

A hypothetical framework for testing phytodiversity in mountainous regions: the influence of airstreams and hygrothermic conditions

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with 12 figures

Abstract. High mountain ranges are considered “hot spots” of phytodiversity due to their geomorphological, petrographical and climatic complexity in relation to the surrounding climate and vegetation zones. The degree of species numbers in high mountains depends on different factors: mass elevation, orographic heterogeneity, location within a floristic region and climate zone, frequency and amount of natural disturbances, as well as the position of the mountain chain against advective airstreams. While these factors are considered as the main triggers driving γ -diversity at a general macro-level, additional stand conditions and processes play an important role for the degree of β -turnover, considering the change of species number in altitude at a meso-level (Fig. 1 and 3) and of α -diversity at a micro-level. After analysing different effects caused by mass elevation (Fig. 7), the second part of the paper focuses attention on the importance of different directions and types of airstreams. A main distinction is presented by the comparison of a species-poor type, given by convective currents and a species-rich type given by obvious climatic differences between windward and leeward exposures (Fig. 8 and 9). Intermediate types result in transitional numbers of species (Fig. 10 to 12). It must be emphasized that the extent of advective airstreams form an important, but only one of the decisive triggers concerning the degree of γ -diversity of a high mountain range.

Keywords: α -, β -, γ -diversity, advective and convective airflows, mass elevation effects; homogeneous, intermediate and heterogeneous exposure types.

1. Mountain ranges as “hot spots” of phytodiversity: criteria for consideration

According to BARTHOLOTT et al. (1996), high mountain ranges are regarded as biodiversity “hot spots” (for details of the term see MYERS (1988)). This concept must first of all be seen as relative to particular climatic or vegetation zones and biogeographic regions, in which mountain ranges occur and rise up to their different altitudinal levels. Global maximum values are reached in tropical mountain ranges, where conditions of tropical species richness in the wake of evolution meet a maximum number of altitudinal belts (comprising montane, cloud, and elfin forest, altotropical shrub- and grassland up to subnival habitats).

Relief formation as a result of mass elevation and dissection controls the extent of the γ -diversity, which, in the sense of WHITTAKER (1972), ex-



Fig. 1. The increased γ -diversity in high mountains results from a large diversity of ecotopes caused by variety in vertical and horizontal direction (altitudinal belts and also dissection by azonal sites). Avalanche ravines in subalpine spruce-larch-forest south of San Bernardino (1200–1600 m a.s.l.) at Misox, Grisons/Switzerland.

presses the overall diversity of a landscape and, according to BEIERKUHNEIN (1998), by extending this approach, can be characterized by way of using the number of species in a larger area (determined by an encircled regional flora). In mountain regions different altitudinal levels lead to an upwardly greater change in the number of species and differentiation in vegetation. In this a multitude of relief features (steep walls, terraces, troughs, spurs, etc.) may in turn cause differences in the level of numbers of biocoenoses or habitats within altitudinal belts. The horizontal gradient of change in species and vegetation is thus joined by a vertical one, which causes a further expansion of the species inventory (Fig. 1).

Variability enlarged to this extent can be described by degrees of heterogeneity or homogeneity. The sum of (dis)similarity in this way is described by the β -diversity. At great altitudes the number of different ecotopes increases thanks to the superimposition of different functional control factors, including the more or less frequent processes of disruption in azonal ecosystems like avalanche tracks, wild streams or active scree slopes. They cause a juxtaposition of different successive stages, thus adding a chronological component to the spatial one (β -turnover according to WILSON & SHMIDA 1984; WOLF 1993 and WITTE 1994 also employ the concept

to characterize a change in altitude). So diversity is less tied to mountain-specific qualities like frequent frost events, longer snow-coverage, elevated wind speed, or minor nutritious soil properties than to a complex structure of small habitats. The micromosaic of phytocoenoses is driven by the pattern of morphotopes that might be highly differentiated in ecotones with a complicated microrelief, microclimate, and microtrophic structure as it is true for many coastal, riparian or mountainous environments (SCHWABE 1997).

The three different dimensions of diversity are at the same time linked to different levels of scale. This paper sets out to consider that scale in greater detail, which includes entire mountain complexes, i.e. the overriding macro-level. Particular attention is paid to the flow of air masses against a mountain range and its significance for hygrothermic diversity and the resulting species richness of a mountain range, i.e. its γ -diversity. To complete the picture, the regional meso-level (particular altitudinal belts) and the local micro-level (individual sites) are considered in the introductory survey (2 and 3).

In part, these considerations are still of a hypothetical nature, though they are at the same time the result of observations which the author was able to make in the Alps and the Pyrenees, in the Cordilleras between Alaska and Tierra del Fuego, in the Atlas Mountains, on Kilimanjaro and in the Drakensberg, in the Blue Mountains of Australia and on Hawaii. Moreover, the Swiss Alps, the Sierra Madre de Chiapas, the north Chilean High Atacama and some high mountain regions of Central Asia supply concrete data from transect recordings, which support the following considerations. Current studies in the Basin and Ranges, in the western Rocky Mountains and in the Sierra Nevada contribute to the consolidation of what is presented here.

MUELLER-DOMBOIS & FOSBERG (1998) present a framework of factors which help to explain vegetation at all scales, in our sense from plant formations of a defined mountain range or from biomes to specific association types. Those factors controlling vegetation by climatic, petrographic and edaphic conditions, as well as by the disturbance regime might be considered as external triggers, others as internal ones defining the vegetation in a narrower sense (flora, access potential of plants, ecological plant type). In the present paper the author submits differentiated lists for each of the three distinguished levels pointing out the most important factors which drive the respective type of diversity.

2. Typification at meso-level (beta-diversity)

With regard to the species richness at different altitudinal levels, i.e. at the meso-level, the following criteria are to be taken into consideration (Fig. 2):

- Evolution = historic-genetic potential of the wider environs.
Example: due to opportunities for migration during glacial times, the nemoral zone in North America presents a more extensive reservoir of taxa than its equivalent in Europe, so that mountainous altitudinal levels

here and there are recruited from different taxa potentials based on different histories of climatic and floristic development.

- Growth climate = altitudinal sector of optimal hygrothermic conditions. Example: in tropical mountain regions the optimal altitudinal location for plant growth (i.e. phytomass that is rather often correlated with highest diversity) tends to be defined by the level of maximal precipitation; in humid mountain regions outside the tropics, it occurs at the warm level at the base.
- Complexity of ecotopes = number of plant communities within one altitudinal level. Example: in the sub-alpine coniferous forest, for example, avalanche tracks and mudflows may lead to the formation of more azonal special sites than at the level of deciduous montane forest not reached any more by destructive events of mass movement.
- Cycles of disturbances = various controlling factors in regeneration processes at each altitudinal level. Example: small disturbances by burrowing and solifluction in alpine mats cause briefer spatial-temporal cycles with more frequent "chances" in the composition of species than long-term processes of self-generation in deciduous forests (disturbance versus autogenesis, BÖHMER 1999).
- Anthropogenic interference = extent and intensity of human influence. Example: relatively untouched, as well as moderately and uniformly utilized, altitudinal sections support a relatively smaller number of species than those where natural space is complemented by a multiple system of land use with a large number of adventitious invaders.

The significance of particular factors varies considerably in the mountain ranges of different zones. The evaluation of factors in Fig. 2 is therefore to be regarded merely as an example and as one of many possibilities. However, the evolutionary contribution to the abundance of species in the extratropics must in principle be held to be comparatively small, whilst playing a much more important role in the tropics (s. Rapoport rule in 4). In respect of climate favourable to growth, all highlands share a reduction in the variety of species at high altitudes, due to increasingly harsh environment. At least in humid mountain ranges outside the tropics the number of species is related to the thermally favourable low levels. In tropical mountain ranges, on the other hand, the optimal zone of phytodiversity per altitudinal level largely follows the vertical precipitation gradient; this is defined by a belt of a maximum amount, the altitudinal position of which depends on the aridity of the base level (LAUER 1976; RICHTER 1996).

Variety of sites at an altitudinal level is determined by the juxtaposition of fragments of numerous zonal and azonal ecotope complexes with its own particular regeneration systems including different stages of succession. In extratropical highlands, subalpine forests on the steep-sided rock walls of glacial troughs may show marked dissection by channels and talus slopes. However, in mountain ranges within and outside the tropics, the sector of maximum β -diversity often occurs above the timberline, where

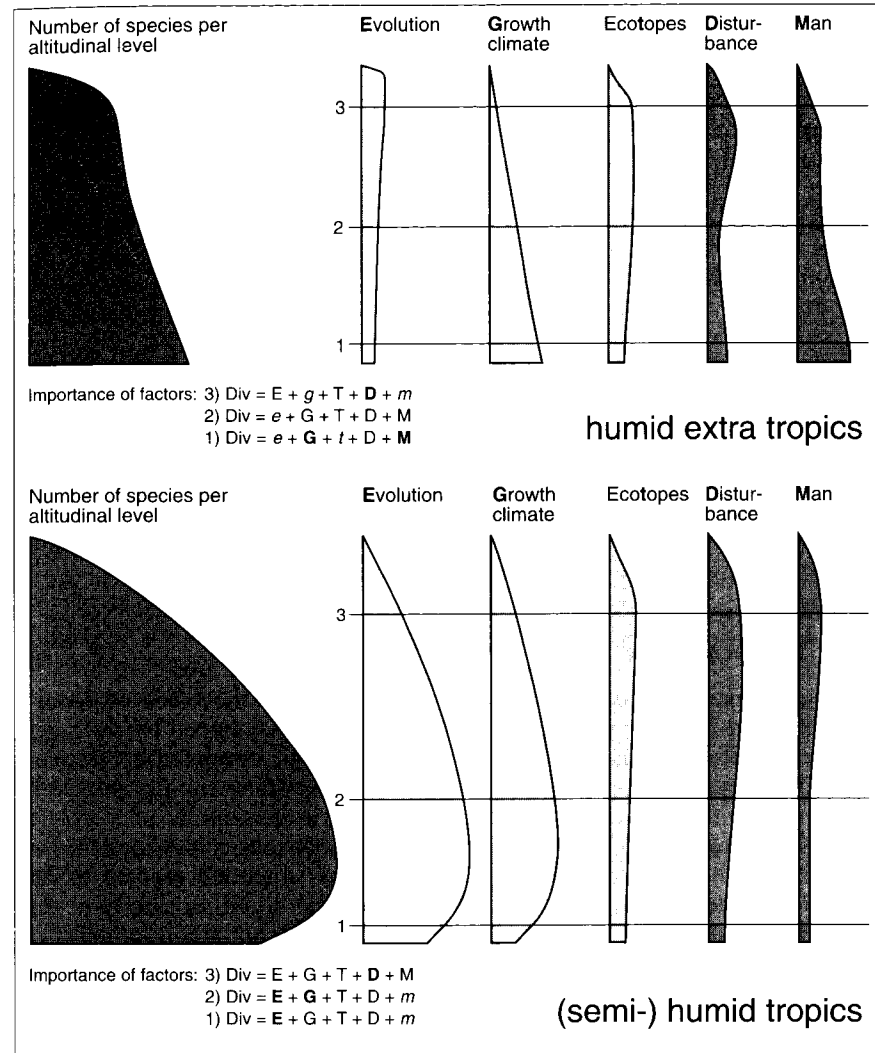


Fig. 2. Vertical change in species richness and factors considered to control the species number per altitudinal level. Generalized variations as expected to occur in the humid extratropics and the humid tropics (theoretical derivations that may vary among specific mountains; for a comprehensive description of disturbance regimes in high mountains see BÖHMER 1999 and BÖHMER & RICHTER 1997). For altitudinal levels 1, 2 and 3 the significance of possible influence of the central factors are expressed in simple summary formulas: small print italics = insignificant to detrimental to species; normal print = normal occurrence; bold print = promoting species.

close morpho-topographical spacing (small ridges and hollows), together with disturbances of several dimensions (influence of burrowers, solifluction, snow anomalies) promote a small-scale mosaic of dry and wet ecotopes, or with different edaphic conditions. In general, disruptive factors in particular prove to be very varied, depending as they do on highly diverse regional accidents. Disturbances have to be considered as a characteristic feature of high mountains, due to the fact that rapid mass movements (mudflows, landslides, rockfalls, rockslides, avalanches) are frequent and extensive, as well as storms or fires bring about gaps in the vegetation.

Human influence on the number of species per altitudinal level may vary from the accidental import of attendant cultural items to intentional introduction of alien pasture plants. In many cases they contribute to an increase in species richness (not to be confused with greater "quality" of the species composition!). The introduction of alien plants from extratropical lowlands affects the high altitudes of the tropics even more than the high altitudes in locations outside the tropics where the supply of alpine ruderals is naturally smaller. If large areas are affected by deforestation, human interference is markedly reducing the number of species in the semi- and euhumid forest areas of tropical mountain ranges even although a number of alien weeds may get in instead.

3. Typification at micro-level (alpha diversity)

The gradients presented above apply only in part to the stock of species per habitat (α -diversity). This level of scale will be well served by the registration of uniform surface areas in order to arrive at a comparable reference base. Differently from the meso- and macro-level, where the floristic composition depends on the immigration of taxa with consequent processes of speciation, most control factors for the number of species per location are subject to habitat-internal ecological rules. This includes vegetation dynamics with its different series of succession. It is worth noting here that in extratropical regions "full series" (DIERSCHKE 1994) of secondary succession in forest belts are in most cases accompanied by a decrease in plant species during its last stages (HARD 1978), whereas in the tropics a tendency towards increases in species can be observed. This concept is resulting in the first case from many annuals within a pioneer phase but fewer woody species within a mature stage, which, in contrast, is characterized by a lot of tree- and epiphyte-species in the tropics.

For the record, it is therefore to be stated that the following characteristics are superimposed upon by internal features of ecosystems, thus ensuring further diversifications in species richness:

– Micro-climate: Small-scale differences in the radiation balance by open sites versus effects of shadowing plants as well as micro-relief govern heat potential and the force of evaporation, and just like small-scale patterns between shaded and sunny positions, they determine the quality of the growing climate, and thus also the inventory of species.

- Availability of water: Together with soil type and form of humus, quantities and types of precipitation regulate the wealth of species insofar as locations which are too wet or too dry may hinder the establishment of many species.
- Soil fertility: At least in regions outside the tropics, in mats of herbs and grasses some types of deep, fertile soils aid the dominance of just a few dominant species, whereas shallow, poor substrates may offer space for plenty of different species. Instead, many forests on infertile soils indicate a minor species richness as the nutritious consumption of woody plants requires an elevated supply, which results in nutrient deficits for most accompanying species; in the tropics and subtropics this factor tends to be of subordinate importance.
- Animal activity: Extent and density of burrowing, digging and treadmill patterns with consequences for transfer of nutrients, zoogenetic processes causing erosion and accumulation, herbivory's eating way, and the distribution of pollen and seed in conjunction with variations in the populations all lead to fluctuations in the composition of species and thus the number of species.
- Ecology of dispersal: The access potential of some taxa to reach a specific site in high mountains is limited; as the steep topography opposes the spreading of propagation types not transmitted by wind or animals, they must be subject to specific facilities of expansion by generative and vegetative processes.
- Structural diversity: The type of formation of a given plant community, i.e. the pattern of distribution of life-forms results in stand densities with different degrees of openness, which determine the variability of irradiation and humus contents for undergrowth and intermediate growth.

Tendencies towards vertical change are most likely to be found in the last-mentioned point, with "leaps" in structure of stands respectively in micro-climate as the chief agents for harsh alterations in species numbers per area in the extratropical humid subalpine-alpine transition: opening up of stands in the timberline ecotone instantly leads to an increase in the diversity of micro-habitats (Fig. 3, top left, and Fig. 4). Here, the tight-knit pattern of overshadowed and open patches provide more complex areal and vertical structures than the mitigating climatic effects in dense dark coniferous forests (RICHTER 1994). In the mountain regions of the semiarid tropics, transitions tend to take place more gradually, since it is entirely a matter of shrub formations, steppes or open forests with higher light levels. In cases of dense forest formations like those in the eastern Great Basin, a maximum of species may appear at the boundary of the lower and upper timberline (double peak of diversity in Fig. 3, top left). In the same system of co-ordinates there are indications of a simple altitudinal change for per-arid mountains as, for example, on the western slope of the Cordilleras above the Atacama (Fig. 5). In this example of the absence of forests, the diversity of species is determined solely by the optimal hygrothermic conditions for plant growth, and focusses on that altitudinal belt, which is not

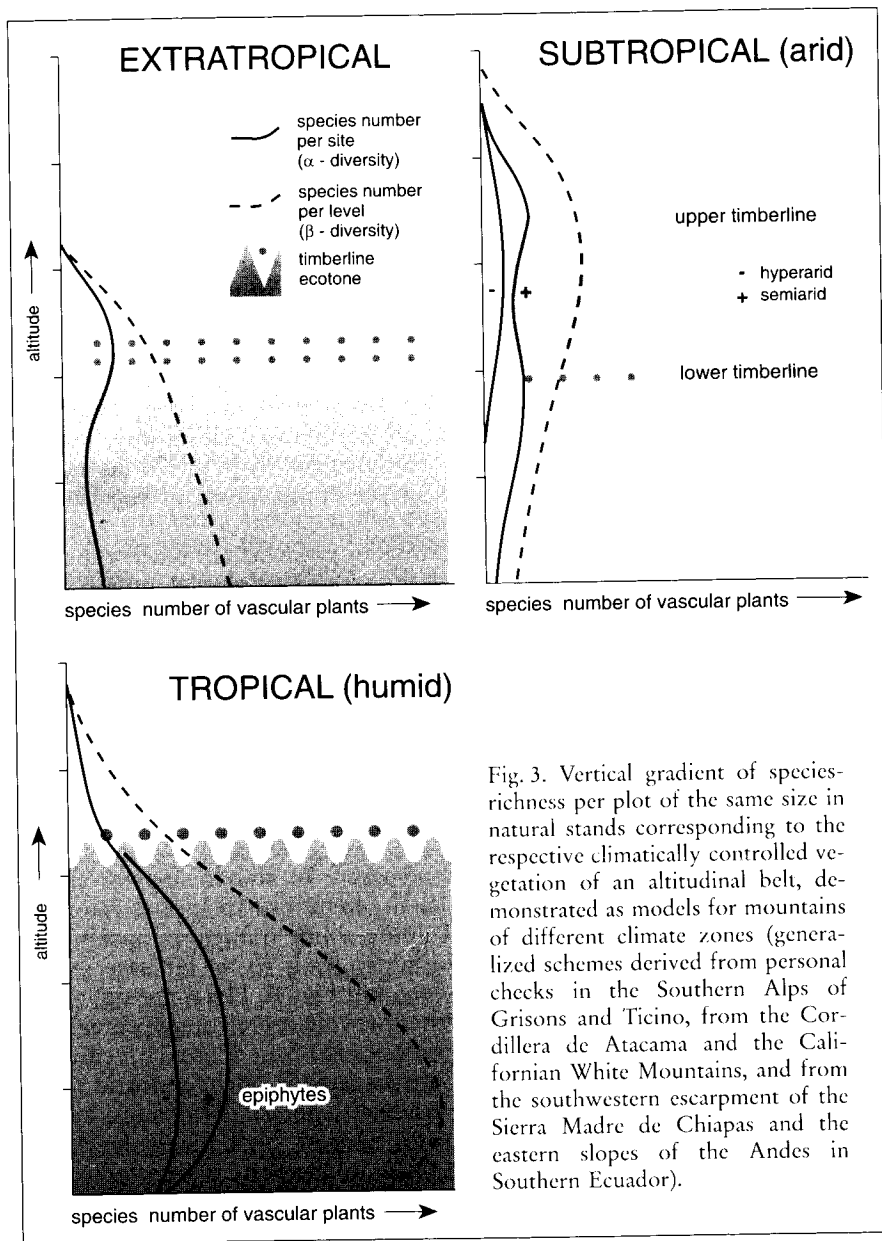


Fig. 3. Vertical gradient of species-richness per plot of the same size in natural stands corresponding to the respective climatically controlled vegetation of an altitudinal belt, demonstrated as models for mountains of different climate zones (generalized schemes derived from personal checks in the Southern Alps of Grisons and Ticino, from the Cordillera de Atacama and the Californian White Mountains, and from the southwestern escarpment of the Sierra Madre de Chiapas and the eastern slopes of the Andes in Southern Ecuador).

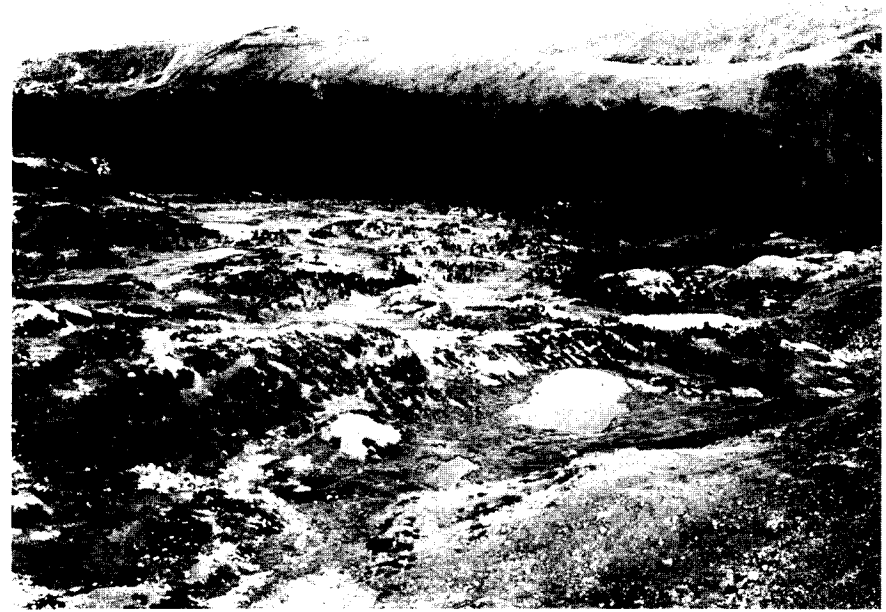


Fig. 4. In extratropical regions, the structural mosaic within timberline ecotone in comparison with subalpine dark coniferous forests (background) and alpine mats provides a complex pattern of habitats (denudation terrace in the foreground) with an ecotonal maximum of species. Forest Canyon in the Rocky Mountains (3600–3800 m a.s.l.) with different phytocoenoses on rock deposits, rounded abrasion rocks, ground moraines, lake shores and bogs.

yet too cold, though distinctly more humid than at the plant-free base level.

In the humid tropics altitudinal change is determined by other features: with the maximum of species occurring at a lower belt (in the example of Fig. 3, bottom left, at around 1200 m a.s.l.) of the two most frequent tropical life-forms, which are trees and epiphytes, here the trend is based on an advanced stage of evolution. The same altitudinal section reveals itself as a region – in the sense of the Rapoport rule (RAPOPORT 1982; STEVENS 1989) – in which many of the present species show only a very limited area of distribution, or a narrow altitudinal spectrum. Whether, and in how far, the maximum of species in the tropical altitudinal profile is simultaneously controlled by an optimal combination of the temperature and humidity supply, remains to be clarified, as does the question of in how far the widely acknowledged “intermediate disturbance hypothesis” (GRIME 1973, and CONNELL 1978) is at all relevant for the number of species per location in tropical mountain ranges (critique by HUSTON 1979, and RICHTER 2000). There is evidence, that at least in forests of lower and intermediate levels processes of an explosive speciation and adaptive radiation on a

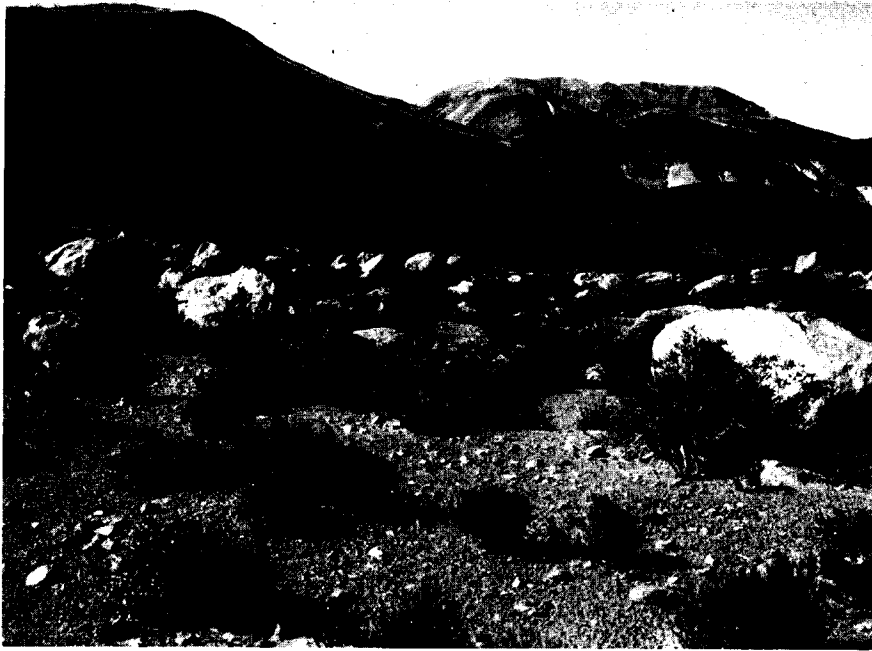


Fig. 5. In high mountains of hyperarid regions without forests, maximum species richness corresponds to optimum climatic conditions. Upper part of the Atacama in Northern Chile (3900 m a.s.l.). Scrub-formation (tola alta) with *Fabiana denudata*, *Parastrephia quadrangularis*, *Baccharis incanum*, *Junellia scriphiooides*.

microgeographic scale might be much more important for differences in diversity ("species swarms", GENTRY 1982). Unlike the extratropical regions, the tropics experience a reduction in species at the timberline, as soon as trees and epiphytes as main supporters of tropical diversity drop out (WITTE 1994; derivations from GENTRY 1988 and ALMEIDA-LEÑERO 1997; Fig. 6).

4. Typification at macro-level (gamma-diversity)

At the macro-level, in this case an entire mountain range, the following criteria are of prime importance for the expression of γ -diversity – again with examples:

- Altitude and extent of a mountain range determine the number of different altitudinal levels.
Example: within the same climatic zone, the higher and more extended Alps host more species than the lower and smaller Sudeten.

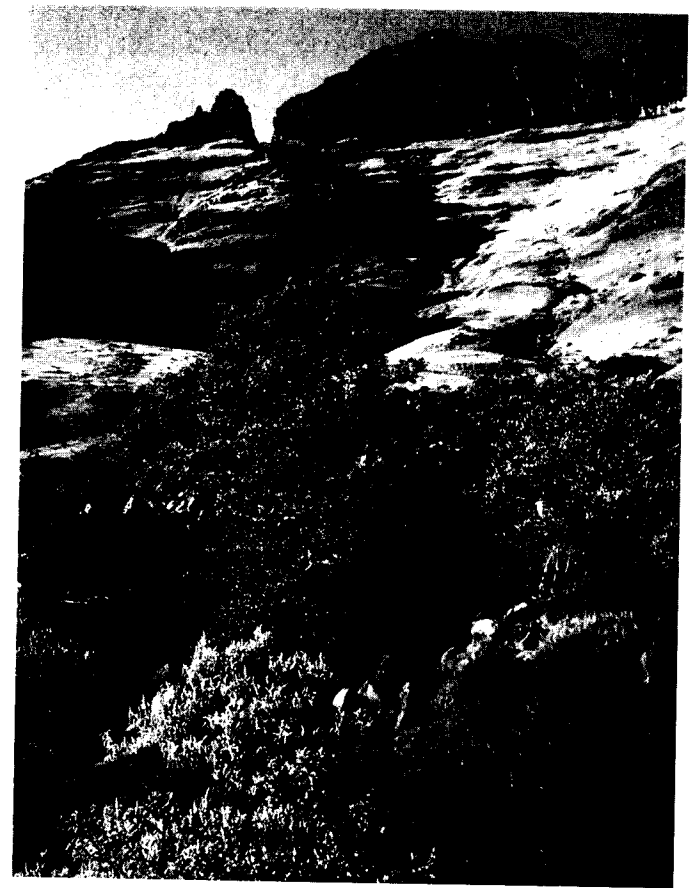


Fig. 6. In contrast to the species-rich afro-montane lowland forests the timberline ecotone at Giants Castle in the Southern African Drakensberg underlies only few tree species (2350 m a.s.l.). Formation along a brooklet with *Leucosidea sericea*, *Buddleia salviifolia*, *Helichrysum trilineatum*, *Erica* spp. within a montane savanna of *Themeda triandra*.

- Internal orography and petrographic heterogeneity of a mountain range.
Example: a straight-forward mountain range structure like the Pyrenees supports fewer species than the highly complex Dinarides, to name a centre of endemism.
- Number of disturbance regimes and their frequencies.
Example: mountain ranges, which are affected by numerous disturbance regimes, (e.g. woodland fires and droughts in the lower reaches, burrowers and solifluction at the higher levels, avalanches at the intermediate level of the Rocky Mountains), present more succession series including complete specific stages than mountain ranges with few disruptive features and less disturbance frequency (e.g. the White Mountains).

- Floristic position of the mountain range.
Example: due to its position between the pontic, euxinic, illyric and east-mediterranean flora, the High Balkans as one more centre of endemism present a higher species potential than the Carpathian Mountains between the pannonic and the pontic floristic provinces.
- Position of mountain ranges in the scheme of climatic zones.
Example: thanks to its actual climate-ecological conditions, and following the Rapoport rule, to its paleo-climatic history a high mountain range in the polar zone cannot host as many species as a tropical one.
- Position of mountain ranges in relation to advective airstreams.
Example: the Sierra Nevada in California, with its marked windward and leeward effects, presents a clear contrast of exposures largely absent from the leeward-facing White Mountains.

While the first points are evidently known in outline, the last one in the list has hitherto scarcely been taken into account; attention is drawn to it here. A distinction is made between three types and several sub-types in one case, where dispositional differences, which in turn differ in the degree of their profoundness, lead to different numbers of species in the mountain ranges in question:

- The heterogeneous type with a predominantly advective influx of airstreams, for instance during frontal wave passages within the westerly wind belt, or monsoonal influences in the subtropics or in the tropics, where trade-winds may show similar effects.
- The homogeneous type with influxes of predominantly convective airstreams during convergent weather situations, prevailing in desert regions.
- The intermediate sub-types featuring vertical change in the ratio of advective to convective flows, or changeable advective directions.

Before going into detail about the way these particular types perform, three different basic principles of the mass elevation effect in relation to flows of air masses will be presented: the continentality effect, the Merriam effect and the blocking respectively foehn effect (Fig. 7).

4.1. Mass elevation effects

The best known, though the least often occurring, type of mass elevation effect is held to be advective airflows running up against a mountain range from various directions. If it is a comprehensive and high mountain complex, screening by sections on the flanks must be assumed, where mild and humid air masses predominate, whilst the less humid mountain centre is marked by greater temperature fluctuations. Though winters are cooler here than on the flanks, the warmer summers contribute decisively to the raising of the timberline in the central area. Circumstances may even encourage the formation of additional plant communities with continental

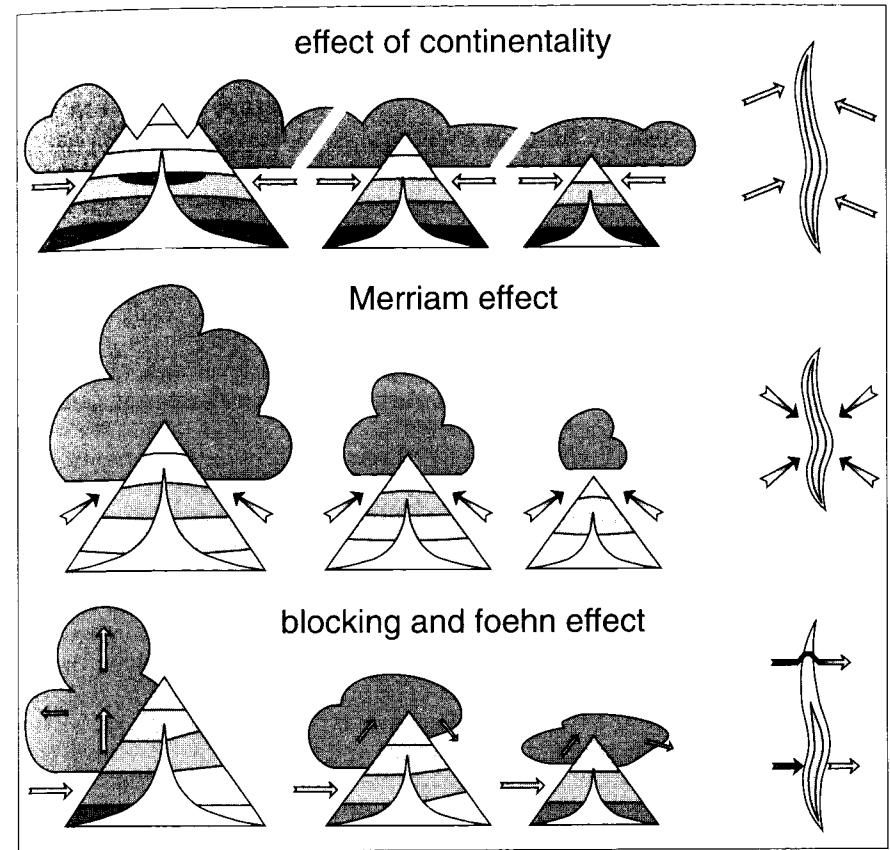


Fig. 7. Three different airstream types related to three mass elevation levels shown as profile sketches with altitudinal belts (dark = dense, light = open vegetation); top view at right.

representatives such as, for instance, *Pinus cembra* as a prototype of the "continentality effect" in the Central Alps.

Only mountain ranges which run parallel to the predominant airflows can cause advective blockages on both sides, though more frequently the influx of humid air masses takes place from one escarpment only and results in occurrences of foehn on the opposite side. However, since such mountain ranges outside the humid tropics are not governed by a definite constancy of direction, blockage and foehn between, for instance, the northern and the southern Alps alternate frequently, so that both sides experience more or less balanced conditions – in contrast to the constancy of the direction of blockage and foehn effect (cf. below). Fig. 7 presents the consequences of the continentality effect by way of the peripheral-central ascent

and some mountains on the South-East Asian Islands. Though here species richness is thought to be very high, due to the tropics, it is conceivable that it is less than the heterogeneous type which predominates in tropical mountain ranges. This hypothesis has not yet been tested, and it may be difficult without considerable input.

4.3. Heterogeneous type

Fig. 9 shows that the “heterogeneous” type stands out thanks to an unambiguously constant advective direction. Quantities of precipitation on the windward side and a dearth of rain on the leeward side are the cause of quite different altitudinal belts on both escarpments, since humid as well as arid sequences exist from the warm low levels to the cold high levels, as shown in the illustration section on the bottom right. This example with its ten different climatic types presents a broad ecological spectrum for the formation of different plant communities. Accordingly, analyses of floristic similarities indicate only minor agreements in the occurrence of species on the two exposures. The dendrogram therefore shows greater values of similarity for altitudinal sequences of species inventories than for the comparison of exposures at equal altitudinal levels (in this example cf. left-hand

position of western slope locations and right-hand ones of eastern slope locations). Floristic assimilation between both exposures only occurs in the crest region where humid air masses cross over to the leeward side; evidence for this can be found in transitory change in high altitude communities on both the western and the eastern side of the crest. Finally the relatively elevated bridges in the diagram symbolize the limited similarity among the plant inventories presented in all the relevés. This points to a high overall species potential, which is recruited from various gene pools, at least on the two slopes of the mountain chain. In this case the multiple hygrothermal conditions lead to fundamentally different sequences of altitudinal belts in one mountain range, or to two different altitudinal belts per level, and thus to a marked increase in γ -diversity.

This type of mountain with a large number of species may occur in all climatic zones. Outside the tropics it can be found in the Alaska Coast Range, in the southern Andes of Patagonia, and in the New Zealand Alps; to a lesser degree it also shows up in Scandinavia. In the subtropics, the mediterranean western sides of the continents are to be separated from the monsoonal eastern sides. In the first case, frontal winter rains provide windward and leeward contrasts in the Medium and High Atlas, in the Sierra Nevada in California and in Spain, and to a lesser extent in the Apennines; in the latter case, monsoonal summer rains cause contrasts between the humid eastern and the arid western slopes, for instance in the Kongur Shan in southern China, in the Southern Drakensberg in South Africa, in the Great Dividing Range in eastern Australia, and to a lesser degree also in the Serra do Mar in southern Brazil. Within the subtropics, parts of the Caucasus and the Pontic Mountains occupy a special position between the mediterranean and the monsoonal types, but also stand out thanks to their considerable vegetation differences, with matching species richness. In the tropics corresponding differences occur, for instance in the Mexican Sierra Madre Oriental, in the Central Andes, or on the high mounts of East Africa and on Mauna Loa and Mauna Kea on Hawaii.

Marked floristic differences also occur between the lower altitudinal level of the western and the eastern slopes of the Rocky Mountains and the Appalachians, while exposure contrasts already decrease at intermediate levels as a result of climatic alignment. Though in these cases climatic differences do occur at base levels, they are less decisive for deviations between species inventories than the floristic limitations, since the mountains separate different floristic regions (TAKHTAJAN 1986).

4.4. Intermediate types

With respect to species richness, “intermediate” types constitute a transition between the two extreme types (heterogeneous and homogeneous). In these cases radiation differences cause a displacement of altitudinal belts at different exposures or one-sidedly interpolated plant communities on mountain slopes. Most mountain ranges can be classified as such, with different causes leading to different patterns. This results in several subtypes

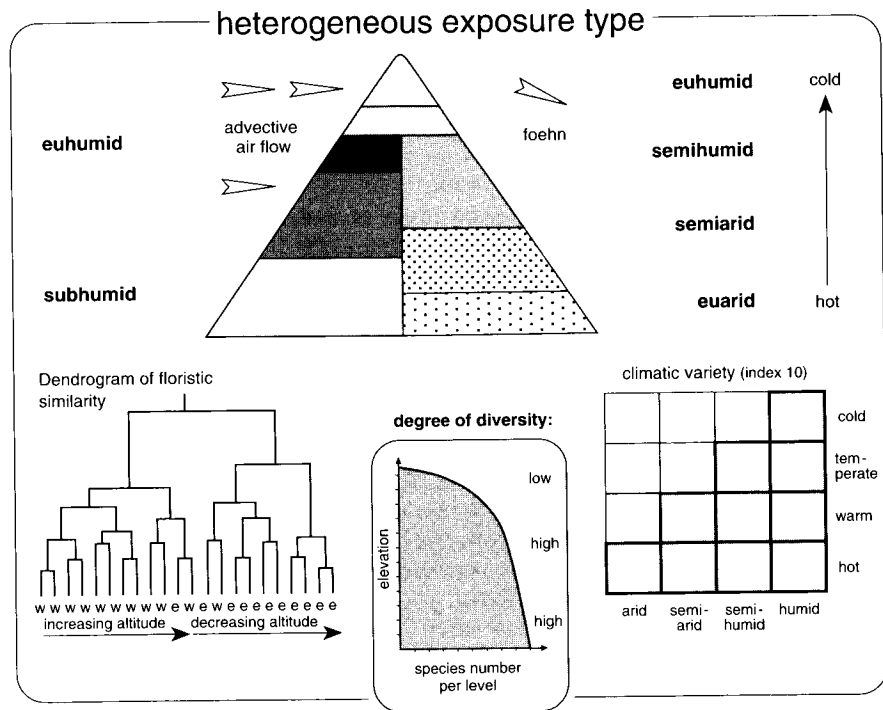


Fig. 9. Heterogeneous type (prototype: Sierra Nevada in California; HETZNER et al. 1998).

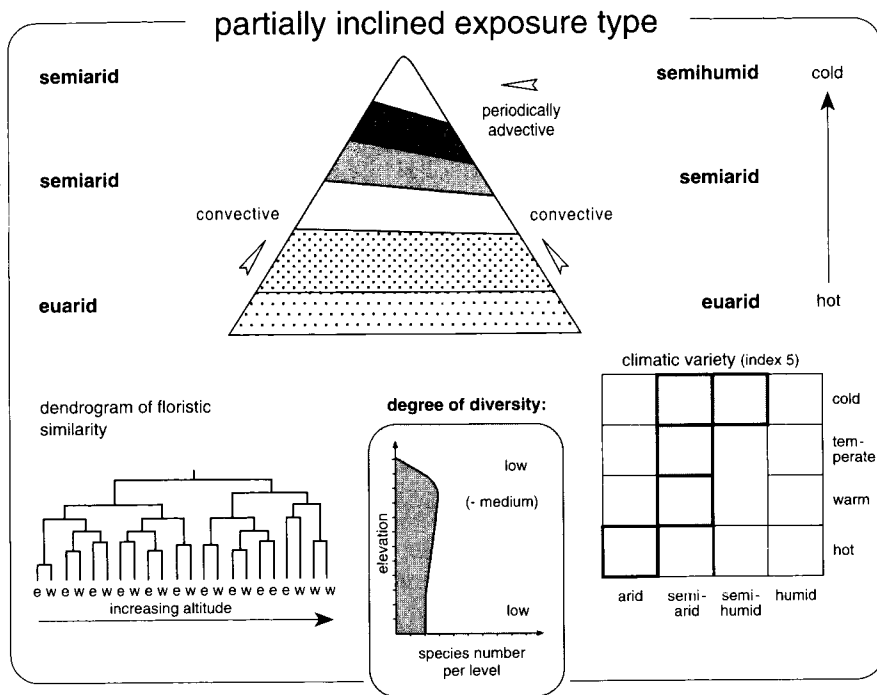


Fig. 10. Intermediate type with partially inclined belts (prototype: Snake Range in Nevada; HETZNER et al. 1998).

depending on the mountain's position against various combinations of airstreams, three of which will be presented here.

The subtype of the partially inclined altitudinal belts differs only slightly from the homogeneous type. The configuration presented in Fig. 10 occurs thanks to a unilateral lowering of the upper vegetation level, which has been caused by an increase of an advective stream in the higher parts of mountain ranges superseding the convective flow of the lower parts. The resulting asymmetry of the upper belts (still) with mesothermal, xerophilous elements on one slope, and (already) microthermal, hygrophilous plants on the opposite one, lead to a transitory increase in species per altitudinal level. This does not, however, necessarily imply an increase in the γ -diversity throughout the entire mountain range. Similar inventories of species or of plant communities, are shown in the dendrogram for both exposures at the low and intermediate levels, whilst at the higher levels divergences become more obvious. Evidence for this situation has hitherto only been established for some mountain ranges of the eastern Great Basin (HETZNER et al. 1997).

An overall even displacement of altitudinal levels from bottom to top occurs when the main airstream direction runs parallel to the mountain

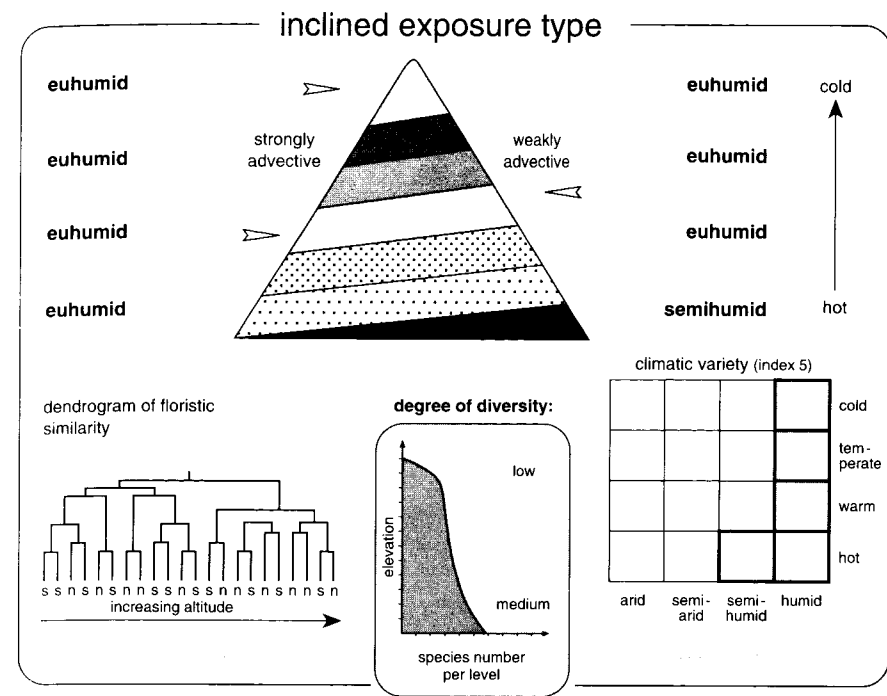


Fig. 11. Intermediate type with inclined belts (prototype: Alps and Pyrenees).

chain. This type is largely confined to regions outside the tropics; it applies mainly to ranges like the Alps or the Pyrenees, which run parallel to the latitude. In these cases humidity supporting westerlies predominate, with the extent of fluctuation varying from southwesterly to northwesterly directions, according to weather conditions and seasons. The fact that in Fig. 11 two arrows indicating airstreams hit the mountain range from opposite directions must therefore not be regarded as a realistic situation; they merely indicate the extent of variations which cause both escarpments to be more or less humid. Throughout this, the rise of altitudinal belts is mainly caused by thermal reasons, so that an additional vegetation zone at base level appears on the southern slope of the two mountain ranges mentioned above. In the Alps it is, for example, the summer-humid insubric complex, and in the Pyrenees the winter-humid meso-mediterranean one, both leading to a rising γ -diversity, as mountain forelands proving to be relatively rich in species on the warmer, southern foot-hills (cf. broader base of the altitudinal gradient in the middle diagram). In the dendrogram the two expositions no longer alternate in facing one another; instead, species inventories have relatively more in common between one and the next higher level, thanks to the rise in altitudinal belts. The conditions described above also apply to some other European mountain ranges such as the Tatra and the southern section of the Carpathian arc.

inserted exposure type

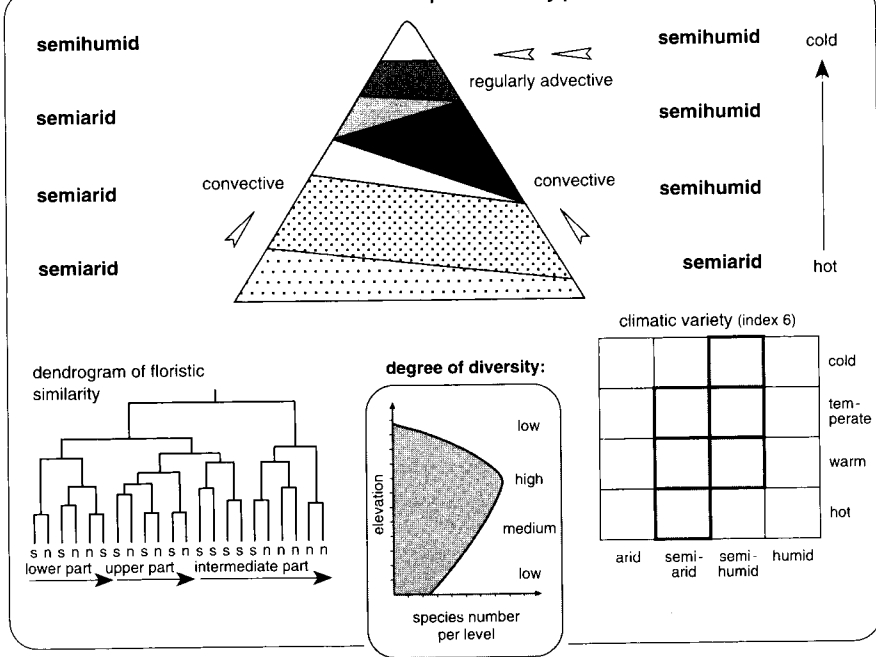


Fig. 12. Intermediate type with increased belts (prototype: Tian Shan; RICHTER et al. 1999).

In mountain ranges where altitudinal belts are inserted on one side only, but are lacking on other escarpments (Fig. 12, upper profile), more sharply defined luff and lee differences must be assumed. Such conditions are found in places where the base level is totally arid and the higher altitudes humid, i.e. in cases where a marked increase of advective airstreams with humidity transfer in the upper levels takes place. Here, the windward side has a hygric advantage in contrast to the enduring dominant convection processes at the leeside, especially if the first one coincides with an exposure on the shady side, where losses through evaporation are less. In such cases the hygrophilous vegetation on the one escarpment and the xerophilous vegetation on the opposite side have little in common. Thus, in the transition zone between the arid and hot low level with few species and the humid and cold high altitudes, there exists a considerable high γ -diversity as a result of the increased climatic variance. Fig. 12 illustrates the latter by presenting six different examples of climatic types, with the dendrogram characterizing the transitory contrast of a dissimilar vegetation between northern and southern slopes by a high bridge. Evidence of the relations of a transitional section at intermediate altitude, which is rich in species, has been proved for most mountain ranges of the Tian Shan, for the western Kuen-Lun and the Hunza Karakoram (RICHTER et al. 1999) and even

applies to low Santa Cruz Island in the Galápagos (MUELLER-DOMBOIS & FOSBERG 1998).

5. Conclusions

The final comment on the significance of the floristic gene pool as a factor contributing to species richness in the mountain ranges shows that airflow aspects form merely one of several controlling factors for phytodiversity in mountain ranges: All the rules mentioned above are theoretically correct, but not necessarily valid. A comparison of the species variety in several mountain ranges also needs always to take into account the other influencing factors mentioned earlier. The seminal work by TAKHTAJAN (1986) suggests itself as a benchmark for the evaluation of paleogeographically derivable floral variety or of endemism, as do the works by BARTHLOTT et al. (1996) and RICHTER (1998) for a zonal evaluation. Climatic altitudinal gradients for the examination of optimal growth conditions can be developed from BARRY (1996) and RICHTER (1996), while the survey by BÖHMER & RICHTER (1997) and RICHTER (2000) provides initial criteria for the evaluation of the significance of disturbing influences and regeneration processes. The position of a mountain range in respect of its climatic zone can be derived from climatic charts, and in this case above all from air-flow maps. As an overall quantity, the altitude and extent of a mountain range result from data on relief energy from topographic maps and the petrographic heterogeneity of a mountain range from geological maps.

This approach allows a framework of key factors controlling the γ -diversity of one particular or of several mountain ranges to be relatively easily devised and assessed in theoretical terms. What is missing, or inadequately known, is hard data on the number of species along altitudinal gradients which provide evidence for or refute the validity of derived values of the ecofactors. Evaluations of potentially existing taxonomic lists may provide initial indications, but due to their varying qualities, rare actualisations and the frequent lack of dividing natural and anthropogenic elements, their sustainability for an examination of the controlling factors is limited. Additionally for many tropical mountain sections the derivation of comprehensive lists will, due to the extreme species richness and to inaccessibility, remain utopian. Thus, a program which envisages transect data collected in releves at fixed altitudinal intervals (for instance at 100 m or 200 m vertical intervals) and agreed surface areas, appears to be more appropriate. Only a comparison of the resulting relative values of such investigations on untouched – or at least near-natural – locations permits more exact testing of the hypothetical framework presented above.

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