EUROPEAN MOUNTAIN BIODIVERSITY: A SYNTHETIC OVERVIEW

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SUMMARY.- This paper, originally prepared as a discussion document for the ESF Exploratory Workshop «Trends in European Mountain Biodiversity – Research Planning Workshop», provides an overview of current mountain biodiversity research in Europe. It discusses (a) biogeographical trends, (b) the general properties of biodiversity, (c) environmental factors and the regulation of biodiversity with respect to ecosystem function, (d) the results of research on mountain freshwater ecosystems, and (e) climate change and air pollution dominated environmental interactions. The section on biogeographical trends highlights the importance of altitude and latitude on biodiversity. The implications of the existence of different scales over the different levels of biodiversity and across organism groups are emphasised as an inherent complex property of biodiversity. The discussion on ecosystem function and the regulation of biodiversity covers the role of environmental factors, productivity, perturbation, species migration and dispersal, and species interactions in the maintenance of biodiversity. Regional and long-term temporal patterns are also discussed. A section on the relatively overlooked topic of mountain freshwater ecosystems is presented before the final topic on the implications of recent climate change and air pollution for mountain biodiversity.

RÉSUMÉ.- Ce document a été préparé à l'origine comme une base de discussion pour l'«ESF Exploratoy Workshop» intitulé «Trends in European Mountain Biodiversity - Resarch Planning Workshop»; il apporte une vue d'ensemble sur les recherches actuelles portant sur la biodiversité des montagnes en Europe. On y discute les (a) traits biogéographiques, (b) les caractéristiques générales de la biodiversité, (c) les facteurs environnementaux et la régulation de la biodiversité par rapport à la fonction des écosystèmes, (d) les résultats des études sur les écosystèmes aquatiques des montagnes et (e) les changements climatiques et la pollution de l'air dominés par des interactions environnementales. Le chapitre sur la biogéographie souligne l'importance de l'altitude et la latitude sur la biodiversité. Les implications des différentes échelles sur les différents niveaux de biodiversité et à travers les groupes d'organismes sont soulignés comme caractéristique complexe de la biodiversité. La discussion sur l'écologie fonctionnelle et la régulation de la

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biodiversité porte sur le rôle des facteurs de l'ambiance, la productivité, la perturbation, la migration des espèces et leur dispersion, enfin les interactions entre espècessur la maintenance de la biodiversité. On discute également les modèles régionaux et les séries temporelles à long terme. On passe rapidement sur les écosystèmes aquatiques de montagne avant de finir sur les conséquences du changement climatique récent et de la pollution dé l'air sur la biodiversité des montagnes.

RESUMEN.- Con este trabajo, originalmente preparado como base de discusión para la reunión organizada por la ESF bajo el título «Trends in European Mountain Biodiversity-Research Planning Workshop», damos una panorámica sobre las investigaciones actuales sobre biodiversidad en las zonas de montaña de Europa. Tratamos los siguientes aspectos, (a) rasgos biogeográficos, (b) características generales de la biodiversidad, (c) factores ambientales y regulación de la biodiversidad en relación con la función de los ecosistemas, (d) resultados de los estudios sobre ecosistemas acuáticos en montaña, y (e) cambio climático y contaminación ambiental dominados por interacciones ambientales. Al hablar de los rasgos biogeográficos destacamos la importancia de la altitud y la latitud en la biodiversidad. Los problemas de escala y su implicación en los diferentes niveles de biodiversidad y en los diversos grupos de organismos se consideran como una característica compleja inherente a la biodiversidad. Desde un punto de vista ecológico-funcional y de regulación de la biodiversidad se contemplan el papel de los factores ambientales, la productividad, las perturbaciones, las migraciones de especies más su dispersión y las interacciones mutuas entre especies para el mantenimiento de la biodiversidad. También se discuten algunos modelos espaciales regionales y temporales a largo plazo. Tras la sección dedicada al tema relativamente poco atendido de los ecosistemas acuáticos de montaña terminamos comentando las implicaciones del cambio climático reciente y la contaminación atmósferica en la biodiversidad de montaña.

Keywords: Mountain biodiversity, review, Europe.

1. Biogeographic trends in European mountain biodiversity

Approximately 20% of the total land area in Europe is comprised of mountains. The high concentration of biotopes in mountain areas is well demonstrated in the CORINE classification maps (COMMISSION OF EUROPEAN COMMUNITIES, 1991). Europe has about 1500 arctic and 10000 alpine plant species which is 4% of all known vascular species (CHAPIN & KÖRNER, 1994).

On a broad European scale the main biogeographical trends in montane biodiversity are altitudinal, latitudinal and longitudinal (PEDERSEN, 1990; BROWN et al., 1993), though, the relative importance of these is still to be established. Differences in species richness along altitudinal and latitudinal gradients are related to ecological amplitude and dispersal capacity which

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determine balances between migration, geographic isolation, speciation and extinction. Mobile taxa capable of migration, extensive gene flow and colonisation will be less subject to speciation or extinction. Less mobile taxa, e.g., apomictic plant species and apterous insects tend to rely on speciation with extinctions more likely.

Species diversity has been shown to decline with altitude in a number of organisms (TERBORGH, 1977; MCCOY, 1990; SFENTHOURAKIS, 1992), though the rarity of species may change. This can have important ecological consequences, e.g., in the Rocky Mountains the Diptera become important pollinators at high altitudes, mainly as the abundance of other pollinators decreases and not because Diptera numbers increase (KEARNS, 1992). Three reasons are commonly given for decreasing diversity with altitude: (i) reduction in area or habitat fragmentation; (ii) severity of environment; and (iii) reduced primary productivity. This pattern of habitat constriction in altitudinal belts also occurs on a latitudinal basis (HUEY, 1978). Habitat constriction on a longitudinal basis is apparent in the west concurrent with increased oceanicity. The more consistent climatological conditions with increased oceanicity could allow species to be distributed across a wider range of habitats than would be possible in more continental regimes. Increased diversity to the west would then be a function of evenness rather than species richness.

BROWN *et al.* (1993) have described a method for biogeographical classification based on 88 sites across the Scottish uplands. They found that the main gradients of variation in plant communities were an east-west (oceanicity) and an altitudinal gradient and latitude with a strong anthropogenic influence. They demonstrated that diversity increased with (i) altitude and (ii) to the west; with a larger number of rare communities in the west and fewer common communities in the east. The approach of BROWN *et al.* (1993) is certainly amenable to a much wider geographic application. Multivariate techniques have also be used to determine the biogeographical distribution of avian species in the Pyrenees (BALENT *et al.*, 1988) where the four main underlying factors were temperature (altitude), atlanticity (east-west gradient), northern penetration and middle-mountain areas.

There is probably sufficient phytosociological data already in existence from a wide enough geographic distribution for an analysis of the nature of these gradients on a European scale (using species or life forms). The difficulties associated with using species in examining the floristic similarities between high mountain regions was pointed out by KOROTKOV (1989) who studied the Caucasus and Western European high mountains.

2. Properties of biodiversity

Questions of scale have become one of the most preoccupying issues in modern ecology (LEVIN, 1992). The diversity of living organisms exists at many scales from the genetic to the landscape scale but it is at the species level that it is most commonly used to define, measure and monitor biodiversity. These scales are not independent of each other; it takes the combination of genetic variation tempered by the environment to produce diversity at the species level. The interactions among species and environmental conditions produce diversity at larger spatial and structural scales.

Measuring genetic diversity, while becoming increasingly easier, is still a complex and laborious process. However, genetic diversity is a preliminary requirement for species diversity and persistence over evolutionary time-scales (VRIJENHOEK, 1985). The genetic diversity of an individual species can be correlated with environmental variability (MCARTHUR et al., 1988). Generally, species with wide ecological amplitudes have reproductive strategies with high outcrossing coupled with high rates of fecundity, and thus tend to have higher genetic variation within rather than between populations (HAMRICK et al., 1991). It may be suggested that genetic diversity within an individual species will decrease with increasing species diversity because at increasing species diversities each species will cover progressively smaller areas and hence a narrower range of environmental conditions. This, in turn will reduce the requirement for having a high genetic diversity. Range limitation of species in mountain ecosystems through either human activities or global climate warming could potentially have serious negative impacts on genetic variation.

At the species scale, there are many types of diversity such as structural, species richness, and evenness, which occur over spatial scales ranging from communities to landscape. Species richness and evenness are commonly determined; species richness has long been established as an area-related measure. However, the species-area relationship is still fraught with theoretical problems. CONNOR & MCCOY (1979) for instance, have demonstrated parameters used to describe species area curves which have no theoretical significance. Despite these difficulties the species-area relationship can still provide insights into species distributions on geographic scales.

Research on species-area relationships in mountain summit systems in Switzerland has shown that, on average, each vegetation stand contained half the Swiss alpine flora (WOHLGEMUTH, 1993). Species-area relationships have also been used to determine the minimum area required for species conservation. SÆTERSDAL et al. (1993) have demonstrated that a smaller area was needed to conserve avian populations in lowland forested systems

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than for conservation of the flora. They have also shown that avian diversity was not maximised in the same stands as vascular plants and that strategies aimed at preserving rare species also tended to maximise diversity at the regional level.

This schism in species centrality could be caused by differences in the functional scale of diversity. A functional cause for an increase in territory size of *Buteo buteo* AUTH (common buzzard) between low altitude wooded hill farms and on higher mountain blocks in North Wales was related to the physical environment through the availability of food resources (DARE & BARRY, 1990). Differences in the functional scale of diversity may be manifested in the reported bias towards female plants of many *Salix* species in northern Scandinavia, which may be caused by a sex related feeding preference of herbivores (HJALTEN, 1992).

The rate at which new species are encountered as area increases has been related to a number of mechanisms, e.g., isolation, immigration, extinction, habitat heterogeneity. Recent synthesis of the patterns in species diversity in Europe and North America have shown that species richness over large scales could usually be correlated with simple climatic variables (CURRIE & PAQUIN, 1987; ADAMS & WOODWARD, 1989; CURRIE, 1991). GRACE (1987) demonstrated how the distribution of plant life forms (sensu RAUNKIAER, 1909; 1934) along geographic gradients also frequently coincided with isometric lines of climate variables. While FELBER & FELBER-GIRARD (1990) have shown that different species-area relationships for peaks of increasing elevation was related to the higher number of biotopes associated with higher peaks in the Jura Mountains.

However, species richness is only one component of biodiversity at the species scale. Abundance and particularly evenness is another important parameter. Species diversity is a concept often used to express the complexities of distribution and abundance within a community. The commonest measure of species diversity is the Shannon-Weiner function based on the use of information theory (see SHANNON, 1948). Despite its theoretical and distribution assumptions, the Shannon-Weiner function (and its encompassing of richness and evenness) is now well established as a standard technique (MACINTOSH, 1967). Many other indices exist which have been extensively reviewed by MAGURRAN (1988) and HUSTON (1994).

For ecosystem functions to be maintained there is a requirement for a minimum number of species. Direct tests of the effects that the reduction of species diversity can have are rare, yet those tests which do exist show these effects can be profound (NAEEM *et al.*, 1994). Although GOODMAN (1975) had questioned whether or not a relationship existed between diversity and ecosystem stability, SCHULZE & MOONEY (1993) have suggested that

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biodiversity ensured ecosystem sustainability in two ways. Firstly, species give an ecosystem its functional properties by providing the channels through which energy and materials flow. Secondly, functional redundancy enables the ecosystem to respond to unpredictable stresses.

A functional group is a group of species in which the same process will consistently have the same effect. The functional attributes of such ecologically equivalent species are either structural or interstitial. Structural species are those which provide syntax in the environment, e.g., trees. Interstitial species are those which occupy the modified environments created by the structural species, e.g., snowbed bryophytes, invertebrates and epiphytes in trees. The distribution of interstitial species is thus inextricably linked to that of structural species yet the processes governing the distribution of both types are likely to be different. Fluctuations in the distribution and diversity of structural species can largely influence the diversity of interstitial species. These impacts will be even more marked in montane and alpine environments where even a minor amelioration of conditions by structural elements can be vital for the persistence of interstitial components. Factors influencing the distribution and diversity of structural species in mountain zones is still largely unresolved despite some ecophysiological research on selected species.

Different functional groups use different resources and competition between groups is likely to be minimal; competition within groups where there are a number of functionally analogous species (SMITH & HUSTON, 1989) creates functional redundancy. At the genetic and species scales redundancy could be considerable. Redundancy within functional groups may be the basis of community stability by enabling the ecosystem to respond to unpredictable stresses on a limited number of species, hence redundancy is contextually a temporal concept.

Functional groups permit a process-based approach for studying biodiversity which is amenable to modelling and from which one can generalise. A functional classification may be one of the first steps to understanding the regulation of species diversity by reducing this complex issue to a manageable level, while allowing the development of a model of montane biodiversity that is applicable over a wide geographic area. A fractal approach opens the possibility of condensing complex pattern based problems, as we find for the pattern and scale of biodiversity, into simple mathematical laws (HASLETT, 1994). However, a prerequisite for modelling is the definition of sufficient parameters within the system for meaningful models to be constructed. The following section will consider recent research on identifying and defining the key processes and mechanisms which regulate biodiversity in montane ecosystems.

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3. Ecosystem function and the regulation of biodiversity

3.1 Environmental factors and biodiversity

Biodiversity cannot be considered in isolation from the environment, and this is particularly true in montane and alpine ecosystems where the environment can be the limiting factor in many aspects of ecosystem function. Slight changes in topography, meteorology, aspect or vegetation cover can shift the controlling balance of environmental variables favouring one species or another. The interactions of these variables along altitudinal gradients generate a highly heterogeneous environment. The temporal dimension adds another layer of heterogeneity associated with soil formation, species flux and stochastic perturbation events. Structural components, either biotic or abiotic, can greatly influence species diversity through altering temperature such as at the upper treeline (JAMES et al., 1994). In a twelve-year study on the distribution of reptiles in the Pyrenees, BORRAS & POLLS (1987) have found that species distribution was underpinned by topology and climate. Soil and vegetation structure were thought to influence the arachnid fauna indirectly in Hesse, Germany, by creating microclimates and through some architectural variations (HOFMANN, 1988). Similar conclusions were reached by DOWNIE et al. (1995) for the distribution of arachnid populations in the North Pennines, England, the mediterranean and eurosiberian faunal complexes of heteroptera at high altitudes (HEISS & JOSIFOV, 1990) and for clausilid rock snail assemblages in the Dolomites (ZEISSLER, 1989). Spatial patterns of avifaunal diversity have also been shown to be associated with gradients in vegetation cover (JAMES & WAMER, 1982; ERDELEN, 1984).

At high altitudes where vegetation cover is reduced, geological features may provide structural diversity. ZAMORA (1991) has shown scale to be important in the study of habitat preferences in different mountain avian species. Vertical structure was the most important factor followed by horizontal heterogeneity with rocky and stony substrates playing a strong role in interspecific segregation. The temperature environment can also be influenced by the thermal properties of substrates such as soils and rocks; soils tend to heat and lose heat rapidly, while rocks (highly dependent on their lithology) will heat slower and lose heat slower. Habitat differentiation of *Proformica longiseta*, Collingwood an endemic ant species of mountains in the Sierra Nevada (IGNACIO et al., 1993) was highly specific for type and thickness of rock to optimise protection against high solar flux or substrate overheating.

However, vegetation is usually the primary determinant of heterogeneity in montane environments. GRACE (1987) stated that the physiological limits of plant distribution are probably climatically determined through disrupting

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some part of the plant's life cycle. The single most important determinant of life cycle processes on mountains is temperature, which shows a gradual decrease with altitude because of reduced insulation from the atmosphere. This general trend belies a marked diurnal variation in temperatures and a less rapid but equally extreme fluctuation from season to season. Spectral composition as well as intensity of solar influx changes with altitude, with more light at the short end of the spectrum and less red and infrared which has implications for phenology at high altitudes.

When photon flux density is not limiting, photosynthetic rates have a unimodal response to temperature. The rate of photosynthesis increases with altitude to a certain elevation. The level of elevation differs between life forms with herbs and shrubs being able to maintain increasing rates to higher elevations than trees (cf. JAMES et al., 1994; WILSON et al., 1987). Species at high altitudes have adapted to have photosynthetic optima at very low temperatures (MOONEY et al., 1964) and they vary on an annual basis suggesting acclimation of plant species (SLATYER & FERRAR, 1977; MOONEY et al., 1978). High saturation and compensation points in high altitude species assist with efficient photosynthesis in a high photon flux, low temperature environment. However, some species have low compensation points and it has been hypothesised that this is an adaptation to utilising low CO_2 partial pressures as CO_2 volume concentration drops by approximately 10% with every 1000 m of altitude (BILLINGS et al., 1961). However, MOONEY et al. (1964) found no effect of partial pressure change in CO_2 on photosynthesis rates in different species, though there may be changes in individual species over an altitudinal gradient. C3 plants tend to increase in biomass with altitude, C4 to decrease and CAM to remain the same (BOUTON et al., 1980). Selection for C3 at higher altitudes can be shown in some alpine succulents which are C3 rather than the expected C4, e.g., Sedum spp. In addition to photosynthesis, temperature influences other physiological processes, notably respiration. Respiration increases with temperature and many high altitude species cannot survive at lower altitudinal stations because of a negative carbon balance generated through high respiration rates (LAFLEUR et al., 1992).

Temperatures at high altitudes are a function of wind speeds (exposure) and net radiation fluxes (KÖRNER & LARCHER, 1988). However, wind can influence vegetation structure through mechanisms other than simple reduction of temperature (GRACE, 1977; 1983). Wind can be a major stress and determine the prevalence of life forms through direct morphological and physiological effects. The principal physiological influence of wind is through changes on the boundary layer coupling by affecting gas exchange

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and the temperature environment of the leaf. The morphological effects of wind can be above- and below-ground as wind can affect architecture of the canopy and root development through mechanical stimulation. Spatial variation in wind speeds is caused by topography and is an important factor in the regulation of biodiversity. The influence of wind on species composition at high altitudes has been tested by WHITEHEAD (1954; 1959) who built stone walls on a uniform montane plateau to create a sheltered environment and reported the migration of taller species into the new habitat.

Exposure and altitude were found to be the primary determinants in the spatial and temporal distribution of populations of rock ptarmigan *(Lagopus mutus pyrenaicus* Hartert, northern and eastern exposures; 1900–2899 m) and partridge *(Perdix perdix hispaniensis* Reichenow southern and south-western exposures; 1400 m-2499 m) in the Carlit Mountains, Spain (GONZÁLEZ & NOVOA, 1989). The species overlapped altitudinally with seasonal changes. Whereas *Lagopus mutus pyrenaicus* stayed mostly at higher altitudes, with minor altitudinal shifts, *Perdix perdix hispaniensis* were found at lower altitudes in winter and spring, moving higher during the summer to cause the ranges of the two species to overlap.

Both temperature and wind have significant impacts on water relations at higher altitudes. Seasonal variation in plant water relations is caused by increased radiation in summer and unavailability of frozen water in winter. Water relations can influence the distribution of vegetation and hence the diversity of associated species assemblages. For example, winter drought stress caused by poor cuticle development at high altitudes has been hypothesised by TRANQUILLINI (1979) to be a determining factor for altitudinal position of the alpine treeline. However, GRACE (1990) has rejected it as a likely determinant of treeline elevation for *Pinus sylvestris* L. in Scotland, where slightly higher leaf transpiration rates in krummholtz and isolated trees were caused by stomatal dysfunction through abrasion damage (GRACE, 1990; VAN GARDINGEN *et al.*, 1991). The level of damage found was not thought to be sufficient to be evoked as a mechanism limiting the altitudinal limit of tree growth.

In addition to locking up available water, snow can have many other impacts on the structure and composition of vegetation. An insulating cover of snow can protect organisms from extreme winter conditions (SONESSON & CALLAGHAN, 1991). Depth and duration of snow cover is particularly important for the persistence of many cryptogamic snow bed species. Changes in the distribution of snow cover will have significant impacts on communities which depend on snow cover for survival.

There are two clear research priorities in relation to understanding the impacts of environmental parameters on species assemblages at high altitude.

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Firstly, the availability and reliability and of climatic data and its spatial and temporal resolution across Europe is considerably patchy. A major commitment to meteorological research across the European mountain ranges is a primary requisite for ecological research. Definitions of mountain climates on geographic scales have been attempted in only a few studies, e.g. BOUCHER (1989) and MCCLATCHEY (1996). Such approaches can show which types of data are required and where this data needs to be collected. Many new methods have been developed recently for estimating meteorological variables at various scales, e.g. surface temperatures (WANG *et al.*, 1991), though it should be remembered that the climate experienced by different life-forms cannot be directly predicted from standard meteorological data (KÖRNER & LARCHER, 1988). This correlation between life form and climate is the second facet of biodiversity-environment relations which requires more research.

3.2 *Species flux, migration, succession and dispersal*

A possible response of organisms to a sustained change in the environment is to migrate to habitats with improved chances of survival. Thus, the composition of communities at any point in time is transitory. Assemblages of organisms can be considered as source-sink structures, an approach which is particularly useful where similar habitats are highly fragmented, as is the case in mountains. Flows between sources and sinks are regulated by process of species interactions and dispersal. As with adaptations, species interactions generally become less important with increasing altitude while dispersal, in both time and space, becomes more essential for species survival. Very little research has looked at mechanisms and rates of species dispersal in mountain environments.

A useful approach for evaluating population vulnerability, which could have wider applications is nested sub-set modelling (CUTLER, 1991). This approach recognises that assemblages at one scale can house small (nested) sub-sets of species in habitats which have become increasingly fragmented. Two interesting properties then become apparent; widely distributed species which are absent from otherwise diverse assemblages (holes), and uncommon species which occur in depauperate faunas (outliers). The «nestedness» of an assemblage is then estimated as a sum of the holes and outliers. In CUTLER's (1991) original example he noted that mammalian distributions tend to be hole-rich, while avian distribution patterns were outlier-rich. The mechanism determining this variation in distribution pattern was selective extinction, with a wide variation in extinction rates.

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Environmental stochasticity is the commonest cause of extinction in small, fragmented populations (FOLEY, 1994) and rates of extinction can be dramatic (TERBORGH, 1990). The mechanism of extinction is usually failure to complete the life cycle (Grace, 1987).

Diversity within migratory paths can be very high, e.g., SIMEONOV & DELOV (1989) recorded 178 avian species (31 of which were rare or endangered) on a main migratory passage in Kyonovska Mountain, Bulgaria form 1973 to 1987. The influence of the Mediterranean, availability of water in the Struma river, and the proximity of a suitable wetland habitat for hydrophilic species were thought to account for the high diversity of species in this mountain region.

Is it the availability of dispersal routes or density-dependent processes that drives species dispersal? Species fluxes must be considered in terms of area. Larger areas have a greater number of habitats where species can flow and more routes for dispersal than smaller more fragmented habitats.

3.3 The productivity-biodiversity relationship

Productivity is defined at the rate of energy flow through a system ($kJ\ m^{-2}\ y^{-1}$). Biodiversity typically has a unimodal relationship with productivity, within the functional domain of the community (ROSENZWEIG & ABRAMSKY, 1993). This unimodal relationship gives rise to the «paradox of enrichment» (*sensu* RIEBESELL, 1974), where biodiversity is usually positively correlated with productivity up to a point after which it decreases when nutrients are added. The mechanism(s) underlying this relationship has (have) yet to be clearly established and the comparatively low species richness in montane systems may offer an ideal system in which to study it.

Variation in the spatial and temporal flow of energy can change biomass distribution, canopy dynamics, and above- and below ground net primary production. The main physiological constraints on energy flow in montane systems are nutrient supply and availability of water. The distribution of nutrients in high mountain ecosystems was investigated by KÖRNER (1989) in nine regions around the globe. Nitrogen was the only nutrient to show consistent variation with altitude, with plants at higher altitudes having higher N concentrations per unit leaf area within life forms. N content expressed on a dry weight basis also increased in herbaceous species with altitude; in contrast woody evergreen species had stable values. N partitioning in 45 species from an altitudinal gradient in the Alps showed that partitioning of N to the leaves was the same at all altitudes. Latitudinally there was a decrease in leaf N from sub-arctic to equatorial mountains, possibly correlated

with leaf longevity. There may be differences between life forms in the efficiency to capture and store nutrients. Protein N content has been shown to be highest in the leaves of deciduous and evergreen bushes and graminoids in the Khibiny Mountains, Russia (LUK'YANOVA *et al.,* 1989).

There are many known physiological relations between water and nutrient availability, production and carbon allocation. BOWMAN *et al.* (1993) have demonstrated that the difference in community response to nutrient enrichments was related to changes in community structure in a dry meadow, and to a shift from a nutrient to a light limitation of production in a wet meadow. N+P treatment in a dry alpine meadow increased species richness significantly compared with a wet alpine meadow. This was in part related to local extinction of *Kobresia myosuroides* (Vill.) Fiori enabling colonisation by other species. In the wet meadow graminoid biomass increased significantly with N and N+P treatments, while forb biomass decreased significantly, suggesting a competitive interaction for light. Another recent study by BOWMAN *et al.* (1995) has shown that community response to nitrogen and water additions was mediated by plant growth form and related to differences in species physiology. This has obvious consequences for species composition and diversity in relation to the combined effects of N deposition and climate warming as graminoids generally have higher quality litter, substantially higher rates of tissue turnover. This may result in enhanced rates of nutrient cycling leading to positive a feedback and thus enhancing the transformation of some ecosystems.

3.4 *Perturbation regimes and patterns in biodiversity*

Perturbation, or disturbance can be defined as any process which removes biomass (GRIME, 1979) and can be biotically or abiotically driven. Biotic processes will be those of grazing, predation and anthropic activity. In mountain environments abiotic disturbances can be climatic, such as wind, rapid and dramatic fluctuation in temperature, weight of snow and frost pruning. In addition, there are inherent perturbations associated with the natural entropy of mountain systems. These include regular disturbances such as solifluction and much more extreme less frequent ones, such as avalanches, mud slides (see RAPP *et al.,* 1991), scree flows and fire.

The frequency of low level perturbation may be required for the maintenance of diversity at the community level. Moving up to a landscape scale, the more extreme low frequency events will generate a mosaic of communities ensuring a reserve of species for colonisation in the locality. Species within communities can evolve strategies for ensuring their survival

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with consistent and low level disturbance regimes, e.g., persistence of *Calluna vulgaris* (L.) Hull in wind stripes on plateaux in the Scottish Highlands (BAYFIELD, 1984).

Recreational pressure in remote mountain areas has increased the frequency of perturbation LANCE *et al.* (1989). Increasing visitor pressure could have very dramatic and detrimental influences on vegetation as has been shown by experimental studies (COLE, 1995) where the response of vegetation to disturbance from trampling fit a second order polynomial function (with considerable variation between life-forms). Reduced vegetation cover would increase vulnerability to soil erosion and hence more extreme disturbances such as mud slides.

The nature of the relationship between perturbation and diversity has still to be elucidated as field evidence for the role of perturbation in maintaining diversity in European mountains is limited (but see JENÍK, 1998). As stress on mountain ecosystem increases monotonically with altitude the assessment of the ability of communities at higher altitudes to persist under increased intensity and unpredictability of perturbation should be a priority.

3.5 *Species interactions and the maintenance of biodiversity*

The role of competitive interactions in determining species diversity has been much debated. Within plant populations the classification of competitive and stress tolerant (GRIME, 1979) functional types for species persistence has been criticised for not making reference to the role of resource limitation (TILMAN, 1990). TILMAN argued that competitive advantage would go to the species which can withstand the lowest concentration of limiting nutrients and therefore competition and stress tolerance were the same selective force in a community. Diversity as an indicator of stress has also been questioned by SCHINDLER (1987).

Predation is a significant process in structuring communities, e.g., the annual reproductive rate of *Buteo buteo* (L.) in Norway has been shown to be coupled to population cycles in various species of voles, but notably, *Microtus agrestis* L. (SPIDO & SELAS, 1988) and to a lesser extent to spring weather conditions. However, there is also competition between predators leading to habitat differentiation, e.g., dispersal of avian species along vertical as well as horizontal gradients can be explained by competition (HAFFER, 1989).

There is a lack of studies on the effects of changes of plant species diversity on the fauna in European mountains. In contrast, in South Africa a fascinating study was reported by FRASER & CROWE (1990) on the disruption to fauna assemblages after the invasion of montane fynbos flora by woody plants. A

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comparison of density, biomass, species richness and composition of the avian fauna in stands which had or had not been invaded by alien plants (primarily *Acacia cyclops* A. Cunn. ex G. Don) demonstrated no significant decrease in the density of avians between fynbos stands, though the density of nectarivorous species did decrease in correlation with increasing density of invasive plants. This trend could have a positive feedback on the status of native plants through disrupted pollination.

More manipulative *in situ* experiments are needed as many of the interrelationships between species are poorly understood. Interactions between organisms and density-dependence has also received little attention.

3.6 *Regional biodiversity*

Regulation of biodiversity may need to be studied on wider geographic scales than merely at the community level, e.g. for migratory species. Indeed, analyses of evolutionary mechanisms in a single genus can provide insight into the processes of migration and speciation that shape regional floras (KELSO, 1992) and faunas. For example, the effects of geographic speciation can be seen in populations of mountain vipers (*Vipera* spp.) along the Anatolian «Diagonal» in Turkey, where a new species of *Vipera, V. albizona,* has recently been described (NILSON *et al.,* 1990). The role of the opilionid, *Mitopus morio* F. in characterising the biocenotic region of the Alps above an altitude of 1500 m was shown by MARCELLINO (1988). For this study the diversity of the Opilionid fauna from different habitats in the Alps was estimated using Sørensen's index, the annual mean of activity density, Simpson's dominance index and the Gleason-Margalef richness of species. Most of the species encountered had a European distribution, though those found at higher altitudes, had a more restricted distribution in the Alps.

Most studies are restricted to a single mountain range or to national or regional boundaries and few mechanisms are evoked from field data. In a rare study of distribution of mammals, ANDERA & CERVENY (1994) found that 41 of the total of 62 species of mammals in the Sumava Mountains, Bohemia, had a continuous distribution. Another seven species were distributed over a considerable part of the region with the exception of the highest mountain areas. Only one species, *Sorex alpinus* Schinz, was restricted to medium and higher altitudes, though this could be an artefact caused by suitable habitat destruction at lower altitudes. It is probably at this scale that anthropic influences are most clearly expressed. In other cases where species have known mechanisms to overcome geographic constraints, e.g. snow

leopards can cross glaciers to get from one mountain range to another (KOSHKAREV, 1988) population restriction must be anthropic.

3.7 *The eclipse of history-long-term temporal patterns*

Environmental changes have contributed to community structure and composition in the long-term, though this important and neglected area of biodiversity regulation has often been overlooked in ecological studies (RICKLEFS & SCHLUTER, 1993). On higher mountain peaks the tops formed refugia and nunataks where a relict flora was able to survive above the ice sheets. There, species underwent speciation in isolation from each other. Then as the ice sheets melted the species gradually moved down to lower elevations where they interacted with species from lowland refugia. Glaciation, fragmentation and rates of tectonic uplift have been probably the major selective events at the continental scale. For example, range expansion of the spider complex *Lepthyphantes annulatus* Kulczynski, which is currently found in the Pyrenees, western and eastern Alps and the Carpathian mountains, is hypothesised to have occurred during the last treeless glaciation with speciation during the current warmer interglacial (THALER *et al.*, 1994).

Endemism is a characteristic feature of both the flora and fauna of mountain regions. A geobotanical synthesis on the incidence of plant endemism in the western Mediterranean demonstrated that there are elements of both patroendemics and schizoendemics in the region, a testament to both an ancient flora which developed *in situ* and to continuing speciation (HINZ, 1990). Continuing speciation will have an obvious impact on future assemblage composition. A synthesis of the carabid fauna in the Western Alps suggested that species richness was related to clado-vicariance events in addition to a heterogeneous environment (CASALE & VIGNA TAGLIANTI, 1992).

Lacerta monticola Boulenger is a glacial relict endemic to three mountain ranges in the coastal region of the Iberian peninsula (BROWN & PÉREZ-MELLADO, 1993). Geographic variation throughout the ranges revealed considerable variability and the Pyrenean population was sufficiently distinct to be considered a different species. Similarly, studies on *Canis lupus* L. in Italy indicated that the population was fragmented into a number of «island» populations on mountain ranges and despite having home ranges of 200-400 km² there was little genetic interchange (BOITANI, 1992). A captive breeding programme has been established to ensure conservation of genetic variability.

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Man has probably had the most significant influence over ecological time scales. THOMPSON *et al.* (1996) recognised the role of changing land management, notably afforestation and traditional heather moorland burning, in declining populations of a number of montane and sub-montane avian species in the Cairngorm Mountains, Scotland. They concluded that more research was necessary on elucidating the links between avian densities and abundance and vegetation composition before the spatial and historical trends could be fully interpreted.

While the role of glacial isolation seems theoretically inherent, it has rarely been tested. BIRKS (1993) using the occurrence and frequency of 109 plant species in 75 grid squares tested the function of nunataks in explaining the distribution of montane plant species in Norway and concluded that unglaciated areas had no significant contribution to current plant distributions.

This may hold true for some elements of the Norwegian flora. However, different groups of organisms will have had completely different routes to their current distributions and the impact of glaciation will have varied from region to region. Mammals and some insect faunas are likely to be relicts, while other elements of insect faunas, avian faunas and plants have probably undergone processes of recurrent colonisation, obscuring the role of glacial processes.

4. Freshwater ecosystems

The flora and faunal diversity of high altitude freshwater ecosystems is little documented, although in many parts of Europe these habitats are used as reference sites for monitoring climatic change and impacts of air pollution.

Water is an important component of many habitats and yet its function in the uplands is poorly studied. One recent review of the ecology of high altitude running water systems has identified melt-water, nature of feeding water, e.g. ground melt etc., temperature, flow fluctuations, turbidity, water chemistry, O_2 concentration, species assemblages as important variables (WARD, 1994). The most important factor on species richness is temperature, with effects mediated through generation time and mutation rate. Abundance and biomass of mountain stream water mites (Hydracarina) have been shown to vary with temperature in Germany (MEYER, 1994) where each taxon had a distinct and seasonal abundance distribution. Examining Molluscan communities in 43 European lakes MOUTHON (1990) has proposed that altitude, latitude and depth were the main factors associated with species

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richness, though they were thought to operate through temperature. Mineral content and temperature, together with historical factors were shown to determine watermite (Hydrachnellae, Acari) distributions in 149 springs in the Pyrenees (ROCA & GIL, 1992).

Temperature is thus important in determining the structure and composition of freshwater populations from community to regional scales. However, at wider geographic scales, speciation and history can have major influences. Many elements of alpine freshwater ecosystems have wide geographical distributions though geographic variation becomes more pronounced with altitude as isolation increases. A Pan-European study on the species composition of sessile algae of crystalline rocks showed that despite similarities in temperature and oligotrophy there was a considerable variation (KAWECKA & ELORANTA, 1988).

Other physical factors can, on occasion, be shown to have stronger influences than temperature. The nature of the stream bottom was the main factor determining the structure of oligochaetes in mountain streams in Poland, but geographic location was also important (DUMNICKA, 1994). Gradient, substratum and presence of flora were the main factors in explaining the variation of *Phagocata vitta* Dugès in fresh water springs in Wales (ARMITAGE & YOUNG, 1992). Ionic strength and current velocity were the main determinants of species composition and abundance of diatom assemblages in 28 springs in the Pyrenees, though modifications in relation to light and temperature were found in some populations (SABATER & ROCA, 1990). Redundancy analysis on environmental factors related to species composition in 116 high altitude lakes in the eastern Pyrenees revealed that water chemistry and altitude explained most of the variance (GRACIA *et al.*, 1994). However, body size and abundance in communities of plankton from La Caldera lake in Spain suggested that ecological and evolutionary processes were more important in structuring the community than physiological factors (size-dependent metabolism) (RODRIGUEZ *et al.*, 1990).

In addition to characteristic spatial distribution patterns related to micro-habitats, species diversity in mountain freshwater habitats can also show clear seasonality. A one-year study on drift density in the fauna of a mountain stream in Lunz, Austria found that the most abundant taxa were Diptera (46.6%; mainly Chironomidae and Simuliidae), Ephemeroptera (24.0%; dominated by *Baetis* spp.) and Plecoptera (16.1%). Drift density (in terms of numbers and wet weights) was significantly higher in spring and summer than autumn and winter (WARINGER, 1992).

Acidification of freshwaters has a detrimental impact on diversity. A study by GUEROLD *et al.* (1991) in the streams of the Vosges Mountains, found that species richness of freshwater macro-invertebrates in acidified streams was 29

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as opposed to 93 in non-acidified streams. Soft waters, which are often found in mountainous areas are more prone to effects of acidification. Diatoms are particularly sensitive to acidity and the diversity of diatom taxa was recently shown to decrease significantly over a decreasing pH gradient in samples from a number of streams in Polish mountains (KWANDRANS, 1993).

The effects of agriculture on high altitude lakes may be very small. CATALAN *et al.* (1993) in a study in the Pyrenees found no significant differences in the water chemistry of disturbed and undisturbed high altitude lakes, except for few cases. They suggested that disturbance by agriculture is only important for small, shallow endorreic lakes. Epilithic diatom communities in Lake Piccolo Naret in the Swiss Alps were considerably influenced by C addition, while N and P supply was of minor importance (NIEDERHAUSER & SCHANZ, 1993). MCKNIGHT *et al.* (1993) indicated that the availability of labile dissolved organic O_2 could be the primary controlling factor of seasonal variation in heterotrophic activity of planktonic microbial populations.

Freshwater ecosystems are important for diversity in the wider landscape. River banks at high altitudes provide habitats for *Sorex alpinus,* the alpine shrew (BRUNNER & BRAUN, 1991) and availability of suitable mountain streams has been shown to effect the population numbers of *Salamandra salamandra* L. in the Carpathian mountains, Poland (SWIERAD & ZAKRZEWSKI, 1990). This species is also dependent on the composition of the arthropod fauna (GUERRERO *et al.,* 1990).

5. Environmental interactions

Industrialisation has been associated with increases in atmospheric concentrations of CO_2, CH_4, N_2O and CFCs (WATSON *et al.,* 1996). Most notable is the increased concentration of CO_2 which has risen from 280 ppm in pre-industrial times, to 350 ppm today and is predicted to increase to 560 ppm by the late twenty-first century (WATSON *et al.,* 1996). Despite the lack of conclusive evidence of causality, there is concern that if CO_2 concentration is driving global climate warming then, as undeveloped nations make the transition to industrialised societies, the increase in mean temperatures and associated climate variables will impact heavily on all biotic natural resources.

One of the key areas where climate changes are predicted to impact is at high altitudes. This section considers the current research on climate change impacts and the impacts of environmental pollutants.

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5.1 *Climate change*

An increase in the mean global air temperature of approximately 0.6 °C since AD 1860 is now broadly recognised (JONES *et al.,* 1986), and future increases are widely predicted. Predicted changes for the 21st century vary from 0.9-1.5 °C hundred years[-1] in Scandinavia (SANTER *et al.,* 1990), to 2-6 °C hundred years[-1] in North America (BONAN *et al.,* 1990), with increases expected to be greater at higher latitudes because of feedback effects due to ice albedo (KUKLA & KUKLA, 1974; HANSEN *et al.,* 1988). These figures indicate a 0.1-0.3 °C rise per decade, though uncertainties are high and 0.2-0.5°C have been mooted. However, these are very general scenarios of climatic change and down-scaling to regional level is generally extremely difficult; more so in montane environments given the influence of topography and the spatial and temporal inconsistencies in available data. One recent study on the potential impact of different climate change scenarios throughout Europe found that the biggest impacts would be along tension zones in mountain regions where oceanic and continental air masses meet (BUNCE *et al.,* 1996).

The role of climate change in determining biodiversity in mountain regions is difficult to predict. Of concern is that the two climate variables most likely to change, temperature and precipitation distribution, are also the two most selective forces with increasing altitude and any change in these variables may have potentially significant impacts. Not only biodiversity but ecosystem stability may also be affected through changes in the C balance. There is an undetermined quantity of the global C pool currently stored in low-temperature ecosystems and releasing even a proportion of this into the atmosphere could have a large impact. The fundamental role of temperature in the structure and composition of montane ecosystems makes them excellent systems in which to monitor climate change.

In a report on the potential impact of future climate changes on Norwegian ecosystems, HOLTEN & CAREY (1992) suggested that ecosystem response would be non-linear because of the stochastic nature of climate variables and the unimodal response of species to temperature. In addition, they concluded that more knowledge of ecosystem processes, particularly demographic processes was necessary before critical thresholds of climatic change could be ascertained.

In a manipulative experiment on the response of *Cassiope tetragona* (L.) L. Don to both changes in temperature and increase nutrient flux that would be associated with global climatic warming, HAVSTRÖM *et al.* (1993) demonstrated a differential response in growth along an altitudinal gradient. At the lower altitudinal and latitudinal limit competition for light and

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nutrients were the limiting factors of growth; at higher altitudes and latitudes it was temperature. Although this set of experiments accounted for the impacts of species interaction through shade, much more research on species interactions and over much longer time scale is required before the full impact of different climatic regimes can be assessed. More recent work in the Scandes has been summarised by SONESSON & MOLAU (this volume).

5.2 *Air pollutants*

The secondary effects of air pollution on the avifauna in the Smrk massif and on avian diversity in the Moravskoslezske Beskydy Mountains has been shown by ČAPEK (1991, 1994). Altogether 77 bird species, of which 71 % were breeders, occurred in the study area. The highest species richness was correlated with relatively undamaged forest stands and least bird species bred in dead stands and in a clearing induced by air pollution. Similarly, the highest total breeding bird density, the highest value of diversity index and the highest number of synecologically important bird species were found in stands resembling virgin forest while the lowest in dead stands and in the clearing. There was a significant correlation between the degree of forest stand damage and the number of breeding bird species. On the other hand, the local forest decline created good ecological conditions for several other bird species.

One of the few studies to compare the chemical composition of cloud events in the Black Forest and at a higher altitude on the Vosges Mts., Germany was conducted by LAMMEL & METZIG (1991). They showed that acidity of cloud water at Vosges was as low as pH 2.8 compared with samples from the Black Forest at 4.9-4.0. Similar findings have been reported from mountain studies in North America, e.g., KIM & ANEJA (1992) found cloud water to have an average pH of 2.4-4.9 compared with rainwater at 3.5-5.5. KIM & ANEJA (1992) concluded that processes of evaporation and transpiration were most important for determining the ionic content of cloud water. Higher concentrations of pollutant ions in cloud water compared with wet precipitation have also been recorded by COLLETT *et al.* (1993a) on Mount Rigi, Switzerland (1620 m a.s.l.). Small drops of cloud water (<10 μm diameter) were found to be enriched in ions. This is important as large cloud droplets are captured by snow crystals. On one occasion, no significant difference could be detected between ion concentrations in cloud water and precipitation. This was during a period of extreme precipitation rimming. The processes involved in precipitation increasing in ionic content during rimming was investigated by COLLETT *et al.* (1993b) in a subsequent study.

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The Mts. Vosges study by LAMMEL & METZIG (1991) also demonstrated that solvents became concentrated in water below the forest canopy. Below cloud gas scavenging has been shown to be consistent among three sites on Mt. Rigi, Switzerland (OBERHOLZ et al., 1993), though scavenging for NH_3 was more important than for NH_4^+. This study also showed strong concentration gradients for NH_3 and NH_4^+, with NH_4^+ highest at high altitude and NH_3 highest at low altitudes. No elevational gradient was found for SO_2. Under conditions of stable atmospheric stratification for some days the contribution of gas scavenging to ionic concentration in precipitation has been reported to be as high as 80% (ZINDER et al., 1988). Snow also scavenges atmospheric pollutants and these can be deposited where snow has accumulated when it melts; this has been demonstrated for snow at the treeline (POMEROY et al., 1993). A flushing of 50 - 90 % of soluble metal ions was found in the first melt-water fraction from mountain snow packs by ECKER et al. (1990) in west Japan. However, the final fraction melt-water fraction contained the highest loading of insoluble metal ions.

As occult deposition in mountainous regions is important for modelling pollutant fluxes cloud rather than precipitation events could be more important. The question arises - how far are these counted in current meteorological accounts? It is also notable that ionic flux studies have been made only in forested habitats and an earlier review of pollutant deposition in eastern North America (LOVETT & KINSMANN, 1990) has highlighted this lack of published data.

The quantity of precipitation has been shown to have effects on pollutant deposition. In an 18-month study at 10 mountain sites in North Wales REYNOLDS et al. (1990) found that although concentrations of SO_4 and NO_3 where lower than those found in more polluted areas of Europe the deposition rates were higher because of higher annual precipitation. However, this relationship was not linear and topography played an important role in the spatial variability of deposition. Seasonal variation in acidity has been detected by BRANTNER et al. (1994) on Mount Sonnblick, Austria (3106 m. a. s. l.). Acidity was higher in May (cloud water pH 4.2, snow 4.4) compared with November (cloud water pH 4.5, snow 5.1) with cloud water being always more acid than snow. High acidity, particularly in spring, may have effects on phenology though no research specifically on pollutants and phenology have been conducted.

Of the few studies that have looked at the influx of the potentially highly toxic halocarbon pollutants, FRANK et al. (1991) reported higher C1 and C2 halocarbon levels at a mountain forest site in Germany than at the Atlantic coast in Portugal. Tetrachloromethane levels were constant at all sites and a

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suite of other halocarbons varied in relation to the industrial characteristics of the sites. How do these accumulate in the food chain?

Air pollution acts on many physiological processes and many levels from lethal toxicity, e.g., death of sub-alpine *Picea* forest and subsequent replacement by *Calamagrostis villosa* (Chaix) J. F. Gmelin (PYSEK, 1993) to interference at cellular level, e.g. change in the ultrastructure of mesophyll chloroplasts after fumigation of plant species from Turkish Mountains (ARNAUTOVA *et al.*, 1990). Most air pollution research has been concentrated on the response of montane forests with relatively few studies of pollutant influx to high montane. Technical equipment for sampling air pollution is readily available, e.g.: VAN-WYK & STOCK (1991) have described a simple sequential (stage) atmospheric deposition sampler for use in remote mountain areas. Unfortunately, it is principally designed to collect precipitation, but could be modified to sample cloud water. The historical impacts of air pollution can also be studied using suitable herbarium material, such as was done by BADDELEY *et al.* (1994) who estimated past atmospheric nitrogen loads and the potential impacts of future N fertilisation on *Racomitrium lanuginosum* (Hedw.) Brid. heaths in Britain. However these authors stressed that heavy grazing pressure, rather than high levels of N deposition, may be associated with the decline and fragmentation of *Racomitrium*-dominated mountain heaths.

5.3 *Ozone*

Ozone concentrations can be correlated with altitude and climatic conditions, with increased ozone concentrations at higher altitudes. Ozone levels which exceed international recommended threshold values have been consistently recorded from European mountains (KRAPFENBAUER, 1991). Mountains typically have a diurnal pattern of low in morning, peak late afternoon; some dependency on the previous days concentration was also observed. In very remote locations, ozone concentrations in mountain environments can be low and show little diurnal fluctuation (PEAKE & FONG, 1990). Within forest canopies at least, ozone has a vertical distribution caused by depletion as ozone interacts with vegetation and soil. In North America there is some evidence for higher ozone concentrations during drier weather (EDWARDS *et al.*, 1991), though the study compared one wet and one dry year only. The absolute maximum average ozone concentration for a single hour was 156 ppb in the drought year, while it was only 107 ppb in the following wet year. There is also the possibility that these results can be interpreted in terms of other climate variables. In a more extensive investigation measurements of

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ozone, NO_x and meteorological variables were made by ANEJA *et al.* (1994), from May to October for 3 years at a network of five high elevation sites (1000 m) in the eastern USA. The data showed that high ozone episodes occurred frequently during June and July, and were strongly correlated to upwind from urban and industrial source areas in addition to meteorological parameters, such as temperature, and relative humidity. The concentrations of NO_x were higher during the high ozone episodes, reflecting the photochemical production of ozone at the regional scale.

Assessing the effects of ozone on vegetation has been tested experimentally using control chambers. LEFOHN *et al.* (1990) have expressed concern over the arbitrary ozone level of 0.025 ppm often used in charcoal-filtration chambers to simulate the natural background concentration of ozone. Their analysis indicated that the seasonal 7-h average values of 0.025 ppm and below, used by some researchers as a reference point, may be too low and that estimates of crop losses and tree damage in many locations may have been too high.

The spatial and temporal variability of results suggest that a long-term monitoring over a wide geographic area and associated experimental programme are required to determine the effects of ozone on high altitude species.

5.4 *UV-B*

Long-term depletion in stratospheric ozone has resulted in increasing solar UV-B flux. Measurements at Jungfraujoch, Switzerland (3576 m a.s.l.) have recorded a sustained 1% yr^{-1} increase in UV-B radiation since 1981 (BLUMTHALER & AMBACH, 1990; AMBACH & BLUMTHALER, 1993). In mountain regions, there is a greater incidence of UV-B radiation as the atmosphere is rarefied and consequently has less of a filtering effect. Research on the effects of UV-B on living organisms has until recently been restricted to humans and economically important crop plants. One of the few early studies on the effects of UV-B on plant species from the Rocky Mountains found evidence of a varying degree of epidermal screening of UV-B (DAY *et al.*, 1992). Herbaceous dicots screened the least and conifers the most, with woody dicots and graminoids in between. A considerable amount of research has been made on natural vegetation recently (see e.g. SONESSON & MOLAU, 1998).

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6. Conclusions

There has been very little synthesis of the processes regulating biodiversity in Europe's mountain ranges. In particular, there is surprisingly little direct information on the mechanisms supporting these ecosystems. Areas of species flux, disturbance and regional or landscape level processes are particularly neglected. This has to be set in the context of significant advances in the theoretical understanding and modelling of diversity in the last decade (RICKLEFS & SCHLUTER, 1993). Models can enable hypothesis generation against which the results of experimental research can be compared. To this end, one needs clearly defined and testable hypotheses (PETERS, 1991; WEINER, 1995) which do not ignore mechanisms (WEINER, 1995), as some argue that a mechanistic approach is probably the only cohesive one to understanding biodiversity (RICKLEFS & SCHLUTER, 1993).

Much of the research to date has been conducted in isolation, in part as a result of national boundaries and language differences, with much data published in obscure publications, or internal reports. In addition, there are some insufficiently studied biological groups or systems, e.g., soil microfauna, inverterbrates, cryptogams and fresh water ecosystems. The soil microfauna could be particularly important as a control mechanism of the C budget in mountain regions (see BROLL, 1998) as it plays a critical role in mineralisation and decomposition.

Above all, however, it seems appropriate to seek much more integration and cross-factoring of ecological and, indeed, molecular histories concerned with mountain biodiversity. This paper has tried to offer a synthesis of some of the work that has been made on mountain biodiversity. If it initiates some new areas of work, thought or synthesis it will have served its purpose.

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