

REVEALING DIVERSITY PATTERNS OF VASCULAR PLANTS AND THEIR CAUSES IN SEMIARID HIGH MOUNTAIN REGIONS. A TOP-DOWN APPROACH FOR GREAT BASIN MOUNTAIN RANGES, USA

With 11 figures and 2 supplements (V, VI)

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Zusammenfassung: Muster der Pflanzendiversität in semiariden Hochgebirgen und ihre Ursachen – ein ‘top-down approach’ für Gebirge des Great Basin, USA.

Biodiversität als Ausdruck der Vielfalt lebender Organismen eines Raumes ist immer abhängig vom betrachteten Maßstab. Häufig sind Mechanismen und Prozesse, die die Diversität eines Raumes beeinflussen, nicht auf allen Maßstabsebenen gleichermaßen wirksam oder ersichtlich. Daher können und müssen sich Untersuchungen auf unterschiedlichen Maßstabsebenen gegenseitig ergänzen, um zu einer Erklärung vorhandener Muster beizutragen.

Die vorliegende Untersuchung versucht anhand von Beispielen Muster und Ursachen der Phytodiversität im semiariden Great Basin im Südwesten der USA aufzuzeigen. Es werden vier Maßstabsebenen unterschieden:

- die *Landschafts-Ebene* betrachtet das gesamte Great Basin als physiographische Einheit. Hier spielen neben klimatischer und petrographischer Heterogenität vor allem florenhistorische Entwicklungen eine große Rolle für die Ausbildung der gegenwärtigen Phytodiversität;
- die *Gebirgs-Ebene* betrachtet die klimabedingte vertikale Zonierung einzelner Gebirge. Anhand dreier Beispiele (White Mts., Spring Mts. und Snake Range) werden Diversitätsmuster der Gesamtfloren sowie der zonalen Vegetation entlang der Höhengradienten aufgezeigt;
- die *Höhenstufen-Ebene* betrachtet Vegetationsmuster innerhalb von Höhenstufen anhand von Dominanzstrukturen und Lebensformzusammensetzung, um strukturelle Gemeinsamkeiten und Unterschiede aufzuzeigen;
- die *Patch-Ebene* betrachtet schließlich beispielhafte Muster, die von exogenen und endogenen dynamischen Prozessen hervorgerufen werden und unterschiedliche Wirkungsspektren aufweisen.

Summary: Revealing diversity patterns of vascular plants and their causes in semiarid high mountain regions – a top-down approach for Great Basin mountain ranges, USA.

Biodiversity, or the richness of living organisms within a particular area, always has to be seen in dependency to the scale of observation. The mechanisms and processes influencing diversity are often not equally effective and / or visible on different scales, hence a multi-scale approach is indispensable for explaining existing diversity patterns. This study tries to reveal patterns and causes of vascular plant diversity in semiarid mountain Ranges of the Great Basin by using the four following observation scales:

- the *landscape-scale* covers the whole region of the Great Basin with its single mountain ranges;
- the *mountain-scale* considers one particular mountain range with its altitudinal belts along environmental gradients;
- the *belt-scale* is employed to describe structural patterns within climate induced altitudinal vegetation belts of a mountain range;
- the *patch-scale* regards the different environmental units formed by dynamic processes within the essential communities of the various belts.

1 Introduction

The scale-dependent aspect of patterns and processes in ecology was recognized long ago, but scale issues as a scientific research topic came to the forefront only within the last 20 years (TURNER et al. 2001). Dependent on the scale of observation, patterns or processes might become prominent or hidden. LEVIN (1992, 1960) states: “That there is no single correct scale or level at which to describe a system does not mean that all scales serve equally well or that there are not scaling laws”. This statement refers to ecology in

general but applies especially well to patterns of biodiversity and vascular plant diversity. 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 another, and a functional interpretation always has to be orientated on the different spheres of influence (CRAWLEY a. HARRAL 2001; HUSTON 1994).

At large spatial and temporal scales plant species richness is controlled by the rates of speciation and extinction (ROSENZWEIG 1995). Based thereon, environmental heterogeneity creates a certain niche diversity

per area and controls species richness as well as other types of phytodiversity (diversity of formations or functional types, evenness, endemism, etc.). On smaller scales however, it might be second in importance to direct environmental variables like water, nutrients or light (PAUSAS a. AUSTIN 2001). Thus, diversity research at varying spatial scales leads to a multitude of – sometimes even contrary – estimations of plant species richness and its causes. Especially in large heterogeneous areas, where generalization is necessary, the resolution is generally too low to detect the important environmental factors involved.

High mountain regions play a special role within diversity research, as they generally show an outstanding geodiversity due to their geomorphological, petrographic and climatic complexity in relation to the surrounding lowlands (BARTHOLOTT et al. 1996; GRABHERR et al. 2000; RICHTER 2000). Based thereon and modified by exogenous and endogenous dynamic processes, high mountains show an enormous spatial and temporal niche-heterogeneity and hence a high species diversity.

Large-scale approaches to explain diversity patterns often cannot cope with those regional characteristics of the environment and flora for several reasons. Often there is a lack of knowledge about the actual amount of existing taxa, as local floras are likely to be either old, incomplete, limited to special areas of interest or simply non-existent. If they are, the gradually changing environment and taxonomic reclassification may cause further confusion for certain areas.

The Great Basin with its numerous small mountain ranges is a good example for this, as discussions about its biodiversity have been controversial ever since and remain so still today. For a long time the Basin Ranges have been treated as “islands” in a “desert-sea” (according to the island biogeography theory of MACARTHUR a. WILSON 1967) with an impoverished flora compared to the surrounding “mainlands” of the Sierra Nevada-Cascades-Axis to the west, and the Rocky Mountains to the east (HARPER et. al. 1978; REVEAL 1979; WELLS 1983). A similar impression is given by the world map of phytodiversity by BARTHOLOTT et al. (1996), which is based on the species richness of vascular plants in standard area units of 10,000 km² and was calculated with a formula including area size and species number. For the western United States it indicates high plant diversity in the westernmost mountain chains (Cascade Range, Sierra Nevada and coastal Southern California, 1,000–3,000 species/area), and for the Rocky Mountain chain (1,000–2,000 species/area). The Basin and Range Region shows an overall lower species diversity of only 500–1,000 species per 10,000 km². Never-

theless, the authors already stress the importance of mountains as spatial elements of increased geo- and thus phyto-diversity, and the problem that “larger ranges [...] are easily portrayable, whereby smaller ranges are represented as a unit and not in detail, for reasons of scale” (BARTHOLOTT et al. 1996, 322).

A local but excellent analysis of CHARLET (1991), based on numerous mountain florulas of the southwestern USA, showed that the vascular plant species richness of the Great Basin mountain ranges was strongly underestimated for a long time and that the mountain flora of the Great Basin is “remarkably similar in species richness and composition” (CHARLET 1991, 212) to both the Pacific Axis and the Rocky Mountains. This opinion is supported by a more recent approach on mapping the plant diversity of the United States by MUTKE (2000), a scholar of the Barthlott school. Using an optimized data set and new methods of data management, interpolation and statistical exploration, as well as advanced modelling procedures, he found high plant diversity within the arid Southwest, with 1,500–2,500 species per 10,000 km² even higher than within the California Floristic Province. MUTKE considers an evenly distributed factorial complex as driving force, that comprises non-measurable historical processes within the environment as well as aridity- and elevation-related gradients next to other unmeasured or too generalized environmental factors. The larger the area investigated, the less detectable the important factors get, particularly if the necessity of generalization creates a resolution too big for them.

All incalculabilities considered, the number of species per area unit is still the most simple expression of phytodiversity. Due to its absolute values it is mappable in contrast to comparative indices over space and time, which are nevertheless very important to show the diversity patterns of an area and therein to detect relative diversity peaks or depressions and their causes.

A solution of this problem is not intended for this paper and is also not feasible by the authors. Nevertheless, we intent to contribute new data on the dependency of plant diversity on environmental processes and gradients at different scales of resolution with special emphasis on the Basin and Ranges region. For implementation we suggest a nested approach with a stepwise reduction of the area surveyed.

2 Which types of diversity?

With his differentiation of alpha-, beta- and gamma-diversity, WHITTAKER (1972) tied together different forms of diversity and their dependence on spatial

scales and environmental gradients. Species richness per area unit is treated as alpha-diversity, if the samples are homogenous entities (i.e. spatial, temporal or functional units). The diversity of an area or sample composed of several of those homogeneous basic units is defined as gamma-diversity. The spatial extension of both sample types is variable, but they have the same dimensional characters with discrete numbers and are subsumed under the expression “within-habitat diversity” (WHITTAKER 1972). If used for data without area-linkage, the “Evenness” (PIELOU 1975; HAEUPLER 1982) can be employed to describe the equitability or dominance of entities (e.g. taxa, life forms) within a vegetation unit.

The beta-diversity, or “between-habitat diversity” is based on the previously ascertained quantities and gives comparative information about the (dis-)similarity between two units, again either spatial, temporal or functional. It has no own dimension and is described by indices (MACARTHUR 1965; WHITTAKER 1972) with algorithms adapted to the research interest. Binary data (e.g. species lists) can be compared, as well as quantitative data (e.g. ground cover of species). Important similarity indices are the JACCARD Index (or “similarity ratio”) or the SØRENSEN Index and their derivatives (for details see e.g. HAEUPLER 1982).

3 Decisive factors and their scale-dependent aspect

A multitude of different factors lead to the existing plant diversity of the Basin Ranges. Within this paper, they are split into environmental factors, recurrent dynamics in vegetation structure (sensu WHITE 1979), and time.

The environmental factors can be divided into resource, direct and indirect variables according to PAUSAS and AUSTIN (2001): the resource variables include all properties that are consumed by plants (e.g. light, water), and plant growth is generally greatest at high resource levels; the direct or “regulator” variables regulate the physiological processes of the plants but are not consumed (e.g. air temperature, soil pH), and plant growth is highest at intermediate levels; the indirect or “complex” variables (e.g. altitude, topography) have no direct influence on plant growth, but are correlated with a variety of resource and / or regulator variables (for details see also HUSTON 1994).

Recurrent dynamics are subdivided into exogenous natural and anthropogenic disturbances, stress, and endogenous cyclic processes. Natural disturbances in the Basin Ranges include wildfire, rapid mass movement, frost-induced soil movement, animal impacts

and gap dynamics. Human activity is generally low above the foothills, but the partial use of natural resources (timber, recreation) and man-made fires have some influence. Stress is indicated if processes occur regularly and the present vegetation is adapted to them, as in avalanche gulches, ravines or on active alluvial fans; endogenous cyclic processes are caused by the system itself and alter the vegetation periodically.

Overlying all other processes is the factor of time: the temporal variation of plant diversity is controlled by episodic, periodic or permanent changes of direct and / or regulator variables or biotic factors.

On larger scales, diversity is governed mainly by the complex environmental variables (climate and its changes along vertical, latitudinal and / or meridional gradients; vertical extension and petrography or “geodiversity” sensu BARTHLOTT et al. 1996), as well as by the floristic history of the region (speciation and extinction). On smaller scales, dynamic processes gain importance in addition to environmental factors and enrich the niche diversity. Bearing this scale-dependent aspect of all the factors in mind, four different observation scales are employed to reveal information about the vascular plant diversity of the Basin Ranges:

- the *landscape-scale*;
- the *mountain-scale*;
- the *belt-scale*;
- the *patch-scale*.

4 Data and sources

Nine representative mountain floras (CLOKEY 1951; MOREFIELD et al. 1988; CHARLET 2001), evenly distributed across the region (see Fig. 1), were analyzed on the landscape-scale concerning richness on different taxonomic levels within and between the different mountain ranges. Additional data is derived from our own studies (~750 samples of 500 m² in vertical distances of generally 150 m, FICKERT in prep., for location see Fig. 1). This data also serves for the general overview about the climate-dependent altitudinal zonation (Fig. 3). The nomenclature of the altitudinal belts used in this paper follows RICHTER (2001).

For observations on the smaller scales, nested samples within the vegetation belts and along the altitudinal gradient (~100 sample units of 2,500 m², 1,200 smaller plots nested therein, GRÜNINGER in prep.) of three representative mountain ranges are used: the White Mts., the Spring Mts. and the Snake Range, for location see figure 1. This data also provides the opportunity to calculate evenness values on floristic and structural levels.

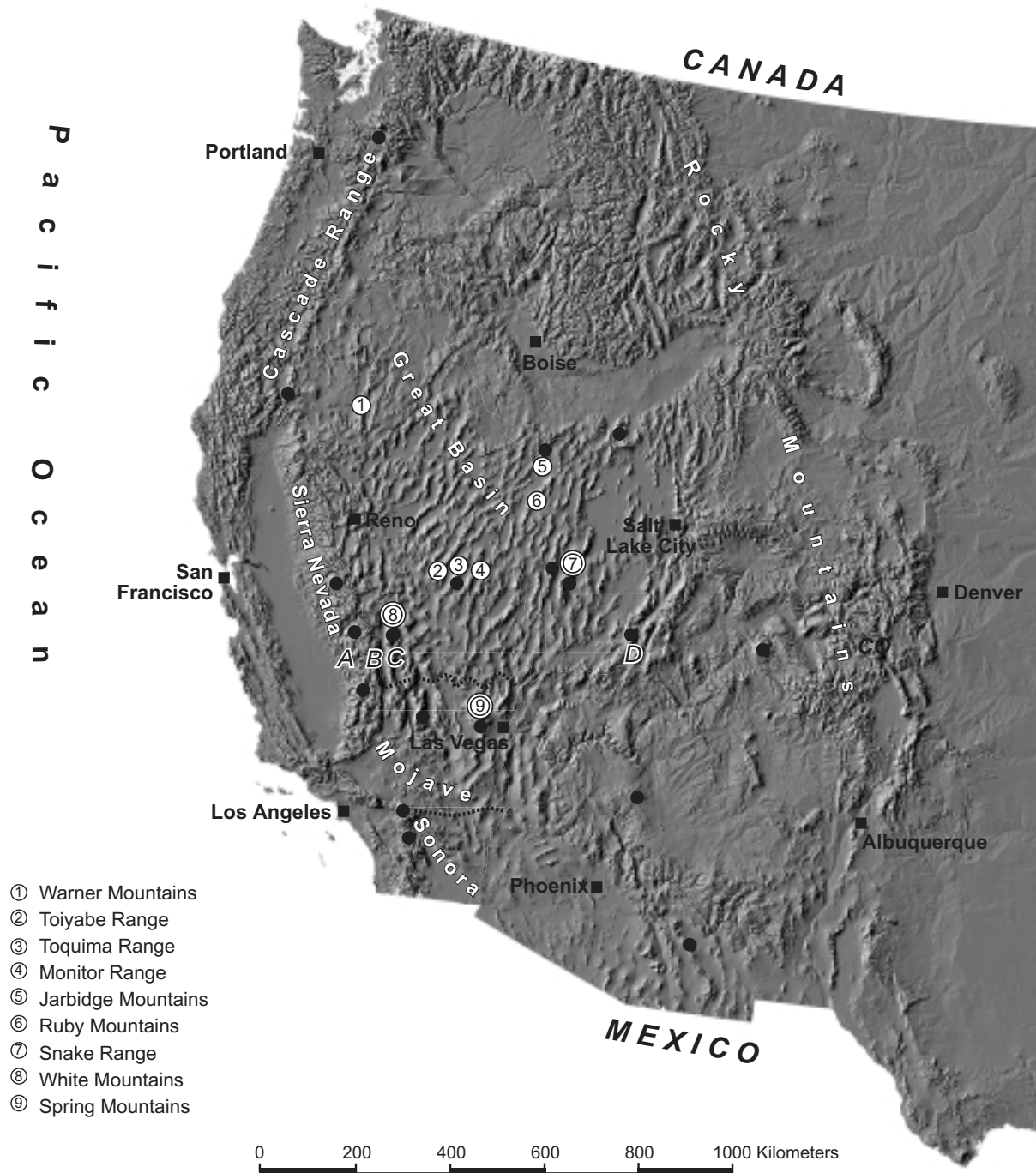


Fig. 1: Outline of the hydrographic Great Basin and location of the mountain ranges studied (1–9 for the landscape-scale, the double-circled 7–9 also for the mountain-, belt- and patch-scale). The black dots indicate the location of transect studies which are the base for Fig. 3 and Fig. 7. The capital letters (A, B, C, D) indicate the location of the precipitation gradients shown in Fig. 2. Shaded relief modified from THELIN and PIKE (1991)

Umriss des hydrographischen Great Basin und Lage der untersuchten Gebirge (1–9 für die Landschaftsebene, die doppelt umrandeten 7–9 auch für die Gebirgs-, Höhenstufen- und Patchebene). Die schwarzen Punkte zeigen die Lage der Transekte an, auf deren Ergebnisse Fig. 3 und Fig. 7 beruhen. Die Großbuchstaben (A, B, C, D) geben die Lage der Niederschlagsgradienten von Fig. 2 an. Kartenhintergrund verändert nach THELIN und PIKE (1991)

5 Study area

The western USA is characterised by two major mountain systems, the Sierra Nevada-Cascades axis along the Pacific and the Rocky Mountains several hundred kilometers inland with the Great Basin in-between. It is hydrographically defined as an area without drainage to the ocean; floristically it encompasses three different deserts (Fig. 1). The largest part in the North belongs to the cold Great Basin desert, while smaller areas in the south are part of the warm Mojave desert and the hot Sonora desert. The Great Basin is characterised by numerous north-south trending mountain ranges that are separated by narrow valleys. This strip-like arrangement of basins and ranges is a result of fault block tectonics which occurred parallel to the Sierran uplift since the late Tertiary. Many of these mountain ranges reach well over 3,000 m a.s.l. and the vertical extension between the lowest (Death Valley, -82 m a.s.l.) and the highest point (White Mountain Peak, 4,342 m a.s.l.) is immense.

Climatically, the Great Basin is characterised by strong continentality. The Pacific Cordillera creates a nearly continuous barrier for the western air masses and most of the humidity is dropped on the windward side. Consequently, vapour content and precipitation on the leeward side is significantly lower (BRYSON and HARE (1974) compare the precipitation gradients of the Sierra Nevada west- and east-sides in figure 2). Reflecting these climatic differences, the Sierra Nevada shows a strong asymmetry of vegetation belts on western and eastern slopes (Fig. 3 “heterogenous type” according to RICHTER 2000, see also HETZNER et al. 1997). Only at higher elevations, where moisture-carrying clouds lap over the crest and differences in humidity are weak, high taxonomic similarities between both expositions are prevalent.

Valleys in the western part of the Great Basin often receive less than 200 mm of precipitation/year, and even at 3,800 m a.s.l. in the White Mts. annual precipitation stays below 500 mm (POWELL a. KLIEFORTH 1991, see Fig. 2). The annual course of precipitation resembles a mediterranean-type climate with maximum values in winter and dry summers. Because of the low vapour content and due to the restricted size of the mountain ranges, rain-shadow effects in the western Great Basin are insignificant, and the similar climatic conditions on both flanks are also borne out by the symmetric assemblage of vegetation belts and the high taxonomic similarities between western and eastern flanks within the belts (“homogeneous type” sensu RICHTER 2000 and HETZNER et al. 1997, see Fig. 3).

In the southern and eastern part of the Great Basin, a secondary peak of precipitation in summer is caused by the influence of humid air masses originating from trade winds crossing the Gulf of Mexico (BRYSON a. HARE 1974). Due to low pressure above the high plateaus and mountains of the Southwest, warm and humid air is diverted inland and rises above the heated surface of the mountain masses, causing short but intensive convective thunderstorms. The more massive the respective mountain, the higher is the amount of convective summer precipitation received, a phenomenon called the “Merriam effect”. Especially the higher elevations profit from this humidity input during the growing season (see station Blowhard in Fig. 2), as reflected by additional vegetation belts missing further west; nevertheless, these mountains still belong to the homogenous type of altitudinal zonation (see Fig. 3).

The lower foothills within the Great Basin are dominated by steppes of either different chenopod shrubs and / or *Artemisia* spp. in dependency on the soil salinity. Only in the lower and warmer southern part, different shrub formations, dominated by *Larrea tridentata* and higher up by *Coleogyne ramosissima*, occur. Above the semi-deserts and steppes, open woodlands of *Pinus monophylla* and *Juniperus osteosperma* are dominant in almost all mountain ranges. In the western Great Basin the Pinyon-Juniper woodlands shift into another woodland consisting of *Pinus longaeva* and / or *Pinus flexilis* higher up, sometimes separated by a narrow conifer-free belt (“balds”, see BILLINGS 1990; HÖLLERMANN 1973).

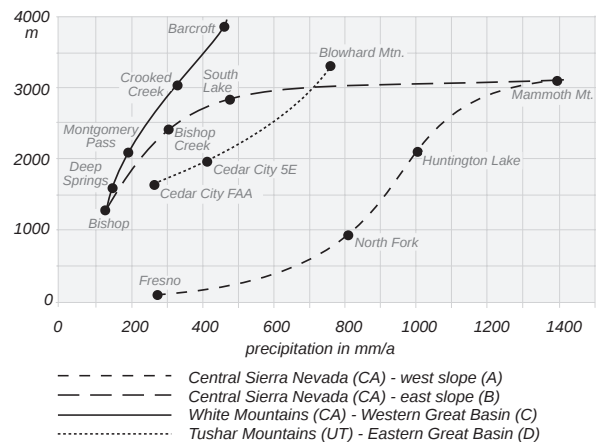


Fig. 2: Altitudinal precipitation gradients in different regions of the southwestern USA. For location compare the capital letters A, B, C and D in Fig. 1

Vertikale Niederschlagsgradienten in verschiedenen Bereichen im Südwesten der USA. Zur räumlichen Einordnung der Gradienten vergleiche A, B, C und D in Fig. 1

In the eastern part of the Great Basin dense conifer forests are located between the two woodlands. These forests are dominated by one or more of the following species: *Abies concolor* var. *concolor*, *Pseudotsuga menziesii* var. *glauca* and *Pinus ponderosa* var. *scopulorum*. Also *Picea engelmannii*, a characteristic treeline conifer of the Rocky Mountains, gains importance in the eastern Great Basin Ranges, sharing sites with *Pinus flexilis*. Above the tree line, loose talus communities are widespread on steep slopes, in some places with more moderate relief, as in the White Mts., alpine steppes with forb-rich turfs, low (sub-)shrubs, and cushion plants are interposed.

6 Scale-dependent examples

6.1 Landscape-scale

For a contemplation of plant diversity on a landscape-scale, richness on different taxonomic levels is

discussed. Figure 4 shows a classification of the nine mountain floras based on their similarity in species composition. All nine ranges rise from (semi-) arid foothills to the timberline (in the case of the Warner Mts. and Monitor Range) or well above.

The highest similarities exist between the three neighbouring Toiyabe, Toquima and Monitor Ranges, that represent the dry western Great Basin. A second group of relatively high similarity is formed by the Jarbidge Mts., the Ruby Mts. and the Snake Rg., characterizing the more humid northern and eastern Great Basin. In contrast, the Warner Mts. (as part of the Modoc Plateau transitional to the Cascades), the White Mts. and the Spring Mts. (rising above the Mojave Desert) are floristically rather independent. The classification roughly reflects a gradient of decreasing precipitation that is verified by climate data for the foothills and which probably also exists at higher elevations. Especially the arid foothills of the White Mts. and the Spring Mts. contain a high number of species which

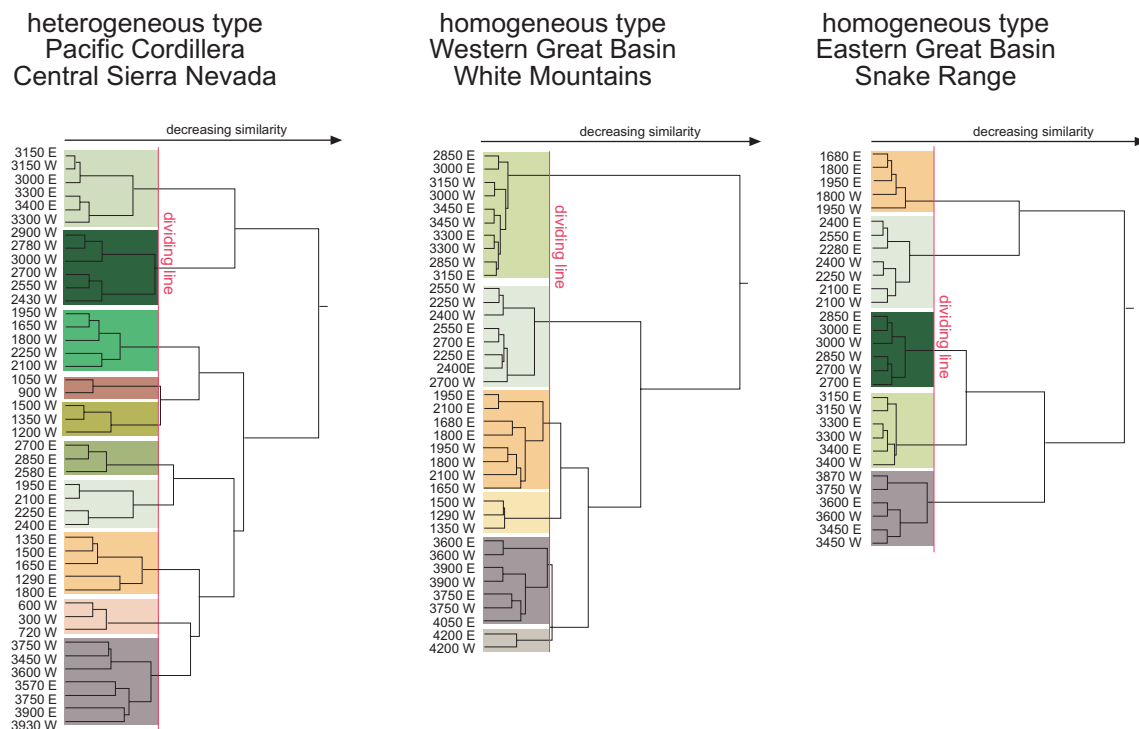
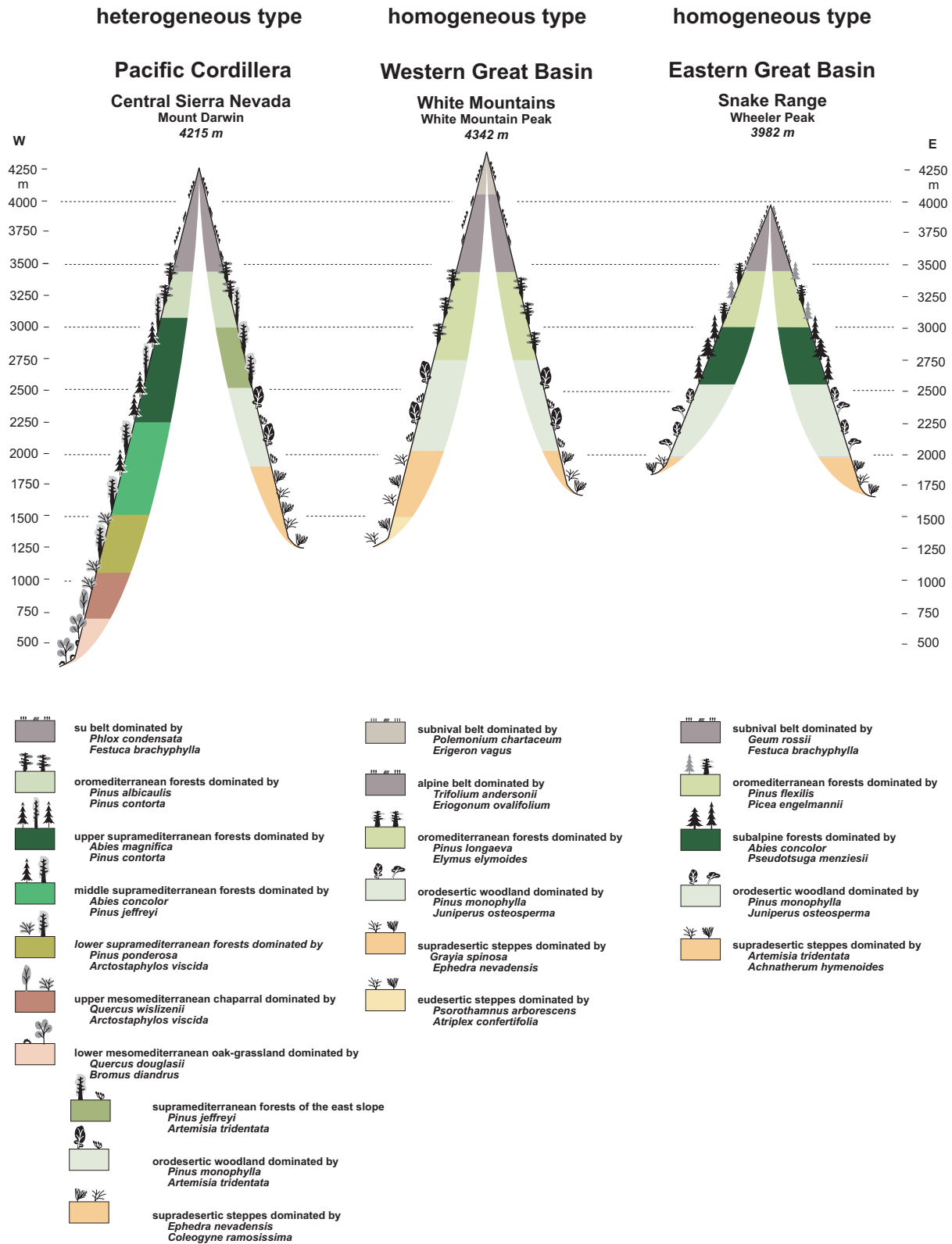


Fig. 3: Classifications of 500 m² samples along transects on west- and east-facing slopes of the Sierra Nevada, the White Mountains and the Snake Range are shown above (data square root transformed, vectors standardized, similarity matrix based on Van der Maarel Coefficient, minimum variance clustering). The thereof resulting profiles to the right indicate homogeneous or heterogeneous types of mountain ranges

Klassifikationen (oben) von Vegetationsaufnahmen (500 m²) entlang von Transekten auf west- und ostexponierten Hängen in der Sierra Nevada, den White Mountains und der Snake Range mit den daraus resultierenden Profilen (rechts) ermöglichen eine Beurteilung, ob homogene oder heterogene Gebirgstypen vorliegen (Daten wurzeltransformiert, Vektoren standardisiert, Ähnlichkeitsmaß: Van der Maarel, Cluster-Algorithmus: minimum variance)



are missing in the other ranges, hence their isolation in the cluster.

Altogether 2,060 species in 586 genera and 107 families were encountered in the nine floras. Due to differences in quality of the species lists, varieties and sub-species for many taxa could not be recognized, thus the actual number of species is expected to be much higher and might come close to the total known number of species of the "main Great Basin State" Nevada (2,850 species according to DAVIS et al. 1997, a fairly large number for a desert state with an area of 286,352 km²).

A high gamma-diversity is reflected in the large number of species present in just one of the floras ($n = 896$, or 43.5%), while only 37 species (1.8%) are present in all nine (Fig. 5). The floristic history of western North America plays an important role for the actual spatial distribution of plants in the Great Basin Region. Climatic changes caused by the Sierran uplift since the Tertiary (and most pronounced since late Miocene / early Pliocene), but also during the Pleistocene, had an important influence on the current species distribution. In Pleistocene times the Rocky Mts. – to a lesser degree also the Sierra Nevada-Cascades axis – as well as the adjoining valleys served as migratory pathways for arctic and boreal plants recessing southwards from advancing continental ice during glacial periods (AXELROD a. RAVEN 1985; BILLINGS 2000).

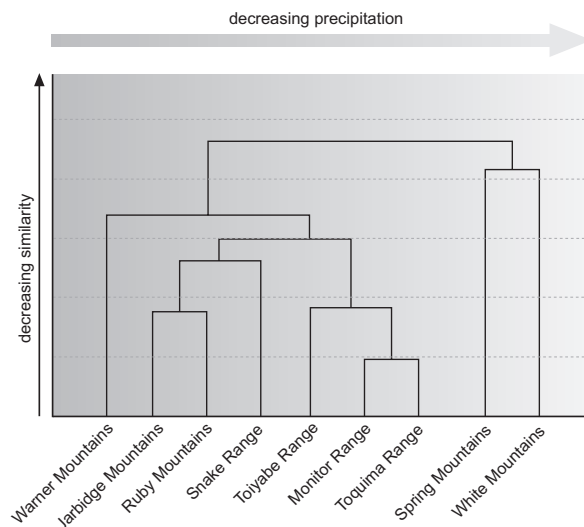


Fig. 4: Classification of the nine local floras (data from CLOKEY 1951; MOREFIELD et al. 1988; CHARLET 2001). Agglomeration rule: Unweighted pair-group average; Distance measure: Euclidean distance

Klassifikation der Gesamtartenlisten der neun ausgewählten Gebirge. Cluster-Algorithmus: Unweighted pair-group average; Distanzmaß: Euklidische Distanz

Many species of northern origin thus reached far south and today are restricted to the higher elevations of the Rocky Mts., the Sierra Nevada and the Great Basin. During warmer and drier interglacials, plants migrating from the south entered the area and contributed taxa to the lowland flora (REVEAL 1979). Additionally – and maybe even more important within the Great Basin Region with its isolated mountain ranges –, there was a cyclic up- and downward displacement of plants responding to the glacial and interglacial climates. Numerous (sub-) alpine plants of Great Basin mountain ranges are thus derived from lowland (desert) species with the ability of adaptation (WEBER 1965; AXELROD a. RAVEN 1985). Vivid and recent speciation is most obvious in the Asteraceae, a plant family known to be in active genetic fluctuation worldwide. With 321 species in 106 genera it is by far the most diverse family in the region.

In contrast to the high gamma-diversity on a species level, gamma-diversity of families is much lower, as 39% ($n = 42$) of the plant families occurring in the data set are present in all nine florulas (Fig. 5). This degree of correspondence, although not extraordinarily high compared to other regions, hints at an equal floral basis within the Great Basin region. Also extinction may have led to a "generalization" on higher taxonomic levels.

As already stated, the third dimension in mountain ranges enhances the climate-induced habitat diversity, and is considered as one of the most important factors for the increased richness of mountains compared to the lowlands. The larger the vertical extension above the base of a particular mountain range is, the more vegetation belts can be developed as a result of the

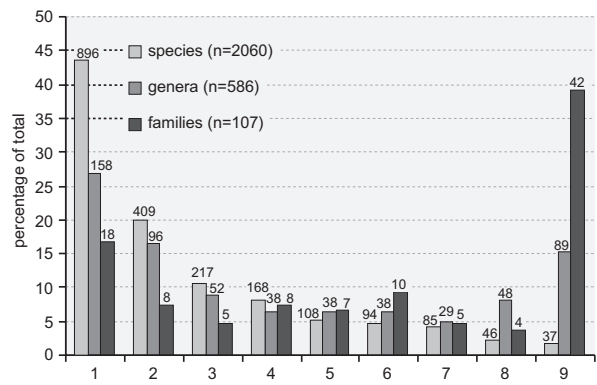


Fig. 5: Number of species, genera and families in regard to the number of mountain ranges where they are present

Arten-, Gattungs- und Familienzahl in Bezug zur Anzahl von Gebirgen, in denen sie vorkommen

changing hygro-thermic conditions with elevation. Figure 6 shows a strong relation between the richness of species, genera and family of the nine floras and the vertical extension of the particular mountain range. A similar pattern is described by BOWERS and McLAUGHLIN (1982) for local floras from Arizona, New Mexico and Western Texas.

An even stronger increase in species number – and also in genera and families – with vertical extension show heterogeneous mountain ranges with their higher diversity of vegetation belts (HETZNER et al. 1997; RICHTER 2000). Examples in figure 7 are the Sierra Nevada and the Transverse and Peninsular Ranges of California. Even if not based on complete species lists – which do not exist in these cases – but on own 500 m² relevés, heterogeneous mountain ranges in general seem to possess higher number of species and genera than homogenous mountain ranges of the same vertical extension. For families this trend is not so obvious, which supports the assumption of the same historical basis.

In addition to climate and floristic history, the petrography of the region plays an important role for the plant diversity. Due to the geologic-tectonic development of the Great Basin, rocks of different age and chemism are exposed in close proximity, creating a wide variety of soils and topography. The result is a high ‘petrographic’ niche diversity within small areas. Especially the limestone ranges like the Spring Mts. (comprising 20% of all endemic plant species of the State of Nevada, BRUSSARD et al. 2001) are centres of endemism (RAVEN 1988; CRONQUIST et al. 1972).

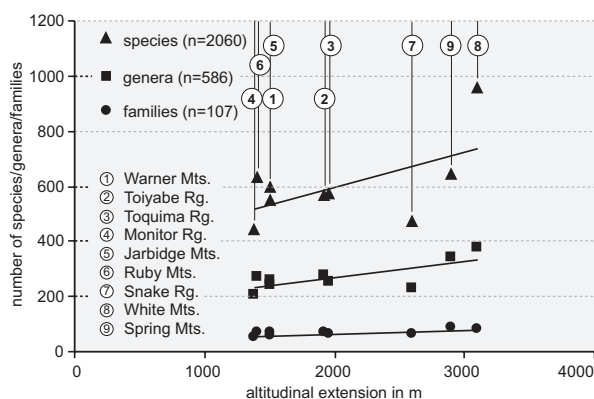


Fig. 6: Relation between number of species, genera and families and elevational range in the nine local floras

Beziehung zwischen der Anzahl von Arten, Gattungen und Familien und der Reliefenergie in den neun untersuchten Gebirgen

6.2 Mountain-scale

In the semiarid mountain ranges of the Southwest, two climatic extremes mainly restrict plant growth along the altitudinal gradient: at lower elevations the restricting force are limited water resources, whereas at high elevations low temperatures limit plant growth. Most of the species present in a mountain range find their ecological niche within the zone characterized by sufficient moisture supply and moderate temperatures. Here, a variety of light-use strategies is possible and many functional types can coexist on a patchwork of habitat types.

Corresponding patterns can be observed in the three selected mountains (Suppl. Va). In general, all three ranges have the highest species numbers at intermediate elevations. The White Mts. show the most ideal and “smooth” curve, with maximum values around the lower tree line, where around 50% of the total flora is represented. In the lower foothill zone, annual and ephemeral plants add to the species richness, but coverage is mainly provided by nanophanerophytes (see Suppl. Vb). Within the whole timbered zone the number of hemicryptophytes is highest in relation to other life forms, while the ground cover is made up

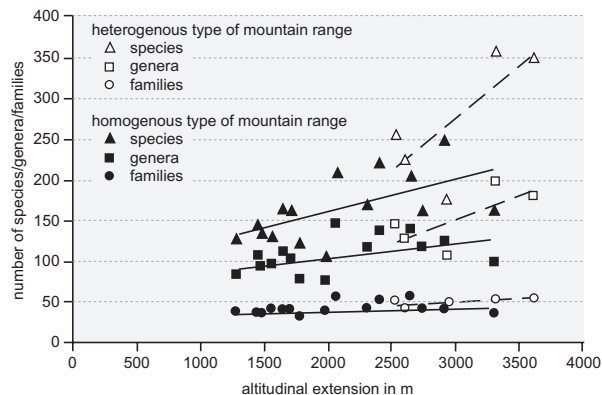


Fig. 7: Relation between number of species, genera and families and elevational range separately drawn for homogenous and heterogeneous types of mountain ranges. The analysis is based on the authors' own vegetation studies along 19 transects in the (South-)Western United States (for location see Fig. 1) rectangular to the main orientation of the mountain ranges (FICKERT in prep.)

Beziehung zwischen der Anzahl von Arten, Gattungen und Familien und der Reliefenergie getrennt betrachtet nach homogenem und heterogenem Gebirgstyp. Die Analyse beruht auf Daten, die entlang von insgesamt 19 Transekten (zur Lage siehe Fig. 1) quer zum Gebirgstreichen im (Süd-)Westen der USA erhoben wurden (FICKERT in Vorb.)

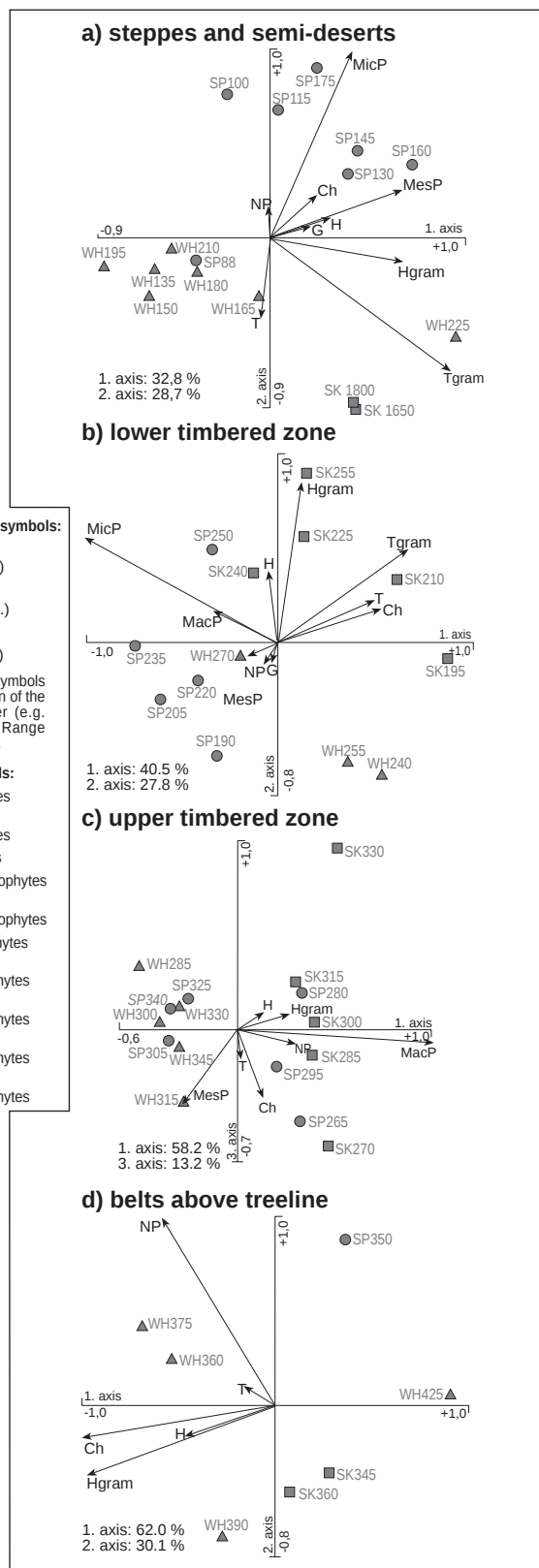


Fig. 9: for description see next page

almost solely by mesophanerophytes. Only above the tree line, where life form richness is reduced, the dominance of herbal species coincides with their dominance in ground cover.

Concerning life forms and species richness, the patterns in the Snake Rg. generally correspond with those of the White Mts. Nevertheless, two differences can be observed: firstly, the presence of conifer forests dominated by macrophanerophytes at middle elevations increases life-form diversity and absolute ground cover; secondly, livestock degrades the steppe vegetation and introduced weedy annuals out-compete native herbs. This pattern is not climate induced as in the other cases described, but is created by a large-scale disturbance. The distribution of species richness in the Spring Mts. is more complex, showing two major diversity peaks and an overall more indistinct pattern of plant distribution. The lowest foothills are species-rich due to their location within the Mojave Desert. The area is especially rich in ephemeral (mostly endemic) plants, that do not contribute much to the absolute ground cover (see Suppl. Vb). A scrub formation dominated by the nanophanerophyte *Coleogyne ramosissima* follows higher up, poor in associated shrubs and herbs. At the lower tree line, it intermingles with the distinct understory of the Pinyon-Juniper belt, creating a secondary peak in species richness. The high species numbers of the upper part of the woodland continue through the mixed coniferous forests and gradually decrease towards the *Pinus longaeva* woodland. As in the Snake Rg., the forests have an increased ground cover and even the lower woodlands show high total coverage. A sharp decline in species number above the tree line indicates

the climate-induced change of environmental conditions with coarse-grained loose debris and the effect of the extensive solifluction and cryoturbation (FICKERT u. GRÜNINGER 2002). The tree individuals stand widely scattered on these slopes and the sparse understorey vegetation is adapted to the soil movement. Although the range has a homogenous petrography, it affects the diversity at these high elevations on the mountain-scale.

Species replacement along the elevational gradients is gradual in all three ranges, but most obvious in the ecotones between two vegetation belts. The species-turnover curves based on the JACCARD Index of similarity (similarity of neighbouring elevation levels on base of plant species, Suppl. Va) generally show higher similarities within the vegetation zones than at the respective boundaries, where similarity values drop.

6.3 Belt-scale

A comparison between the climate-dependent vegetation belts of the three different ranges is conducted on this scale to reveal structural similarities of undisturbed vegetation in corresponding zones. The evenness is an appropriate tool to show and compare dominance-structures of the communities. The correspondences observed are not fixed on similar taxa in this case, but on similar degrees of dominance or entropy in the compared vegetation units. The graphs in figure 8 show “dominance structure-species richness diagrams” (“Dominanzstruktur-Artenzahl-Diagramme” according to HAEUPLER 1982), that are a result of calculated evenness-values plotted against the observed species numbers per site. The evenness is based on SHANNON’s Entropy but comprises the absolute species richness as well. Low values indicate high dominance of few (or only one) species; an increase in species richness lowers the dominance automatically. For a detailed description see HAEUPLER (1982).

Certainly, these evenness plots do not reveal the “nature” behind, i.e. which plants determine the degree of dominance. This can be done by an ordination biplot as in figure 9, where four principal component analysis (PCA’s) are drawn. The sites are arranged in a coordinate system according to their similarity in composition and structure; the taxa are drawn as arrows which are the longer, the more they explain of the total variance within the data set. As a comparison on the basis of species is meaningless, the data is reduced to life form groups.

For clarity reasons, the different vegetation belts are subsumed under four units and described separately: steppes and semi-deserts; lower timbered zone (i.e. the Pinyon-Juniper woodlands present in all three ranges);

Fig. 8: Dominance structure-species richness diagrams according to HAEUPLER (1982) of undisturbed zonal vegetation along the elevation gradient of the three mountain ranges

Dominanzstruktur-Artenzahl-Diagramm nach HAEUPLER (1982) von Aufnahmen ungestörter zonaler Vegetation entlang des Höhengradienten der drei Gebirge

Fig. 9: PCA-ordination diagram of aggregated lifeform composition data in co-variance biplot scaling with life forms represented by arrows (logarithmic data transformation, vectors centered). Data is used also in Fig. 8 and Suppl. Vb
PCA-Ordination der aggregierten Lebensformdaten in Kovarianz-Matrix (Werte logarithmisch transformiert, Vektoren zentriert). Der Biplot zeigt neben den Aufnahmen auch die Lebensformdaten, die als Pfeile dargestellt sind. Die hier verwendeten Daten werden auch in Fig. 8 und Suppl. Vb verwendet

the upper timbered area (encompassing both forests and upper woodlands); the zone above the tree line.

Steppes and semi-deserts:

The lower foothills in all three ranges are characterised by shrub steppes and semi-deserts with nanophanerophytes as the dominant life form. The PCA in figure 9a shows a rather clear separation in three distinct groups. With the exception of the lowest sample (SP88), all Spring Mts. sites are located above the first axis due to the presence (not abundance!) of the microphanerophyte *Yucca brevifolia*, which is a typical Mojave element and a life form missing in all other foothill-samples (see Suppl. Vb). Furthermore, these sites are characterized by high evenness values and species numbers (Fig. 8a). Only the highest steppe sites in the Spring Mts., which are clearly dominated by *Coleogyne ramosissima* (SP160, SP175), show lower evenness values.

The relatively high contribution of weedy, often introduced annual grasses (mainly *Bromus tectorum*) and forbs (e.g. *Erodium cicutarium*) as a result of grazing activity in the foothills isolates the samples of the Snake Rg. (SK165, SK180) in figure 9a and causes rather low species numbers and low evenness (Fig. 8a).

All but one of the White Mts. sites are located in the lower left quadrant of figure 9a, representing the typical Great Basin shrub steppes dominated almost purely by nanophanerophytes. The differing highest sample (WH225) reveals the problematic classification of ecotonal plots: pine is already present (hence the separation), but all other associates indicate a steppe character. Evenness and species numbers are variable in the White Mts. (Fig. 8a), affected by the unhomogeneous petrographic and topographic conditions, as the homogenous broad alluvial fans of the Snake Rg. and Spring Mts. are much less widespread.

Lower timbered zone:

The Pinyon-Juniper woodland sites show a compact assemblage in figure 8b. Low evenness values in combination with few species characterize the White and Spring Mts: *Pinus monophylla* dominates the overstorey, associated with *Juniperus osteosperma*; shrubs are present but do not reach higher amounts of coverage; herbs only contribute to the species richness but barely nothing to the ground cover. In contrast, the distinct plots of the Snake Rg. show both a higher species richness and a more even distribution of species: the herb layer is better developed and characterized by different annual or perennial grasses and forbs (Fig. 9b), indicating more

plant-available water. Since the samples were taken on slopes with generally high run-off and low storage capacities, the higher contribution of summer precipitation to the total annual in the Snake Rg. is supposed to be crucial.

Upper timbered zone:

The upper timbered zone comprises two different coniferous formations: mixed coniferous forests (only present in the Spring Mts. and the Snake Rg.) above the Pinyon-Juniper woodland, and again an open woodland dominated by *Pinus longaeva* in the White and Spring Mts. and by *Pinus flexilis* and *Picea engelmannii* in the Snake Rg.

The darker, more dense forests in the Snake Rg. and the Spring Mts. stand out on the righthand part of the graph in figure 9c with their clear dominance of macrophanerophytes. *Abies concolor* var. *concolor*, *Pinus ponderosa* var. *scopulorum* and *Pseudotsuga menziesii* (only in the Snake Rg.) are accompanied by an open understorey of shrubs and subshrubs as *Ribes* div. spec. or *Juniperus communis*. The highest woodland plots of the Snake Rg. (SK315, SK330) also appear to the right, but are separated by the dominance of the macrophanerophytic *Picea engelmannii* (Fig. 9c). As several tree species coexist and contribute rather equally to the total ground cover, the evenness is higher than in the open upper woodlands of the Spring and the White Mts. (Fig. 8c). Especially in the White Mts., dominances peak and drop only at WH315, where *Pinus flexilis* shares the site of *Pinus longaeva*. The similar life form composition in the woodlands of the Spring and White Mts. determine their position on the left side of the graph in figure 9c.

Above tree line

Above the tree line either alpine steppes or more common loose talus communities are characteristic for all Great Basin mountain ranges. Species numbers vary but in general decrease from the tree line towards the summits (compare Fig. 8c and 8d, see also Suppl. Va). Due to the overall low ground cover, evenness values of the samples are high. Higher species numbers are reached only in the alpine steppes of the White Mts. (WH 360 and WH 375). Deeper soils on rather flat ridgelines support the occurrence of sub-shrub communities with up to 30% ground cover (see Suppl. Vb). Here *Artemisia rothrockii* occurs with associated shrubs and other life forms (Fig. 9d). On the loose talus slopes near the summits the species numbers drop significantly, and the ordination reveals no distinct grouping. Geological

differences between the three ranges create distinct debris in subnival sites and thus a number of dissimilar niches for adapted plants.

This detailed explanatory description might appear rather confusing to a reader unfamiliar with the study area. Nevertheless, these different community and life-form structures are very obvious in the field. For the visualization of these differences, see photographs of the formations described above in figure 10.

6.4 Patch-scale

Dynamic changes in vegetation are most obvious on the patch-scale, even if not restricted to it. They are caused by exogenous disturbances and endogenous cyclic processes and thus are a result from periodic or abrupt changes of environmental factors, or from the interaction of changing susceptibility and existing unaltered environmental factors of a community that come to gain importance (WHITE 1979). The spatial (and also temporal) heterogeneity in ecosystems is increased, and a high niche diversity supports the co-existence of many species in areas of limited size. The spatial extension of dynamic processes is variable and depends not only on type, but also on the severity and frequency of the process, and the patch size examined has to be orientated thereon.

Exogenous processes: wildfire

Wildfires are a characteristic and widespread exogenous disturbance of the semiarid American Southwest. Supplement VIa shows an undisturbed zonal stand within the Pinyon-Juniper woodland and adjoining mid-successional stage after fire in the Spring Mts. at 1,900 m a.s.l. Most obvious is the different vegetation structure of the burned sites. Mesophanerophytes dominate under undisturbed conditions and barely appear in the burn, where nano- and microphanerophytes have the highest coverage. Total ground cover, however, is almost equal.

The modified values of different resource and regulator variables in the burned area (higher radiation input, reduced competition for the resources water and nutrients) support the establishment and maintenance of several shrubby genus like *Amelanchier*, *Arctostaphylos* and *Purshia* next to the prevalent *Artemisia*, creating a chaparral-like community. Several disturbance-affiliated herbs increase the species richness and temporarily replace the zonal components. With only 4 species in common and 11 or 16 species restricted to one sample (see Suppl. VIa), the calculated similarity (JACCARD Index) is 17.4%. If the area of investigation is extended

(GRÜNINGER in prep.), the increase in niche diversity becomes even more obvious: the tripled area within the old growth reveals only 2 additional species (total of 13), but 13 species more species occur within the burned site (total of 29).

Endogenous processes: animal activity

The yellow-bellied marmot (*Marmota flaviventris*) occurs between 2,700 and 4,100 m a.s.l. in the White Mts. and causes small-scale endogenous dynamic processes. It inhabits rocky terrain near vegetated areas and forages on different herbs to store fat for hibernation. Figure 11 shows a sketch and a photograph of a marmot-inhabited site at 3,500 m a.s.l. The 100 m² plot comprises 9 vascular plant species with a total ground cover of 35%. The marmot holes are protected by small boulders and near the bare, rocky "central area". Several degraded pathways connect entrances with each other, neighbouring burrows, a debris slope and a forage area at a nearby spring. The immediate surroundings of the central area shows not only a shift in the dominance of certain species, but also by their modified habit. *Muhlenbergia richardsonis* is a minor associate of the community, but dominates near the holes and its grazed stalks indicate heavy forage activity; *Elymus elymoides* can be found with moderate coverages throughout the area but its cover and growth is increased; the abundance of *Artemisia rothrockii* is also slightly higher (Fig. 11).

Even if these observations are no quantitative investigations on the influence of marmots on plant diversity, some processes may be detected: the enrichment of nutrients due to excretions near the burrows and the bioturbation (as generally described by HOLTMEIER 1999) support the growth of individuals of *Elymus* and *Artemisia*; *Muhlenbergia* seems to be a favoured forage of the marmots, and the excreted seeds germinate in high numbers under these nutrient-rich conditions. In contrast to the previous example with a larger spatial extension, here a small-scale disturbance creates a vegetation mosaic and a shift in dominance in an otherwise homogenous vegetation unit, rather than increased species richness.

Endogenous processes: interaction of plants

Supplement VIb shows a comparison of various micro-habitats in the subnival zone of the Spring Mts. and their structural differences. The talus slopes are sparsely vegetated in general (less than 5% coverage) and low in life form diversity (Suppl. Va, b). The nine

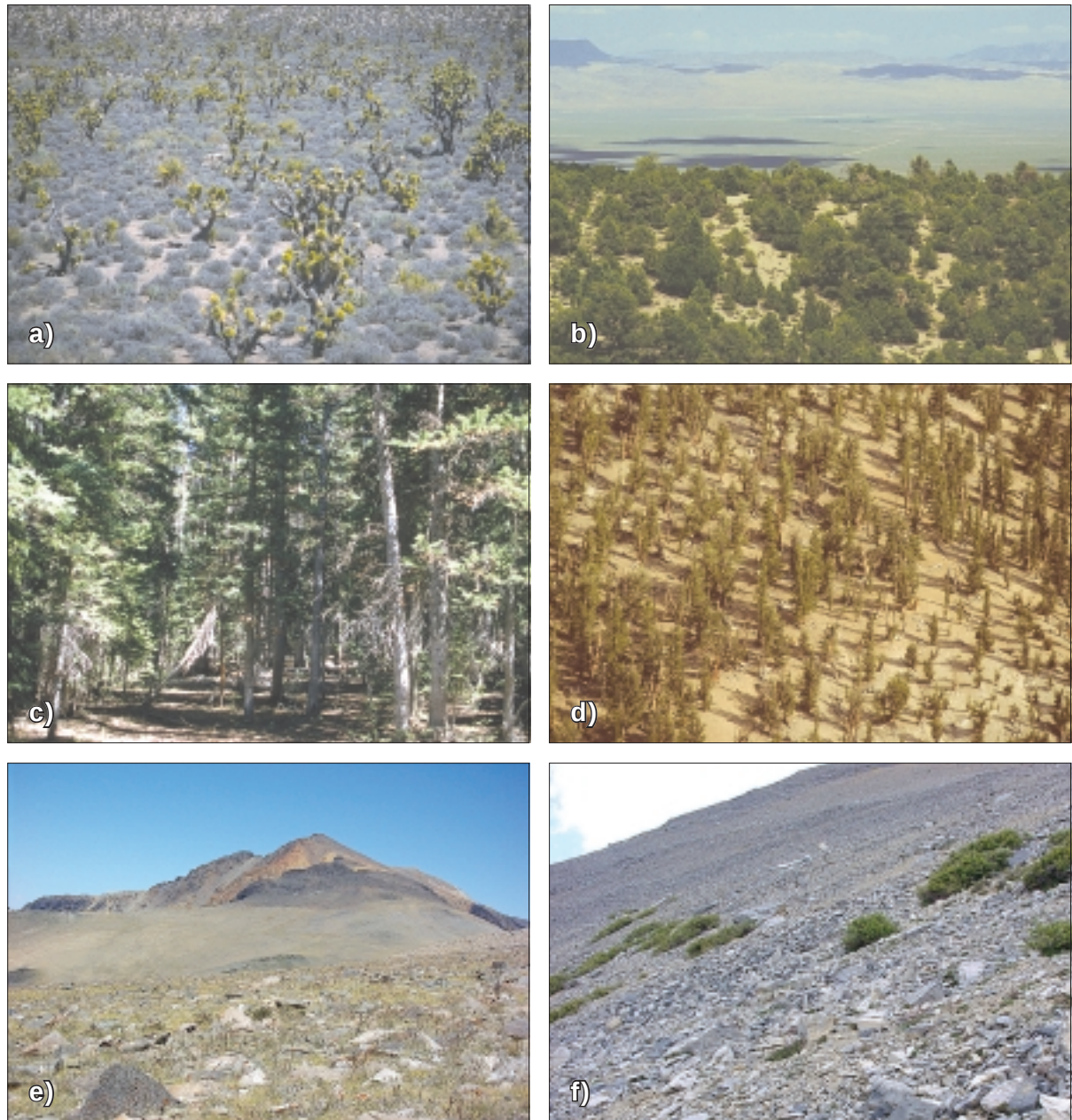


Fig. 10: Photographs of characteristic plant formations of the Great Basin mountain ranges

- a) shrub steppes / Strauchsteppen (here: *Coleogyne ramosissima* a. *Yucca brevifolia*, Spring Mountains 1,400 m a.s.l., Photo: FICKERT 2000)
- b) Pinyon-Juniper woodland / Kiefern-Wacholder-Offenwald (*Pinus monophylla* a. *Juniperus osteosperma*, Snake Range 2,100 m a.s.l., Photo: FICKERT 2001)
- c) subalpine forests / subalpine Wälder (*Abies concolor* a. *Pseudotsuga menziesii*, Snake Range 2,750 m a.s.l., Photo: FICKERT 2001)
- d) oromediterranean woodland / oromediterraner Offenwald (*Pinus longaeva*, White Mountains 3,000 m a.s.l., Photo: FICKERT 2001)
- e) graminoid-rich alpine steppes / grasreiche alpine Steppen (*Poa glauca*, *Elymus elymoides*, *Muhlenbergia richardsonis*, White Mountains 3,800 m a.s.l., Photo: GRÜNINGER 2001)
- f) subnival talus community / subnivale Schuttfuren (*Ribes montigenum*, Spring Mountains 3,500 m a.s.l., Photo: GRÜNINGER 2001)

plots have a mean species richness of 3.1 species and a mean ground coverage of 15.6%, both with a high mean variation, (Suppl. VIb table and graph). The plots comprising *Ribes montigenum* show high species numbers and high ground cover of associated species compared to the plots without this gooseberry. The drawings reveal the reason for this: the shrubs block the moving debris and hence create a sheltered micro-environment just beneath themselves, in which most of the accompanying species grow. The same effect can be caused by boulders (see plot p11 in Suppl. VIb). Processes like these do not increase the overall species richness, as all species grow unsheltered on the slopes as well; nevertheless, they lead to niche diversity connected with structural diversification in an otherwise homogenous habitat shaped by extreme environmental conditions.

7 Résumé

The influence of the floristic-historic development within the region is most obvious on the landscape-scale, if different taxonomic hierarchies are observed. Some general differences in geological development are also apparent, and the dependence of vegetation

on general precipitation patterns is manifested in the diversity of climate-related vegetation belts.

The complex gradient of altitude is crucial for plant life within a mountain range since its range and intensity determines the diversity on the mountain-scale. In the Great Basin, extreme climatic conditions at both ends of the gradient lead to a relatively high equitability in plant cover and to a lower diversity in life forms within the respective elevation belts. Also, the gamma-diversity of plant species is lower at both extremes.

In the dry and hot foothill areas, the amount of plant-available water and its high variability is the limiting factor for plant growth. Nevertheless, annuals are at an advantage over other life forms due to their short life cycle and contribute to the gamma-diversity of species, but not much to total cover (as seen on the mountain- and belt-scale). Under disturbance this ratio may become inverted: few weedy annuals lower species diversity due to competition but reach higher ground cover.

Moderate climate conditions increase the gamma-diversity of the vegetation belts, the dominance within undisturbed vegetation units and their life form diversity (apparent on the mountain-scale). Abundant precipitation and intermediate temperatures allow a variety of light-use strategies and a more successful use of niches created by the distinct topographical features

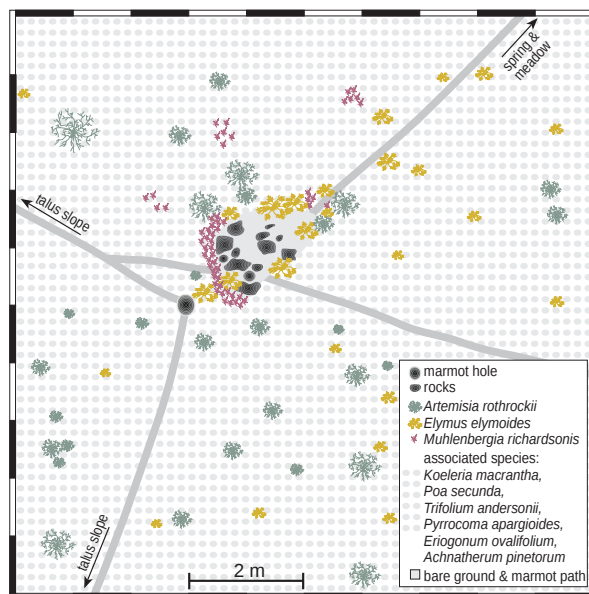


Fig. 11: Sketch and photograph of a marmot-inhabited site in the White Mountains at 3,500 m a.s.l. (slope angle 3°, WNW), showing an example for a small-scale endogenous dynamic process

Aufsichtsskizze und Photographie einer durch Murmeltiere überprägten Fläche auf 3.500 m Meereshöhe in den White Mountains (Hangneigung 3°, Exposition WNW) als Beispiel eines kleinräumigen endogenen dynamischen Prozesses

and soil properties. Many species and functional types can coexist on a patchwork of habitat types that is further enriched by exogenous and endogenous dynamic processes. These are also able to link neighbouring vegetation belts and serve as transfer channels for floral elements (see JENTSCH a. BEIERKUHNLEIN in this issue).

At the highest elevation, the direct variable temperature constrains the physical processes of the vegetation. Productivity and ground cover are low, as is gamma-diversity of species and life forms. There is an extraordinary diversity in micro-habitats, determined by steep environmental gradients and dynamic processes. Some of these gradients appear on the belt-scale, like the varying soil development in the White Mts. Others become obvious if the structures of individual sites are studied on the patch-scale, like the structural changes near the marmot burrow or the increased niche diversity within the mobile debris in the Spring Mts. caused by the sheltering shrubs. Micro-topography also contributes to the niche diversity in the highest zones of the Great Basin mountain ranges in creating a small-scale mosaic of varying temperature, moisture or nutrient conditions. This factorial complex can lead to a locally increased alpha-diversity of species in the Great Basin ranges (details will be given by GRÜNINGER in prep.).

The type, frequency and intensity of dynamic processes determine the prevalent vegetation patterns and

its temporal variation. High dominance of few species and increased productivity, high species richness with a more even ground cover, as well as all stages in-between can occur on the patch-scale. Endogenous processes are not separable from the environment they act on, and mostly create a rather fine-grained mosaic of habitats. In the relatively sparse vegetation of the Great Basin ranges above tree line, the processes are sometimes rather easily detectable on the patch-scale; but they can just as well be hidden or obscured by overlying factors and processes. If the affected vegetation is adapted to exogenous processes occurring within, the following stages of succession and the changes in diversity are mostly well documented. Under natural conditions such ecosystems are generally a patchwork of different successional stages at varying spatial scales.

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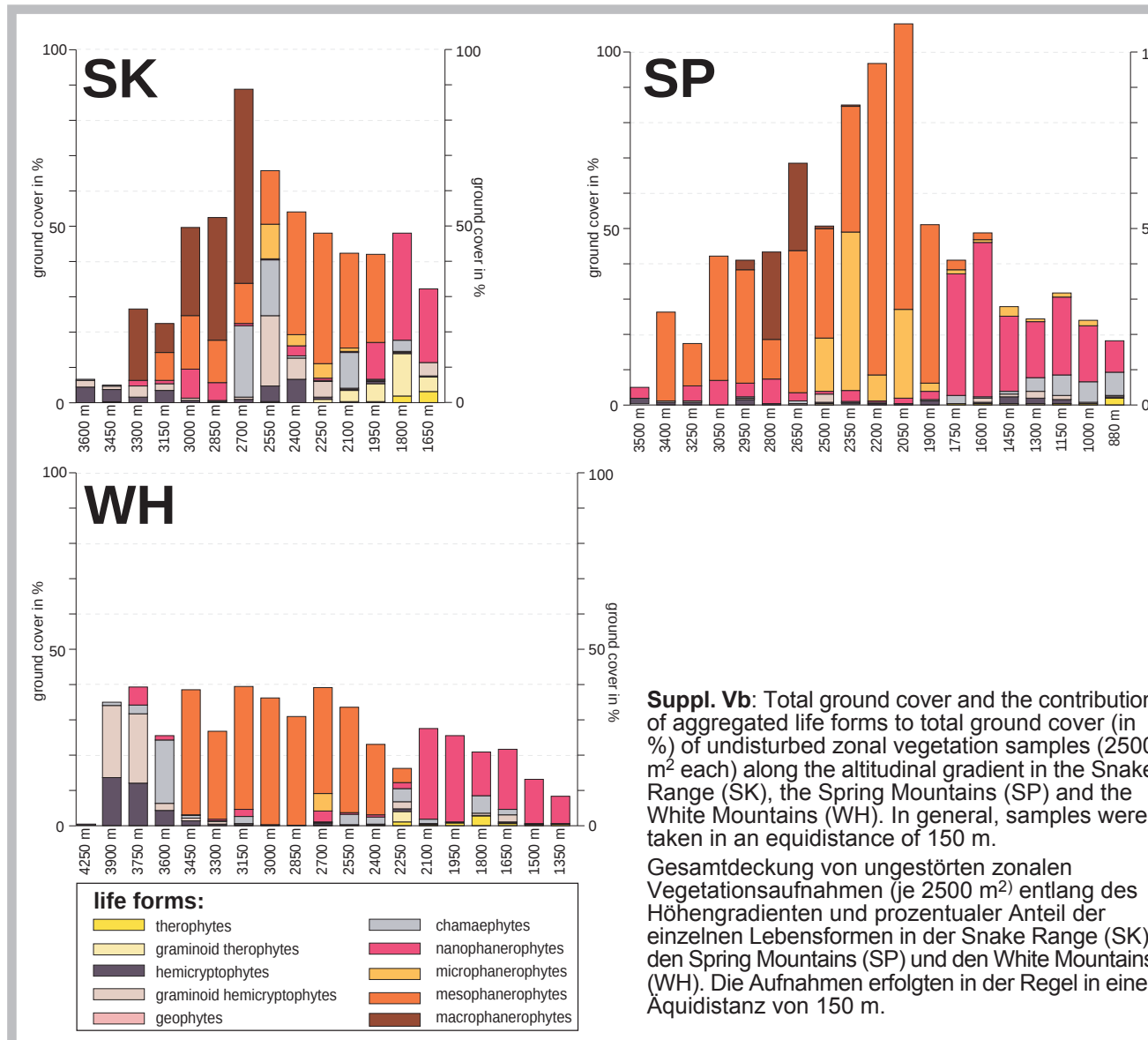
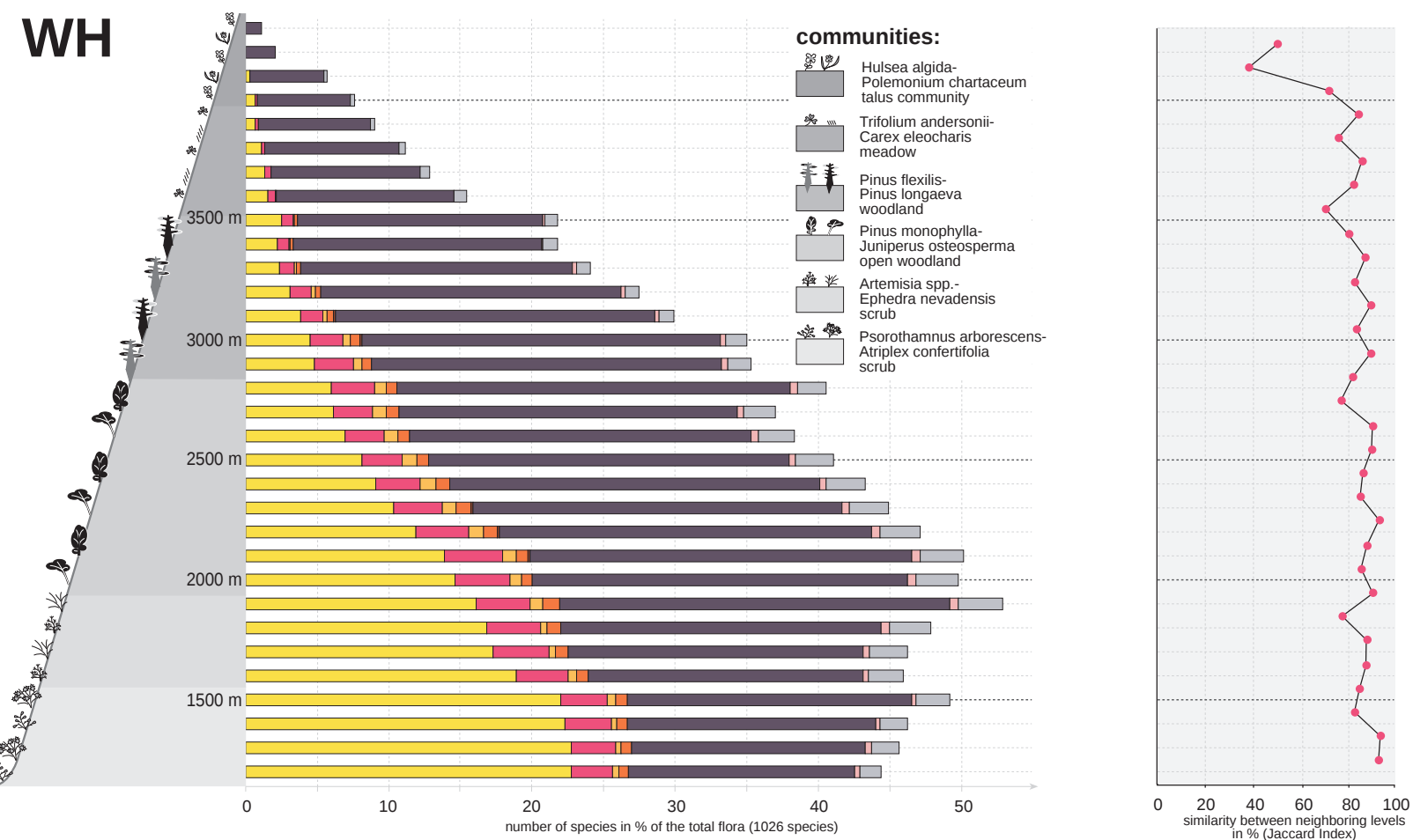
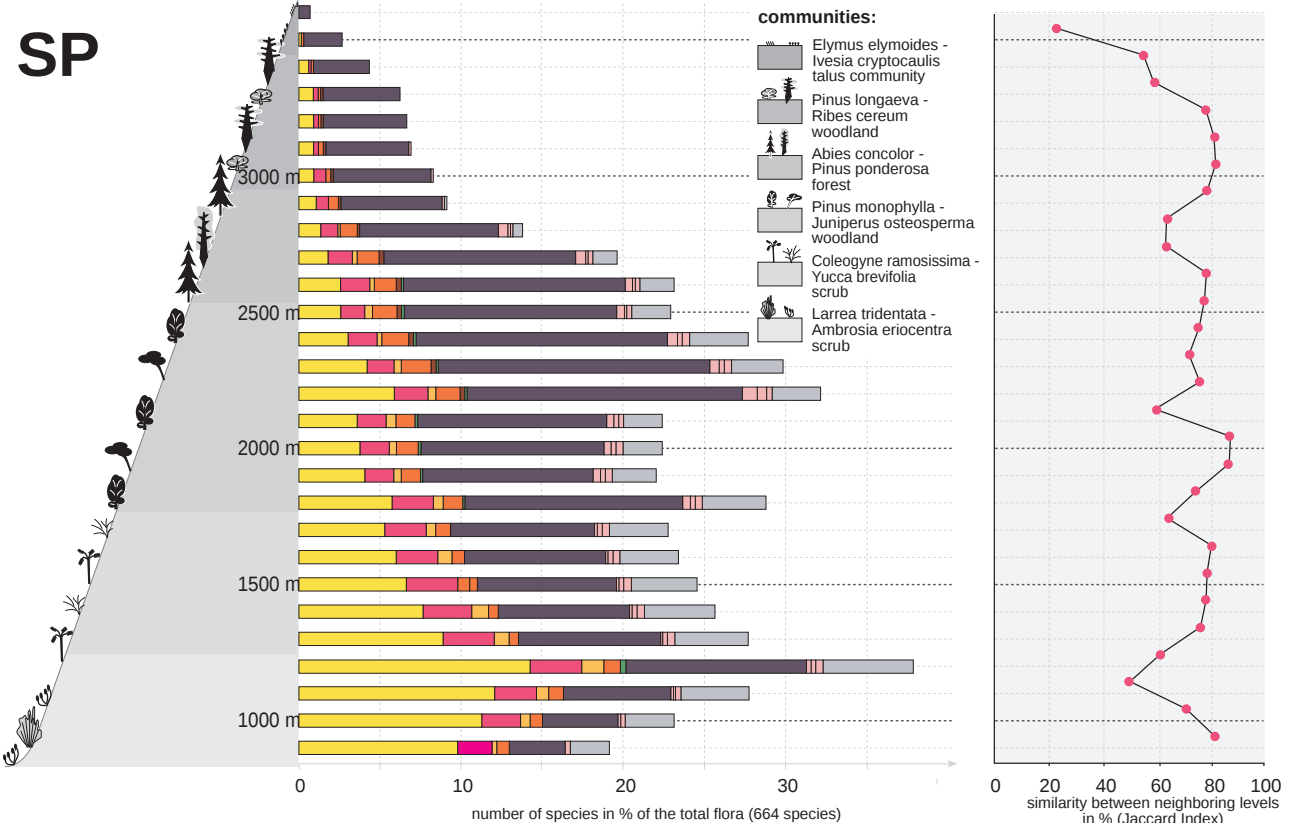
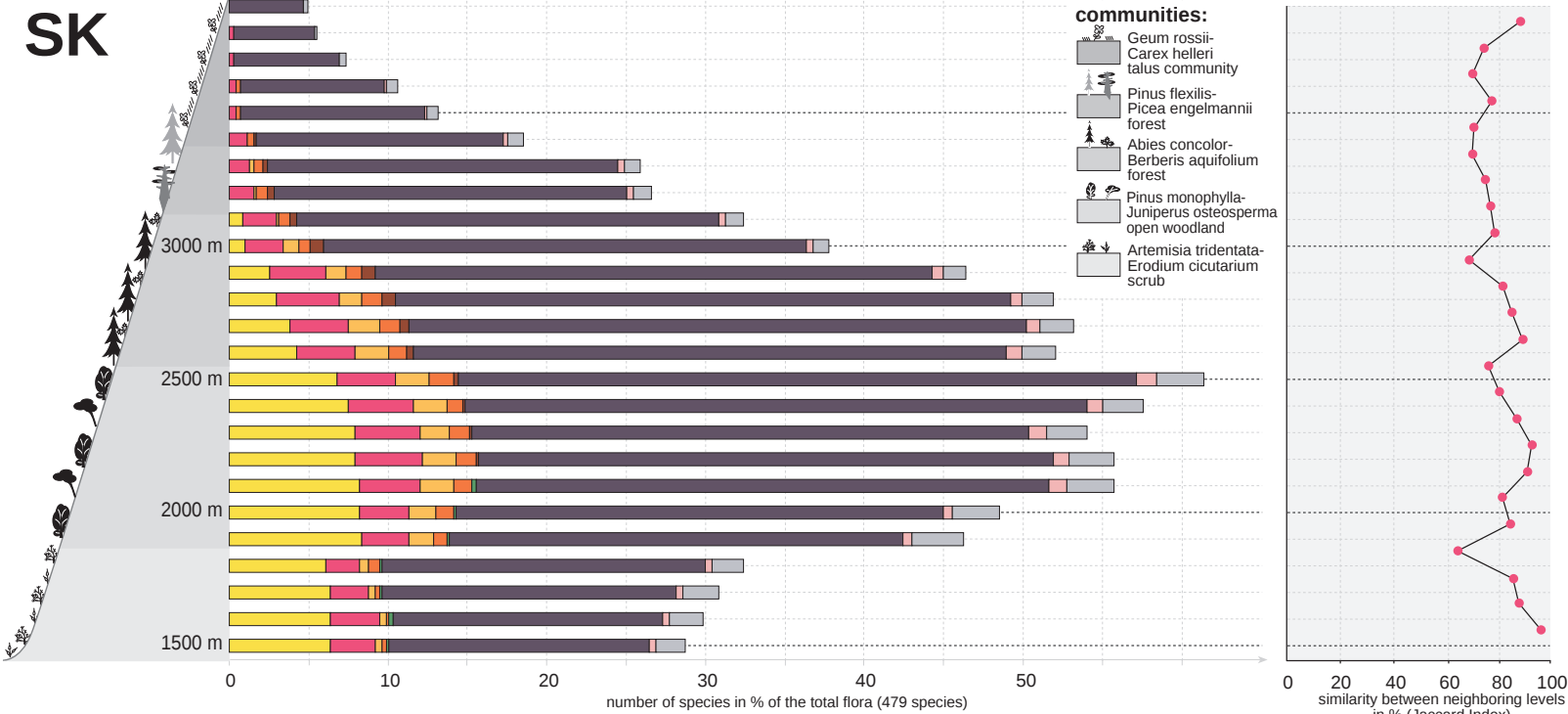
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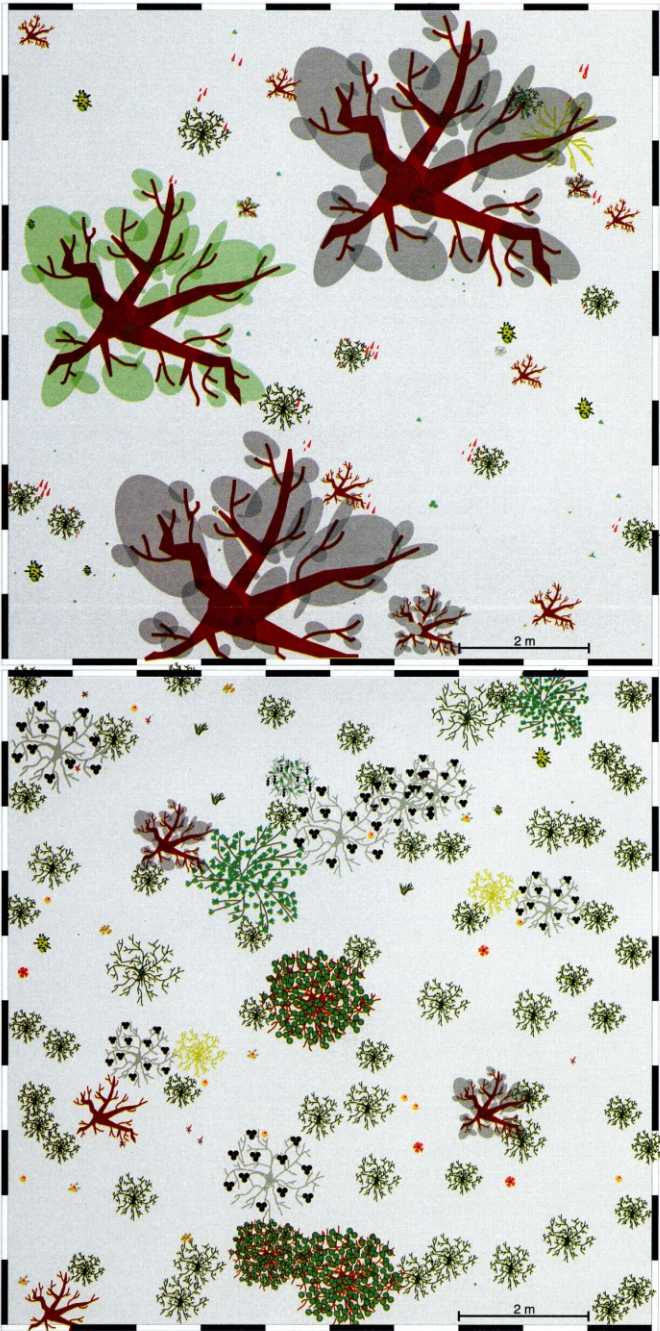
Suppl.Va: gamma-diversity of vascular plant species (in % of total flora) and their life form affiliation in equidistances of 100 m along the altitudinal gradient in the Snake Range (SK), the Spring Mountains (SP) and the White Mountains (WH). The graphs to the right show the beta-turnover in flora of neighbouring elevation levels in % of similarity (calculated by JACCARD Index). Data sources: SK: CHARLET 2001, SP: CLOKEY 1951, WH: MOREFIELD et al. 1988.

Gamma-Diversität der Gefäßpflanzen (in % der Gesamtartenzahl) und ihre Lebensformzugehörigkeit in Abständen von je 100 m entlang des Höhengradienten der Snake Range (SK), der Spring Mountains (SP) und der White Mountains (WH). Die zur Rechten stehenden Kurven zeigen den beta-turnover der Flora benachbarter Höhengschnitte in ihrer prozentualen Ähnlichkeit (berechnet mittels JACCARD Index). Datengrundlage: SK: CHARLET 2001, SP: CLOKEY 1951, WH: MOREFIELD et al. 1988.

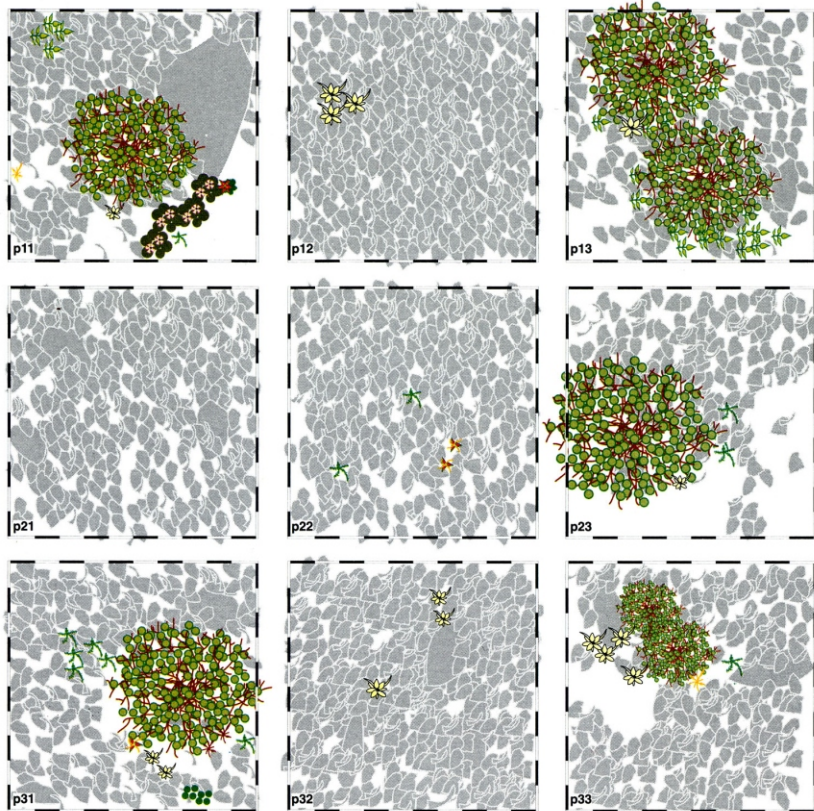
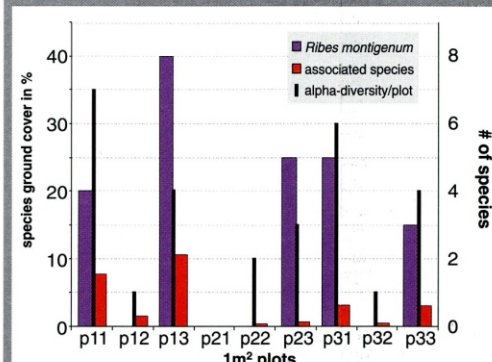
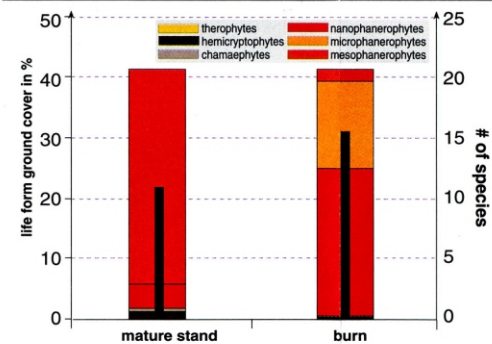


Suppl. Via: example of a exogenous dynamic process. Comparison between an old growth forest (upper plot) and a stand disturbed by wildfire (lower plot) in the Pinyon-Juniper woodland of the Spring Mts., 1900 m a.s.l. The table indicates the life form of the species as well as their ground cover per plot. The graph shows the alpha-diversity of species and the total ground cover of the aggregated life forms per plot.

Beispiel eines exogenen dynamischen Prozesses. Vergleich zwischen einem reifen (obere Aufsichtsskizze) und einem von Feuer gestörten Bestand (untere Aufsichtsskizze) im Pinus-Juniperus Offenwald in den Spring Mts. auf 1900 m ü. NN. Die Tabelle zeigt die Lebensformzugehörigkeit der Arten sowie ihre Deckung. Das Balkendiagramm zeigt die alpha-Diversität der Flächen auf Artenbasis und die Deckung der Lebensformgruppen.



Species	life form	cover old growth	cover burn
<i>Artemisia tridentata</i>	NP	3	20
<i>Amelanchier utahensis</i>	MIp		9
<i>Arctostaphylos pungens</i>	MIp		5
<i>Purshia stansburyana</i>	NP		3
<i>Pinus monophylla</i>	MesP	25	2
<i>Chrysothamnus asper</i> ssp. <i>parryi</i>	NP		1
<i>Garrya flavescens</i>	MIp		0,2
<i>Gutierrezia sarothrae</i>	Ch		0,1
<i>Heliomeris multiflora</i> var. <i>nevadensis</i>	H		0,1
<i>Opuntia erinacea</i>	Ch	0,3	0,1
<i>Achnatherum hymenoides</i>	Hgram		0,05
<i>Bahia dissecta</i>	T		0,05
<i>Caulanthus cooperi</i>	T		0,05
<i>Elymus elymoides</i>	Hgram		0,05
<i>Ephedra viridis</i>	NP	1	0,05
<i>Sphaeralcea grossulariifolia</i> ssp. <i>pedata</i>	H		0,05
<i>Castilleja angustifolia</i>	H		1
<i>Chamaesyce fendleri</i>	H		0,1
<i>Cryptantha tumulosa</i>	H		0,05
<i>Eriogonum umbellatum</i> var. <i>subaridum</i>	Ch		0,2
<i>Juniperus utahensis</i>	MesP		10
<i>Streptanthus cordatus</i> var. <i>cordatus</i>	H		0,05
<i>Swertia albomarginata</i>	H		0,05
dead wood			2



Species	p11	p12	p13	p21	p22	p23	p31	p32	p33
<i>Ribes montigenum</i>	20		40			25	25		15
<i>Aquilegia scopulorum</i>	0,2	1,5	0,5			0,05	0,7	0,5	2
<i>Ivesia cryptocaulis</i>	0,3		0,1		0,2	0,5	1,5		0,8
<i>Draba jaegeri</i>					0,1		0,1		
<i>Valeriana acutiloba</i>	3		10						
<i>Antennaria soliceps</i>	4								
<i>Trisetum spicatum</i>	0,05						0,3		0,2
<i>Heuchera rubescens</i> var. <i>alpicola</i>	0,2								
moss	0,5						0,5		
debris									

Suppl. Vlb: example of a endogenous dynamic process. Comparison between nine micro-sites with varying shrub cover in the Spring Mts. at 3500 m a.s.l. The table indicates the life form of the species as well as their ground cover per plot. The graph shows the alpha-diversity of species per plot and the ground cover of *Ribes montigenum* vs. the associated species per plot.

Beispiel eines endogenen dynamischen Prozesses. Vergleich zwischen neun Standorten in den Spring Mts. auf 3500 m ü. NN mit verschieden hoher Strauchbedeckung. Die Tabelle zeigt die Lebensformzugehörigkeit der Arten sowie ihre Deckung. Das Balkendiagramm zeigt die alpha-Diversität der Flächen auf Artenbasis und die Deckung von *Ribes montigenum* im Vergleich mit den Begleitarten.