst ihre wahre Bedeutung zeigen.

Die Interaktionen zwischen all den angesprochenen Komponenten zeigen sich vielfältig, hoch komplex und sind zu-meist nur schwer durchschaubar. Generelle Erklärungsversuche zur erhöhten Vielfalt in Hochgebirgen müssen daher meist modellhaft bleiben und können oft keine endgültigen Aussagen über ihre Entstehung und Variabilität in einem realen Landschaftsausschnitt machen. Detailuntersuchungen hingegen liefern wirklichkeitsnahe und gut verwertbare Ergebnisse für kleine Bereiche mit eng gefassten Umweltbedingungen, sind jedoch aufgrund ihres Designs und Arbeitsaufwandes nur bedingt auf größere Gebiete anwendbar. Die vorliegende Untersuchung versucht aufgrund dessen einen Mittelweg zu finden und theoretische Aussagen über maßstabsabhängige Aspekte der Pflanzenvielfalt in Hochgebirgen auf Grundlage einer umfassenden Datenbasis zu verifizieren.

Als Untersuchungsraum dient der semiaride Bereich des Great Basin im Südwesten Nordamerikas. Seine vorwiegend N-S-streichenden Gebirgsketten liegen eingebettet zwischen der westlich vorgelagerten Sierra Nevada/Cascade Range und den Rocky Mountains, die den Großraum nach Osten hin begrenzen. Innerhalb des Arbeitsgebietes wurden Vegetationsdaten entlang von Transektstudien in drei „Kern“gebirgen aufgenommen (in den White Mountains im Osten Kaliforniens an der Grenze zu Nevada, den Spring Mountains in Südnevada nordwestlich von Las Vegas und in der Snake Range in Ostnevada). Die Aufnahmen erfolgten in festgelegten Höhenabständen von 150 m Äquidistanz innerhalb zentraler Beständen sowie an Standorten mit abweichenden Umweltvorgaben, in verschiedenen Sukzessionsstadien und auf ausgewählten Sonderstandorten. Das für diese Untersuchung entwickelte Aufnahmedesign umfasst drei genestete Aufnahmeformen, deren Auflösung 1 m<sup>2</sup> (Mikro-Plot), 10 m<sup>2</sup> (Meso-Plot) und 2.500 m<sup>2</sup> (Makro-Plot) beträgt. Insgesamt flossen Daten von knapp 1.400 Aufnahmeflächen in die Untersuchung ein. Neben floristischen Aspekten wurden Lebensformspektren und Formationscharakteristika aufgenommen und in die Auswertung einbezogen, das erhobene Datenmaterial wird außerdem durch weitere Transektstudien im Westen der USA und durch kommentierte Florenlisten verschiedener Autoren ergänzt.

Um den maßstabsbedingten Wahrnehmungsunterschieden der Steuergrößen Rechnung zu tragen, wurden die Untersuchungen zur Phytodiversität in vier Maßstabsebenen aufgliedert:

- Die *Landschafts-Ebene (landscape-scale)* betrachtet das gesamte Great Basin als physiographische Einheit. Neben den eigenen Vegetationsaufnahmen wurden Sekundärdaten verwendet um den Einfluss großräumiger Faktorenkomplexe auf die Ausbildung der gegenwärtigen Phytodiversität zu bestimmen. Florenhistorie und petrographische Differenzierung des Great Basin haben entscheidend auf den Artenreichtum der Gebirge eingewirkt. Latitudinale und longitudinale Veränderungen des Klimaregimes, die Massenerhebung und die vertikale Erstreckung der Gebirge sowie menschliche Eingriffe sind außerdem maßgeblich entscheidend für die floristischen und strukturellen Vielfaltsmuster innerhalb des Gebirgsraumes.
- Die *Gebirgs-Ebene (mountain-scale)* betrachtet die klimabedingte vertikale Zonierung einzelner Gebirge entlang ihrer Höhengradienten. Strukturelle und floristische Vielfaltsmuster werden beispielhaft für die Kerngebirge vorgestellt, anhand von Arten-Arealkurven verdeutlicht und hinsichtlich von Gemeinsamkeiten und Unterschieden in ihren Steuergrößen verglichen. Neben florenhistorischen und klimatischen Komponenten verstärkt sich hier der Einfluss der Petrographie auf den Artenreichtum der Gebirge. Natürliche und anthropogene Störungen wirken sich vor allem auf die strukturelle Vielfalt der Gebirge aus.
- Die *Höhenstufen-Ebene (belt-scale)* wird benutzt, um in den Kerngebirgen standörtliche Gemeinsamkeiten und Differenzen der Höhenstufen aufzuzeigen. Artenzusammensetzung, Dominanzstrukturen und Lebensformspektren werden dabei innerhalb der Vegetationsstufe und zwischen den korrespondierenden Stufen betrachtet. Während der Einfluss großmaßstäbiger Faktorenkomplexe in den Hintergrund tritt, gewinnen petrographische (soweit vorhanden) und topographische Differenzierung weiter an Bedeutung. Natürliche Störungen und Stress bestimmen maßgeblich die Ausbildung von kurz- bis mittelfristigen Mustern, starker anthropogener Einfluss kann zu nachhaltigen Degradationserscheinungen und Verlust an Vielfalt führen. Die Durchmischung von Vegetationsstufen in den Ökotonbereichen fördert die floristische und strukturelle Vielfalt in hohem Maße. Störungen sowie azonale oder extrazonale Standorte, die bestimmte Vegetationsstufen entlang des Höhengradienten miteinander vernetzen, können ebenfalls zu einer lokalen Erhöhung der Diversität beitragen.
- Die *Patch-Ebene (patch-scale)* stellt schließlich beispielhafte Muster vor, die durch kleinräumig vorherrschende Standortbedingungen, Störungen oder dynamische Prozesse mit variierenden Wirkungsspektren hervorgerufen werden. Eine Bewertung der Einflussfaktoren ist hier nurmehr über Einzelaussagen möglich, da sich die floristische und strukturelle Vielfalt je nach Standort auf kleinstem Raum maßgeblich erhöhen oder reduzieren kann.

Natürlich können die erhobenen Daten auf den verwendeten Skalenebenen bei weitem nicht alle Vielfaltsmuster aufdecken oder erklären, die entwickelte Methodik eignet sich jedoch hervorragend für vergleichende Betrachtungen in den naturnahen, relativ stabilen Ökosystemen der Great Basin Gebirge. Mit Hilfe der erworbenen Raum- und Prozesskenntnisse können diversitätsprägende Faktoren besser verstanden, ihre

Wirkung in zukünftigen Analysen schneller erkannt und eventuell auf klimatisch vergleichbare Räume übertragen werden. Neben einer Vergrößerung des ökologischen Basiswissens bieten sich die gewonnenen Einsichten weiterhin als Grundlage für nachhaltige Schutzkonzepte zur Erhaltung der überraschend hohen Phytodiversität an, die der Großraum aufgrund von ökologischem Fehlverhalten zu verlieren droht.

HERAUSGEGEBEN VON

ERNST STRUCK, DIETER ANHUF, WERNER GAMERITH UND KLAUS ROTHER

Schriftleitung: Erwin Vogl



HEFT 21

Friederike Grüninger

# Scale dependent aspects of plant diversity in semiarid high mountain regions

An exemplary top-down approach for the Great Basin (USA)

With 85 figures, 33 tables, and 30 photos

Selbstverlag Fach GEOGRAPHIE der Universität Passau

The book at hand documents high mountain biodiversity using the sparsely populated Great Basin region in the southwestern United States as a field laboratory. Its numerous small mountain ranges are separated by low-lying arid valleys. The repeated contrast between alpine and desert environments across one quarter of the North American continent gives rise to a surprisingly rich flora. These alternating basins and mountain ranges are a perfect match to explain patterns and processes in plant diversity using a multi-scale approach. Through this unique methodological concept, the nearly natural and relatively stable ecosystems of the Great Basin Ranges are introduced and important triggers of plant diversity are discussed and evaluated on four different observational scales from micro to macro.

Fundamental ecological principles of the Great Basin region are clearly explained and set the stage for conservation of its rich biotic resources. High mountains of the world possess an outstanding biodiversity as compared to their surrounding lowlands and are indeed “hotspots” of plant diversity as clearly presented here. Just as mountains physical properties are manifold, so are the reasons for mountains being biodiversity hotspots: The complex patterns and processes of plant diversity vary with the scale of observation, just as the driving mechanisms may gain or lose or importance with those same changes in scale. The text explains how the multitude of abiotic and biotic environmental factors coexist and change along an altitudinal and latitudinal gradient as they are accompanied by different disturbance regimes and other dynamic processes in an exceptional setting, the American Southwest.

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GRÜNINGER, FRIEDERIKE: Scale dependent aspects of plant diversity in semiarid high mountain regions: An exemplary top-down approach for the Great Basin (USA). 143 S., 86 Abb., 33 Tab. und 31 Photos. Passauer Schriften zur Geographie 21. Selbstverlag Fach Geographie der Universität, Passau 2005, € 25,-

In recent years, many studies on gradients of plant species diversity and related evolutionary and environmental controls have been published. High mountain regions of the world turned out to represent hotspots of biodiversity due to the small-scale environmental heterogeneity and the compression of climatic zones along elevational gradients. However, our knowledge of elevational diversity gradients and scale-dependent diversity patterns in high mountain regions is still deficient. F. GRÜNINGER takes up this research deficit and provides a much-needed study on floristic and structural diversity patterns in the mountainous Great Basin region of the southwestern United States. In her dissertation, she reveals diversity patterns based on transect studies along altitudinal gradients and explains respective patterns by environmental factor complexes. An outstanding feature of her thesis is the consistent application of a multi-scale approach in order to verify general theoretical statements regarding causal explanations of diversity patterns. She succeeds in identifying triggers of plant species diversity over a range of observational scales, from landscape-scale, mountain-scale and belt-scale up to patch-scale.

The thesis is divided into 9 chapters. The first two chapters provide the theoretical background on species richness models along elevational gradients and on the role of environmental factors and disturbances. It is a good introduction, although recent discussions of different schools on elevational diversity gradients could have been touched in greater detail. Chapter 3 illustrates the physical setting of the study area, and deals in particular with the core mountains of the study (White Mts., Spring Mts., Snake Range). Data sampling and exploration methods are described in chapter 4. The nested sampling design (micro-, meso-, macro-plots), developed in order to operationalize the multi-scale approach for analysing diversity patterns, proved to be well suitable for that purpose. It is the methodical highlight of the study. Likewise, the highly sophisticated multivariate data analyses are quite convincing. The only methodical question that remains is why soil physical and chemical parameters had not been assessed. This would have substantially extended the set of explanatory variables for diversity patterns and enhanced the data interpretation, in particular at patch-scale. The results of the three core mountains are presented in chapters 5, 6, and 7, follow-

ing the multi-scale approach. It is impressively elaborated how patterns and processes are linked to changing factorial complexes as one proceeds from larger to smaller observational scales. E.g., vegetation history, petrographic heterogeneity or latitudinal, longitudinal, and altitudinal changes of major climate patterns play a major role at landscape- and mountain-scales, whereas petrographic and topographic differences, natural disturbances, small-scale dynamic processes, and human impact are decisive factors at belt- and patch-scale. However, each core mountain shows distinct patterns and processes pointing to the difficulties that arise when searching for generalizations and ultimate simple explanations for observed spatial patterns. Comparing the explained patterns and processes of the three core mountain ranges, the final chapters (comparative discussion, concluding remarks) highlight the respective similarities and differences, and review theoretical implications of the results.

In conclusion, F. GRÜNINGER's thesis is a significant contribution to biodiversity research and to comparative high mountain research. Elucidating the role of scale in observing and interpreting patterns and processes is a particular strength of the book. It is to be recommended to anyone who seeks a deeper understanding of spatial diversity patterns in mountainous regions.

UDO SCHICKHOFF