MOUNTAIN ECOSYSTEM RESPONSE TO GLOBAL CHANGE

Jörg Löffler, Kerstin Anschlag, Barry Baker, Oliver-D. Finch, Bernd Diekkrüger, Dirk Wundram, Boris Schröder, Roland Pape and Anders Lundberg

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Summary: Mountain ecosystems are commonly regarded as being highly sensitive to global change. Due to the system complexity and multifaceted interacting drivers, however, understanding current responses and predicting future changes in these ecosystems is extremely difficult. We aim to discuss potential effects of global change on mountain ecosystems and give examples of the underlying response mechanisms as they are understood at present. Based on the development of scientific global change research in mountains and its recent structures, we identify future research needs, highlighting the major lack and the importance of integrated studies that implement multi-factor, multi-method, multi-scale, and interdisciplinary research.

Zusammenfassung: Gebirgsökosysteme gelten generell als sehr empfindlich gegenüber dem Globalen Wandel. Allerdings sind aufgrund der Komplexität der Systeme und wegen vielfältiger Interaktionen der Einflussfaktoren sowohl das Verständnis gegenwärtiger Reaktionen als auch Vorhersagen zukünftiger Änderungen sehr schwierig. Unser Ziel ist es, potenzielle Effekte des Globalen Wandels auf Gebirgsökosysteme zu diskutieren und Beispiele für die zugrunde liegenden Reaktionsmechanismen zu geben, soweit sie derzeit verstanden sind. Basierend auf der Entwicklung und den heutigen Strukturen der „Global Change"-Forschung in Gebirgen zeigen wir den Forschungsbedarf auf und betonen insbesondere das weitgehende Fehlen und die Bedeutung integrativer Studien über verschiedene Faktoren, Methoden, Maßstäbe und Disziplinen hinweg.

Keywords: High mountain ecology, arctic-alpine environments, climate change, land use and land cover change, tree line alteration, range shifts, altitudinal zonation

1 Introduction

The current debate on regional and local responses that might occur under future global change is often focussed on sensitive landscapes, such as the Arctic, coastal regions, and mountains, especially the Alpine (ACIA 2004; IPCC 2007a, b). In this context "global (environmental) change" refers to changes having both natural and anthropogenic causes and encompass, among other factors, climate change, land use cover change, industrialisation, urbanisation, and changes in atmospheric chemistry (Goudie and Cuff 2002). Becker and Bugmann (2001) classify global environmental change affecting mountain ecosystems into two categories: systemic changes that operate at a global scale (such as trace gas-induced climate change) and cumulative changes caused by processes at a local scale but that are globally pervasive (such as land use cover change). In this article, we will concentrate on the effects of climate change, as well as on increasing levels of CO_2, nitrogen input, and land use change. We use the term "ecosystem" according to the definition of Tansley (1935), including the organism complex and the complex of physical factors (with climate and soil as important determinants) involved and considering that these systems are characterised by constant interchange between organisms and between organisms and inorganic factors.

Mountain ecosystems are expected to react very sensitively to climate change (IPCC 2007a), with both natural and social systems being influenced (Beniston 2000, 2006). In the case of thresholds being exceeded, these changes can be irreversible (Beniston 2003). While long-term predictions are not possible, scenarios can be used to describe potential future conditions. These scenarios cover a broad range of possible developments, which makes obtaining distinct conclusions difficult. Furthermore, potential non-linear feedbacks and species interactions can influence and possibly override autecological responses to climate change (Rial et al. 2004; Burkett et al. 2005; Nogués-Bravo et al. 2007; Wookey et al. 2009). For example, Suttle et al. (2007) describe how an increase

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of precipitation that extends the rainy season in an area with a Mediterranean climate and long summer droughts initially causes an increase in plant biomass in an ecosystem and, thus, also increases the habitat quality for herbivores, predators and parasitoids, but after a few years, an altered plant species composition leads to changes in the timing of food availability and a decline in the habitat quality for higher trophic levels.

In addition to climate change, changes in land use and land cover are widely regarded as one of the main drivers of global change affecting mountain ecosystems (e.g., Bugmann et al. 2007; Zierl and Bugmann 2007; Batllori and Gutierrez 2008). Economic growth and demography will have a major impact on agriculture and grazing regimes in mountain areas. In some regions, this may lead to environmental deterioration due to, e.g., deforestation, over-grazing and the cultivation of marginal soils (Beniston 2000, 2003), while other regions may experience extensification and reforestation (OcCC and ProClim 2007). For example, the European Alps have experienced dramatic changes in land use and land cover over the last decades because of increasing machine deployment, the abandonment of less accessible land and the intensification of more productive areas (Tasser et al. 2005; Börst 2006; Giupponi et al. 2006). The associated impacts on vegetation, including alpine tree lines, are expected to be huge. Moreover, nitrogen availability and mobility have been altered substantially on a global scale by industrial N fixation, the combustion of fossil fuels, the cultivation of nitrogen-fixing crops, and land conversion (Vitousek et al. 1997); atmospheric nitrogen inputs are predicted to further increase considerably (Galloway et al. 2004; Lamarque et al. 2005). This will have major impacts on frequently nutrient-limited mountain ecosystems (Wookey et al. 2009). Furthermore, the nitrogen concentration in rivers and lakes may increase, with major effects on aquatic ecosystems (Rogora et al. 2003).

Therefore, to contribute to solving future problems in a changing world, research on mountain responses to global change is a top priority. Thus, after giving an overview of the development of global change research in mountains, this review article aims to discuss potential effects of globally triggered changes in mountain ecosystems and our current scientific understanding of the underlying response mechanisms. Moreover, based on this analysis, we aim to derive future mountain research perspectives.

2 Development of scientific global change research in mountains

We conducted a bibliometric analysis of scientific publications (peer-reviewed articles, proceedings, and reviews) listed in the ISI Web of Science (Science Citation Index Expanded, 1899 to January 11, 2010) database, which showed that global change research is growing at an exponential rate, and this is reflected in the number of publications on the thematic complex of mountains, climate change, and land use and cover change (Fig. 1). However, we are aware that this analysis provides trends rather than exact figures because not all publications dealing with global change in mountains necessarily use these key words. Although publications covering these topics extend back well into the early part of the 20th century, this integrated approach to studying global change in mountainous terrain is relatively recent (Tab. 1). Of the 74,316 publications we found on mountain research, only 224 records contained each of the three research topics, the earliest of which was published in 1991.

Interestingly, between 1990 and 1991, there was a dramatic shift in the number of publications in all three thematic areas (Fig. 1), which can be linked to several important developments that occurred in the latter half of the 20th century (Fig. 2). Mountain and

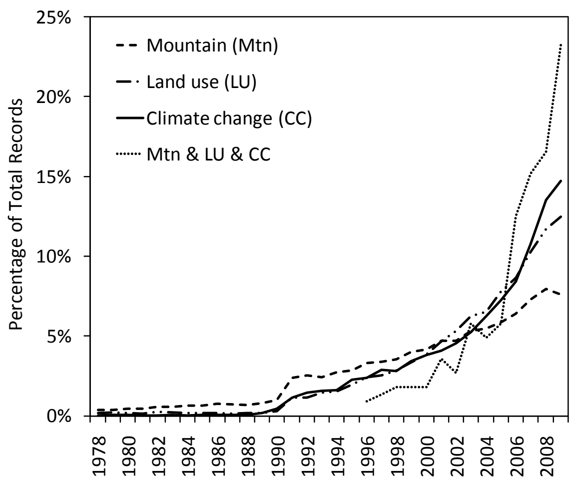

Fig. 1: Plot of the percentage of the total number of papers published per year from a search of the key phrases: i) "mountain* OR alpine (74,316 total since 1900; 95% of total published after 1978), ii) landuse OR "land use" OR "land cover change" OR "landcover change" (24,643 since 1993; 99% of total published after 1978), iii) climate change OR "climatic change" OR "global warming" (39,678 since 1910; 99% of total published after 1978), and iv) all previous three combined (224 since 1991) in the ISI Web of Science (Science Citation Index Expanded, 1899 to January 11, 2010) database

Tab. 1: Total number of records and year of first record for publications listed in the ISI Web of Science (Science Citation Index Expanded, 1899 to January 11, 2010) using various keywords or phrases

Terms	Number of ISI publications	Year of first record
mountain* OR alpine	74,316[a]	1900
landuse OR "land use" OR "land cover change" OR "landcover change"	24,643[b]	1933
"climate change" OR "climatic change" OR "global warming"	39,678[b]	1910
(mountain* OR alpine) AND (landuse OR "land use" OR "land cover change" OR "landcover change")	1,563	1978
(mountain* OR alpine) AND ("climate change" OR "climatic change" OR "global warming")	3,175	1989
(mountain* OR alpine) AND (landuse OR "land use" OR "land cover change" OR "landcover change") AND ("climate change" OR "climatic change" OR "global warming")	224	1991

[a] 1978–2010: 95% of all records

[b] 1978–2010: 99% of all records

alpine research began to flourish during the 1960s and continued through 1980s with the development of several international programmes that fostered collaborative transdisciplinary research in mountains (Lauer 1984; Ives 1992; Price 1995; Messerli and Messerli 2007, 2008), such as the International Biological Programme (1964–1974), the International Geographical Union (IGU) Commission on High-Altitude Geography (founded by Carl Troll in 1968), and the UNESCO Man and the Biosphere Programme (MAB) Project 6 (1973–1987). Further milestones were the development of the International Centre for Integrated Mountain Development (1984), the creation of the International Geosphere-Biosphere Programme (1986), under whose auspices (among others) the Mountain Research Institute was founded (Becker and Bugmann 1997, 2001), and the inclusion of chapter 13 on "Managing Fragile Ecosystems: Sustainable Mountain Development" in the UNCED Agenda 21 in Rio de Janeiro (1992). Moreover, the UN proclaimed the year 2002 to be the "International Year of Mountains". Another step was the constitution of the IGU Commission "Mountain Response to Global Change" in 2008. Furthermore, the development of the field recently reached a new milestone with the conference "Global Change and the World's Mountains", held in Perth in September 2010. All of this underlines the importance of global change as an "emerging field" in mountain research.

Similarly, technological advances (e.g., the start of the Landsat program in the early and mid-1970s) have provided datasets that allow for the detection and monitoring of change, which correlates well with the increase in the rate of publications during the mid-to-late 1970s addressing land use and cover change topics (Fig. 2). Regarding advances in climate change research, the publication of "the Charney report" in 1979 (Charney et al. 1979) marked the beginning of a concerted effort to scientifically understand the impacts of climate change caused by anthropogenic carbon dioxide emissions and culminated in the first of four reports by the Intergovernmental Panel on Climate Change (IPCC) in 1991.

3 Potential effects on mountain ecosystems

The intensified research described above has indicated numerous potential effects of global change on mountain ecosystems. Climate change will have a strong impact on the cryosphere, while impacts on glaciers, permafrost, the altitudinal snow line and cryospheric processes will in turn cause changes in hydrology, vegetation and geomorphology (Price and Barry 1997; Beniston 2003; IPCC 2007a). Permafrost degradation and glacier retreat lead to the destabilisation of mountain areas that can result in mass movements, such as rockfalls, landslides, and debris flows (Kääb 2008; Harris et al. 2009). Hydrological processes (e.g., precipitation, evapotranspiration, soil moisture, runoff, discharge, sediment loads, and pollution loads of runoff water) will not only be affected by climate change, but also by vegetation transformations caused by land use and land cover change (Price and Barry 1997; Beniston 2000; López-Moreno et al. 2008; Stehr et al. 2010). Overall, water discharge from mountains will be altered with respect to timing, volume

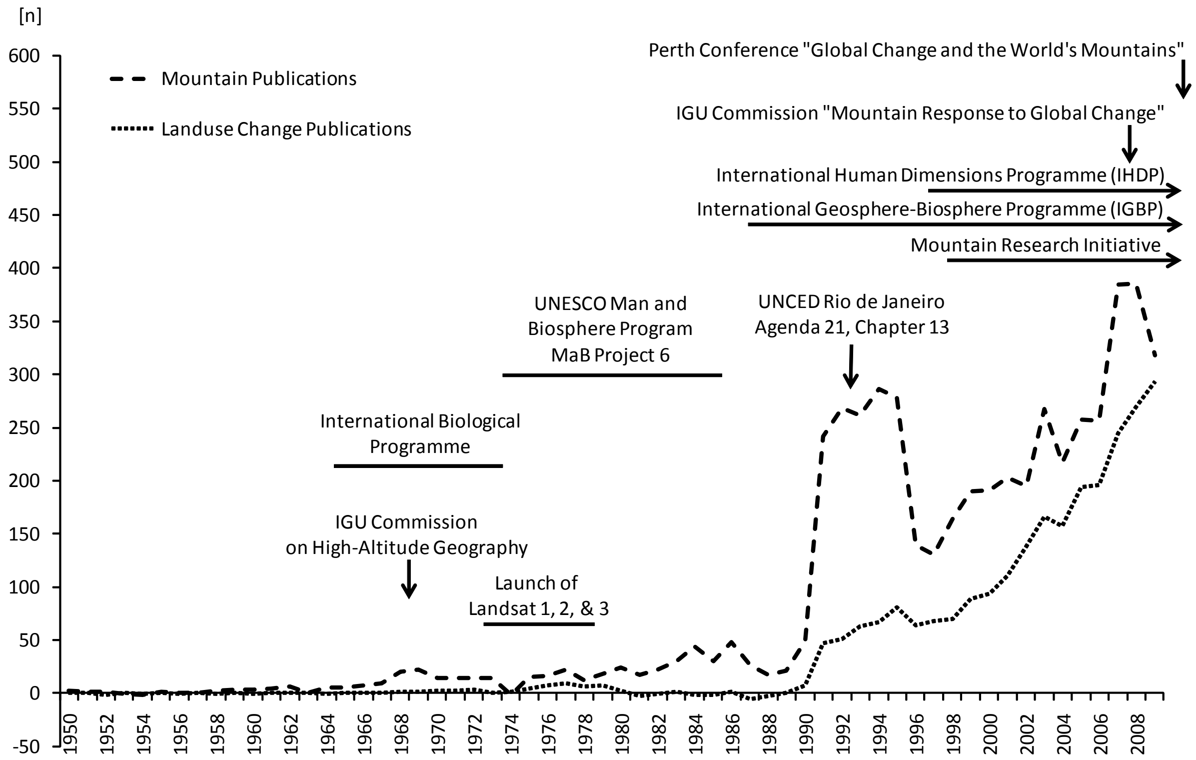

Fig. 2: Plot of the 5 year running mean (assumed average time from start of research through publication of results) of the rate of publication (difference between number of publications in the respective year and the previous year) of papers listed from two searches of the ISI Web of Science (Science Citation Index Expanded, 1899 to January 11, 2010) database with the key phrases: mountain* OR alpine and landuse OR "land use" OR "land cover change" OR "landcover change"

and variability (Messerli et al. 2004; Viviroli and Weingartner 2004; Viviroli et al. 2007; López-Moreno et al. 2008).

Another major issue is the impact on biodiversity (Price 2008). Mountain ecosystems are highly vulnerable to climate change, regarding both average climatic values and extreme events (Diaz et al. 2003). As a consequence, range shifts, modifications of assemblage compositions, and species extinctions are expected (Nogués-Bravo et al. 2007; Sekercioglu et al. 2008; von dem Bussche et al. 2008; Richter et al. 2009; Schöb et al. 2009; Bendix et al. 2010; Kreyling et al. 2010; Kullman 2010). For instance, vegetation is influenced by climate change (temperature, snow cover, soil moisture) and by land use cover change (e.g., succession, regrowth in some regions, afforestation or deforestation and fragmentation in others; fire management; the provision of artificial snow for winter tourism) (Beniston 2000; Keller et al. 2000; Wipf et al. 2005). The effects of these processes will concern physiology, primary productivity, food quality, and decomposition, but will also concern diseases, plant-animal-interactions, and species composition (Price and Barry 1997; Beniston 2000; Theurillat and Guisan 2001; Albert et al. 2008). For example, an upward shift of alpine plants and an increase in the plant species richness of high alpine and nival vegetation are already observable (Walther et al. 2005a; Pauli et al. 2007; Parolo and Rossi 2008), with not only upper margins, but also optimum elevations and lower distributional margins being affected (Kelly and Goulden 2008; Lenoir et al. 2008, 2009). The effects on mountain forests will also be complex due to impacts on productivity, pests, competition, frosts, windthrows, and fires (Price and Barry 1997; Bigler et al. 2005; Bugmann et al. 2005; Kurz et al. 2008b). Moreover, potential tree line shifts related to global change will affect carbon sequestration (with rising tree lines leading to an increase of carbon storage), the cycling of water and nutrients, and the maintenance of biodiversity (MILLENNIUM ECOSYSTEM ASSESSMENT 2005; Malanson et al. 2007).

Similarly, animals can react to altered conditions with physiological, behavioural and genetic adaptations or migration, or they may become extinct (Price and Barry 1997; Zurell et al. 2009). A growing number of studies report an upward shift of species ranges (and occasionally an associated range contraction for high-altitude species) of, e.g., birds, amphibians, insects, reptiles, and mammals (Seimon et al. 2007; Wilson et al. 2007; Moritz et al. 2008; Raxworthy et al. 2008; von dem Bussche et al. 2008; Chen et al. 2009). Further faunal changes are projected to be especially pronounced in mountain regions, not only due to the strong environmental variation over short distances, but also because of the occurrence of many species' range edges and the large number of small-range endemic species (Lawler et al. 2009).

4 Underlying response mechanisms

The above-mentioned vast number of potential global change effects in mountains highlights the relevance of understanding the underlying mechanisms. However, in many cases, these are still not well understood. Investigations often focus on eye-catching topics, such as shifts in glaciation or the altitudinal tree line, although permafrost thawing and related hazards have also increasingly been attracting interest. Instead of collaborative studies across disciplines, which are demanded for ecosystem research in general (e.g., LTER – Long Term Ecological Research, cf. http://www.ilternet.edu/) and environmental observations in mountains in particular (e.g., GLOCHAMORE Research Strategy, cf. Grabherr et al. 2005), we usually find sectoral research. In the following sections, we thus present an overview of response mechanisms to global change (comprised of alterations of climate, CO_2 levels, nutrient availability, and land use) structured according to cardinal fields of research. Supplement I illustrates the given examples and interdependencies.

4.1 Snow, ice, and permafrost

The response of the cryosphere to global change is of the utmost importance for mountain ecosystems because of its effect on micro-climate, hydrology, vegetation, and carbon balance.

Snow cover, for example, via its spatial and temporal distribution, determines the timing of water runoff (Rössler and Löffler 2010) and disturbances associated with avalanches (Slaymaker and Kelly 2007). It has also been proven to be important for the ecologically relevant near-surface temperatures, as well as their decoupling from boundary layer conditions (Löffler and Pape 2004; Wundram et al. 2010). Thus, the impact of climate change on mountain ecosystems is likely to be modified by snow cover and its alterations.

A highly prominent feature of the impact of global change in mountain regions is the retreat of glaciers (Slaymaker and Kelly 2007). The resulting processes and landforms are not only of interest for paraglacial geomorphology (Ballantyne 2002), but they also have important direct (e.g., primary succession on recently deglaciated terrain, cf. Matthews 1992; Cannone et al. 2008; Töwe et al. 2010) and indirect (e.g., timing and volume of water discharge) effects on mountain ecosystems.

Melting glaciers are a global phenomenon (IPCC 2007a) and are regarded as key indicators of climate change, although the determining climatic variables differ in space and time (Barry 2006). Their mass balance is generally influenced by atmospheric conditions, such as solar radiation, air temperature, precipitation, wind, cloudiness, and individual glacier characteristics. As a rule, changes in glaciers at low latitudes primarily depend on variations of atmospheric moisture content, which in turn influence solar radiation, precipitation, albedo, atmospheric long wave emission, and sublimation. On the other hand, temperate glaciers in mid-latitudes are mainly affected by winter precipitation, summer temperature, and summer snow falls influencing their albedo (Zemp et al. 2008). For example, the importance of glacier surface albedo was shown by Oerlemans et al. (2009): especially in years with low snow precipitation, the accumulation of dust (originating from exposed moraines) on retreating glaciers leads to a decrease of the glacier surface albedo, further enhances glacier melt and, thus, intensifies glacier retreat in a positive feedback cycle. However, the exact mechanisms underlying glacier responses to climate change (especially to short-term extreme situations) are generally complex, and sudden regime shifts in glacier mass-balance drivers have to be considered as possible (e.g., Winkler and Nesje 2009; Winkler et al. 2010).

Permafrost changes due to global change not only have effects on slope stability; they also cause changes in carbon balance, the release of trace gases, and hydrology (Slaymaker and Kelly 2007). Therefore, permafrost response mechanisms are also important from the ecosystem point of view.

Mountain permafrost is very sensitive to climate change, especially in areas where ground temperatures are only a few degrees below zero (Harris et al. 2009; Christiansen et al. 2010). However, in spite of clear evidence that warming permafrost causes destabilisation, it remains difficult to attribute individual events to this phenomenon (Gruber and Haeberli 2007). Thawing is known to be more pronounced in convex areas, but the highly complex topography of mountain regions, the influence of snow cover, geological discontinuities, and massive ice bodies in rockwalls cause complicated three-dimensional effects on the subsurface thermal field (Nötzli et al. 2007). Moreover, in addition to being influenced by heat conduction, mountain permafrost is also affected by heat transfer via percolating water in fractures and deep-reaching cleft systems, further hindering predictions of response to climate change (Krautblatter and Hauck 2007).

4.2 Water

Hydrological processes in mountains are tightly linked to the cryosphere. For example, in areas where snow melt hydrology dominates the water cycle (especially where winter temperatures are close to 0 °C), the seasonal timing of runoff is sensitive to projected changes in the snow pack associated with warming trends. In contrast, volume changes in projected annual runoff are chiefly associated with alterations in precipitation and evapotranspiration (Adam et al. 2009). Snow sublimation is an important process in mountain regions with high solar radiation and low relative humidity, such as the High Atlas Mountains in Morocco (Schulz and de Jong 2004; Klose et al. 2010a). Climate change may result in a decrease in sublimation due to higher temperature and, therefore, faster snowmelt (Klose et al. 2010b). In contrast, Wimmer et al. (2009) expect an increase in the sublimation rate in Mongolia, but due to high variability between different Global Circulation Models, no non-ambiguous projection was possible.

A prominent example of a large-scale impact of climate change on hydrology is the projected decrease in the mean upstream water supply from the upper Indus, Ganges, Brahmaputra, and Yangtze rivers, as well as an increase of the water supply from the upper Yellow River (Immerzeel et al. 2010). This is attributed to the contrasting influences of decreasing meltwater production and increasing rainfall, which are of different importance in the various catchments of the Himalaya region (Bookhagen and Burbank 2010; Immerzeel et al. 2010).

Vegetation changes due to global change will also affect hydrological systems. For example, reforestation of abandoned farmland has been shown to cause higher evapotranspiration and, thus, decreases in water discharge and stream flow (López-Moreno et al. 2008). This may also slightly reduce flood risk (Ranzi et al. 2002).

4.3 Vegetation

4.3.1 Alpine vegetation

Studies on the impact of climate change on alpine vegetation have frequently implemented warming experiments using, for example, open top chambers, heating cables, and infra-red lamps (for an overview of methods, see Shen and Harte 2000; Shaver et al. 2000). The reactions shown by vegetation in these experiments include changes in plant growth and reproduction (e.g., Kudernatsch et al. 2008), phenology (e.g., Dunne et al. 2003, 2004), vegetation structure, and assemblage composition (e.g., Klanderud and Totland 2005; Erschbamer 2006, 2007). Because these manipulation experiments usually last a relatively short time, they allow only short-term conclusions to be made. Longer-term monitoring programmes have revealed an increase of vegetation homogeneity (Jurasinski and Kreyling 2007; Britton et al. 2009) and an upward migration of species (Klanderud and Birks 2003; Pauli et al. 2007; Holzinger et al. 2008; Parolo and Rossi 2008; Erschbamer et al. 2009). However, due to low species' dispersal capabilities, dispersal limitations due to fragmentation and a lack of migration routes, the observed upward movement of alpine plant species generally lags behind changes in climatic conditions (Theurillat and Guisan 2001; Walther et al. 2005b). Dendroecology, which is another useful long-term method for detecting climate change responses in mountains (e.g., Becker et al. 2007), has recently also been applied in treeless alpine ecosystems. For example, the radial growth of the dwarf shrub *Empetrum nigrum* ssp. *hermaphroditum* is strongly dependent on summer temperatures (Bär et al. 2007, 2008). However, caution is recommended when relating the growth of nontree woody life forms to summer warming, as a number of methodologically induced constraints exist (Büntgen and Schweingruber 2010). Moreover, potential positive effects of climate warming on plant growth (via a longer vegetation period and higher summer temperature sums) can be overridden by negative effects on growth and reproduction, such as an increased danger of frost damage due to reduced snow pack and earlier snow melt (Inouye 2008; Wipf et al. 2009). In general, because of its importance regarding microclimate (Löffler 2007), snow cover and its response to climate change is highly relevant with respect to the future development of alpine vegetation.

The effects of elevated CO_2 on alpine plant growth appear to be transitory. However, via decreased stomatal conductance, higher CO_2 levels can generally influence transpiration and soil moisture and reduce drought stress in plants (Körner 2006). Additionally, individual responses of plant species can differ, potentially causing changes in vegetation structure and composition (Theurillat and Guisan 2001) and in forage quality for associated herbivores (Handa et al. 2005). Overall, nutrient availability appears to be the key factor that limits carbon-driven enhancement of alpine plant growth (Diemer 1994; Diemer and Körner 1998).

Nutrient regimes can be altered by both warming and atmospheric inputs. Particularly elevated levels of nitrogen are expected to modify vegetation structure and composition through differential responses of species and to accelerate ecosystem responses to climate change (Theurillat and Guisan 2001). For instance, lichen richness has been shown to decline in areas with high N deposition (Britton et al. 2009). Ultimately, higher nutrient levels are expected to increase the importance of plant species interactions in alpine ecosystems, which have previously been characterised by comparatively low competition (Klanderud and Totland 2005).

4.3.2 Tree line

The global cause of tree line formation is heat deficiency, which is regionally modulated by moisture conditions, wind, avalanches, grazing, fire, and human influences (Körner and Paulsen 2004; Walther et al. 2005b; Körner 2007; Wu et al. 2007; Miehe et al. 2008; Holtmeier 2009; Holtmeier and Broll 2010). Thus, the influence of climate change depends on exact site conditions. For example, warming in combination with increased precipitation is expected to be advantageous for tree growth in sites that are now too dry for tree growth, while warmer and dryer conditions could foster tree growth in currently wet areas (Holtmeier and Broll 2007; Malanson et al. 2007).

Mean temperatures have frequently been used as indicators of tree line position. For example, the tree line has been correlated with growing season mean ground temperatures between 5.4 and 7.8 °C (Körner and Paulsen 2004; Körner 2007). However, the importance of winter temperatures has also been reported (Kullman 2007; Harsch et al. 2009), and extreme temperatures (as opposed to means) have been suggested to have a major impact on the tree line, e.g., related to the freezing resistance of seedlings (Piper et al. 2006).

The exact role of temperature versus that of CO_2 fertilisation in tree line dynamics is controversial. The growth of many tree line species seems to be limited by tissue formation and, thus, by temperature rather than by photo-assimilate provision ("sink limitation hypothesis"; cf. Grace et al. 2002; Körner 2003a, b, 2007; Shi et al. 2008). However, some species appear to be carbon-limited, at least in the short term or during winter ("carbon balance hypothesis"), and potential long-range effects of increased CO_2 concentrations on competition and forage quality might influence community composition and food webs (Handa et al. 2005; Li et al. 2008a, b). The discussion regarding sink limitation and carbon balance hypotheses thus continues, demanding further research (Bansal and Germino 2008; cf. review in Smith et al. 2009). Another pathway related to how increasing temperatures might influence the tree line is through the acceleration of nutrient cycling, which in addition to enhanced atmospheric nitrogen deposition, could stimulate tree growth at the tree line (cf. Grace et al. 2002).

Because of time lags, threshold effects, and feedback mechanisms, the tree line is not necessarily in equilibrium with climatic conditions, and thus, it will not automatically immediately respond to climate change. Established trees can survive climate deteriorations for long periods, while tree line advance in response to warming depends, among other factors, on successful tree regeneration, species dispersal, and the availability of soils and generally suitable and invasible sites at higher altitudes (Dullinger et al. 2004; Löffler et al. 2004; Walther et al. 2005b; Kullman 2007; Holtmeier 2009). Additionally, tree line response to climate change can be hampered by pathogens (Tomback and Resler 2007) or herbivores (Cairns et al. 2007). Regarding tropical American tree lines, several feedbacks that prevent tree line advance to higher altitudes have been described; for example, conditions for tree seedlings in the open Páramo are adverse because of extreme radiation, severe night frosts (in comparison to a less extreme microclimate within the forest), and the occurrence of fires (Bader et al. 2007a, b). All in all, Theurillat and Guisan (2001) suggested that warming of merely 1–2 °C will not cause any major tree line shifts and that a temperature increase of 3–4 °C will be required to trigger distinct altitudinal changes.

The influence of land use on the tree line due to, e.g., grazing, agriculture, fire management, or forestry, can interact with the impact of climate change (Baker and Moseley 2007) or even override it completely. For instance, the spatial expansion of forest fragments within the alpine tree line ecotone can be a result of declining pastoral use and should not be confused with the effects of a warming climate (Löffler et al. 2004; Lasanta-Martinez et al. 2005; Gehrig-Fasel et al. 2007; Rössler and Löffler 2007; Rössler et al. 2008; Vittoz et al. 2008; Leonelli et al. 2009; Hofgaard et al. 2010). However, potential vegetation response to climate change can be counteracted by maintaining traditional land use (Theurillat and Guisan 2001; Anschlag et al. 2008; Baniya et al. 2009). In conclusion, in contrast to the assumptions made in many studies, tree lines cannot necessarily be regarded as good indicators of climate change. Beyond this, more research is necessary to fully understand the mechanisms acting at the current tree line. Self-enforcing effects, e.g., resulting from enhanced snow deposition within newly established tree populations due to reduced wind velocities (Holtmeier and Broll 2010) or from higher temperatures within a dense growing tree line, should be addressed in future studies.

4.4 Soils

The warming of soils triggers increased microbial activity, net N mineralisation, and nitrification (e.g., Rustad et al. 2001; Makarov et al. 2003; Löffler et al. 2008). Additionally, Hagedorn et al. (2010) showed that experimental soil warming throughout a single growing season increased the CO_2 efflux from treeline soils by intensifying the decomposition of soil organic matter to a greater extent than carbon gains through plant growth. However, winter snow cover is of great importance for soil processes (Edwards et al. 2007), and under certain conditions, climate warming could reduce snow packs, which in turn can lead to colder soils and an increase in the frequency of freeze-thaw cycles (Freppaz et al. 2008). Consequential reductions of soil respiration may cause an increase of carbon sequestration (Monson et al. 2006). In contrast, nitrogen leaching from soils has been reported to increase with decreases in the snow pack, which is potentially attributable to reduced root uptake and/or to physical (rather than microbial) degradation of soil organic matter (Freppaz et al. 2008). Contrary to assumptions of soil cooling due to climate change, a study by Henry (2008) (covering sites across Canada up to an elevation of 1,100 m a.s.l.) indicated that warmer winters have historically caused a reduction of soil freezing days, in spite of declining snow packs. This may lead to a stimulation of soil respiration and the decomposition of organic matter.

Generally, due to the different experimental conditions used, the results from various studies on soil warming are often contradictory. Moreover, decomposition depends not only on temperature, but also on soil moisture (Sjögersten and Wookey 2004; Aerts 2006); other important factors are climate change effects on soil fauna communities and migration abilities (Aerts 2006; Hågvar and Klanderud 2009). In general, indirect effects of warming on soil processes via changes of litter quality due to plant species composition and range shifts are expected to be substantial and possibly even more important than direct physical warming (Shaw and Harte 2001; Aerts 2006; Wookey et al. 2009). Moreover, CO_2 fertilisation has been shown to stimulate soil respiration and microbial activity in tree line soils (Hagedorn et al. 2008). Soil fauna has also been shown to react to increased nutrient availability and associated changes in plant litter production, at least in the short term, with an increase of biomass, a reduction of species richness, and modified dominance structures, with the fastest responses being seen in species with short life cycles (Hågvar and Klanderud 2009).

4.5 Fauna

Warming effects on fauna can generally be direct or indirect. Increases in temperature over the last century have clearly been linked to shifts in species distributions (Lawler et al. 2009). While certain species are exhibiting poleward shifts in the latitude of their ranges, other species have been observed moving upward in elevation at rates that are consistent with recent temperature increases (Parmesan and Yohe 2003). In some regions, lowland birds have begun breeding in montane habitats (Crick 2004). In addition to homoeothermic species, ectothermal species of invertebrates are also moving upwards: Parmesan (2003) reported upward shifts of butterfly populations in North America, which face a higher risk of extinction at lower elevations. Range-restricted species, such as mountaintop species of animals and plants, have been observed to show particularly severe range contractions. Presumably, these are among the first groups in which entire species have gone extinct due to recent climate change, as they are pushed against an altitudinal limit (Parmesan 2006). Documented examples of this are small mammals and insects (Beever et al. 2003; Wilson et al. 2005). However, it is still unclear for many taxa how closely changes in their distributions match climate changes (Popy et al. 2010), and dispersal limitations are considered to have an important impact on range shifts (Holzapfel and Vinebrooke 2005; Oertli et al. 2008).

For mountainous regions in particular, large changes in fauna have been predicted due to the strong gradients in environmental conditions that exist over relatively short distances and due to the fact that the edges of many species' ranges occur in mountainous regions. In mountains and other regions where species encounter their lower latitudinal-range margins, climate warming, together with other drivers of biological change, could lead to significant losses in biodiversity (Wilson et al. 2007). General species richness may decline, and communities may become dominated by widespread species. For example, in Europe, butterflies found in central and southern European mountains have been shown to be more sensitive to climate change than most other butterfly species (Heikkinen et al. 2010). Additionally, the ranges of endemic species can be influenced, especially when they are cold-stenophilous. Turnover rates caused by climate change effects in communities of birds, mammals, and amphibians in mountainous regions can be as high as 90%. Therefore, especially in these habitats, faunal distributions in the future will change drastically when compared to those of today (Lawler et al. 2009).

Host-plant interactions, as well as other biotic interactions, food availability, habitat quality, and the abundance of enemies can be altered by a changing climate. For instance, different climate change responses of host plants and herbivores or of prey and predators may lead to a mismatch between resource availability and suitable climatic conditions and may possibly lead to future range contractions of animal species (Merrill et al. 2008; Schweiger et al. 2008; Green 2010). A rather prominent example of these biotic interactions is the decline of amphibian species in various mountain areas that has been attributed to the pathogenic fungus *Batrachochytrium dendrobatidis*, which benefits from climate change (Pounds et al. 2006; Bosch et al. 2007). However, this climate-linked epidemic hypothesis is controversial, as it has been suggested that extinctions could be explained by the spreading of an invasive pathogen, independent of environmental change (Lips et al. 2008). Nevertheless, habitat alterations connected to climate change, e.g. the desiccation of wetlands, have a major influence on amphibian populations (McMenamin et al. 2008). Climate change has also been shown to influence the winter habitat conditions of high latitude rodents. For instance, altered conditions in the subnivean space affect the population cycles of lemmings (*Lemmus lemmus*), making rodent peaks less regular (Kausrud et al. 2008). The importance of snow conditions and spring temperatures for the onset of the vegetation growth and thus for the body mass of reindeer calves is another example of such effects (Pettorelli et al. 2005).

Furthermore, as in lower altitudes, the phenology (seasonal timing) of the activity of ectothermal animals can be influenced by climate change. For insects, the ability to gain sufficient heat energy to complete their life cycle has been suggested to limit their altitudinal distribution (Hodkinson 2005). Thus, the life cycles of insects and other arthropods could be altered drastically. A well know example of this, because of its function as a vector for transporting fungi to forest trees, is that of the mountain pine beetle (*Dendroctonus ponderosae*), which has been found to have shortened its generation cycle from two years to one year in the Rocky Mountains of the United States, resulting in increased population abundances (Logan et al. 2003; Kurz et al. 2008a). Another example is the altitudinal range expansion of the winter-active pine processionary moth (*Thaumetopoea pityocampa*) in the Italian Alps. This is attributed to warmer average winter temperatures, accelerating early larval development, allowing for increased winter feeding, shorter starvation periods and an overall enhancement of survival (Battisti et al. 2005).

For the migrating bird species the American robin (*Turdus migratorius*), the date of their first sighting in their mountain habitats was found to be 14 days earlier on average in 1999 compared to 1981 (Inouye et al. 2000). In parallel, for mountainous bird species, it has been observed that the mean laying dates of first clutches has advanced (Hendricks 2003; Potti 2009). In the Colorado Rocky Mountains, hibernating yellow-bellied marmots (*Marmota flaviventris*) ended their hibernation period up to 38 days earlier at the end of the 1990s than in the middle of the 1970s, apparently in response to warmer spring air temperatures (Inouye et al. 2000). For both hibernating and migrating species, earlier activity in mountain habitats could pose problems, as asynchrony with the disappearance of the winter snow pack and with vegetation can increase. This could occur due to higher precipitation during winter and a resulting constant, or even later date of snow melt, although air temperatures might generally rise. After these animals initiate activity in the spring, they thus face longer periods of snow-covered ground and of resources being hidden before the summer growing season begins (Inouye et al. 2000). However, various alpine species can show very different phenological responses to changing climatic conditions. For example, migratory bird species may react either to low-altitude temperature regardless of high-altitude snow pack conditions, or to alpine snow conditions regardless of low-altitude warming (Green 2010).

5 Future research needs

The multitude of examples given above highlights the fact that there are many uncertainties regarding future ecosystem behaviour due to ecosystem complexity (Walther et al. 2005b). Many detailed studies have generated highly specific data related to response mechanisms to global change in mountain areas, but these results were often obtained under a narrow range of environmental conditions. Additionally, in spite of a large number of local-level studies, there are no consistent data on whole mountain regions, and there is a serious need for further research in this regard (Sonesson and Messerli 2002, 93). Moreover, current studies raise the question of whether alpine ecosystems will actually react as sensitively to climate change as predicted (see above), or may be much more resilient towards warming than generally expected. For example, the important effect of local topographic heterogeneity on factors such as microclimate, snow cover, soil conditions, vegetation patterns and animal diversity has frequently been reported (Holten 2003; Löffler and Finch 2005; Löffler 2005, 2007; Löffler et al. 2006; Löffler and Pape 2008; Wundram et al. 2010; Fig. 3), and it has been shown that the effects of microtopography on soil and surface temperatures can greatly override the effects of slope and region (Löffler et al. 2006). It is suspected that this topography-dependent temperature mosaic might offer refuges to species in the course of climate warming (Scherrer and Körner 2010, 2011). Moreover, it is possible that climate change will mainly influence exposed and wind-blown ridge sites, while areas associated with thick snow cover will largely remain unaffected by climate change (cf. the "conservative nature of snow", Gjærevoll 1956). This debate emphasises the need for a further thorough examination of these highly differentiated mountain ecosystems. Standardised approaches across different mountain regions, as postulated for comparative mountain research by Carl Troll quite some time ago and others since, are vital for these types of in-depth studies (e.g., Troll 1988; Sonesson and Messerli 2002; Winiger and Börst 2003).

Generally, we strongly advocate conducting multi-factor studies, which should account for the potential physical and biotic effects of not only climate warming, but also of land use cover change and atmospheric nitrogen input (Theurillat and Guisan 2001; Löffler et al. 2004; Rustad 2008). Such studies would therefore represent the broad spectrum of global change-related factors affecting mountain ecosystems as comprehensively as possible. Research in this field must also cover various spatial and temporal scales (from micro-scale to macro-scale, cf. e.g., Pape et al. 2009, and long-term studies with high temporal resolution) to understand the functioning of mountain ecosystems with respect to their spatial heterogeneity and configuration and to comprehend the spatial interactions between these systems.

Methodically, different approaches (observations, experiments, and models) associated with particular advantages and disadvantages (cf. Rustad 2008) have to date often been used exclusively. Ideally, the integration of the various methods will allow for a better understanding of ecosystem response to global change for both ecosystems in general and mountain ecosystems in particular (Theurillat and Guisan 2001; Harte 2005; Bugmann et al. 2007; Rustad 2008; Seppelt et al. 2009). Concerning experiments on climate warming, with regard to the disadvantages of in-situ warming experiments (for an overview, see Shaver et al. 2000), a thus far rarely investigated possibility is transplanting (preferably large) monoliths of soil and associated vegetation between different elevations, thereby using the natural climatic transition along mountain slopes to simulate climate change (Bruelheide and Flintrop 2000; Bruelheide 2003; Körner 2005; cf. Fig. 4). Experiments on other types of global change-related factors include artificial fertilisation (to account for changes in atmospheric chemistry) or fencing (to manipulate grazing impacts, thus simulating land use change). Field research can also be complemented with growth chamber experiments, which have rarely been applied for studies on mountain ecosystems (e.g., Lokupitiya et al. 2000; Marty et al. 2009).

Global change research cannot be conducted without modelling. Models allow projections of system states for global change scenarios. They integrate data from observations and experiments, gen-

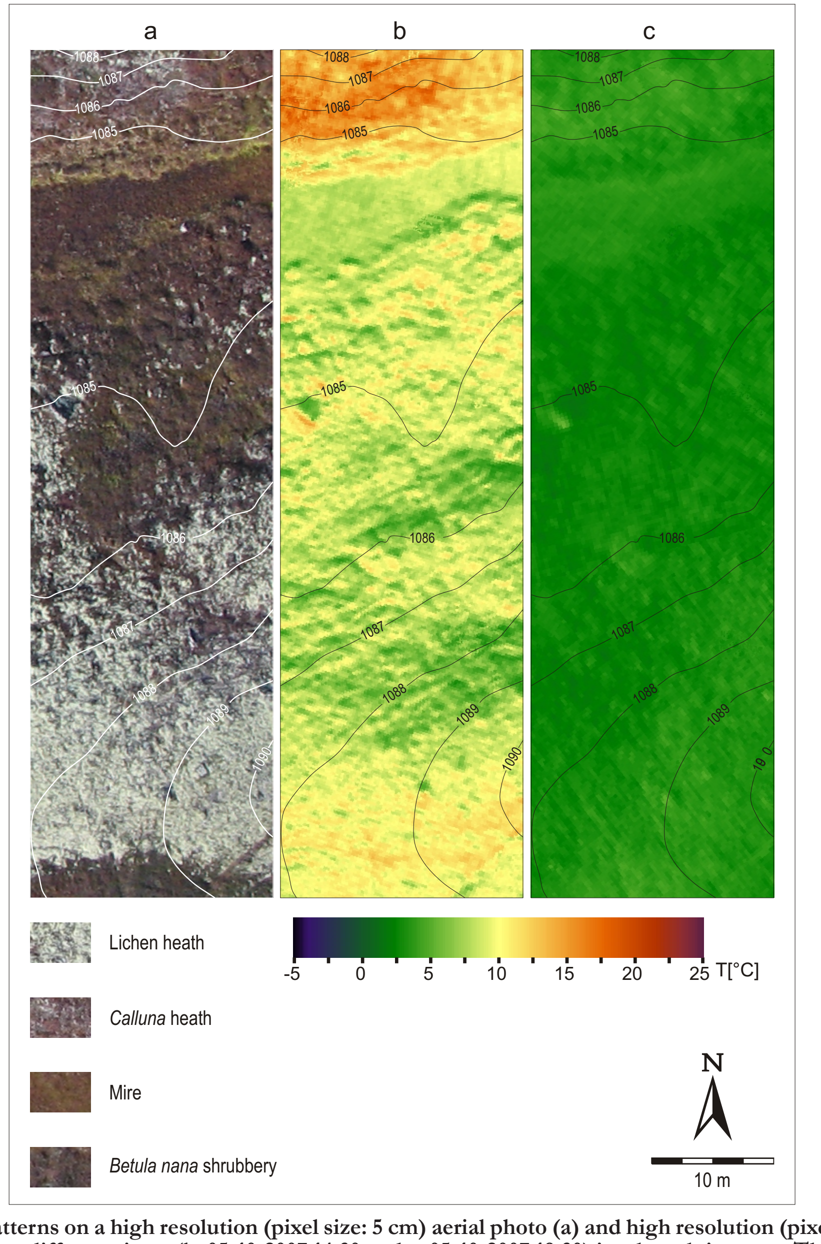

Fig. 3: Land cover patterns on a high resolution (pixel size: 5 cm) aerial photo (a) and high resolution (pixel size: 15 cm) thermal surface patterns at different times (b: 05-10-2007 14:30 and c: 05-10-2007 18:30) in a low alpine area. The real colour photo was captured by a simple 7 megapixel digital compact camera (Canon Powershot S70) and the thermal images were taken with a MIDAS thermal infrared camera (320 × 240 uncooled microbolometer; 8 µm to 14 µm). The cameras were attached to a simple camera platform carried by a helium balloon. All images were taken from an altitude of approx. 200 m above ground. The raw pictures were orthorectified based on a precision (about 10 cm accuracy) digital elevation model that was generated from aerial stereo pictures from the same field campaign (Wundram and Löffler 2008). Simplified topographic conditions are illustrated by one meter interval contour lines extracted from the digital elevation model

erate hypotheses motivating new observational and experimental approaches, and allow an interdisciplinary approach to be employed by using mathematical equations as a common language. Modelling generally covers a range of approaches, starting either with the description of patterns or processes (Schröder and Seppelt 2006).

In global change research, phenomenological/statistical species distribution models (also referred to as environmental niche models or habitat models) have been successfully applied in landscape ecological, biogeographical, and macroecological contexts for describing species distributions or species richness patterns, as well as in predicting range shifts

Fig. 4: Transplantation of 1.5*1.5*0.5 m³ monoliths to a lower altitude (Vågå/Oppland, Norway, summer 2008)

(e.g., Guisan and Theurillat 2000; Dirnböck and Dullinger 2004; Nogués-Bravo et al. 2008; Trivedi et al. 2008; von dem Bussche et al. 2008). To overcome limitations, such as the lack of direct implementation of ecological processes and biotic interactions, as well as the underlying equilibrium assumption (for a general discussion, cf. Pearson and Dawson 2003; Araújo and Guisan 2006; Zurell et al. 2009), more mechanistic approaches have been developed recently (e.g., Anderson et al. 2009; in a general context, cf. Keith et al. 2008; Kearney and Porter 2009). Here, distribution models are linked with process-based approaches.

Process-based models have been very successfully applied in describing population dynamics or forest dynamics responding to all aspects of environmental change in mountain areas, explicitly considering species interactions, dispersal, and other processes (e.g., Lischke et al. 1998; Weisberg et al. 2005; Rammig et al. 2006; Bugmann et al. 2007; Wallentin et al. 2008; Dislich et al. 2009). These kinds of models provide a mechanistic understanding of and deep insights into processes (e.g., Grimm et al. 2003; Rickebusch et al. 2007b). Therefore, they enable sound predictions of future developments and reconstruction of past developments to be carried out (e.g., Bugmann and Pfister 2000; Lischke 2005; Heiri et al. 2006).

The dynamics and interactions of water, carbon, vegetation, disturbances, and land use need to be considered in process-based ecosystem models and in integrated landscape models, which is the next logical step to achieve a mechanistic understanding of global change impacts on mountain landscapes. Promising examples of this are provided, for instance, by Zierl and Bugmann (2005), Lischke et al. (2007), Schumacher et al. (2006), Quétier et al. (2007), Rickebusch et al. (2007a), Zierl and Bugman (2007), Albert et al. (2008), and Schröder et al. (2008).

A large range of scales is involved in assessing the impact of global change on mountainous ecosystems. Global driving forces, such as climate change, are supplemented by demographic and economic changes on regional to local scales. Therefore, modelling efforts must consider these scale issues, especially because GCM outputs cannot be used directly for local-scale impact assessment. Downscaling (e.g., Xu 1999; Benestad 2002; Steinacker et al. 2006; Quian 2010) is an important issue when analysing the impact of climate change on mountain ecosystems, but this is challenging because these systems are characterised by extreme small-scale heterogeneity (Ihse 2007; Pape et al. 2009). Although most scenarios agree regarding the warming of mountains, the future development of precipitation is often unclear. Modelling frequently concentrates on large spatial scales and long-term effects on factors such as water availability (e.g., Barontini et al. 2009). The challenge is to model the impact of global change on local (micro and meso) scales, including soil moisture patterns and their temporal dynamics as important factors for local energy balance and plant growth.

Programmes and networks that support the implementation of mountain research are often highly specialised. For instance, a focus on biodiversity and vegetation is shown in the GMBA (Global Mountain Biodiversity Network) and the associated initiatives GLORIA (Global Observation Research in Alpine Environments, e.g., Pauli et al. 2005) and MIREN (Mountain Invasion Research Network, e.g., Pauchard et al. 2009). Changes in glaciers are addressed by the WGMS (World Glacier Monitoring Service) with its Global Terrestrial Network for Glaciers (GTN-G), while permafrost issues are dealt with by the IPA (International Permafrost Association) and its GTN-P (Global Terrestrial Network for Permafrost). CEOP-HE (Coordinated Energy and Water Cycle Observation Project – High Elevations) concentrates on energy and water cycles in mountains. The sometimes unidimensional focus of these research networks and organisations is frequently reflected in highly specialised research. However, an ecosystem approach demands integration across compartments, such as the atmosphere, hydrosphere, cryosphere, pedosphere, and biosphere, with all disciplines focussing on the same functional phenomena (cf. Margraf 1987). Accordingly, interdisciplinarity is recommended by e.g., the MRI (Mountain Research Initiative, Becker and Bugmann 1997, 2001; cf. GLOCHAMORE Research Strategy, e.g., Grabherr et al. 2005; Price et al. 2006), CIRMOUNT (Consortium for Integrated Climate Research in Western Mountains), and NOROCK (Northern Rocky Mountain Science Center). This recommendation might appear self-evident, but so far, large interdisciplinary research projects on global change in mountains have been rare. Exemplary exceptions are (i) the CLIMET Project, in which research on climate, biology and hydrology in mountain areas along a continentality gradient in the northwestern USA are incorporated (Fagre et al. 2007), and (ii) a current study on gradients in tropical mountain ecosystems and their anthropogenic replacement systems in Ecuador, combining research on patterns and processes related to climate, soils, water relations, biodiversity, vegetation, fauna, disturbances, and land use (Beck et al. 2008; Bendix and Beck 2009; Dislich et al. 2009; www.tropicalmountainforest.org).

In conclusion, we suggest future research on mountain ecosystem response to global change to account for the following aspects simultaneously:

- multi-factor studies: taking various global change triggers into account (climate change, land use cover change, change in atmospheric chemistry, etc.);
- an integrative, multi-method approach: linking experiments, observations, and problem-specific models;
- multi-scale research: conducting studies across various spatial (micro, meso, macroscale) and temporal (long-term research, high temporal resolution) scales;
- interdisciplinarity: focussing on the same functional phenomena, taking a large set of driving factors of natural and human systems and their feedbacks into account and considering effects on different aspects of the socio-ecological system.

Ultimately, complex studies are required to fulfil the standards of truly comparative mountain research. This is still not an easy task, and attempts to do this have often not led to a set of integrated conclusions. We therefore advise conducting localised studies across different mountain areas, covering various factors, methods, and scales, in which experts on natural and human systems should formulate common research questions to be dealt with in the same study area.

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Authors

Prof. Dr. Jörg Löffler
Dr. Kerstin Anschlag
Dr. Roland Pape
Dr. Dirk Wundram
Department of Geography
Climatology and Landscape Ecology Research Group
University of Bonn
Meckenheimer Allee 166
53115 Bonn
Germany
joerg.loeffler@uni-bonn.de

Dr. Barry Baker
Director, Canyonlands Research Center
The Nature Conservancy
820 Kane Creek Blvd.
P.O. Box 1329
Moab, UT 84532
USA
bbaker@tnc.org

Dr. Oliver-D. Finch
Animal Biodiversity and Evolutionary Biology
University of Oldenburg
Carl-von-Ossietzky-Straße 9-11
26111 Oldenburg
Germany
oliver.d.finch@uni-oldenburg.de

Prof. Dr. Bernd Diekkrüger
Department of Geography
Hydrology Research Group
University of Bonn
Meckenheimer Allee 166
53115 Bonn
Germany
b.diekkrueger@uni-bonn.de

Guest Prof. Dr. Boris Schröder
Institute of Earth and Environmental Science
University of Potsdam
Karl-Liebknecht-Str. 24-25
14476 Potsdam-Golm
Germany
boris.schroeder@uni-potsdam.de
and
Leibniz Centre for Agricultural Landscape Research
(ZALF) e.V.
Eberswalder Str. 84
15374 Müncheberg
Germany

Prof. Dr. Anders Lundberg
Department of Geography
University of Bergen
Fosswinckelsgate 6
5020 Bergen
Norway
anders.lundberg@geog.uib.no

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The interdependencies shown are based on the examples given in the text.