GLOBAL CLIMATE CHANGE AND LOCAL DISTURBANCE REGIMES AS INTERACTING DRIVERS FOR SHIFTING ALTITUDINAL VEGETATION PATTERNS

With 9 figures and 4 photos

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Zusammenfassung: Globale Klimaveränderungen und lokale Störungsregime als interagierende Steuergrößen sich verschiebender höhenzonaler Vegetationsmuster

Klimaveränderungen werden im kommenden Jahrhundert eine wesentliche Steuergröße für Ökosystementwicklungen sein. Sie werden sich vor allem in Gebieten wie Hochgebirgen mit engen klimatischen Gradienten deutlich bemerkbar machen. Allerdings werden die Lebenszyklen und Ausbreitungsmöglichkeiten von Arten sowie die Langlebigkeit ortsgebundener Organismen die Anpassung an graduelle, aber bezogen auf die Skala von Ökosystemen relativ schnelle Veränderungen, begrenzen. Lebensgemeinschaften werden wahrscheinlich eine gewisse Trägheit in der Veränderung ihrer Artenzusammensetzung zeigen und die Entwicklung langfristig konkurrenzstärkerer Gemeinschaften verzögern. Dies kann wiederum zu einem Verlust von Biodiversität und zu Einschränkungen von Ökosystemfunktionen und Resilienz führen. In Hochgebirgen könnten dann Störungsereignisse, wie Murenabgänge und Lawinen, vermehrt gravierende Einschränkungen menschlicher Interessen bewirken (Landnutzung, Siedlungen, Infrastruktur). Im Kontrast zu dieser Sichtweise entwickeln wir hier den Gedanken, dass in einem sich verändernden Klima Störungen zu einer raschen Anpassung von Lebensgemeinschaften beitragen. In einer sich verschiebenden Umwelt können einzelne Störungsereignisse, die Teil eines übergreifenden Störungsregimes darstellen, Trägheit aus einem System entfernen (z.B. nicht reproduzierende, langlebige Individuen) und die Etablierung neuer Arten und Strukturen fördern. Dies ist vor allem in Gebieten bedeutsam, in welchen natürliche Prozesse der Ökosystementwicklung vorherrschen und kurzlebige menschlich gestaltete Ökosysteme von geringer Bedeutung sind, wie dies in den meisten Hochgebirgen der Fall ist. Landwirtschaftliche Landnutzung ist hier auf geringe Flächen beschränkt. Störungen können folglich zum Erhalt von Biodiversität und ökosystemarer Stabilität beitragen.

Summary: Climate change will be a major driving factor for ecosystem development during the next century. It will be most prominent in areas with narrow climatic gradients such as high mountains. However, the life cycles and dispersal potential of species and the longevity of non-mobile specimen are likely to limit the adaptation to gradually but, compared to the temporal scale of ecosystems, rapidly changing environments. Communities may perform inertia to the shift of species composition and delay the development of more competitive communities on a long-term perspective. This in turn may promote a loss of biodiversity and restrictions in ecosystem functioning and resilience. Then in high mountains disturbances such as mud flows or avalanches might cause hazardous effects on human interests (land use, settlements, and infrastructure). In contrast to this perspective, we suggest in this paper that in a gradually changing climate, disturbances will contribute to a faster adaptation of communities. In a shifting environment, single disturbance events, that are part of a specific disturbance regime, can remove inertia (e.g. non-reproductive long-lived individuals) from a system and support the establishment of new species and structures. This is most important in regions where natural processes of ecosystem development predominate and ephemeral anthropogenic ecosystems are of low importance, which is generally the case in high mountains. Here agricultural land use is limited to small areas. Thus disturbances can contribute to the preservation of biodiversity and ecosystem stability.

1 Introduction

Despite the development of regional scenarios of relative atmospheric warming and altered precipitation patterns, there is growing uncertainty about the consequences of climate change for biodiversity and ecosystem functioning. Special concern is put on the major drivers for the loss of biodiversity and to biogeographical hotspots of biodiversity, to which many high mountains of the world belong. High mountains are as well highly fragmented refuges as corridors of cross-continental migration (BARTHLOTT et al. 1996; KÖRNER 1999).

Although high mountain ecosystems are assumed to be highly vulnerable due to their combination of harsh environment, short vegetation period and slow growth rates, the high diversity in species and functional types contributes to their persistence in face of land use pressure and changing climatic conditions (KÖRNER 1995). Thus, the preservation of biodiversity is a key factor to ensure functions and services at the ecosystem and landscape scale.

After addressing (1) the accelerating speed and extend of global change as a general dilemma, we identify (2) the drivers for current biodiversity changes. We then discuss biodiversity properties and dynamics, focusing on altitudinal vegetation patterns in high mountain ecosystems. We develop spatially explicit ideas on (3) the possible consequences of climate change. Synergistic effects of (4) shifting altitudinal vegetation patterns and (5) the alteration of local disturbance regimes due to atmospheric warming and locally increased precipitation may enhance ecosystem dynamics and promote (6) the loss of biodiversity. Finally, we develop the rationale of (7) ecological inertia represented by long-lived, slow-growing organisms being both risk and potential for the future of biodiversity and the stability of ecological systems.

2 *The dilemma of accelerating global change for the persistence of biodiversity*

2.1 *The "crisis of biodiversity"*

About ten years ago, in 1992, international political awareness of the need to protect biodiversity was condensed in the „Convention on Biological Diversity" (CBD). The diffuse fear of losing species worldwide was based on scientific findings pointing to a severe "crisis of biodiversity" (e.g. WILSON 1985, 1989). The turn of the century is to witness a species extinction period, whose dimension is comparable to the major natural extinction events, which are documented in shifts of fossil species composition in geological strata during the last 500 million years. Such phases were mainly triggered by extreme climatic changes caused by impacts of extra-terrestrial objects (LEVINTON 2001). Just as in the past, the current period of extinction goes along with a rapid loss of species across different groups of organisms. It is estimated to happen at a rate 1,000 times greater than the natural background rate of extinction (PRIMACK 1993; ROSENZWEIG 1995). However, it has a new quality according to the driving processes. The modern loss of biodiversity is directly related to human activities such as habitat destruction.

2.2 *Interacting mechanisms promoting global change*

Various mechanisms enhancing global change are interacting and self-accelerating. Anthropogenic modifications of biogeochemical cycles lead to substantial responses of the physical and chemical properties of the atmosphere. Such global change phenomena will in turn affect biodiversity, leading to ecosystem responses and ecosystem functioning at the regional scale (Fig. 1).

Global changes affects for example climate and air purity, water cycles and water quality, nutrient availability and microbial activity in soils at the regional scale. The general set-up of land use will be altered. These changes will generate a repercussion in the species composition of communities and ecosystems. More effective vectors such as infrastructure and transport will promote such processes. On the other side, mainly in semi-natural ecosystems, fragmentation of habitats will restrict the dispersal of species and thus the potential of ecosystems for adaptation to new site conditions.

Global warming is an indirect effect of resource exploitation, the release of CO_2 out of fossil fuels. The accelerated melting of ice shields and glaciers gives dramatic evidence of this large-scale phenomenon. In the tropics glaciers are near extinction (DYURGEROV a. MEIER 2000). The melting of the terrestrial Antarctic and Greenland ice shield is presumed to cause a subsequent rise of the sea level.

Altered precipitation patterns may influence the functioning and stability of ecosystems, for example if drought periods are further elongated in semi-arid savannas. A shortened period of frost and snow cover in mountain biomes will be a substantial challenge to the highly specialised life history cycles of alpine organisms.

In addition, landscapes are increasingly homogenized due to land use and cover change. Particular ecosystem types are disappearing. This can be observed for traditional coppices in Central Europe. Unfragmented primary forests are dissected due to oil-exploration and logging in Canada. Remote habitats in high elevation zones are threatened by diffuse settlement in Central Latin American. Shrub- and heathlands on resource-limited soils are exposed to atmospheric nitrogen deposition. Homogenization and fragmentation are affect–ing the heterogeneity of landscapes and the related niche diversity. The change of physical and chemical properties of the biosphere, as followed by changes of human land use, results into a cascade of consequences for all living biota.

2.3 Global Change Dilemma: accelerating speed and increasing spatial extent

Current biodiversity research is facing the dilemma that (1) the speed of ecosystem change is accelerating, and (2) anthropogenic pressure on biodiversity is of global extent. There is a sensitive threshold to the ongoing speed of change. As soon as species cannot cope with the speed or the spatial extent of environmental change, they are likely to go extinct. A decrease of local biodiversity is to be expected if the spatio-temporal mechanisms of migration, phenotypic plasticity and dispersal, meta-population dynamics or evolutionary development do not meet the scales of global change. Consequently, ecosystem functioning may be permanently altered regarding biotic feedback, matter and energy cycles. The limited scales of organisms in contrast to the speed and extend of global change are visualised in figure 2.

Obviously, the organismic potential to change its current location by large-distance migration or fast alteration of life history cycle and growth form will offer survival mechanisms in the face of global change to a certain fraction of species. Still, the shift of distribution areas (decades, centuries) will most likely cover only short distances, and evolutionary adaptation mechanisms will probably require many generations (millennia). The expected spatio-temporal dynamics of global change clearly exceed such low-speed and short-range reactions for most species.

Communities will respond in a specific way to global change. Aside from the potential loss of species, diversity within communities and species richness may increase as well. New environmental conditions may favour the invasion of species with high competitive ability, high potential for large-distance dispersal or migration to a novel habitat. Thus, in order to cope with changing environmental conditions, species need particular adaptive, dispersal and migratory abilities.

2.4 Drivers for the loss of biodiversity

Ongoing discussions about global change phenomena and their local effects on biodiversity have currently been alerted by the report of the Intergovernmental Panel for Climate Change (IPCC 2001). In the face of the accelerating speed of global change, future research outlines such as the 6th framework programme of the

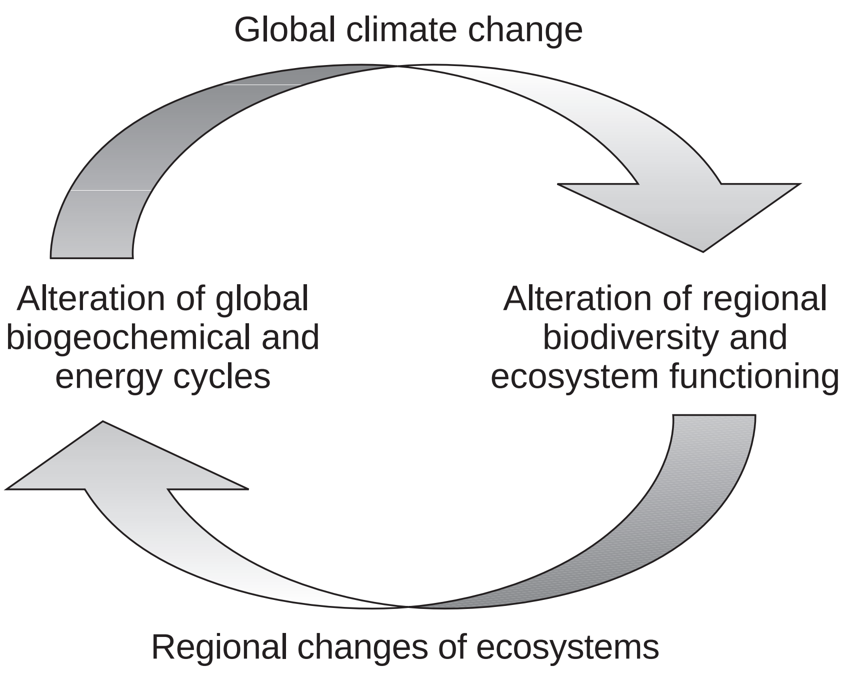

Fig. 1: Alterations of the physical and chemical conditions of the atmosphere are followed by regional changes in biotic diversity and species composition of ecosystems. This will influence ecosystem functioning. This in turn will have feed back on biogeochemical and energetic global cycles

Veränderungen der physikalischen und chemischen Bedingungen der Atmosphäre werden regionale Veränderungen der biotischen Vielfalt und der Artenzusammensetzung von Ökosystemen zur Folge haben. Dies wird wiederum negative Rückkoppelungseffekte auf globale biogeochemische und energetische Kreisläufe haben

European Union address the "drivers" for biodiversity loss as an essential focus of science.

The major anthropogenic drivers of global change are land use dynamics, fragmentation, invasion, and disturbance regimes, nitrogen deposition and atmospheric carbon-dioxide enrichment. Relative atmospheric warming and altered precipitation patterns are indirect effects of human activities, too. These drives are likely to develop combined effects on the physico-chemical, ecological or biomechanical processes. Avalanches, for example, may likewise be caused by climatic or human impact. Both, natural and anthropogenic drivers that are responsible for the loss of biodiversity may be enhanced in near future.

In alpine environments, the drivers most threatening to biodiversity are estimated to be climate change, increased atmospheric nitrogen deposition and changes in traditional land use (Sala et al. 2000) (Fig. 3).

3 *Biodiversity in high mountains*

3.1 Mountain biodiversity research

Current scientific approaches in biodiversity science extend from numerical to functional biodiversity research (Myers et al. 2000; Ernst et al. 2000; Loreau et al. 2001). Several syntheses of international discussions about biodiversity and ecosystem functioning have been published since Rio (e.g. Schulze a. Mooney 1993; Davis a. Richardson 1995; Vitousek et al. 1995; Mooney et al. 1996; Solbrig et al. 1996; WBGU 1997; DIVERSITAS 2002), including high mountains (Chapin a. Körner 1995; Körner a. Spehn 2002; SWISS BIODIVERSITY FORUM 2002). Biodiversity patterns at the landscape scale and functional attributes in the alpine zone have been reported (Beck et al. 1984; Lawton 2000; Nagy et al. 2003).

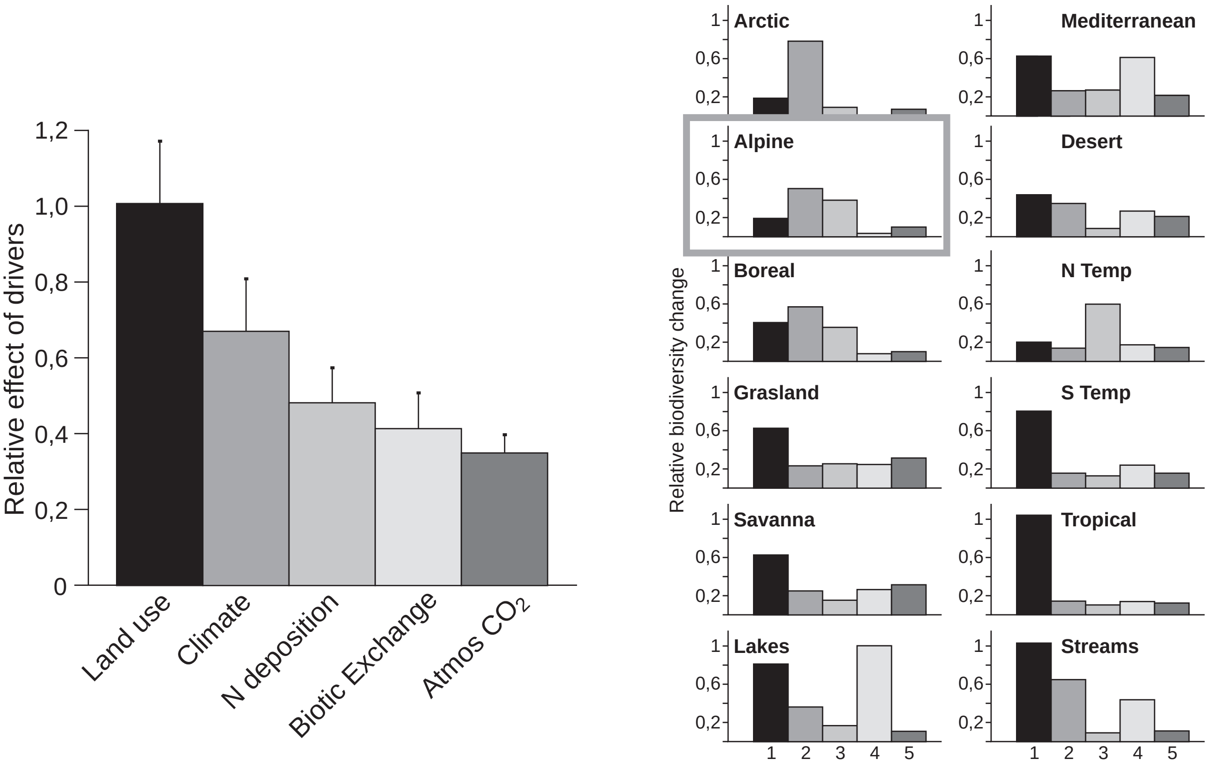

Fig. 2: Relative effects of global drivers for biodiversity change. Prognosis until 2100 (left), and their significance for the loss of biodiversity in different ecosystems (right). Alpine ecosystems are marked on the right side. Note the stronger importance of climate change and changes of nutrient cycles in high mountain ecosystems (after Sala et al. 2000)

Prognose bis 2100 zum relativen Effekt globaler Veränderungen auf die Veränderung der Biodiversität (links) und ihre spezifische Bedeutung in einzelnen Ökosystemen (rechts). Auf der rechten Seite sind alpine Ökosysteme hervorgehoben. Bemerkenswert ist die dort deutlich erhöhte Bedeutung klimatischer und stofflicher Veränderungen (nach Sala et al. 2000)

Mountain ecosystems are identified as highly sensitive indicators for the ecological implications of climate change, particularly atmospheric warming, because low temperatures reflect essential limits to living conditions (HAEBERLI et al. 1999). International networks aiming to monitor effects of climate change in high mountains have been established. Examples are the "Global Mountain Biodiversity Assessment" network (GMBA 2000) or the "Global Observation Research Initiative in Alpine Environments" (GLORIA 2001).

3.2 Why are high mountains so diverse?

Which factors cause the extraordinary diversity of high mountain ecosystems? (1) In comparison to lowlands, mountains are characterised by heterogeneous site conditions regarding parent rock, soil, exposition, inclination, microclimate, hydrology and slope position. Their three-dimensional organisation in space shows a higher variability. This promotes the co-existence of various growth forms and life-history types in close proximity. (2) Due to the vertical compression of thermal life zones, there is a small-scale mosaic of micro-habitats, each inhabited by a set of specialists. This can lead to sympatric speciation. Transitional zones between altitudinal belts, e.g. the forest-alpine transition are particularly rich in taxa. (3) Furthermore, limiting ecological factors such as the short vegetation period due to frost and snow cover, missing organic substrate or sharp wind impede competitive dominance and rather promote species diversity. (4) In high mountains, spatial isolation of habitats explains the occurrence of paleo- and neo-endemism. Due to plate tectonics, many high mountains are organised in linear structures and thus serve as networks for the dispersal of species. For lowland species, these linear structures act as barriers. (5) Adding to the highly compressed diversity of geomorphologic, petrographic and climatic conditions, mechanical disturbances are the major drivers that do shape evolution, and the maintenance and loss of biodiversity (DARWIN 1859; CONNELL 1978; CHRISTENSEN et al. 1989; WHITE a. JENTSCH 2001). Documenting the connection between climate and disturbance will improve our ability to predict ecosystem dynamics and assess the potential impact of climate change on mountain biodiversity.

3.3 Disturbance promotes biodiversity in high mountains

Altitudinal zones of vegetation are believed largely to correspond to temperature isolines. This has been demonstrated for the non-topography limited tree-line (KÖRNER 1995). However, disturbance is omnipresent in mountain ecosystems, so that new approaches focusing on this dynamic ecological factor need to be applied to explain existing vegetation patterns. WESCHE et al. (2000) have indicated that in Eastern African high mountains the local tree-line ecotone is disturbance dependent and rather fire-induced and fire-maintained than due to temperature limitation. The same was found for the tree-line of the Andes in the tropics

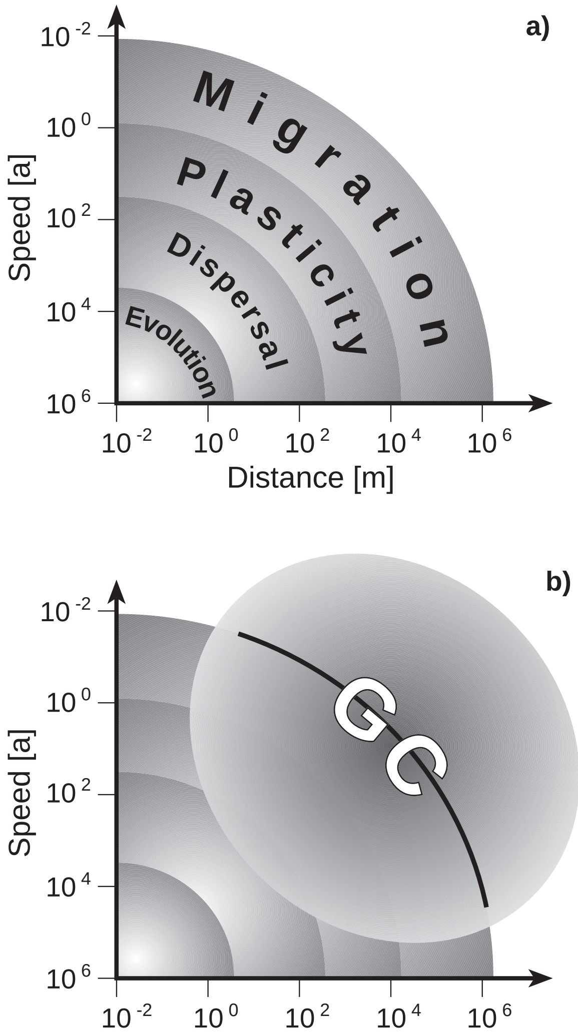

Fig. 3: Spatio-temporal scales of biotic mechanisms to cope with changing environmental conditions: migration, plasticity, dispersal, and genetic evolution (left) versus the spatio-temporal scale of global change phenomena (right). Note the log/log scale

Skalen des Reaktions- und Entwicklungspotenzials von Lebewesen als Reaktion auf sich ändernde Umweltbedingungen: Abwanderung, Ausbreitung, ökologische Plastizität und genetische Evolution (links) in Kontrast zu Geschwindigkeit und Ausmaß der Phänomene des globalen Wandels (rechts)

Photo 1: Tree-lines can by caused by a multitude of zonal and azonal ecological features, including thermal limitation, human land use and recurrent natural disturbances such as flooding regimes and continuous rock-fallings. Rocky Mountains, Canada. (Photo: JENTSCH)

Ursachen für eine Waldgrenze im Hochgebirge können eine Vielzahl zonaler oder azonaler Einflussgrößen sein: zum Beispiel thermische Grenzen, anthropogene Nutzungsrhythmen oder wiederkehrende Störungsereignisse wie Hochwässer oder häufiger Steinschlag. Rocky Mountains, Kanada

Photo 2: Within a particular ecozone each altitudinal belt is prone to various kinds and intensities of mechanical impact. Natural disturbances are prominent in upper altitudinal belts, while human land use typically shapes lower altitudinal belts. Rocky Mountains, Canada. (Photo: JENTSCH)

Innerhalb einer Ökozone unterliegt jede Höhenstufe charakteristischen mechanischen Einflüssen unterschiedlicher Art und Intensität. Die oberen Höhenstufen sind durch vorwiegend natürliche Störungsregime geprägt, während mittlere und tiefere Lagen durch anthropogene Landnutzung überformt sind. Rocky Mountains, Kanada

Photo 3: A combination of low-magnitude earthquakes and water-saturated soils after days of high precipitation caused hazardous mud-flows in central Latin America in 1998. The material covered entire settlements by several metres. Mexico. (Photo: JENTSCH)

Die katastrophalen Schlammlawinen in Mittelamerika 1998 wurden nach einer langen Niederschlagsphase durch leichte Erdbeben ausgelöst. Von Berghängen abgehende Schlammmassen begruben ganze Siedlungen. Mexiko

Photo 4: Ecological inertia despite changing environmental conditions is represented by a few extremely long-lived, slow-growing plant species typical of arctic and alpine vegetation. Here, scattered individuals of *Pinus aristata* var. *longaeva* are shown, that reach several thousand years of age. White Mountains, USA. (Photo: JENTSCH)

Sehr langsam wachsende Arten mit hohen Lebensspannen – typisch für alpine und arktische Lebensräume – repräsentieren ökologische Trägheit trotz sich verändernder Umweltbedingungen. Auf diesem Bild sind verstreute Individuen der Grannenkiefer (*Pinus aristata* var. *longaeva)* zu sehen, die mehrere tausend Jahre alt werden. White Mountains, USA

(Joergensen et al. 1995). It is hypothesised, that isolated trees above the actual upper limit of continuous forest, may at least in tropical high mountains be explained as relicts of formerly higher reaching forests that survived in favourable habitat, where they are less vulnerable to fire, grazing and wood-cutting (Miehe u. Miehe 1994). Lowland limits of continuous forests are in many cases due to human land use activities. Additionally, a fourfold tree-line has been identified in the Sierra Nevada, USA, (Richter 2001) in the sense, that elevational forest zones are separated by intermediate "balds" (Höllermann 1973). The explanation for such large gaps is non-climatic, but rather based on historical limitations; suitable tree species for that particular altitudinal belt may not have reached the location (Richter 1996). Natural, recurrent disturbances such as flooding regimes and unstable slopes may further shape tree-line ecotones and restrict forest development beyond zonal features as shown in photo 1.

Disturbances occur across a wide range of spatial and temporal scales, and on all levels of ecological organization (e.g. Darwin 1859; Connell 1978; Sousa 1984; Picket a. White 1985; Tilman 1996; Walker et al. 1999; review White a. Jentsch 2001). The sum of all disturbances in an ecosystem – including their spatial patterns and temporal return intervals – is called the disturbance regime. In high mountains, cryoturbation, solifluction, erosion, snow, glacial and fluvial action, avalanches, mud flows, mass movements are typical mechanical impacts of various magnitudes and frequencies that create heterogeneous patches of varying size, distribution and biotic legacy. Additionally, fires, insect calamities, herbivory, and anthropogenic disturbances (e.g. traditional land use, logging, settlements, climate induced altitudinal transhumance, hunting, skiing, road tracks, hiking trails, water catchments) add to the broad spectrum of dynamic factors.

Disturbance events are often destructive on the local scale. However, they create spatial heterogeneity and temporal niche diversity. They affect interactions among organisms and act as evolutionary force for the development of life history attributes and functional traits (Nobel a. Slatyer 1977). They selectively promote the ability to cope with a highly dynamic environment. Biodiversity in turn contributes to functional resilience of mountain ecosystems despite disturbance ('Insurance-Hypothesis' by Walker 1995; Naeem a. Li 1997; 'Resilience-Hypothesis' by Peterson et al. 1998; Walker et al. 1999, and review on stability concepts by Grimm a. Wissel 1997).

A few hypotheses regarding the effect of disturbance on biodiversity have been proposed so far (review e.g. Petraitis et al. 1989; Mackey a. Currie 2000). The most prominent 'Intermediate Disturbance Hypothesis' (Connell 1978; Huston 1994; Hubbel et al. 1999) states that highest species diversity will occur at an intermediate level of disturbance intensity, frequency or spatial extend. A substantial alteration of disturbance regimes such as floods, fire or traditional land use, can be a severe threat to the maintenance of biodiversity and may result in changes of the abundance of many species (Tilman 1996; Beierkuhnlein 1998).

As explained above, disturbances can cause both stability at larger scales and change of ecological functions and patterns at smaller scales (Turner et al. 1998; Walker et al. 1999; Jentsch et al. 2002). To assess the significance of particular disturbances for biodiversity in mountain ecosystems, two scales are appropriate for analysis: the 'patch scale' created by a single disturbance event and the 'multi-patch scale' comprising a pattern of disturbed and undisturbed patches (Jentsch et al. 2002). Temporal rhythms of recovery vary with resource availability and environmental constraints. The disturbance history of a patch and organic legacies after disturbance events determine the mode of regeneration. At the multi-patch scale, comprising both disturbed and undisturbed patches, biodiversity properties and patch dynamics emerge. Interactions between disturbed and undisturbed patches can ensure dynamic stability within an altitudinal zone and the persistence of species, as long as the zone is not compressed beyond a certain threshold or shifted to other environmental conditions.

Ecosystem dynamics including disturbance can generally be thought of as a function of two ratios (Turner et al. 1993): the relationship of disturbance extent (patch size) to landscape extent (multi-patch pattern); and the relationship of disturbance interval (frequency) to recovery interval (time needed for recovery). In mountain ecosystems, the extent of the landscape is determined by the continuity of the vegetation of a particular altitudinal zone. Stability is promoted when the disturbance extent is small relative to the extent of the altitudinal zone, and when the disturbance interval (the time between disturbances) is long relative to the recovery interval of the dominant vegetation (the time needed for recovery to the pre-disturbance state). Often, ecosystems characterized by high species diversity are believed to exhibit higher functional resilience in the face of disturbance (e.g. Connell a. Orias 1964). In high mountains with steep slopes soil stability is an important property. Soil stability highly depends on plant cover and rooting patterns. The more diverse root growth forms are the less likely will extreme events promote soil erosion (compare the Insurance Hypothesis, Yachi a. Loreau 1999).

Biodiversity patterns, as well as disturbances vary along latitudinal, altitudinal and environmental gradients. Within a particular biome (ecozone) each altitudinal belt is prone to various kinds and intensities of mechanical impact, such as natural disturbance regimes at higher elevations or anthropogenic land use at lower elevations (Photo 2). Plus, azonal disturbances connect different altitudinal belts. Due to the greater number of altitudinal belts in tropical high mountains; more disturbance types can be expected there than in subpolar mountain ranges (RICHTER 1998). This coincides with the general phenomenon of increased phytodiversity towards the equator (RAPOPORT 1975). Also, the spatio-temporal scale of disturbance, and accordingly the number of secondary successional stages differs among high mountains of various ecozones.

4 *Consequences of climate change in high mountains*

4.1 *Shifting of altitudinal vegetation patterns and loss of biodiversity*

The common underlying assumption that present plant distributions reflect their climatic limitations, which would also apply under future conditions, is considered operational over regional scales where orographical diversity is expected to offer refugia for species with low competitive abilities or presently at the limits of their contributions (LAVOREL 1999). This cannot be applied to high mountains, where vegetation is organised in clear altitudinal belts or elevational zones due to the narrow vertical climatic gradient. Elevational zones carry specific plant communities, combinations of species where certain life forms dominate. OHLEMÜLLER and WILSON (2000) develop generalized linear models to detect shifts in plant species richness parallel to the ongoing climate warming. They show that altitude may serve as a major parameter to explain species richness in high mountains of New Zealand. The boundaries between adjacent altitudinal zones are not sharp. In most cases, a disperse pattern of individual trees is found and tree height may gradually be reduced. Hence, it is more adequate to see this "line" as an area of gradual change of individual performance, and species composition respectively.

Post-Pleistocene upward shift of species in high mountains along with climate warming is well documented. It was already in 1957 when BRAUN-BLANQUET pointed out that further changes will occur if warming will take place.

Fluctuations of climate occurred during the last centuries. It is indicated by historical documents and land use patterns (e.g. distribution of vineyards) and by dendrochronological and palynological data sets. As high mountain vegetation is closely connected to climatic features, it is obvious that we can not expect constancy under scenarios of relative atmospheric warming. Even recently, during the 20th century, vegetation is reacting to climate warming. Climate response surfaces are developed for individual species distributions (GOTTFRIED at al. 1999). Species moving upward can initially enrich the diversity on mountain tops (GOTTFRIED et al. 1994; GRABHERR et al. 1994). It is evident that there is a natural physical upper limit for this shift. If such a process would continue some specialized communities of high mountains could run out of space. They could "drop from the top". Thus, the pressure of ubiquitous strong competitors migrating upwards with increasing temperature could cause biodiversity losses in high mountain biodiversity hot spots. In many cases these regions also bear endemic species which are sensitive to complete extinction.

Due to slow regeneration rates and short-distance dispersal of orobiotic plant species, anthropogenic decline of communities and the related lowering of the tree line, as it has been documented for afro-alpine vegetation by MIEHE and MIEHE (2000), can hardly be compensated in such a harsh environment within short time periods. This is also true for the scale that is relevant for the ongoing climate changes, where decades and centuries are discussed and not thousands of years. However, the data basis to generalize such a prognosis is rather poor. Perhaps, pressing affairs will not allow extensive mapping and investigations in the field. Predictive models are needed to get a clue on the future local reaction to global change of sensitive regions.

A further approach considers vegetation types as an entity that will move as a structural unit, though the exact floristic composition may vary over time (HILBERT a. VAN DER MUYZENBURG 1999 cited in LAVOREL 1999). Still, there is an indication that an upward shift will not occur at each altitudinal level and communities with the same speed (GOTTFRIED et al. 1999). Species of different vegetation belts show varying adaptations to the constancy of their natural communities and environment, most important in our case: specific life time, strategies for dispersal, phenotypical plasticity, and competitive ability.

4.2 *Climate warming experiments*

Specific reactions of various life forms of vascular plants can be depicted from warming experiments in alpine vegetation at the Rocky Mountains. HARTE and SHAW (1995) applied permanent but moderate infrared heating to previously established plant communities in the field. The experiment was carried out along a soil moisture gradient to prove modified reactions under various site conditions, because it is expected that climate change will also effect precipitation and moisture regimes. Life forms that can be understood as functional types respectively performed in a specific way. Grasses and herbs were more strongly controlled by moisture than by temperature. The biomass of grasses remained higher over three years on the dry sites compared to the moist ones. Herbs performed complementarily; they were more productive on moist sites. However, woody species, such as dwarf shrubs, were strongly influenced and promoted by heating (Fig. 4, Fig. 5, and Fig. 6). This suggests that the moisture regime will strongly modify warming effects. On the other side, it indicates that species-specific reaction patterns will occur.

Alpine vegetation is strongly differentiated within one vegetation belt by small-scale microtopography (Körner 1995). Such microsites would respond differently to global climate changes. Thus, the reaction of plant species to warming has to put autecological site requirements in relation to the plausibility of microsites to change substantially.

4.3 Towards the top

Along with a shift of populations towards higher altitudes there may be a decline of adequate area, which would reduce space for populations and subsequently population size. This will reduce the viability of populations. The new establishment of individuals may become a serious bottleneck as well. If seeds are transported uphill by specific vectors, as known for the mountain bird *Nucifraga caryocatactes* and *Pinus cembra* in the Alps, specific climate conditions such as wind speed or night time frost events may still be too harsh for a successful establishment, even if mean temperatures would increase. Current comparisons focusing on adult trees are obviously too simple as a basis for future scenarios.

Many species have co-evolved within certain communities. Hence, these species would depend on other species to move upward. Specific site conditions are not likely to change rapidly together with climate change, as the depth and capacity of the substrate. If there is no comparable site evolved at higher altitudes, only a shift in temperature alone will not provide appropriate conditions for migrating species. New kinds of disturb-

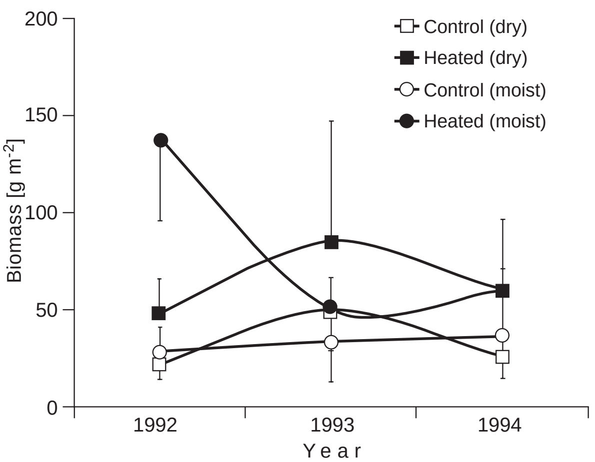

Fig. 4: Development of shrub species during a warming experiment in natural high mountain vegetation of the Rocky Mountains on dry (squares) and moist sites (circles). Shrubs respond positively to heating under different soil moisture conditions (based on data from Harte a. Shaw 1995)

Entwicklung der strauchigen Arten im Verlauf eines Erwärmungsexperimentes in natürlicher Hochgebirgsvegetation der Rocky Mountains auf trockenen (Quadrate) und feuchten Standorten (Kreise). Sträucher reagieren positiv auf Erwärmung unter verschiedenen Feuchtigkeitsverhältnissen der Böden (nach Daten von Harte a. Shaw 1995)

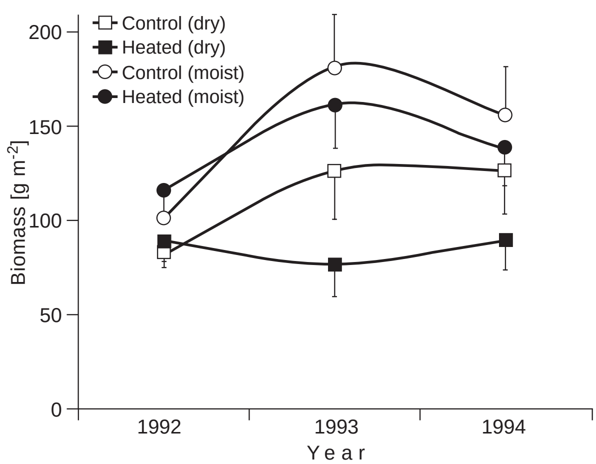

Fig. 5: Development of herbaceous species during a warming experiment in natural high mountain vegetation of the Rocky Mountains on dry (squares) and moist sites (circles). Herbs respond stronger to moisture than to heating. They are promoted on moist sites (based on data from Harte a. Shaw 1995)

Entwicklung der krautigen Arten im Verlauf eines Erwärmungsexperimentes in natürlicher Hochgebirgsvegetation der Rocky Mountains auf trockenen (Quadrate) und feuchten Standorten (Kreise). Krautige reagieren stärker auf die Bodenfeuchte als auf Erwärmung und werden unter feuchten Bedingungen gefördert (nach Daten von Harte a. Shaw 1995) ances could occur at such sites, constantly creating open soil for ruderals to establish but restrict the survival of K-strategic long-lived woody species. Communities would also lose species with a reduction of occupied area. If environmental heterogeneity, the internal pattern within certain ecosystems, would remain constant, the reduction of area with increasing altitude will most likely cause a decline of species diversity. Finally, at mountain tops, the communities run completely out of space. If the amplitude of altitudinal distribution should also be reduced, this effect would become even more prominent. We realize, that a variety of scenarios of community shift can be imagined (Fig. 7).

Plus, disturbances play an important role according to the creation of temporal niches, as discussed further below. They promote complementary use of ecological niches. As species will not adapt within short time periods to new disturbance regimes, the development of new niches will not be answered directly in species distribution and richness (Fig. 8).

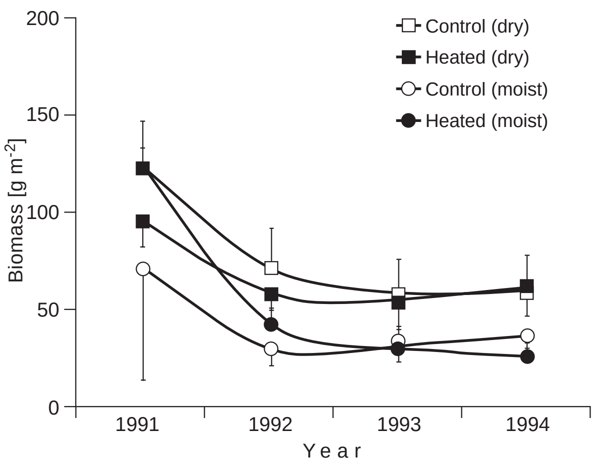

Fig. 6: Development of graminoid species during a warming experiment in natural high mountain vegetation of the Rocky Mountains on dry (squares) and moist sites (circles). Grasses respond stronger to moisture than to heating and is more important on dry sites (based on data from HARTE a. SHAW 1995)

Entwicklung der Gräser im Verlauf eines Erwärmungsexperimentes in natürlicher Hochgebirgsvegetation der Rocky Mountains auf trockenen (Quadrate) und feuchten Standorten (Kreise). Gräser reagieren stärker auf die Bodenfeuchte als auf Erwärmung und werden unter trockenen Bedingungen gefördert (nach Daten von HARTE a. SHAW 1995)

In the northern and southern hemisphere, altitudinal belts are generally not symmetric and constant over expositions and slopes. They are modified by mesoclimatic conditions. In consequence, the upward shift of communities with changing environmental conditions may disrupt populations and isolate smaller populations from a formerly interacting unit. The loss of connectivity within a community can be due to a shift of asymmetric altitudinal zones or to growing isolation and fragmentation (Fig. 9). Positive long-term effects on speciation are possible.

Comparable processes enhanced speciation during the Pleistocene. Nevertheless, again such processes need more time to have positive effects on species diversity. The probability is high that small populations will get extinct and that the fragmentation of communities will increase.

Even so, we can expect that within human life span there will be no significant shift of complete communities or vegetation units. Either the higher altitudes will not supply adequate site conditions or new disturbance regimes will not be answered by evolutionary processes and dispersal within short term. In total, a severe loss of genetic diversity and species diversity is predicted with climate change (GOTTFRIED et al. 1999).

We have to keep in mind that climate change may also promote communities of minor importance today due to the decline of recently dominant and more competitive communities. This decline may be caused by internal destabilization, shifting dominance patterns of contributing species and by modified external factors as a new disturbance regime. Land use will sensitively react to climate change and thus also produce new patterns of cultivated crops in high mountains of the world.

4.4 Alteration of disturbance regimes with climate change

Climate change can have multiple effects on the ecosystem dynamics of high mountains including enforcement and suppression of particular disturbance regimes. Models incorporating the relative atmospheric warming indicate that major parts of the current glacier cover could disappear, permafrost could degrade, slopes could develop instabilities, and river run-offs could be enhanced (HAEBERLI et al. 1999). Thus, atmospheric warming might induce a stronger magnitude of extreme short-term climatic events and natural hazards (MESSERLI a. IVES 1997) such as the disastrous mud flows in central Latin America covering entire towns in 1998 (Photo 3), the catastrophic flooding of the Elbe river in Germany in 2002 and the large bush fires in Australia in 2002. Referred to the life span of individ-

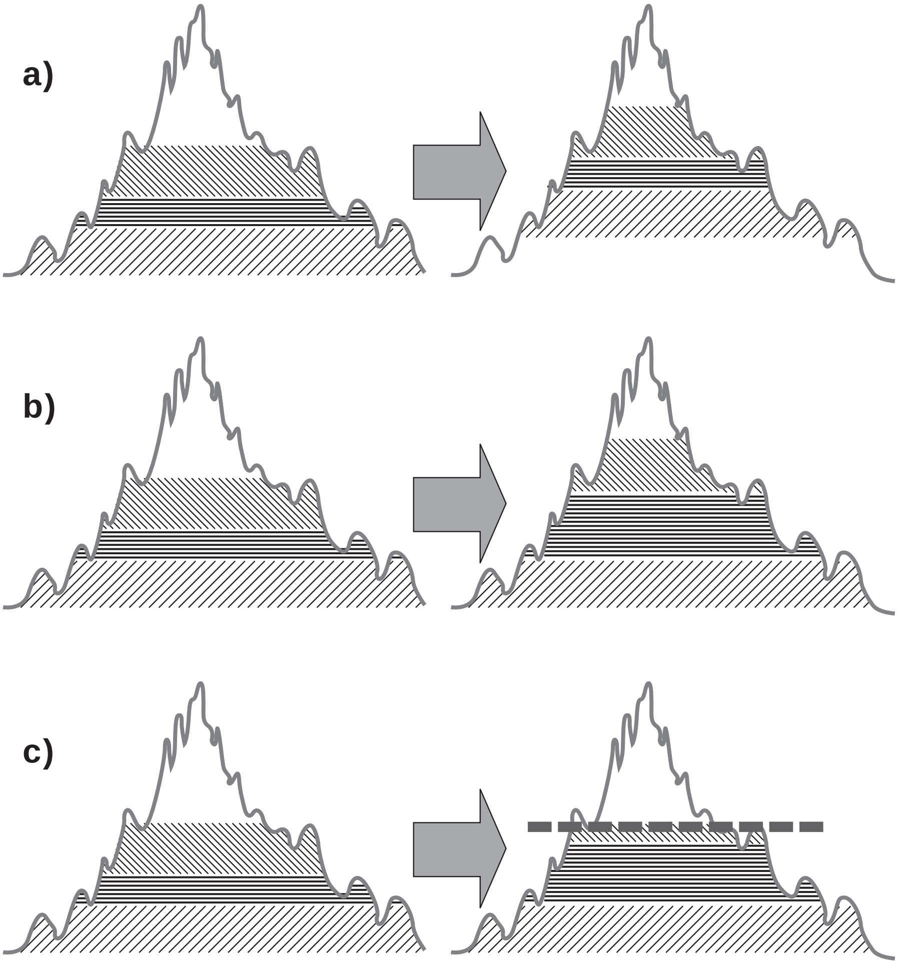

Fig. 7: Temporal sequences for three cases of shift of altitudinal zones. The figure is related to two communities and an intermediate transitional zone between them (ecotone): a) Communities and transition zones move upward in the same way. b) Upward expansion of one community and expansion of the transitional zone due to specific individual reactions of species from both communities. c) Limitation of upward shift and expansion of transitional zone together with a loss of area of the upper community

Zeitliche Sequenzen für drei Fallbeispiele der Höhenverlagerung von Lebensgemeinschaften (oder Höhenstufen). Die Abbildung bezieht sich auf zwei Lebensgemeinschaften (Schrägschraffur) und eine intermediäre Übergangszone (Ökoton) (waagerecht schraffiert): a) Lebensgemeinschaften und Übergangsbereich verschieben sich gleichermaßen. b) Aufgrund unterschiedlicher Ausbreitungsgeschwindigkeiten einzelner Arten verbreitert sich der Übergangsbereich. c) Begrenzung der Aufwärtsbewegung durch absolute Obergrenzen und Flächenverlust der oberen Lebensgemeinschaft

ual organisms, events with a short duration may seem to have limited importance. Nevertheless, their effects and repercussions can be long-lasting and severe, accompanied by ecosystem instability as related to water cycle and slope processes.

Anthropogenic disturbance regimes can significantly add to the development and maintenance of high species diversity in mountain ranges. However, climate changes will also influence land use practices and land cover in high mountain ecosystems. The tropical mountains, for example, have been widely transformed into cultural landscapes (MIEHE u. MIEHE 1994). With changing environmental conditions, azonal disturbances may increasingly bridge or dissect altitudinal vegetation patterns and promote the invasion of species that were formerly not able to persist under the natural limitations of climate and disturbance regime. Typical examples of species migration across altitudinal zones can be found after logging or cattle-grazing (RICHTER 2001).

Fig. 8: Two cases of upward shift restrictions and modification due to novel environments: a) shift of a community out of a zone with a specific disturbance regime (e.g. out of the zone where land use is possible due to soil and relief – arrow), b) shift of a community into a zone with new site conditions (e.g. lack of soil, rocky outcrops – arrow)

Zwei Fälle der Begrenzung und Modifizierung von Höhenverschiebungen bedingt durch das Antreffen nicht vergleichbarer Umweltbedingungen: a) Verlagerung einer Lebensgemeinschaft auf einer Höhenzone mit spezifischem Störungsregime heraus (z.B. Höhenstufe, in welcher Ackerbau aufgrund edaphischer und geomorphologischer Gründe möglich ist – Pfeil), b) Verlagerung einer Lebensgemeinschaft in eine Höhenstufe mit neuartigen Standortverhältnissen (z.B. geringe Bodenmächtigkeit, anstehender Fels – Pfeil)

With climate change we can predict an alteration of disturbance regimes. This may lead to (1) an upward pressure of human land use. It can (2) increase disturbance magnitude and disturbance frequency. This means a faster rotation and the exclusion of late successional communities. In arctic and alpine environments climate warming can also go along with (3) the suppression or slowing down of essential disturbances such as cryoturbation. (4) New competitors might reach communities that were former ecologically isolated. Autotrophic communities known at 6,000 m altitude (HALLOY 1991) will not perform a high competitive ability.

More scenarios related to the interactions between an altered disturbance regime and biodiversity patterns could be thought of. Future climate warming may allow increased biomass production within plant communities that were formerly limited by low temperatures. This will provide an increase in standing fuel for burns, which might occur in regions sensitive to fire. Climate change has been predicted to control fuel supply and therefore the fire regime in the sub-tropical Andes (GRAU 2001).

As we can not expect, that entire communities of plants, soil fauna, fungi and microorganisms will adapt with the same speed, a loss of ecosystem functions and

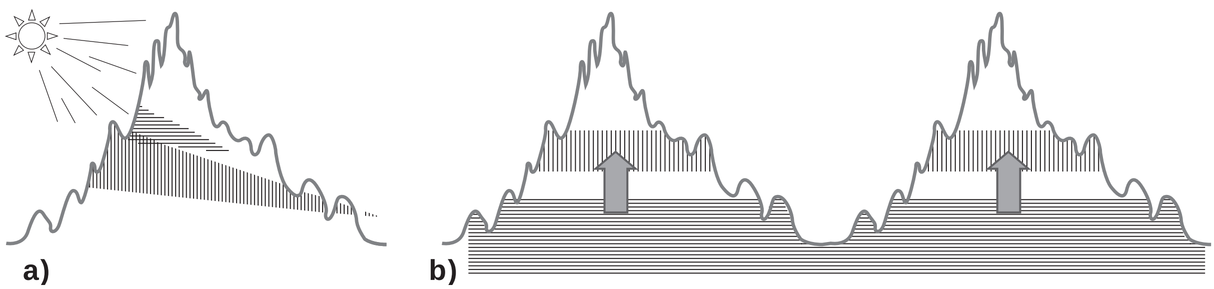

Fig. 9: Loss of connectivity within a community a) due to the shift of asymmetric altitudinal zones, b) due to the growing isolation and fragmentation of shifting altitudinal zones. Positive long-term effects on speciation are possible

Verlust von Verbindungen a) durch die Verschiebung asymmetrischer Höhenstufen, b) durch die wachsende Isolation und Fragmentierung sich verschiebender Höhenstufen. Langfristig sind positive Effekte auf die Artbildung möglich general performance is inevitable. It takes time for soil organisms that mineralize organic litter to establish. So, one effect of climate warming could result in a decreased activity of soil organisms and to the accumulation of litter on the soil surface, serving for initial ignition of fires.

We know about the vulnerability of mountain ecosystems to land use changes and about the spatial limitation of shifting vegetation patterns. However, we are not informed about the overall ecological plasticity of mountain ecosystems in face of altered site conditions, of altered disturbance regimes and of their synergistic interaction.

5 *Ecological inertia: risk and potential for the future of biodiversity*

In high mountain ecosystems, a few dominating species reach very long life spans, ranging from several hundred to several thousand years. Examples are found among trees, shrubs, dwarf shrubs, and clonal grasses. Long-lived, slow-growing individuals of species such as *Betula nana, Pinus aristata* var. *longaeva* (Photo 4) or *Carex curvula* may not be able to adapt to changing environmental conditions. However, they might not completely die off due to some unfavourable decades. They represent ecological inertia in face of altering conditions or competitive pressure by new species. This can mean both, risk and potential for the future of biodiversity.

The risk of not being able to cope with changing environmental conditions by adaptation or migration is simply the fate of extinction. On the other hand, evolutionary inertia may provide temporal refuges in repeatedly changing environments. The potential of enduring novel conditions via long-term survival is an option of "a better future", in which conditions could become favourable again, although this strategy seems currently not adequate.

Species with very long life-spans exhibit genetic stability through time. When trends of alteration return again to past conditions, their particular traits may be most successful and even ensure the persistence of these species during cyclic alterations. Especially in alpine zones, there is a high variability of climate between years. Extreme conditions reappear with a certain probability and have been selective evolutionary processes in the past. As most alpine species are long-lived, they will have experienced such conditions within their lifetime. GASTON et al. (1998) conclude that the higher the climatic variability of the site, the larger the probability that species will have the adaptive potential of a wide distribution. However, we cannot expect a simple transfer from RAPOPORT's rule (1975) to the altitudinal range of species, as STEVENS (1992) suggested. If there is no competition by fitter species, many species of high mountains could tolerate a higher frequency of warmer seasons. They will develop inertia within the system even if species composition and vegetation structure will not respond to climate warming. However, strong disturbances such as avalanches may remove long-lived organisms. Disturbance can thereby contribute to a reduction of inertia in ecosystems.

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List of Acronyms

GLORIA: Global Observation Research Initiative in Alpine Environments
GMBA: Global Mountain Biodiversity Assessment
IPCC: Intergovernmental Panel on Climate Change
WBGU: Wissenschaftlicher Beirat der Bundesregierung Globale Umweltveränderungen