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Ecological and Land Use Studies Along Elevational Gradients

Mountain regions and UNESCO Mountain Biosphere Reserves (MBRs) encapsulate broad elevational ranges, cover large gradients of geological, topographical and climatic diversity, and thus host greater biodiversity than the surrounding lowlands. Much of the biological richness in MBRs results from the interaction of climatic contrasts and gravitational forces along elevational gradients. External forces such as atmospheric change and human land use interact with these gradients, and result in distinct landscape patchiness, ie mosaics of land cover types within and across elevational belts. The management of MBRs influences land use and land cover, which affects biodiversity and ecosystem processes, both of which provide goods and services to society. Due to their broad environmental and biological diversity, MBRs are ideally suited for global change research and will be increasingly important in illustrating biodiversity conservation. This article summarizes the ecologically relevant results of an international workshop on elevational gradients that aimed to achieve a synthesis of the major ecosystem and biodiversity conditions and drivers in an altitude context. The workshop developed a core research agenda for MBRs that prioritizes long-term research and changes in land use across a broad elevational range.

Keywords: *Elevational gradients; biodiversity; elevational belts; global change research; land cover change; Mountain Biosphere Reserves.*

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Introduction

A characteristic feature of high mountains is their vertical zonation into elevational belts with distinct climates: (1) the snow- and ice-covered nival belt, (2) the alpine belt (treeless, above treeline), (3) the mainly forested montane belt (below treeline), and (4) the valley floors and forelands. This sequence of belts, and their differences and interactions along elevational gradients, contribute to the environmental and biological diversity of UNESCO Mountain Biosphere Reserves (MBRs), which offer unparalleled challenges and options for geophysical and biological research, and for conservation and ecosystem services in the context of global climate change (UNESCO 2006). They share a common concept, are distributed all over the world, and are capable of performing special investigations, including research (see Table 1 below and Reasoner et al 2004). These issues were discussed at a Global Change and Mountain Regions (GLOCHAMORE) Workshop in 2005 (Becker et al 2007, in this issue).

Biota and soils along elevational gradients reflect the outcome of multiple interacting environmental factors over long periods of time. They are more likely to approximate steady-state responses to such conditions than experimentally manipulated systems, hence they have frequently been referred to as model test systems (Garten et al 1999) or experiments by nature (Körner 2003, p 7). Here we shall summarize the major ecological and biodiversity trends across elevational gradients in mountains and their research implications for MBRs.

Slope stability and biodiversity gradients

The trivial fact that mountains have slopes causes them to directly or indirectly influence the life of half of the earth's human population (Messerli and Ives 1997; Meybeck et al 2001; Körner and Ohsawa 2006). Slopes provide gravitational power to water, which can be converted to electrical energy. Slopes guard, guide or constrain, and endanger traffic routes. They stop clouds (advection) or create them (convection). Slopes also exert mechanical force on any organism, installation or activity located on them. Unless made of solid rock, the only way in which loose substrates can be secured to slopes is through vegetation: these living claws, screws, and nails sustain slope stability, protect soils, and prevent slope dangers (Körner and Spehn 2002). Hence, slopes are only as stable as their vegetation (including material stability beyond the vegetation). Consequently, the integrity of upslope vegetation, achieved through a multitude of plant structures and plant functional types, ensures downslope welfare and safety.

The hump-shaped elevational species richness pattern, illustrated in Figure 1, has several potential reasons. Mild climatic conditions at mid-elevation (high humidity, moderate temperatures) permit the co-existence of taxa which otherwise have high-, mid- or low-elevation centers of distribution (Kessler 2001; Körner 2003; Bhattarai et al 2004). This "range overlap effect" is particularly pronounced in the zone of gradual or patch-wise transition from montane forests to alpine vegetation. Land area fragmentation (Rosenzweig and Ziv 1999), metapopulation interactions (Stevens 1989), source-sink effects of taxa (Kessler 2001; Grytnes 2003), and historical and evolutionary processes (Ricklefs 2004) all favor maximum organism diversity at mid-elevation. The elevation at which the richness peaks varies with the taxonomic group as determined by its ecophysiology, reproductive requirements, and evolutionary history. For instance, the diversity of certain cryptogamic plant groups peaks at higher elevation than diversity in woody angiosperms. As mountains become narrower with increasing elevation, the habitat area per eleva-

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tional belt gets smaller (Körner 2000; Colwell et al 2004), and species richness decreases. The loss of angiosperm species above the treeline is approximately 40 species per 100 m across a wide spectrum of mountain ecosystems (Körner 2003).

As mountains get steeper and higher, species diversity usually declines (Körner 2003, 2004; Nagy et al 2003). However, this is only true above the climatic treeline and not for all groups of organisms. For example, the diversity of lichen and moss species often increases beyond the treeline (Theurillat et al 2003; Virtanen et al 2003). Over transects covering the full gradient from low to high elevations, about 75% of all studies show "hump-shaped" patterns as mentioned before, with a mid-elevation peak of species richness across all groups of organisms (Figure 1), whereas about 15% show monotonic declines; the rest increases or shows idiosyncratic patterns (Rahbek 1997; Hemp 2002; Grytnes 2003; McCain 2005).

Mountain soils

Most of the services provided by mountain ecosystems, such as protection of slopes by vegetation cover and the productivity of forests and agro-ecosystems, are driven by the intimate linkages between plants, soils, and associated soil biota (Bardgett et al 2002). Some key species of soil fauna (eg earthworms), often called "ecosystem engineers," drive soil structure and soil hydrology in the upper soil layers, and decline in abundance and activity as altitude increases. Likewise soil microbial processes are a function of temperature (Townsend et al 1995; Winkler et al 1996). As a consequence, litter layer turnover rates decrease with elevation (Alps: Schinner 1982; Tibet: Wang et al 2005).

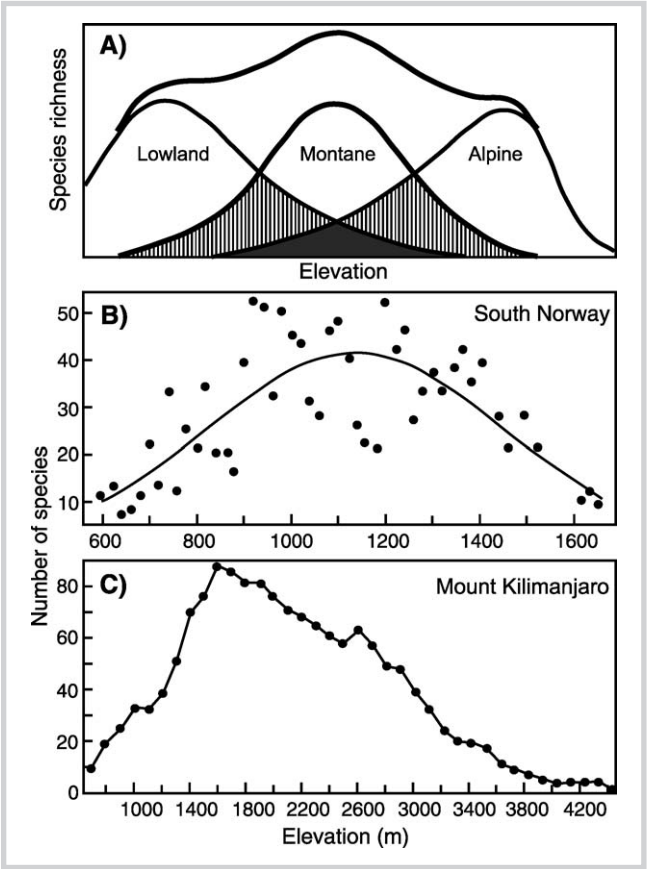
In many mountain regions, the upper montane forest has the maximum soil organic matter pool of a whole region: mountain forest replacement by pastures can mobilize this carbon (Bolstad and Vose 2005). Above the treeline we often find extremely high soil humus concentrations per unit dry weight (50% or more), but the total carbon pool size declines as soil depth becomes shallower. These humic soils are rather fragile and rapidly eroded if vegetation is disturbed. Above the treeline, profile depth and stone content are particularly limiting factors for carbon and water storage (Körner 2003; Leifeld et al 2005). For an overview including biological indices see Knoepp et al (2000) and Parisi et al (2005). Currently, geo-referenced, harmonized data on soil organic carbon and other soil quality and soil biodiversity data in mountain regions are lacking; they are needed as a baseline reference for future trends.

The treeline ecotone

The most prominent biogeographic boundary in mountains is the upper limit of tree growth, often termed treeline. The treeline represents a life form boundary that limits regional tree growth irrespective of the species. In regions that lack tree species adapted to the cold, the actual tree limit does not represent a natural climatic treeline (eg Hawaii). While a great variety of local environmental factors may modify high-elevation forest distribution (eg drought, fire, avalanches, and land use), the growing season mean temperature of 6.7±0.8°C sets the over-arching upper limit at a global scale (Körner and Paulsen 2004). The climatic tree limit also represents the best biological reference against which other elevational belts in mountains can be defined.

The treeline ecotone is ideally suited for climate change monitoring. Although all evergreen tree species

FIGURES 1A TO 1C Elevational gradients of organism diversity often show a mid-elevation peak related to the overlap of distributional ranges and the absence of extreme life conditions: A) curves symbolize range spectra for groups of taxa centered at 3 different elevations with the resultant sum given at the top (see Körner 2003); B) examples for boreal latitudes (grassland plants; Grytnes 2003); and C) equatorial latitudes (ferns; Hemp 2002).



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studied at the treeline so far have been found to be better supplied with carbon under current atmospheric conditions than trees at lower elevation (for reference see Hoch and Körner 2005), the deciduous larch (*Larix decidua*) was found to still take direct advantage at the treeline from atmospheric CO_2 enrichment (Handa et al 2005). The warming trend during the past century has also clearly enhanced tree growth at the treeline (Rolland et al 1998; Paulsen et al 2000). Since the treeline determines the lower boundary of the alpine belt, any upward shift of the treeline will restrict the overall alpine area and impact the distribution of alpine species with a lower altitude affiliation. Monitoring and modeling treeline shift is a prerequisite to modeling the future ranges of alpine species in response to climate change (Dullinger et al 2004).

Genetic diversity and isolation

Mountains are often considered archipelagos of isolated environments in an ocean of "hostile" low-elevation terrain, with mountain species adapted to the cold (Nagy et al 2003). As with island biogeography, this isolation exerts constraints on evolution and species diversity, resulting in a higher ratio of endemics at higher elevations (Kessler 2000; Vetaas and Grytnes 2002; Pauli et al 2003). Important questions for research are: How has human land use fragmented mountain environments? Do mountain species suffer more from lower populations, more frequent genetic bottlenecks and drift than species at lower elevations? Is genetic diversity at risk as natural habitat fragmentation increases with elevation?

Recent genetically based ecological research in the European Alps illustrates that the adapted reproductive systems of mountain plants ensure high genetic diversity despite frequent spatial isolation (Escaravage et al 1998; Plüss and Stöcklin 2004). In addition, mountain plants can compensate periodic reproductive failure by clonal spreading, and with this, survive both short- and longer-term periods of unfavorable climate (Steinger et al 1996; Weppler and Stöcklin 2005).

Biotic changes

Mountain biota will respond to climatic change in various ways (Theurillat and Guisan 2001). There is consensus that climate change drives species rather than communities (Huntley 1991). Monitoring of a high summit in the eastern European Alps (Schrankogel, Tyrol) for 10 years revealed complex community dynamics, with a recent gain in pioneer species from the alpine grassland belt and unexplained losses of otherwise well-adapted cold climate species (H. Pauli, personal communication). Overall, these summits have been found to host more species of pioneer vegetation than they did 40–100 years ago (Grabherr et al 1994; see also Bahn and Körner 2003). One of the obvious risks is the loss of species from mountains not high enough to offer escape routes in the case of upward shifts of taxa less adapted to the cold (Theurillat and Guisan 2001). The worldwide GLORIA network (www.gloria.ac.at) aims to assess such trends on a long time scale (Pauli et al 2004). MBRs offer suitable long-term monitoring sites in this regard, with 10 GLORIA sites established within MBRs or in their close vicinity.

It is far more difficult to assess migratory responses to warming climate at lower than summit elevations, where historical observations are more difficult to locate accurately (Guisan and Theurillat 2005). Yet an upward shift of lower elevation boundaries of species was recently documented for butterfly species in Spanish mountains (Wilson et al 2005), and for plants and other taxa (Walther et al 2005). Hence, appropriate observation programs are also required to monitor such changes along the full elevation gradient, as a way to complement the "summit view" (Guisan and Theurillat 2005), and MBRs could play a major role in establishing them.

On much larger regional scales, climate-driven species distribution models (Guisan and Thuiller 2005) can provide useful primary estimates of potential impacts over large areas and complex landscapes. This empirical approach statistically relates current species distribution to environmental conditions, such as topography, climate, geology, and land use. It has been successfully applied to predicting plant species distribution at a fine scale in alpine landscapes (eg Gottfried et al 1999; Guisan and Theurillat 2000; Dirnböck et al 2003), suggesting sharp range reductions for many species, and possible local extinctions for some very high-elevation species.

Species losses were also predicted in several European mountain ranges by similar models fitted at the Europe-wide continental scale (Thuiller et al 2005). Such model-based scenarios help envisage future change in mountain biota and can reveal areas of high predicted turnover and species loss where monitoring activities should be prioritized. While more mechanistic models including population dynamics and dispersal (eg Dullinger et al 2004 for *Pinus mugo*; Bugmann 2001 for various tree species) would be desirable, our knowledge is still insufficient to parameterize these for most species in a spatially explicit way (Guisan and Thuiller 2005). Yet, to be realistic, future projections should at least include individual species' ability to migrate at a sufficient speed to keep pace with rapid climate change. To make development of such models possible, a priority task for MBRs should be to set up appropriate GIS databases of species observations and environmental maps.

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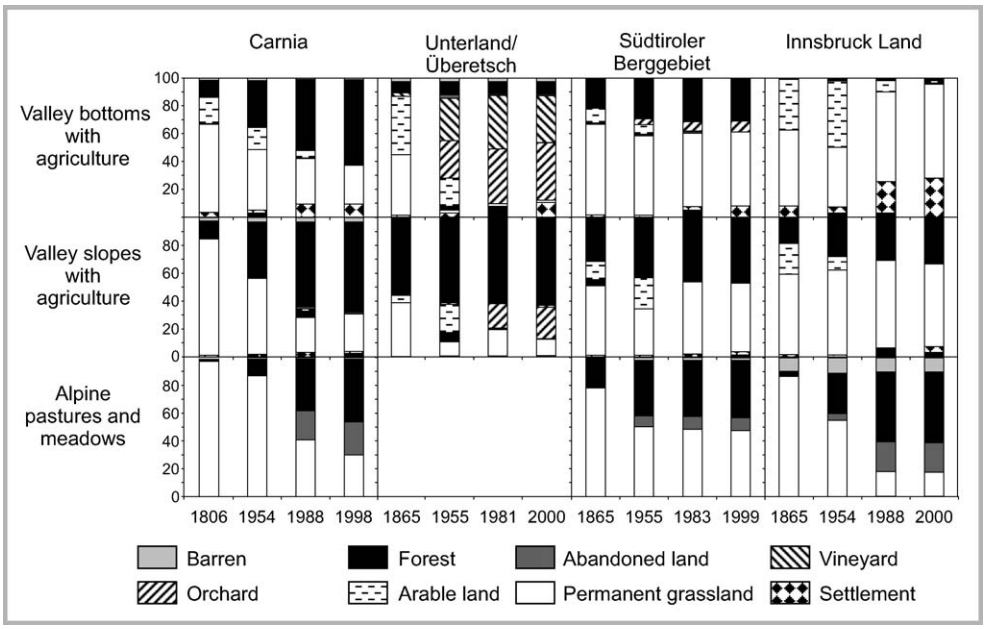


FIGURE 2 Historical land use development in 4 different agrarian regions of the European Alps: 1) the agricultural retraction region of Carnia (Italy), 2) the South-Tyrolean wine and fruit cultivation region Unterland/Überetsch (Italy), 3) the South-Tyrolean grassland region Südtiroler Berggebiet (Italy), and 4) the Innsbruck Land region (Austria). (Based on Tasser et al 2005)

Socioeconomic impacts on elevational gradients in land use and biodiversity

For biodiversity and ecosystem processes, the type of land cover (extent and quality) is considered the main manageable feature in MBRs. Hence, assessments and measures need to address the extent (spatial coverage) as well as the quality (biological inventory, ecosystem processes, services) of certain land cover types. A good example of such an investigation was given by the recent analysis of ecological and land use changes in various elevational belts in the Alps along with the elevational decline of agricultural and forestry activities (Figure 2 and Tappeiner et al 2006). With the exception of one region, the investigated sites underwent agricultural intensification on the valley floors, while the settlement area expanded (Figure 2). On steeper slopes, agricultural area is increasingly being taken out of cultivation and 39–80% of former managed areas in the alpine pasture region has already been abandoned. These human-driven land use and land cover changes affect important ecosystem services (vegetation shifts, biodiversity, phytomass production, carbon sequestration, and water relations). The subalpine belt (1700–1900 m) experienced massive increases of forest due to natural reforestation, and thus the fraction of cultivated and grazed land is rapidly decreasing, along with its related biodiversity.

The studies in Tyrol by Tappeiner et al (2006) indicated that land cover changes, as observed by Dirnböck et al (2003), combined with human-induced changes, far exceeded the effect of climatic influences. On a plot basis, intensification of land use by grazing (and overgrazing) commonly favors grasses to the disadvantage of herbs, ultimately leading to low diversity tussock grassland of low palatability (Tasser and Tappeiner 2002; Tasser et al 2005). In the tropics, subtropics, and the southern hemisphere humid temperate zone, the combination of inevitable fire management and animal trampling in combination with overgrazing may lead to the complete loss of inter-tussock space vegetation and increase the risk of soil erosion (Spehn et al 2006).

A principal paradigm for these assessments is that vegetation cover ensures soil protection and slope stability. Net benefits of sustainable land use are maintenance of productivity, habitat integrity, down-slope safety, and water yield (Spehn et al 2006). Therefore maps of land cover type and other features (eg topography, geology, soils, land use intensity, population density) are of prime importance. Biological inventories need to be weighted by taxon abundance (starting with vascular plants, megafauna, and charismatic species). These maps should be supplemented by sets of meteorological data (at least precipitation and temperature) at several altitudes, and remote sensing data, such as thematic scanner data (eg Normalized Difference Vegetation Index, NDVI).

Conclusions and recommendations

Elevational gradients and transect establishment should be primary subjects of mountain research (see Becker

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TABLE 1 Suggested global change research in MBRs (core research agenda).

(A) Biodiversity and ecosystems

What?/Why?	How?/Priority (P)?
(1) Secure scientific reference locations for future research in MBRs (reference study sites of past global change research in international programs such as IBP, IGBP, MAB, GLORIA, etc)	Management to keep study sites with original land use states. Previous studies should be repeated over decades using the same protocol without affecting the site.
(2) Document land surface conditions and archive landscape changes to increase public awareness and visualize management consequences. Calibration of remote sensing data.	Aerial photographs, remote sensing, plus digital images taken from fixed positions in clear weather for characteristic landscapes. **P**: 2 cemented posts and 2 photos per year and location.
(3) Monitoring of land use: grazing intensity, agriculture, tourism. Land use is one of the main determinants of plant community composition and function as well as landscape structure, and interacts with climatic change in complex ways.	Records of type and rough numbers (stocking rate), time and duration of presence of animals and recording of important shifts in land use practices. Take records of visitor numbers/activities. **P**: Presence/absence, and estimates such as low, medium, high.
(4) Install permanent plots including exclosures of animals at different elevations: grazing and browsing are the key drivers of land cover type and species diversity. Long-term exclosures illustrate the impact of animal disturbances in both positive and negative directions, even to lay persons.	Fenced and/or durably marked (control) plots replicated in each elevational belt in grazed terrain as well as in areas without domestic animals. Measure biomass and species abundance, and take photographs. **P**: 2 pairs of high- and 2 pairs of low-elevation plots for both grassland and forestland. Surveyed every 5th year.
(5) Establish permanent plots in the treeline ecotone, which is a prominent biotic and natural climatic boundary in MBRs. It may have disappeared due to land use and/or be restricted to relic stands (to be identified). Tree dynamics are expected to exert high sensitivity to ongoing and future atmospheric changes, important for erosion and avalanche protection and thus down-slope ecosystems and human settlements. Emphasis on recruitment and stand density changes within the ecotone.	GPS and/or durable land marking of at least two 20-m-wide and 50-m-long elevational corridors centered at the treeline (as defined by a line connecting the uppermost patches of forest trees at least 3 m high), capturing recruitment above as well as below the current treeline in areas with no land use. **P**: 2 corridors surveyed at decadal intervals for number and height of trees.
(6) Plant species diversity monitoring at summit locations (GLORIA). GLORIA adopts a standardized, global, and cheap method for global change assessments in sensitive MBR locations. After establishment and initial inventories, the value of the sites increases with time.	Establishment of a GLORIA site requires 4 sub-sites (ie summits). Monitoring should be done every 5–10 years. Ideally, soil temperatures are logged at least at one, preferably at all sub-sites (http://www.gloria.ac.at). **P**: All MBRs should have a GLORIA site.
(7) Records of plant phenology (time of sprouting, flowering, senescence) and date of arrival of migrating or hibernating animals at the station, preferentially at different elevations. Phenology and migration are among the most sensitive indicators of climatic conditions and are easily recorded at negligible cost. Phase shifts in phenologies of interacting species can have severe consequences for biodiversity and ecosystem functioning. Effects are likely to differ across elevations.	At the minimum, such observations should be made near an MBR station. Only abundant and persistent species are suitable. The standardized MBR diary is the primary place of record, followed by an annual synthesis on a standardized spreadsheet. **P**: 3 plant and 3 migratory bird species monitored. Advanced: monitoring at several different elevations and larger numbers of species.
(8) Attributing "indicator values" to existing plant species inventories. Species abundance-weighted community means of such indicator values have proven to be highly sensitive to environmental conditions and their change. Once inventories are annotated with indicator values, it is easy to quantify abiotic conditions at a site and to monitor long-term changes. Because plants integrate conditions over time, this method is often more informative than direct measurements of abiotic conditions as such.	Based on expert knowledge, environmental preferences of taxa will be attributed using a 5 or 10-rank scale for preferences in soil moisture, temperature, winter snow duration, soil fertility, soil reaction (pH), light requirement, and ruderal nature (early vs late), in essence following the concept of Ellenberg (1974). This is a "the more species the better" activity, hence there is no minimum or optimum research intensity.
(9) Arrival and altitudinal position of invasive species. These may be a threat to native species and vegetation assemblages. Impacts at higher elevations and effects of climate warming are largely unknown. Given the potential threat, early warning (and action) is important in MBRs.	Some taxonomic knowledge by MBR personnel is required (notes to be made in MBR diary). **P**: Regular surveys for new taxa along invasion corridors (roads, trails, rivers). Advanced: tracing abundance semi-quantitatively (http://www.miren.ethz.ch).
(10) Monitoring radial tree growth (seasonal change and impact of weather). Dynamics of tree growth are the most sensitive indicators of current climatic conditions in a seasonal course. To assess extreme events, growth monitoring tapes should be installed on stems as continuous devices (easy and simple, high time resolution). The general public has great interest in learning about the well-being of forests. Longer-term trends will remain the classical domain of forest inventories and tree-ring analysis.	Calibrated girth tapes are installed on straight, smooth-barked tree species at undisturbed, representative locations. Monthly readings are taken. The inclusion of treeline trees would greatly enhance the impact of such readings (high elevation trees are more responsive to temperature, low elevation trees more to moisture). **P**: 5 individuals for each of 3 contrasting tree species, monthly readings during the season. Advanced: more trees, sites and species.

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(B) Hydrology and water resources

What?/Why?	How?/Priority (P)?
(11) Assess the areal and temporal pattern of precipitation as the main driver of hydrological and other associated processes, with special attention to gauged catchments across elevational transects.	Establish a network of precipitation stations, with at least 1 recording station (pluviometer) and several totalisators. **P**: Altitudinal variation of precipitation.
(12) Determine streamflow (river discharge) and runoff (water yield) as key variables of mountains (and MBRs) dependent on space and time (seasonality), also during extreme events (floods, droughts), and perform micro-catchment studies. Lowland to highland revenues may assist MBR financing in the long run and encourage sustainable catchment land use.	Establish continuously recording discharge monitoring stations (gauges) at suitable river cross sections. Maintain these stations continuously, in particular during floods. **P**: Quantify catchment yield and peak runoff-producing areas in at least 1 major MBR catchment.
(13) Assess water quality (biology, chemistry, sediments) in rivers at least at main (representative) discharge gauging stations (budgets, undesired developments).	Design a sampling and analysis program (eg once per month peak flow). **P**: Flask sampling after extreme events.
(14) Identify major sources of runoff and problems with water quality (risks) within the MBR.	Assess input–output relations, retention capacity and water balance. **P**: Quantify the water balance equation for at least 1 MBR catchment.
(15) Explore (and improve) the capacities of the landscape for flood retention. Develop flood management strategies.	Assess (introduce) functional floodplains, maintain the capacity of main channels, reduce the extent and connectivity of quickflow producing areas. **P**: Current floodplain maps.
(16) Assess the influence of land cover types and land use on amount and quality of runoff. Quantify the influence of sustainable grazing practices in catchments in terms of hydropower gains (potential economy-based subsidies to MBR budgets via highland–lowland linkages).	Test areas should be selected in MBRs that use special hydrological installations (lysimeters, runoff plots, rain gauges, soil moisture monitoring). **P**: Simple balancing bucket-lysimeters (seepage collectors).
(C) Special land surface characteristics	
(17) Assess the geographic/geomorphologic landscape conditions and changes across elevation.	Establish a digital terrain model and satellite imagery analysis. **P**: Create an MBR GIS database.
(18) Apply GIS for spatio-temporal analysis and simulation of snow, glaciers, permafrost, slope and rock wall, rockfall, debris flows, runoff, lake formation and outbursts, flood propagation, slope, and river erosion/sedimentation to understand teleconnections across elevational transects and dangerous developments.	Use satellite and ground data, quantify surface changes, use time series analysis and simulation of projections into the future. **P**: Assess time series of changes in key source and sink areas.
(19) Establish a soil and soil erosion database and monitoring scheme across elevational belts.	Define sensitive zones (slopes), establish a monitoring protocol for slope movements and soil condition. **P**: Establish an MBR soil map. Identify major mass wasting areas.

et al 2007). Besides great biological richness and biodiversity, slopes that reach up to the treeless alpine belt are prime sources of avalanches, landslides, and other hazards, making the protection function of high elevation forests crucial. Changes in land use practices are possibly the most influential changes MBRs can envisage. Because empirical data such as monitoring time series of events and conditions will always remain limited in time and space, any projections of future developments will require modeling, which in turn depends on monitoring data.

The presentations and discussions at this GLOCHAMORE workshop led to a list of research activities recommended as "core research agenda for MBRs" (Table 1; similar to a questionnaire developed for the UK by Sutherland et al 2006). The list highlights a few central themes relevant and practicable for MBRs, often at little extra cost. Basic environmental, biological, and hydrological activities are highlighted, in particular monitoring, and also a few integrative activities such as monitoring catchment processes (hydrological as well as surface processes, including land use). Due to their regional nature, assessments of human activities beyond land use and their economic, social, and ethnological background have not been specified here.

A priority on monitoring activities has been emphasized for 2 reasons. First, monitoring data are a prerequisite for understanding processes. In addition, monitoring data are essential for modeling and thus for the validation of current concepts of natural and socioeconomic developments. Combining monitoring and modeling with cross-disciplinary syntheses will assist knowledge-based land use planning and management of MBRs.

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