

Climate change and mountain ecosystems

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Introduction

Over the past decade, the issue of climate change has risen rapidly to an important position on international scientific and political agendas. A number of key events in this process may be identified, beginning with the 1988 Conference on "The Changing Atmosphere" (World Meteorological Organization 1989), and the consequent establishment of the Intergovernmental Panel on Climate Change (IPCC). The three Working Groups of the IPCC presented their first reports (Houghton et al. 1990; Tegart et al. 1990; IPCC Working Group III 1990) to the Second World Climate Conference in 1990 (Jaeger and Ferguson 1991), which provided a major impetus to the formulation of a Framework Convention on Climate Change. This was signed by the heads of state of most of the world's nations at the 1992 UN Conference on Environment and Development. Yet, although mountains occupy a considerable part of the world's land surface and are directly or indirectly vital for a significant proportion of the global population, little explicit attention has been given to the possible implications of climate change for mountain ecosystems. Only one international meeting, held in 1992 in Davos, Switzerland, has been entirely devoted to this topic (ProClim 1992).

For those who make decisions concerning the future of mountain regions, recognition of the likelihood of rapid climate change leads to some of the greatest uncertainties they are likely to face. The purpose of this chapter is to

outline the complexities and implications connected with climate change and its potential results for mountain areas. This chapter considers, first, climate change and climates; second, potential changes in mountain ecosystems—particularly their vegetation—resulting from climate change and, third, methods for assessing these changes. It concludes with a discussion of some of the long-term implications to be considered by those responsible for managing mountain protected areas.

Climate Change and Mountain Climates

Climate is usually described, for convenience, in terms of long-term (typically 30-year) averages of a range of parameters. It varies continuously, at all scales of time and space; the variation at daily and local scales we call the weather. Both climate and weather are ways of describing the variety of states of the Earth's atmosphere, which is a non-linear (chaotic) system (Gleick 1987). The atmosphere's chaotic nature represents one of the greatest problems in climatology. While recognition of this problem means that specific predictions of the rate and degree of future changes in climate are not possible, it does not prevent projection of a range of likely future climates and the study of the responses of ecosystems to these.

There is now a general consensus within the scientific community that the global climate—and therefore its regional components, including mountain climates—is likely to change over coming decades, at rates unprecedented in human history (Houghton et al. 1990, 1992, Schneider 1989b). This means that, at any point on Earth, over the next few decades, significant changes in long-term averages (e.g., temperatures, rainfall, sunshine) and in frequencies of extremes (e.g., floods, droughts, storms) may occur. It appears likely that the global average temperature will rise to the highest level of the past 100,000 years, during which most mountain ecosystems have evolved (Huntley and Webb 1988; Schneider and Bonder 1984). Yet, even if the average global temperature rises, there may be—at least for some decades—places where average temperatures will stay the same, or even decrease. In addition, it is very unclear how the projected increase in average global temperature would affect patterns of rainfall, snowfall, and soil moisture (Mitchell et al. 1990).

The definite identification of climate change will be based on a certainty that significant changes have been, and are occurring over all parts of the globe over a period of many years. Yet, for a number of interlinked reasons, it is not possible to specify whether a period of rapid climate change has begun. Even though available data show an upward trend in average global temperature, these data neither extend far enough back in time, nor do they provide adequate coverage around the Earth, to allow the conclusion that statistically-significant changes in the global climate are occurring (Folland et al. 1992, Wigley and Burnett 1990). Nevertheless, three undeniable facts suggest that an

era of climate change is likely in the near future, if it has not already arrived (Shine et al. 1990, Watson et al. 1990).

The first fact is that two independent types of research show that atmospheric concentrations of a number of gases are increasing. Polar ice sheets include air bubbles that record the chemical composition of air trapped for many millennia. Ice cores from these glaciers show that concentrations of carbon dioxide (CO₂), nitrous oxide (NO₂), and methane (CH₄) have increased over the past three centuries. For the past two to three decades, these upward trends have been corroborated by analysis of air samples collected at isolated locations far from centers of population or industrialization. These data show increasing concentrations of not only CO₂, NO₂, and CH₄, but also man-made chlorofluorocarbons (CFCs). The second fact is that laboratory experiments show that the addition of any of these gases to a volume of air permits it to absorb additional infrared radiation. The third fact is that the Earth emits infrared radiation. Added together, these facts suggest that, as the atmospheric concentrations of these gases increase, the energy balance of the Earth-atmosphere system is likely to change, so that the atmosphere as a whole will warm—the phenomenon described as "global warming."

The principal causes for the increasing concentrations of the infrared-absorbing gases (or "greenhouse gases") are found not in natural processes, but in human activities (Watson et al. 1990). The combustion of fossil and organic fuels releases CO₂ and NO₂. During the production and distribution of fossil fuels, the cultivation of wetland rice, and the raising of livestock, CH₄ is released. All three gases are released as a consequence of forest clearing and agricultural activities. Finally, CFCs are released from leaking refrigerators and air conditioners and during the manufacture of electronic components. Thus, the precursors to likely climate change—increasing concentrations of greenhouse gases—derive not only from industrial processes and the use of fossil-fuelled transport, but also from the daily activities of all of humankind: growing, harvesting, preserving, and cooking food; and heating and cooling homes and workplaces.

It is inconceivable for human populations to cease these daily activities. There are however, technological, economic, and policy solutions that may be used to limit emissions of greenhouse gases, and therefore likely rates of climate change. The identification and implementation of such solutions are a major focus of current developments in global environmental policy (Andresen and Wettestad 1992). Given the likely implications of climate change for protected mountain areas, those concerned with the management of these areas should consider how they might contribute to the creation and implementation of policies to limit emissions of greenhouse gases.

For mountain climates and the likely implications of climate change in mountain regions, one should note that these climates are characterized by

marked diurnal and seasonal cycles, with high variability at all spatial scales. In any mountain region, the diverse relief, aspect, and slope further increase both temporal and spatial variability (Barry 1986, 1992b). The availability of long-term year-round climatological data for mountain regions is highly variable (Barry 1992a), and such data tend to be available more readily from settlements close to the mountains or in valleys than from mountain sides and peaks. Consequently, even when data are available, they often do not provide a good overall description of the climate of an entire mountain area, because relationships between climatic variables in mountains and neighboring areas are highly complex (Barry 1990).

Some mountain areas contain quite dense networks of meteorological stations at many altitudes. Such networks, however, often record only data for part of the year (e.g., winter, for providing information useful for predicting avalanches), and measurement at individual sites may not have taken place for long enough to provide a statistically valid—or useful—description of the local climate. Very small changes in the location of measurement sites can result in considerable changes in the data collected. To summarize, it is evident that there are considerable difficulties in describing mountain climates even under current conditions. Yet, research on possible future climates requires baseline descriptions of current climates from which projections can be made.

Apart from the chaotic nature of climate, there are other reasons, of more regional importance, why scientific projections of global climate are not likely to be available in the foreseeable future. These reasons are all more pronounced in heterogeneous regions, such as mountains. The first has already been noted: the lack of climate data sets for locations around the globe over an adequately long time period. Clearly, this problem is particularly difficult in mountain areas, though it also applies to much of the world's oceans (Folland et al. 1990). A second is the inadequate knowledge of the interactions of the atmosphere and the Earth's other systems, particularly with regard to the roles of clouds and vegetation in influencing the Earth's radiation balance and of the oceans in absorbing heat (Cusbach and Cess 1990, Gates et al. 1992). Both of these cause problems in constructing climate models from which projections could be drawn. Yet another reason relates specifically to the computers in which such models are constructed. These models are known as GCMs: General Circulation Models or Global Climate Models, depending on their history and who is describing them.

GCMs require immense computational capacity. For example, a state-of-the-art GCM that portrays the Earth's surface and atmosphere as a grid of cells spaced at 4.5° latitude and 7.5° longitude (about 500 by 640 km at 40° latitude), with nine vertical levels, has 17,280 cells. To calculate a year of climate statistics for all of these cells at realistic intervals (thirty minutes), using one of the most powerful current supercomputers, which can add nearly a billion numbers a second, requires ten hours (Schneider 1989a). In more concrete terms, each

cell in this model is approximately the size of Colorado, which has an altitudinal range of nearly 3000 m. and a great diversity of landscapes including deserts, mountains, and plains. Yet Colorado's great variety of climates is, because of the model's constraints, described by a single set of statistics. To create GCMs with a finer spatial resolution will require far more powerful computers. Even if the power of computer processing continues, however, to increase as fast as in recent years, it is improbable that the spatial resolution required for projections relevant to mountain regions will be attained this century.

A number of additional problems remain to be addressed before GCMs would be able to produce information useful for assessing the potential effects of climate change in mountain regions. First, GCMs are typically used to produce outputs which represent a new equilibrium climate resulting from an atmospheric concentration of CO₂ which is double that of the pre-industrial era. Although some scientists foresee the possibility of sudden change as a result of global warming (Broecker 1987), and abrupt changes in regional climates have occurred in the past (Dansgaard et al. 1989), the general consensus is that climates will change gradually. "Transient" model investigations of gradual changes are a relatively new area of research (Gates et al. 1992), and suffer from all of the problems described above. A final problem is that the statistical outputs of GCMs are typically in the form of average values. For many ecosystems and their components, including people, extreme values are often more important. To provide such values would require considerable reconceptualization of the design and use of GCMs (Katz 1988).

In summary, given the non-linearity of the climate system, the considerable research needed to provide basic understanding of the complex interactions between its different parts, the problems of GCMs, and the great variability of mountain climates over both space and time, computer models will remain exploratory tools for defining potential future mountain climates for the time being. This applies not only to GCMs, but also to new approaches, such as the "nested models" being developed for the western United States and the Alps (Giorgi 1990, Giorgi et al. 1990). However, this does not mean that projections of possible future mountain climates cannot be constructed. The primary alternative approach is to develop scenarios: internally consistent descriptions of future climatic conditions over space and time. These may be derived from the output of GCMs, from geological, historical, or current analogies, or through the application of ex-fungi (e.g., O'Neill et al. 1987); and other soil organisms (Whitford 1992). To summarize, it appears likely that, even though the possible effects of CO₂ enrichment on mountain ecosystems may be very important, only a very generalized understanding of these effects will be available for a long time to come.

Table 1: Shortcomings of Approaches for Assessing Ecological Effects of Climate Change on Natural Ecosystems (Based Primarily on Street and Semenov 1990).

Direct transfer function approach

(Analysis of current bioclimatic distribution of assemblages of flora and fauna to assess future distributions in response to climate change)

- 1) Species respond individually to climate change:
 - Current assemblages will not move
 - key species (pollinators, symbionts etc.) may be absent
- 2) Responses to CO₂ will probably alter responses to climate
- 3) interactive effects of climate change are not considered: wildfire frequency, air pollution, herbivory, pathogenicity
- 4) Impacts of barriers to migration are not considered

Historical approach

(Inferences from past and present distributions of plant and animal species sensitive to critical levels of heat and moisture)

1. Climate change may evoke genetic responses, creating divergent races of species to take over newly evolving niches
2. Rates of climate change affect rates and degree of response
3. Range shifts in response to climate change depend on dispersal strategy
4. individual species may respond differently to climate change in different ecosystems

Paleoreconstruction

1. Projected amount/rate of climate change is unprecedented
2. CO₂ variations in the past did not drive climate change
3. Dating uncertainties
4. Mean temperatures of past eras are only rough estimates
5. Projected climate change will occur with other pressures without precedent in previous eras: air/water pollution, human population growth

-> Paleo-based scenarios for species migration may give indications of mechanisms and patterns of dispersal, but not rates

Simulation models

1. Do not examine interactions at the landscape level: migration, dispersal, substrate change, spread of fire, pests, pathogens
2. Do not incorporate interactive effects of changes in: Fire frequency, air quality, greenhouse gas concentrations, pest potential on multispecies perennial communities

Ecophysiological understanding

1. Long-term effects of increased temperatures and greenhouse gas concentrations are unknown
2. Inability to account for interactive effects: competition, herbivory, etc.

Direct Physical Responses to Climate Change

This section discusses the interactions of climate and the various components of ecosystems. It uses the chapter on natural tent phases. It is beyond the scope of this paper to discuss in detail potential changes in all of these components. Initial assessments for glacial, geomorphological, and hydro-systems, in particular, were prepared for conferences in 1989 in the Netherlands (Rupke and Boer 1989) and Armenia (Barry 1990, Kotlyakov et al. 1991, Luckman 1990, Slaymaker 1990) and the International Conference on Mountain Environments in Changing Climates, held in Davos, Switzerland in 1992 (ProClim 1992). This section concentrates on the vegetation of natural and semi-natural ecosystems, bearing in mind the comment of IPCC Working Group II that, for the reasons shown in Table 1, "...assessing the ecological and socio-economic consequences of climatic changes for natural terrestrial ecosystems is a highly speculative endeavor" (Street and Semenov 1990).

Mountain ecosystems may be affected by climate change in two ways: first, by the increased concentrations of CO₂ available for photosynthesis (i.e., physiological responses); and second, by the actual changes in climate (i.e., physical responses). These two types of response are very closely interlinked, since physiological processes such as photosynthesis and respiration are closely influenced by temperature, water availability and, in the case of photosynthesis, sunlight. A basic assumption of assessments of the potential impacts of climate change on species is that, for each, there is an optimum range—and also threshold values—of climatic parameters for growth and reproduction and that, as climates change, species will be able to follow this optimal "climatic zone" with a lag from years to centuries. Physiological or behavioral adaptation, however, or even genetic adaptation, to changing climate are also possible.

Physiological responses to CO₂ enrichment

Before considering how changes in climate might affect the distribution of plant and animal species, it is essential to briefly consider the potential effects of increasing atmospheric concentrations of CO₂ that would be partly responsible for these changes.

Very many experiments on the potential effects of CO₂ enrichment on vegetation have been performed. Most have taken place under highly artificial conditions, however, often using only one species, usually seedlings; avoiding extremes of temperature and light; without limitations of water and nutrients; and excluding herbivores and pathogens. There have been few studies of complete ecosystems: none has been in a mountain environment (Koerner 1992b, Street and Semonov 1990). The results of the experiments show that responses to CO₂ enrichment are very species-dependent (Melillo et al. 1990). These responses include changes in photosynthesis, respiration, water use efficiency, reproduction, growth rate, form, nutritional quality (for herbivores), and ratios of roots:shoots and of seed production:vegetative growth (Curtis et al. 1990, Strain and Cure 1985). In real-world situations, all of these changes will be relevant, but many interactive processes will also come into play: between plants (e.g., competition, symbiosis, mycorrhizal infection); between plants and animals (e.g., herbivore, pollination); and between plants and microbes (e.g., disease, decomposition) (Street and Semonov 1990).

Reviewing the literature, Koerner (1992b) concludes that, because of diverse negative feedback processes, long-term responses of plant canopies to increased levels of CO₂ will be markedly different from the immediate responses of leaf photosynthesis. He proposes a hierarchy of criteria for delineating the differential sensitivity of different types of vegetation to increased CO₂. This approach leads to the initial conclusions that the effects of CO₂ enrichment are likely to be much greater for high-altitude plants than for most low-altitude plants, and that alpine plants are likely to be particularly sensitive. These hypotheses are now being tested at an altitude of 2500 m. near the Furka Pass, Switzerland, using open-top chambers in the most common alpine vegetation type (*Caricetum curvulae*) of the Central Alps (Koerner 1992a).

For forests, which compose a large proportion of mountain vegetation, the likely direct effects of increased atmospheric CO₂ concentrations are also unclear (Eamus and Jarvis 1989, Fanta 1992, Gale 1986, Peterson et al. 1990). These effects have been described as "the factor which is most difficult to evaluate in forest ecosystems" (Fischlin 1991). While research in subalpine forests in the western United States concluded that radial growth was enhanced in response to increasing CO₂ concentrations (LaMarche et al. 1984),

similar research in the Alps found only vague relationships (Kienast and Luxmoore 1988). The possibility of conducting experiments to resolve this question is restricted by very substantial resources that would be required to construct experimental areas to provide statistically-valid data, by the long life-times of trees, and the myriad interactive processes of forest ecosystems.

A final important, but almost unknown, group of responses of mountain ecosystems to CO₂ enrichment involves their below-ground components. These include the below-ground parts of plants, which comprise a large proportion of the biomass of many mountain communities (Billings 1974b, Klug-Puempel 1989); their associated mycorrhizal fungi (e.g., O'Neill et al. 1987); and other soil organisms (Whitford 1992). To summarize, it appears likely that, even though the possible effects of CO₂ enrichment on mountain ecosystems may be very important, only a very generalized understanding of these effects will be available for a long time to come.

Direct Physical Responses to Climate Change

This section discusses the interactions of climate and the various components of ecosystems. It uses the chapter on natural terrestrial ecosystems in the report of IPCC Working Group II (Street and Semonov 1990) as a primary source, with specific discussion of the implications for mountain ecosystems wherever possible.

The component of climate change on which most attention has been focused is increasing temperature. There are a number of reasons for this. First, it is the most obvious change, which would result in other changes (e.g., soil moisture, evapotranspiration, fire frequency and severity). Second, it is the change for which there is the greatest agreement between GCMs. Third, it is the change that can be most easily assessed for past (paleo-) and recent climates, from which parallels for future climates can be drawn. Fourth, there is a large literature on the influences of temperature on the distribution of species and on ecological processes. This last point also applies to water; and the distribution of vegetation types can be treated as determined by the interaction of temperature and water regimes (Ellenberg 1988, Holdridge 1964, Ozonnda 1988). Furthermore, for the distribution and survival of many flora and fauna, temperature may be a less important factor than moisture (Billings 1974a, Woodward 1992). Yet, while water is crucial in all ecosystem processes and interactions, the outputs of GCMs vary greatly in their projections of changes in precipitation and soil moisture, as noted above.

Like any climatic variable, temperature can be described in a number of ways: means, ranges, extremes, etc. As mentioned above, GCMs primarily provide information about possible changes in means, and assessments of future

distributions of flora and fauna have primarily been based on such information. Yet, for many animal and plant species, both actual extremes and the length of the period over which organisms experience them are critical. For instance, while excessively low temperatures can prevent the germination of scads (Bewley and Black 1982), very high soil surface temperatures can prevent seedling survival. Equally, temperature extremes are significant for the dynamics and distribution of many fauna, particularly insects (Maui 1968, Rubinstein 1992). Overall, the greatest concern is that rates of change in temperature may be greater than the ability of species to adapt or migrate; although this may be a lesser problem in mountain regions, where species may only have to move a few hundred meters upslope, rather than a few hundred km, as would be the case in flatter areas (Boer and de Groot 1990). Consequently, species may become extinct and, at the least, it is probable that ecotypes and genetic variation will be lost. Some species may become more abundant, however, and speciation may occur in response to new conditions (Smith and Tirpak 1989).

In addition to requirements for suitable temperature and precipitation regimes, a number of other factors limit the distribution of plant species. Among these, a suitable substrate is particularly critical. In temperate mountain regions, soils have had a relatively short evolution since the last ice age (Retzer 1974) and, even if scads can reach new habitats whose climatic conditions are suitable, soil conditions may be inappropriate. This may be because soils have not evolved sufficiently; because their chemical or physical characteristics are unsuitable; or because they have deteriorated as a result of human activities. The latter, for instance, is the case in Berchtesgaden National Park in the Bavarian Alps, where soil has been eroded from areas whose forests have been cleared. Consequently, even if the climate improved, trees could not grow again in these locations (d'Oleire-Oltmanns 1990). Conversely, even under

current climates, in areas from which trees have been cleared and where soils are appropriate, the growth of trees above the current anthropogenic timberline may be limited by fungal infections as, for instance, in the Alps (Schoenenberger, Frey and Leuenberger 1990).

In an era of climate change, the characteristics of soils would be expected to change gradually. Changes in temperature would probably lead to changes in the relative abundance of soil biota, thus affecting trophic relationships in soil food webs. Up to threshold levels, increases in temperature and available moisture would be likely to amplify the chemical and biological processes of soil development, promoting the decomposition of organic matter and thus accelerating soil formation (Whitford 1992). Changes in chemical composition would also be likely. Excessive precipitation can limit decomposition, however, and/or lead to increased erosion and downstream sedimentation (Melillo et al. 1990). Thus, estimates of average values of precipitation may not be useful in developing assessments of the effects of such changes; estimates of the

intensity and amount of precipitation in extreme events may be of greater importance. Finally, changes in precipitation and temperature regimes could change the heights of water tables: a critical factor in the distribution of some species.

In some mountain ecosystems, another important ecological factor deriving from the interaction of temperature and precipitation is fire. The frequency of fires in many mountain ecosystems has been modified considerably by human actions, further complicating the projection of frequencies under new climates. Since photosynthesis is often limited by current temperature and CO₂ concentration, one can hypothesize that increases in these variables will lead to increased growth of vegetation and therefore to increased fuel loading. This problem could be exacerbated if mortality increases because trees are living in less optimal conditions and, particularly, if evapotranspiration increases (Franklin et al. 1992, Street and Semonov 1990). Over time, the distribution of certain species could be significantly changed as a result of new fire frequencies; as has happened as a result human actions, for instance in the Rocky Mountains (Daubenmire 1943).

In addition to temperature, precipitation, soil moisture and type, and fire frequency, there are other physical constraints on the ability of organisms to disperse in response to changing climates and survive in their new environments:

- a. changes in the frequency of other disturbances, such as avalanches, heavy snowfalls, major storms, floods, and droughts (Franklin et al. 1992);
- b. changes in the depth and duration of snow-cover and in the length of the snow-free (growing) season. These are vital factors in the distribution of mountain flora and fauna (Ellenberg 1988, Holten and Carey 1992);
- c. changes in cloud cover, which could alter the sunlight available for photosynthesis and also have other effects, such as changing rates of snow melt;
- d. the availability of potential habitat. This is a major issue for species which would have to move to higher altitudes in response to a warmer climate, since mountain peaks are smaller than their bases. Not only is there a smaller area in each successive elevation zone, but potential habitats might not be available for species currently restricted to the tops of mountains (Peters 1992);
- e. the availability of migration corridors. This is a crucial issue for species in the complex topography of mountains, and is exacerbated by the east-west orientation of many chains (e.g., Alps, Pyrenees, Himalaya).

Both of the last two constraints could be ameliorated or exacerbated by human actions. For instance, while corridors for migration could be kept open by appropriate land use management practices and policies, the expansion of

agricultural land use to higher altitudes could decrease possibilities for dispersal (Street and Semonov 1990, World Resources Institute 1990).

The ability of organisms to disperse also depends on their own characteristics and their interactions with other organisms. A species' ability to disperse depends on its reproductive capability, its dispersal strategies and, for animals, its mobility (Gadgil 1971). Paleo-climatic studies suggest that few forest tree species would be able to disperse as fast as the projected changes in climate (Davis and Zabinski 1992, Roberts 1989). In addition, every species interacts with others in a wide range of relationships, to which must be added the multifarious intentional and unintentional human actions which can limit or assist species dispersal.

Individuals of a species not only have to be able to disperse successfully, they also have to become established in large enough numbers to reproduce and persist in their new environment, where they may encounter new competitors, predators, pests, or pathogens against which they have few, if any, defences; a situation which may have parallels in the introduction of exotic species by man (Mooney and Drake 1986, Vitousek 1988). Furthermore, obligate species may become unavailable because of responses to different components of climate change. Harte et al. (1992) cite the example of the subalpine plant *Delphinium nelsonii*, which is pollinated by broad-tailed hummingbirds. While the timing of the birds' migration is determined by photoperiod, the annual growth and development of the plant is a function of temperature and snowmelt. If the latter changed, the hummingbird might not arrive at the right stage in the plant's annual life-cycle to pollinate it, thus potentially leading to the latter's extinction.

A further suite of factors to consider are the differences in the life-history strategies of the organisms that compose any ecosystem (Rubinstein 1992). For instance, many insects and other small organisms, including microorganisms, have generation times much shorter than the plants and animals they utilize as sources of food. This means they could adapt to new climatic conditions more quickly, leading to increased pressure on "host" organisms (Franklin et al. 1992). In addition, the mortality rates of many insects are affected by temperature (Bale 1991), so that population sizes might be changed directly. This is likely to be of major importance for many phytophagous insect species and of particular relevance to the long-lived trees of many mountain forests, which tolerate a current climate that is far from optimal for regeneration and growth and therefore could be especially sensitive to the direct and indirect effects of climate change. Yet such trees could also benefit from climate change: a number of recent studies suggest that the growth rates of trees in high altitude forests have increased in recent decades because of higher summer temperatures, the most important determinant of tree growth in these environments (Innes 1991).

The considerations of this section lead to three general conclusions. First, a "negative" response, such as local extinction, to changing environmental conditions is generally quicker than a "positive" response, such as colonization of new habitat (Smith and Tirpak 1989). Second, many of today's assemblages of organisms (communities, ecosystems, etc.) will not exist under future climates. This understanding derives particularly from theories of dynamic biogeography that suggest, as species respond in individualistic ways to changing environmental conditions, both plant and animal communities change continuously over time (Brubaker 1989, Hengeveld 1990, Sprugel 1991). These theories are based on a large number of paleo-ecological studies of a wide range of species (Birks 1989, Coope 1979, Davis 1983, Graham 1986, Van Devender and Spaulding 1979). Third, certain characteristics of species are likely to make them particularly sensitive to changes in climate. These include those which are at the edge of their range; geographically localized; genetically impoverished; poor dispersers; slow reproducers; localized and annual; highly specialized; or migratory. Many mountain species fall into a number of these categories; and many are relicts, having been isolated by past changes in climate (McNeely 1990, Street and Semonov 1990).

Approaches to the Assessment of Ecological Responses to Climate Change

There are clearly many difficulties in starting to assess the potential distribution of mountain flora and fauna in response to changing climates. Even with incomplete understanding, however, it is important for such research to be undertaken as an input to policy processes relating to the management of protected areas and other resources, and also to define future topics of research. The approaches described in this section principally refer to case studies for the future of the Alps. Comparable studies are beginning in many of the mountain National Parks and National Forests of the USA (e.g., Halpin 1993, Key and Marnell 1990). It is also likely and desirable that similar studies are planned or underway in other mountain regions where adequate data sets are available to permit the methods described.

Cartographic Approaches

Cartographic approaches are based on the assumption of optimal climatic zones mentioned above. The simplest method begins with maps of existing assemblages of species (e.g., plant species as described on vegetation maps). First, the spatial relationships between these assemblages and specific climatic variables are defined. Then, scenarios are used to determine possible future distributions of these variables. Finally, these are used to define the resulting new locations of the assemblages, taking other site factors into account. Such a study has been started for the Alps (Beniston and Price 1991, Ozenda and Borel 1991). Given the fact that today's animal and plant communities are likely to

disassemble in response to a changing climate, however, this type of method can be, at the best, exploratory and illustrative (Boer and de Groot 1990).

More realistic cartographic approaches start from the current distributions of individual species (rather than species assemblages), from which possible changes in response to changes in one or more climatic variables are assessed. One method uses physical and bioclimatic assumptions (e.g., the adiabatic lapse rate and species-area curves) to define new climatic zones. This circumvents the need for detailed information on the spatial distribution of climatic variables—which is unavailable for many mountain regions. Such a region is Nevada's Great Basin, where this approach has been used to examine potential changes for animal species, assuming that a warming of 3°C would cause potential habitats to shift upward by 500 m. The study suggested that numbers of mammal species would decrease most, followed by butterflies and resident birds (Murphy and Weiss 1992).

A second method, developed in Norway, uses a simple model that correlates the presence of plant species in 5 km (horizontal) x 100 m (vertical) grid cells with January and July mean temperatures and mean annual precipitation. The model has been used to predict shifts in the distribution of species in response to a 2°C increase in July and a 4°C increase in January temperatures. Initial conclusions are that most alpine plants will retreat upwards and some will be threatened, either by loss of habitat at high altitudes or of suitable microclimates, or through competition, especially from species moving uphill (Molten and Carey 1992). This work is being continued through monitoring and experimentation.

This single-species approach can be made more realistic, and therefore more complex, by incorporating a range of climatic variables, together with actual climatic data sets, and geographic information systems (GIS). In the Alps, bird atlases are being used, in conjunction with the development of climate scenarios, to investigate possible future distributions of sensitive bird species. A comparable study for the plant species of the Alps will be possible once the projected Flora of the Alps is completed, and statistical correlations are made between climatological variables and the distributional data contained in the Flora (Beniston and Price 1991).

Mechanistic Approaches

Mechanistic approaches use computer-aided modeling to determine the likely composition of future ecosystems in response to changing environmental conditions. The models, however, cannot provide information about possible future distributions of species in space. For the Alps, a first attempt to assess the potential effects of changes in climate used a forest stand simulation model incorporating the results of seedling experiments to assess the concurrent effects of CO₂ enrichment. The results of model runs, each for

1,000 years suggest that deciduous trees would invade the current montane and subalpine belts, resulting particularly in a reduction of the dominant conifer species. Given favorable seedbed conditions, however, conifers could expand beyond their present upper limits into the current krummholz and alpine zones (Kienast 1991). While these results are interesting, plausible, and useful for suggesting future research, one should note the exploratory nature of this approach. It is based on a mixture of empirical data and arbitrary rules derived from highly simplified representations of the complex processes of forest ecosystems and furthermore, on the questionable assumption that the responses of seedlings to CO₂ enrichment are applicable to adult trees.

Further Approaches

Two studies are currently starting to provide more realistic assessments of the future vegetation cover of the Alps. One of these will develop climate scenarios for the Alps, based on GCM outputs, and incorporate these into new simulation models of subalpine forest ecosystems. These models, including primary producers, decomposers, and dominant herbivores, will be more realistic than those used for previous studies (Fischlin 1991). A second study will link the mechanistic and cartographic approaches for both forest and alpine vegetation. In a first stage, a number of modeling and statistical approaches will be combined to provide statistical information about likely patterns of succession in plant communities, using vegetation, soil, climate, and topographic data. These outputs will then be introduced into a GIS in order to produce maps of possible future vegetation covers in response to climate change and other disturbances, including insect infestations and fire (Kienast and Brzeziecki 1992).

Implications for the Management of Protected Mountain Areas

The discussions above may appear to provide more problems than answers. Yet there is a considerable wealth of knowledge that is relevant for developing policies for the management of protected mountain areas, both for mountain regions in particular, of which the references cited above provide a very preliminary synthesis—far more in-depth compilation and synthesis is needed—and for the conservation of biodiversity and protected areas in general (McNeely 1990, Peters and Lovejoy 1992, Wilson 1988). Yet, in defining management policies for protected areas, it must be clear what is to be protected, and why: species, biodiversity, or societal benefits (e.g., landscapes, stable watersheds). The following paragraphs attempt to provide some suggestions in these three directions, any of which may, of course, be either complementary or exclusive.

The ecology of a species is critical in determining the possibilities of maintaining populations that include a genetic variation that is adequate for the species' indefinite survival. Each species requires a particular set of interacting species and environmental conditions, including sufficient habitat. Thus, for instance, small invertebrates tend to require very different management strategies than large mammals (Haslett 1993b). The preservation of individual species in an era of climate change may require the maintenance of corridors for migration, active introduction to new potential habitats or, in the most extreme case, creation of appropriate habitats. Given the costs of the latter approaches, their scientific and political complexities, and competing demands for resources, it seems unlikely that great attention will be given to preserving individual species - although this may be an unintended result of legislation in certain countries, such as the Endangered Species Act in the USA.

In many cases, the most realistic method for preserving **individual species** may be within initiatives to maintain biodiversity, however it is defined and valued (Solbrig 1991, Wilson 1988). In this respect, not only number of species must be considered; the maintenance of functional groups (guilds) of organisms is also an essential criterion. One feature of protected mountain areas that may be of particular benefit for maintaining biodiversity is that they tend to cover a wide range of altitudes. Thus, if appropriate habitats can change fast enough, or can be created with the help of human intervention, it may be possible to maintain higher levels of biodiversity than in flatter areas (McNeely 1990). Conversely, because the area of habitat within each elevational zone tends to decrease with altitude, it may be difficult to preserve adequately large populations for long-term survival. While methodologies to design optimal reserve systems for maintaining biodiversity exist (Margules 1988), these assume unchanging environmental conditions and will therefore have to be modified to take climatic changes into account—once adequately detailed information becomes available. Research such as that presently beginning in the Alps and Norway may be of great importance in developing such new methodologies. Nevertheless, it must be realized that the establishment of protected areas is rarely based on such objective criteria; political decisions are usually determinant.

Given the individualistic responses of species to environmental change, it may only be possible to maintain ecosystems typical of the late twentieth century through considerable human manipulation, using techniques such as prescribed burning, artificial fertilization/insemination, and restoration ecology. Nevertheless, it is difficult to reproduce ecosystems in new environments, and more difficult to introduce and maintain component populations of animals than of plants (Jordan 1988).

Habitat mosaics of mountain areas are characteristically extremely complicated at a wide range of spatial scales, and this heterogeneity has a direct bearing on the structure of the ecological communities (Haslett 1993a).

Thus in order to maintain biodiversity, it is essential to maximize not only the area and altitudinal range of protected areas, but also the heterogeneity of their topography and of the associated sets of conditions and resources (e.g., soils, microclimates). In forested areas, individuals of each tree species should be represented by as wide a range of age classes as possible. Particularly in developing countries, however, these rules may be difficult to implement, as growing populations are likely to want to use land, previously unsuitable for agriculture, to produce crops in the new climatic regime. In industrialized countries, the possible expansion of agriculture, as climate changes, are already being assessed (Carter et al. 1991). Such land use problems also apply to the establishment of migration corridors between protected areas; in any case, it is uncertain whether enough corridors could be created (Graham 1988). One implication of these issues is that local people must be involved in defining and implementing management policies for protected mountain areas.

As well as preserving valued species and biodiversity, protected mountain areas are important for providing other public goods to human populations, and policies will have to evolve to reflect the changing importance of these different goods. In an era of climate change, the preservation of stable watersheds, a valuable role fulfilled by many protected mountain areas, may become even more critical. As discussed above, changes in climate may lead to considerably increased mortality of the vegetation on which human populations have traditionally relied to regulate the quality and quantity of water flows. Such problems may be further exacerbated if, as appears possible, episodes of extreme precipitation increase in number. Thus, just as policies for managing mountain forests originally reserved particularly to ensure long-term supplies of wood had to change as other societal functions became more important (Price 1990b), policies for managing protected mountain areas may have to find a new balance between "traditional conservation" objectives, such as the maintenance of biodiversity, and other functions such as the maintenance of an adequate cover of vegetation in watersheds. Compounding the challenges of defining new management strategies for protected mountain areas will be either changes in demands, especially for recreation and tourism, some of which are also likely to derive from climate change (Price 1990a).

Climate change is a likely response of the Earth's systems to human activities, and will result in fundamental changes in the Earth's ecosystems. As mountain ecosystems are likely to be particularly sensitive to climate change, and have a world-wide distribution, it is vital that their biological and physical components be monitored to provide both an indication of climate change and its effects and inputs to the definition and implementation of management policies. This applies especially to areas where intensive research has been undertaken in the past. With greater recognition being given to the interdependence of all of the Earth's systems—atmospheric, biological, and societal—policies for managing protected mountain areas will have to be flexible and reflect the growing

societal demands on the new ecosystems which our descendants will find in the mountains of the twenty-first century.

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