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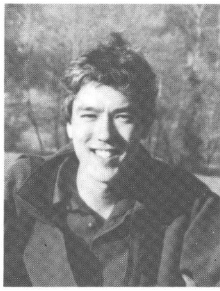

LAST YEAR, according to the World Meteorological Organisation, was the hottest since records began in 1861. Siberia was 3°C warmer than average and the exceptionally hot summer in India, northern Europe and the midwestern United States caused droughts and more than a thousand heat-related deaths in the US. It was also a year of extreme weather events. The hurricane season in the Atlantic was the most active since 1933, causing billions of dollars worth of damage in the Caribbean and the south-east coast of the US. North-west Europe suffered massive flooding in January and February. Over parts of central South America, however, rainfall was 50%–75% below normal for most of the year, and significantly below normal over the Iberian peninsula, north-west Africa and southern Africa in the first half of the year, leading to water shortages. But there was relief in Australia as normal rains made a welcome return to drought-stricken areas following the end of prolonged El Niño conditions in the South Pacific. So, is the climate changing, and if it is, what are the implications for protected areas and biodiversity conservation?

In December 1995, the Intergovernmental Panel on Climate Change (IPCC), the UN-mandated body responsible for reviewing the state of the science of climate change, met in Rome to finalise its Second Assessment Report (SAR). The work of over 2,000 scientists worldwide, and running to over 2,000 pages, this report is the most comprehensive document on the causes, impacts and mitigation of climate change published to date.

The conclusions of the IPCC make sobering reading. The concentrations of greenhouse gases in the atmosphere are still rising. Carbon dioxide (CO_2) is about 30% above its pre-industrial level. It is responsible for around 70% of the enhanced greenhouse effect (the other important greenhouse gases being methane, nitrous oxide and CFCs, HCFCs, HFCs etc.). The main source of CO_2 is the combustion of fossil fuels, and the IPCC states that the balance of evidence now suggests that there is a discernible human influence on the climate system.

Average surface temperatures around the world have risen by about 0.3–0.6°C over the past 100 years and by about 0.2–0.3°C over the last 40 years. Recent years have been among the warmest since 1860, i.e. since instrumental records began (IPCC 1996; see graph on front cover). Perhaps the clearest evidence of climate change comes from glaciers, which are in retreat on every continent of the globe. The changes in glaciers today can be compared directly with the ongoing warming of the atmosphere: the global glacier recession of the past 100 years corresponds to a global warming of about 0.66°C, and has added about 2–4 cm to the sea-level. In the European Alps, glaciers have shrunk by about 50% in volume since the middle of the nineteenth century.

The greenhouse effect is offset in some parts of the world by aerosols (dust and small particles) released into the lower atmosphere by the combustion of coal, oil and biomass. The aerosols act like a giant parasol until they are washed out of the atmosphere by rain after a few days or weeks. Sulphate aerosols, which are primarily responsible for the cooling effect, are also the principle cause of acid rain. The areas most strongly affected by sulphate pollution are the industrial regions of the US, Eastern Europe and China.

General circulation models of the global ocean and atmosphere system project an additional increase in global mean temperature of 1–3.5°C over the next century, given a mid-range scenario of population and economic growth, with a best estimate of 2°C. Thermal inertia of the oceans, however, means that even if greenhouse gas levels in the atmosphere stabilised today, some further global warming is inevitable. Thermal expansion of the oceans and the melting of icecaps will lead to a rise in sea-level of about half a metre by 2100.

IPCC Working Group 2 has looked at the likely impacts of climate change on ecosystems. Many of the ecological models used to make future projections are based on a doubling of the pre-industrial atmospheric CO_2 concentration, which is expected to occur by the year 2050. The following points highlight some key findings with respect to four important biomes.

Forests

- Between a seventh and two-thirds of all forest areas, depending on their location in the world, and on average one third of the global forested area will undergo major changes in vegetation type as a result of changes in temperature and water availability.
- The greatest impact will be on boreal forests, two-thirds of which are likely to be affected and 25%–40% of which are expected disappear altogether, mainly through fire and pest attack.
- Climate change is expected to proceed at an order of magnitude faster than the rate at which many tree species are able to respond by dispersal and re-establishment.
- Carbon stored in forests undergoing transition will be lost as CO_2, causing a positive feedback on the greenhouse effect.

Wetlands

- Increased variability in the hydrological cycle is expected, leaving inland wetlands highly vulnerable to drying. Studies show that wetland species diversity is reduced in dry years.
- Warming of 3–4°C could eliminate 85% of all remaining wetlands.
- Drying of peatlands, especially tundra, releases CO_2 causing positive feedback on the greenhouse effect.

Coastal zones

- Half of all coastal wetlands of international conservation importance could be lost (assuming a 1 metre sea-level rise).
- Mangroves can adapt to up to 10–12 cm sea-level rise a century – about five times slower than the projected rate.
- Coral reefs can cope with projected sea-level rise, if healthy, but are temperature-sensitive: prolonged exposure 1°C above normal causes bleaching, and recovery is rare.
- Mangroves and coral reefs are the first line of defence against storms and sea-level rise.

Deserts

- With few exceptions, deserts are expected to become hotter and, in the Sahara, Arabia and central Asia, drier too.

- Desertification is likely to accelerate in sub-Saharan Africa.

It is clear, therefore, that not only are ecological changes to be expected, but also that the protection of natural and semi-natural ecosystems could help to control the greenhouse effect. Planning for conservation in a changing climate, in other words, is important both for its own sake as well as for mitigating the impacts of climate change elsewhere, on agriculture and human health for example.

The papers written for this special edition of *PARKS* provide guidance on planning for the projected changes and come from all corners of the world, as is appropriate for an issue of global dimensions. Bridgewater stresses the role of monitoring, especially of species at their ecological limits and ecosystems at the edge of their biogeographic boundaries, and the management of protected areas within the context of the wider landscape matrix. He emphasises the importance of conservation outside of reserves and particularly the maintenance of corridors which allow species dispersal and migration as a response to climatic changes.

The paper by Ellison discusses the impacts of climate change and sea-level rise on mangrove ecosystems. She too stresses the need for monitoring, and recommends possible management strategies to mitigate the expected impacts. In a review commissioned by WWF, Stone describes some of the observed and expected impacts on European ecosystems, which could imply significant vegetation community changes in at least 16% and as many as 60% of existing nature reserves. Finally, Malcolm and Markham examine the extent to which either species diversity or the maintenance of ecological functions performed by keystone species confer ecological resilience in the face of external changes. They argue that special attention must be paid to the responses of species which individually or collectively have a disproportionate effect upon ecological structure.

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Protected area management in the face of climate change

PETER B. BRIDGEWATER

Climate change will have significant impact on protected areas and on their management. Particular impacts will include loss of community and ecosystem types which are at climatic limits (e.g. montane communities), change in proportion of community types from climatic and landform changes (e.g. coastal communities), increasing aridity and an overall loss of biological diversity. It is possible that novel communities will become established, following a sorting of indigenous species' mixtures and the establishment of exotic species.

For conservation managers, it will be essential to use a landscape ecological framework, to monitor changes and design remedial measures. Particular attention should be given to boundary, barrier and corridor elements of ecological infrastructure. Monitoring of biota will be an important aspect of climate change detection, especially over the 20–50 year timeframe. For species thought to be at risk, modelling approaches should be used. Options for endangered species include translocation, or, for plants, propagule or germplasm storage for eventual translocation.

To ensure that natural adjustments to communities and biota continue it will be vital to understand clearly the nature of patch dynamics, and the need for appropriate linkages between protected areas. It may also be necessary to accept that some protected areas may become depauperate during the process of climate change, while other areas, currently less valuable, should be added to the protected area network. Protected Area Management Agencies should be prepared to use the full range of IUCN-CNPPA Protected Area Categories, and expect to move protected areas between categories, as appropriate. The advantage of using a landscape ecological framework is that such a broad view may be taken. A flexible approach of this kind will be vital for the protected area manager under a regime of changing climate.

DIRECT AND INDIRECT impacts of climatic change may take many forms, apart from temperature rise (see, for example, Houghton *et al.* 1990). Such impacts will lead to changes in species composition and dominance, ecosystem structure (especially length of growing season) and in the distribution and abundance of species. Palaeoecological work on several continents has demonstrated that, during previous warmer climates, distributions and relative abundances changed, and changed again, as cooling cycles and thus cooler climates became established.

Work on 'fossil' carbon dioxide in the ice caps of Greenland and Antarctica has shown a past increase in carbon dioxide levels coincident with the warm periods in the last 160 000 years. However, concentrations were apparently never as high as at present and the effects from nitrous oxide and methane would have been less pronounced or, in the case of CFCs, absent. There are presently no clear scientific indications regarding rates of ecosystem change relative to climate change; such changes could be gradual, but many argue they could equally be abrupt and rapid (Pearman 1988).

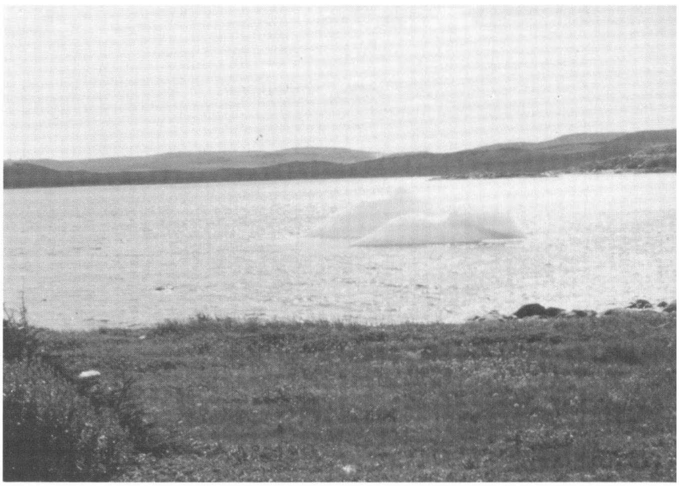
A particularly important point to make at the outset is that climate change is but one component of global change. It may well be that climate change is actually less of a concern for protected area management than other components of global change, such as eutrophication, change in hydrological balance and poor land-use practice. Nonetheless, climate change continues to occupy the world's attention, and protected area managers, from what we know of the potential impacts on biodiversity, should be in a phase of contingency planning (Bridgewater 1993).

Bridgewater (1991) reviewed the general consequences of climate change and concluded that suggested change would result, among other things, in the disappearance of montane and coastal habitats, together with their component plant and animal species. There would also be general degradation of the conservation value of these ecosystems, perhaps through invasion of alien species (Macdonald 1992). Urban *et al.* (1992) note that "the geographic extent of vegetation types might shift through the stationary boundaries of established nature reserves".

Using global models, Neilson and Marks (1994) suggest hydrologic changes in areas of North America, eastern Europe and Russia, Siberia, northern India, Australia, central South America, northern Africa, the Middle East and New Zealand. While it is too simple to suggest an increase or decrease of drought incidence, that may be a consequence for these areas. Neilson and Marks (1994) also note that "it seems reasonable that regions which differ substantially in background climate should have different levels or types of sensitivities to climate change. Regional climatic features result from the large-scale flow of the atmosphere over and around mountain ranges and continental margins, and are features that will remain relatively stable, even under climatic change".

Stock (1992) discusses the climatic change at the boundary of the Oligocene and Miocene geological eras, some 30 million years ago. He notes biodiversity changes resulting from climatic changes in that period as being fairly drastic but, that, in the end, they were recoverable. He suggests less drastic changes will simply cause species to change their distribution boundaries, or migrate to refugia. In refugia, actual increases in biodiversity will occur, in a relatively short time, due to normal evolutionary processes. But to quote him directly "I feel that the direct human threat, e.g. the land use, and the pollution and poisoning of rivers, sea and land, presents a much greater threat to biodiversity on global scale than the greenhouse effect. Many rare species, e.g. now living in nature reserves, especially in wetlands, will not be resistant to a drier and warmer climate, whereas suitable new habitats which can act as refugia, are not available, being already in use by man."

Global warming certainly presents the opportunity for the development of new plant and animal communities. It is, after all, quite likely that in previous geological eras new communities arose as a result of environmental changes brought on by warming or cooling of atmospheres, changes in the amount of water available, in precipitation patterns etc. (Delacourt and Delacourt 1988). Huntley (1990), in a paper on climatic change effects in European post-glacial



A blanket peat ecosystem near L'Anse aux Meadow, Newfoundland, Canada in early summer, with inshore ice block! Ecosystems such as these are under great threat, as most models predict greater warming in higher latitudes. Coupled with changes in rainfall, forest would be a more likely landscape in 100–200 years.

forests, notes changes in species composition, dominance and ecosystem structure, and in the distribution and abundance of species over time.

However, it is much more likely that affected communities will remain in a 'metastable' (Naveh and Lieberman 1983) state until some dramatic environmental perturbation causes a severe dysfunction in the landscape or ecosystem. Perry *et al.* (1990) give a useful analogy of the ecosystem being a ball balanced on a peak, which requires little effort to dislodge. This is a graphic illustration of metastable, rather than the often-presumed stable, nature of ecosystems. Dramatic perturbation events may well become more frequent, since some 'greenhouse' scenarios have included increased climatic variability and environmental perturbations as a consequence of the 'greenhouse effect' (Wigley 1985, Bolin *et al.* 1986). So, we can expect to see versions of ecological communities (possibly somewhat poorer in species – or richer, but less stable) continuing to exist until a dramatic event such as a hurricane type wind, a wild fire, excessive drought, flooding or other environmental catastrophe occurs.

It is also likely that exotic species already present in restricted sites, or not yet established, will achieve range extensions. New species interacting with existing communities will give rise to novel communities for which effective conservation measures will need to be defined. This will be one aspect of 'creative conservation' in the future – giving rise to the 'global garden' (Bridgewater in press).

Management plans for potentially threatened ecosystems, whether in protected areas or not, therefore need to be drawn up with a specific focus on the need to monitor environmental change. In some cases it may not be possible to provide a viable management regime to ensure protection for all aspects of the conservation resource. In these cases protection from dramatic impacts is vital. Such views are implicit in the European Community Habitats Directive, which states that conservation of a site will be considered favourable only when "the specific structure and functions which are necessary for its long-term maintenance exist and are likely to exist for the foreseeable future".

It is important to emphasise that the remaining areas of natural and semi-natural habitats, and the protected area estate in particular, represent reservoirs or islands of biological diversity. Many of the natural and major semi-natural communities in intensively settled countries are included in some form of protected areas. In Australia, large areas of natural and semi-natural landscape are within multiple use land, on private land, on Aboriginal land or subject to rangeland grazing (see Graetz *et al.* 1988, Hobbs and Hopkins 1990). The importance in all countries of private land managers to the long-term survival of the protected area system cannot be stressed enough.

Karijini National Park, Western Australia. A National Park established in semi-arid country, with a rich flora and fauna. This area, according to some models, will receive enhanced rainfall. Such an outcome may result in a significantly decreased biodiversity, as endemic species are outcompeted by exotic plants and animals, with appropriate native species unable to colonise.

Significant effects are also likely in the marine and coastal environment. The rise (or fall) in air and sea temperatures in any of the currently accepted scenarios (see Pearman 1988) will cause biogeographical changes in marine communities. It has even been suggested, for example, that some ocean currents (e.g. the gyre of the Atlantic) could reverse. In these circumstances, the structure and diversity of communities in European and American marine ecosystems would change drastically – to say nothing of indirect effects on terrestrial communities which would result.

It has been suggested that the major effect of climate change on marine and littoral systems will be the inundation of coastal and estuarine systems, consequent upon a projected sea-level rise. Pirazzoli (1986) has analysed tidal gauge records globally and noted a high degree of consistency of annual sea-level rises. Even allowing for natural variation, such changes will alter tidal heights with ultimate effects on littoral and shallow sublittoral communities.

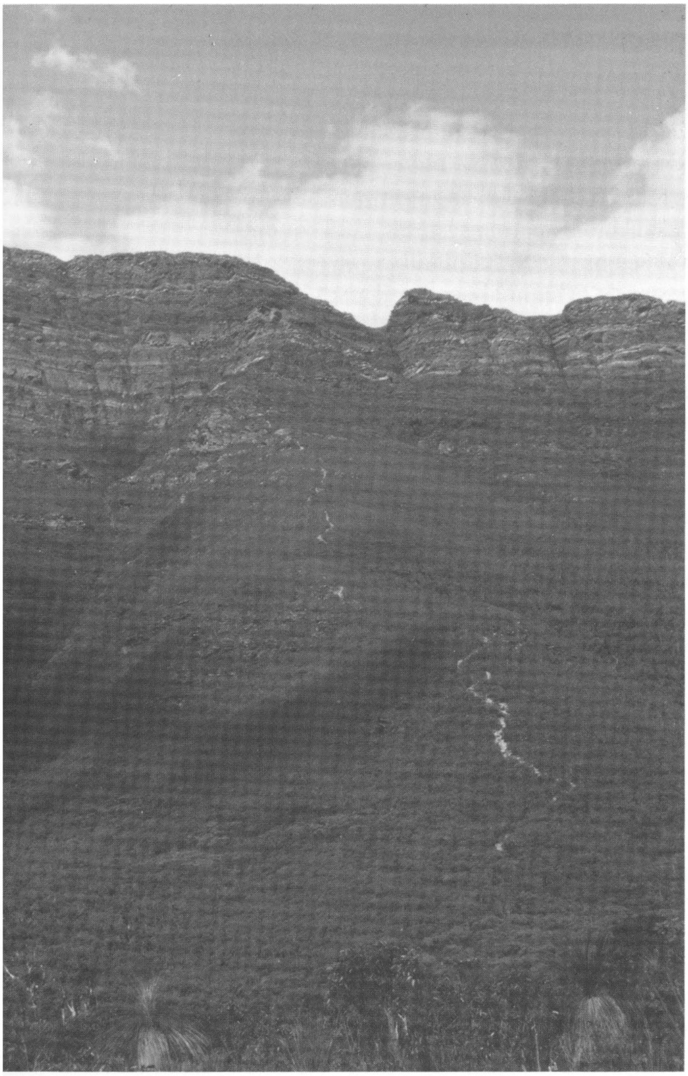
Where there is a limited sediment supply for natural beach replenishment, the sediment shores will not only be gradually immersed, but also become steeper, further reducing the intertidal area and, at some sites where artificial barriers exist (such as the low-lying coasts of eastern England and much of the coastline of the Netherlands), destroying coastal land forms. In tropical regions coral reefs are frequently cited as being in considerable danger from global warming. Yet sedimentation from poor land use, overfishing and other aspects of global change may have a potentially greater impact. Such scenarios are already evident in Australia (Ningaloo Marine Park and the Great Barrier Reef Marine Park) as well as the northern hemisphere reefs (Jackson 1991).

Research and monitoring

Work on the physiological and behavioural responses of plant and animal species under various changes in climatic regimes would help the understanding of likely impacts of climate change. Invertebrates are sensitive indicators of environmental change. Research would help to establish more clearly the parameters affecting the autecology of individual species or species groups, especially those at the edge of their range, so that the influence of climatic change can be recognised in the context of other factors, particularly management. Arnold (1988) and Busby (1988) give details of possible techniques and trends.

BIOCLIM (e.g. Longmore 1986, Busby 1991) is a valuable technique for forecasting species at risk under varying climatic scenarios. BIOCLIM is a system developed in Australia to predict species ranges from a limited set of collected specimens in museums or herbaria, and matching them to bioclimatic envelopes on a latitude/longitude grid. The bioclimatic envelopes are derived from a set of attributes covering both temperature and precipitation, and emphasising attributes which reflect seasonality (e.g. wettest quarter mean temperature, wettest month mean precipitation). The same system can be used to predict ranges given the current climate, by adjusting the parameter values to simulate various postulated changes (Busby 1988). Such modelling, supported by an adequate, user-focused Geographical Information System (GIS), can be very helpful to protected area managers. It is a truism, though, that despite the existence of many such systems, none yet provide the support at the scale and level of sophistication needed by site managers.

Some plant and animal species will give 'early warning' of changes, in much the same way as lichens and bryophytes provide sensitive air pollution indicators. Other 'markers' of changes will include thermophilous (warmth loving) insects (such as some



Lepidoptera and Odonata) which should benefit from global warming and migrate to new areas; species which may be at their ecological limits and thus suffer readily from additional stress caused by climatic and associated environmental change; communities localised at their limits and coastal communities. Global monitoring needs to be more formally established and centred on the protected area network, emphasising sites which are known biogeographic/ecosystem boundaries, for it is across such sites that changes are likely to be first detected.

Undoubtedly a change of climate will favour some terrestrial and marine species presently rare or endangered, provided other environmental features are also favourable to their expansion. Other species may need to be temporarily stored as seeds, propagules, germplasm or ex-situ in botanic and zoological gardens. Coping with increased plant and animal immigration, and the vexed question of sponsoring translocations as a response to climate change, will be one of the most pressing concerns for wildlife agencies. Such organisms that may arrive or change their range in an expansionist way will undoubtedly include a number which pose a threat to native plant and animal species, further emphasising the potential for ecosystem instability.

Bluff Knoll, Stirling Range National Park, Western Australia. This isolated peak has many endemic plant species at the summit, which in extreme winters has occasional snow lie. Any change in climate which stresses the summit flora will have immediate impacts on biodiversity.

Implications for site management

For protected area managers the difficult problem is to assess the risks of loss and the costs of retention of the nature conservation resource. We must attempt to predict the outcomes of climatic change, but cannot then wait until the prediction is proved. A choice must be made between courses of management actions, each of which will have a financial cost as well as a cost and potential benefit to the conserved biota. No firm prescription can be given, as the scenarios are still far from clear.

In Australia and other megadiverse (McNeely *et al.* 1990) countries, effort will be concentrated on endangered species now confined to remnant vegetation in an alien landscape matrix. Wetlands, grasslands and montane ecosystems are likely to be key global ecosystems demanding attention.

Because rapid change may be likely many managers assume nothing can be done and little is known about the effects of current climatic fluctuation. Main (1988) notes that:

> *... [climate change] effects cannot be manipulated easily, if at all. Thus it would be prudent to acknowledge this and make recognition of the cases where natural adjustment or adaptation is to proceed as the first dichotomy in a decision process. However, natural adaptive response can only proceed if it is established that:*
>
> - *The necessary variability and diversity are present in the ecosystem.*
> - *Response can take place even though some species cannot migrate because of habitat fragmentation in nature reserves.*
> - *Where ranges can change readily the adaptive response is unlikely to be negated because the biota will come into conflict with human activities.*
> - *Where the above occur, minimal intervention management is possible.*
>
> *Nevertheless, there will remain a great number of cases where active management is required for maintenance of patch dynamics or the mitigation of the perturbations caused by climatic change, introduced predators, or competitors. The management action taken must then be chosen to give the biota conserved within reservations the best chance of responding dynamically as ancestral populations did to what are assumed to be analogous past climatic changes.*

One *caveat* to that elegant summary by Main must be that past climate changes may have been much less rapid than those forecast – although there still seems dispute on this issue. Huntley (1990) emphasised this in his discussion of post-glacial forest changes. The rate of climate change is certainly going to be a major factor in developing viable strategies. Nevertheless, a knowledge of the response of the biota to past variations in climate, how ecosystems responded to exotic predators, competitors and to disturbances at a range of time intervals is available for some ecosystems.

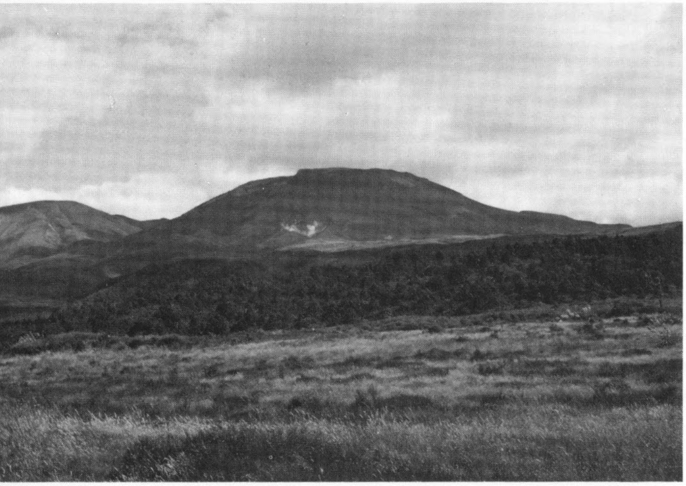
It is possible to express preferences for conservation management goals, for example that a high population number is preferred to a small number or to extinction; that high levels of biodiversity are preferred to depauperate biodiversity and that similar species mixtures are retained in several reserves. To quote Main (1988) again:

> *Furthermore, it is possible to make probabilistic statements based on personal judgement about the likely outcome of any management action as it will affect our preferred management goals. Thus it should be possible to make choices between courses of action so that retention of conservation values is maximised and possible loss minimised.*

A strategy for protected area management under climate change

Until recently the landscape scale has been the poor relation of biodiversity – it has been much overshadowed by the fixation of attention at the species and genetic levels (Bridgewater *et al.* 1996). Risser *et al.* (1984) give a definition of landscape ecology: "Landscape ecology considers the development and dynamics of spatial heterogeneity, spatial and temporal interactions and exchanges across heterogeneous landscapes, influences of spatial heterogeneity on biotic and abiotic processes and management of spatial heterogeneity."

This suggests that the most important features of conservation management strategy for biodiversity into the future will require a fairly sophisticated understanding of conservation biology at the landscape level, as well as an understanding of the dynamics of the species populations (Bridgewater 1993). Integral to the conservation of biodiversity is the connectivity of landscapes. The use of the term landscape



Tongariro National Park, New Zealand, the first World Heritage listed cultural landscape. The Park has several exotic species, including heather (Calluna vulgaris) *and bell heather* (Erica cinerea). *Climatic change will alter the balance between native and exotic species, which will need careful management and development of proactive management strategies.*

follows Forman and Godron (1986): "kilometres-wide area where a cluster of interacting stands or ecosystems is repeated in similar form."

If protected areas are isolated in the landscape or seascape, their purpose is defeated. Also, living associations and their environments change. Corridors provide avenues for dispersal, replacement and formation of new associations in response to and as part of change (see Noss and Harris 1986, Harris and Eisenberg 1989, Bennett 1992, Spellerberg and Gaywood 1993).

Conservation outside reserves not only conserves biodiversity, but also has significant influence on the landscape matrix. Erosion control, catchment security, land reclamation, soil fertility improvement, modifications to air temperature and humidity, control of soil salts, water table levels – all are affected by properly placed and designed corridors, which then need careful management (Forman and Godron 1986). Resilience provided by adequate ex-reserve conservation will alleviate the problems which will spring from global change.

The best examples of natural and semi-natural areas are usually included in a protected area network, but all such habitat is important as a reservoir of biological diversity. It is important that as much as possible of this resource should be conserved, so that the maximum range of opportunities exists for wildlife to adapt to the effects of global warming. The landscape matrix which contains these prime sites for nature conservation will also be subject to changes. New species may be grown in afforestation and new types of agriculture introduced, as existing systems are replaced. Again, specificity is difficult but it is likely that changes will be considerably complex and regionally variable. For example, in Europe good wildlife habitat areas where semi-natural habitat has been substantially modified include hedgerows, ditches and recent plantations. Such areas are widely distributed through rural and suburban areas and represent a substantial part of the total wildlife resource.

Good wildlife habitat often provides linkages between areas of natural and semi-natural vegetation and will be of great value in providing a matrix of corridors and stepping stones for the more mobile species to use in adjusting to climatic change. It may be that some species will move from protected areas to the surrounding good wildlife habitat, and thus conservation strategy must address both the protected areas and the surrounding matrix. However, that matrix has distinctly different landscape infrastructure features. Examples include fencerows, hedgerows, vacant lots, easements, streams and creeks.

Corridors would be part of a general landscape matrix, with benefits for the wildlife resource in facilitating adjustment to climatic change. In Britain the Nature Conservation Strategy for Tyne and Wear (Nature Conservancy Council 1988) is an example of planning which should extend more widely. This study identified, in a highly urbanised area, considerable areas of wildlife potential, and attempted to develop linkages between the areas. The areas themselves, and their linkages, now form an important part of the regional planning process.

Developing these specifics into a general strategy for nature conservation through protected area management in the face of global warming, we should look to the science of landscape ecology. Such a general strategy could well be founded on the 11 principles of landscape ecology enunciated by Forman (1995). I have chosen four of particular relevance in managing for climate change. The principles deal with species, landscape texture, inherent ecosystem change and overall landscape design:

- For subpopulations on separate patches, the local extinction rate decreases with greater habitat quality or patch size, and recolonisation increases with corridors, stepping stones, a suitable matrix habitat, or short inter-patch distance.
- A coarse-grained landscape containing fine-grained areas is optimum to provide for large-patch ecological benefits, multihabitat species including humans, and a breadth of environmental resources and conditions.
- Land is transformed by several spatial processes overlapping in order, including perforation, fragmentation and attrition, which increase habitat loss and isolation, but otherwise cause very different effects on spatial pattern and ecological processes.
- Land containing humans is best arranged ecologically by aggregating land uses, yet maintaining small patches and corridors of nature throughout developed areas, as well as outliers of human activity spatially arranged along major boundaries.

For Australia, this last principle is especially relevant to the recently announced National Reserve System, to be managed by the Australian Nature Conservation Agency. This will expand the protected area system, within a strategic landscape design approach, to ensure that maximum value from each is obtained. Such a strategic approach needs not only good science, but also government support and strong community participation. These four principles are the cornerstone for design strategies we must put in place for whole landscapes – including protected area networks.

Is there a unifying programme that can help draw together these themes, given the range of jurisdictions within which protected area managers must work? What is needed is a bioregional approach, which recognises the role of protected areas, and works within a national protected area system.

A national protected area system should aim to:

- maximise the conservation of biodiversity
- view protected areas as part of the landscape matrix, rather than as islands
- put into place an integrated landscape management framework
- move from a cadastral to a bioregional approach.

The concept of protected areas within a bioregional or integrated landscape management framework is not new. The biosphere reserve concept, formulated to wed conservation and sustainable development, has been developed and championed under the UNESCO Man and the Biosphere Program (MAB). Following a major conference in Seville last year new direction and focus are evident (UNESCO 1996). Biosphere Reserves are a special kind of conservation area – traditionally a nested series of zones with differing management intensities (core area, buffer zone and transition area), designed to include people within an overall conservation framework. They may comprise any mix of terrestrial and/or marine elements. The combination of the Biosphere Reserve concept with the protected area categorisation of IUCN (CNPPA/WCMC 1994) provides a new and powerful tool for managing protected areas within the bioregional approach (Bridgewater and Walton 1996). An important consideration in the present context is that it is the conceptual basis behind Biosphere Reserves which is important, not necessarily the proclamation.

In conclusion, we need to act promptly to assess our stock of biological/ ecological information to respond to what is clearly a crisis which will impinge on an existing crisis of poor land use. As Recher and Lim (1990) have said so clearly for Australia, "We need to act now. We do not have time, or the money, for many of the traditional survey and research techniques. *We need to improve our management of ecosystems outside the reserve system*. We need to urgently consider fauna more adequately than in the past. We need to utilise new technologies which will permit cost effective and accurate data sets to be examined simultaneously" (emphasis mine).

I cannot but agree. The task for the protected area manager will be not only to manage carefully the protected resources, but also to ensure the surrounding landscape is managed appropriately. In this process new working alliances must be forged, and old enmities forgotten. If nature conservation is to achieve its twin aims of maintaining biodiversity and improving ecological infrastructure we must act now to ensure that climate change does not accelerate the extinction process we have already set in train by poor land use allocation and management.

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Potential impacts of predicted climate change on mangroves: implications for marine parks

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Mangrove forests occur on low energy, sedimentary shorelines of the tropics, providing habitats for a specialised group of flora and fauna. Mangrove trees have physiological and morphological adaptations to the environmental stresses of their intertidal habitat, of high salinity, low oxygen, poor nutrient availability and substrate mobility. The main impacts of climate change that can be expected to affect mangrove ecosystems are sea-level rise (primarily through altered sediment budgets), changes in precipitation, temperature rise, and the direct effects of higher levels of atmospheric carbon dioxide.

It is indicated from past analogues that the close relationship between mangrove swamps and sea-level renders them particularly vulnerable to disruption by future sea-level rise. Those of low, oceanic islands are likely to be most sensitive, due to low sedimentation rates. Sea-level rise may cause erosion of sediments at the seaward edge, and increased inundation and salinity may cause stress symptoms in mangrove species, such as reduced growth, reduced litter production and reduced resistance to pests and storms.

Rise in temperature and the direct effects of increased CO_2 levels are likely to increase mangrove productivity, change phenological patterns, and expand the ranges of mangroves into higher latitudes.

Certain identification of climate change and sea-level rise effects on mangroves requires long-term monitoring of biological and physical parameters at a network of locations using standard techniques. This would provide environmental managers with ecological data to allow for informed management of mangrove ecosystems.

WHILE THE consequences of greenhouse-induced climate change are probably not as dramatic as feared in the late 1980s, climate change and sea-level rise remains an issue for coastal ecosystems such as mangroves.

Climate changes that can be expected to occur are detailed in the findings of the WMO/UNEP Intergovernmental Panel on Climate Change (IPCC 1996). In summary, CO_2 levels have risen about 30% since pre-industrial levels, and this is believed to have caused an increase in mean equilibrium temperature of the earth's surface since 1860 of 0.3–0.6°C. As emissions continue, a mean equilibrium surface temperature increase of 1.0–3.5°C (mid range 2.0°C) is projected by 2100. In the last 100 years there has been a rise of 10–25 cm in eustatic sea-level; the IPCC working group predicted a future sea-level rise of 15–95 cm by 2100 (mid range 50 cm). This would imply mean rates of rise of around 5 cm/decade over the next century.

The term 'mangrove' is used to describe a taxonomically diverse group of tree species that grow in the intertidal zone of sheltered shores in the tropics. The extent of their cover has been estimated to be 14,197,635 ha (Lacerda *et al.* 1993). Adaptations developed for their saline wetland environment such as aerial roots, halophytic strategies and vivipary distinguish mangrove trees as a specialised minority within their respective families. There are 34 true mangrove species in nine families, each with a limited geographical distribution around two centres of diversity, in Indo-Malaya and Central America (Tomlinson 1986).

Mangrove species show different preferences for particular habitats. These are defined by elevation as this generally controls salinity, groundwater availability, frequency of inundation and strength of wave action. This results in the zonation of species according to the elevation of the substrate, within the intertidal ranges of mangroves. Within their general habitat of sheltered sedimentary coastlines, mangroves occupy a variety of physiographic settings including deltas, estuaries and coastal lagoons (Thom 1982), with heterogeneous conditions of river discharge, tidal and wave energy regimes and coastal morphology. A separate case is that of mangroves occupying low islands; with no sources of sediment from fluvial or along-shore sources, they accumulate autochthonous sediment on top of reef flats (Woodroffe 1987).

The importance of mangrove ecosystems is now well understood. They act as sediment traps, thus maintaining the clarity of coastal waters. This process promotes vertical accretion and seaward progradation of the mangrove margin, and thereby provides a natural breakwater which protects coastlines from erosion. Mangrove ecosystems also offer a natural resource base for silviculture and a large range of economic products, provide habitats for rare fauna, and act as nurseries for commercially valuable fish and crustacean species. These uses are described in detail by Hamilton and Snedaker (1984) and Tomlinson (1986).

The main aspects of climate change that can be expected to have an impact on mangrove ecosystems are sea-level rise, temperature rise, changes in precipitation and changes in frequency or intensity of tropical storms, as well as changes in productivity caused by higher levels of atmospheric carbon dioxide. These changes will occur in combination with each other as well as with the stresses on mangrove communities consequent from sharing the tropical coastal zone with the majority of the world's human population. Mangroves are today one of the most threatened of the world's natural communities, as they share lowland coastal areas with large, high density human populations (IUCN 1989).

The consequences of climate change impacts on mangrove ecosystems, the identification of the processes that will respond to climate change, the direction of community response, the maximum rates of change that can be withstood, and implications for management and planning in mangrove national parks and protected areas are addressed below.

Sea-level rise

Growing in the upper half of the tidal range, their close relationship with sea-level position renders mangrove swamps particularly vulnerable to disruption by sea-level rise. Furthermore, mangrove species have different preferences of micro-elevation, which determines salinity and frequency of inundation, resulting in species zones. Substrate elevation can be increased under mangroves, by the accretion of peat or mud. If the sedimentation rate keeps pace with rising sea-level, then the salinity and frequency of inundation preferences of mangrove species zones will remain largely unaffected. If the rate of sea-level rise exceeds the rate of sedimentation, then mangrove species zones will migrate inland to their preferred elevation, and the seaward margin will be subject to erosion. With rising sea-level,

Roots of the mangrove Rhizophora mangle. Photo: WWF/Nancy Sefton.

sediment from the upper part of the tidal range is eroded and deposited sub-tidally in the same manner as beach erosion (Ellison 1993, Bird 1993).

The sedimentation rate is a factor of the physiographic location of the mangrove swamp. Drawing examples from the Great Barrier Reef Marine Park, where a variety of mangrove physiographic locations exist, low island mangroves on reef cays such as Low Isles and Pipon receive little externally derived sediment, accreting primarily by their own vegetative production. High island mangroves such as Magnetic Island and Hinchinbrook Island receive terrigenous sediment from soil erosion and smaller catchment rivers, but not to the same extent as mainland deltaic mangroves such as the Daintree and Murray rivers, which receive sediment from a larger catchment.

The rates of sea-level rise which mangrove systems can accommodate can be obtained from stratigraphic evidence of mangrove system response to sea-level changes of the last 7,000 years (Ellison and Stoddart 1991). On low islands mangrove ecosystems could keep up with sea-level rise of up to 11 cm/100 years. For example, in Bermuda, Ellison (1993) found an accretion rate of 8.5–10.6 cm per 100 years over the last 3,000 years. In Tongatapu, Ellison (1989) found an accretion rate of 7.7 cm per 100 years through a mid-Holocene mangrove peat. Each of these developed during conditions of slowly rising sea-level, of less than 12 cm per 100 years. Tide gauge records show relative sea-level rise in Bermuda to have occurred this century at rates equivalent to future globally predicted rates, and mangroves there have died back. Ellison (1993) identified elevation relative to the tidal spectrum as the key indicator of problems related to rising sea-level, such as substrate erosion and inundation stress.

On high islands such as Viti Levu and Lakeba, Fiji, and Kosrae, Caroline Islands, sediment supply has been accelerated by anthropogenically enhanced rates of soil erosion inland. This gives more rapid sediment accumulation rates of up to 19 cm per 100 years. These cases indicate that mangroves of high islands and continental coasts can be dominated by input of terrestrial sediment such that the effects of sea-level rise are lessened. Because of these externally derived sediments, mangrove substrates are accreting at a faster rate than the peats of low limestone islands. Stratigraphy indicates that few large mangrove systems existed in the earlier Holocene, when rates of sea-level rise were rapid, from 25 to 100 cm per 100 years.

If sea-level rise exceeds the rate of sedimentation, then the following responses can be expected.

Erosion

Three types of erosion can be expected:

- Cliff erosion of the sediment at the seaward edge, undercutting mangrove roots and leading to windthrows. Loss of the seaward zone leads to truncated zonation and narrower fringes. Management responses could be stabilisation and protection from further erosion, by use of biodegradable matting placed on the sediment surface. Once sediment built up against the eroding edge is stabilised, it can be replanted with mangrove propagules.

- Sheet erosion across the swamp surface of leaf litter and sediment. This causes migration of pioneer/seaward mangroves into more landward zones. Loss of leaf litter impacts the faunal foodchain, and introduces a positive feedback as litter cannot accumulate to form peat. Park managers should monitor sedimentation rates within the mangrove ecosystem, by long-term observation of calibrated stakes, and litter fall should be quantified (English *et al.* 1994). Leaf litter retention on the substrate surface can be monitored (CARICOMP 1992), and the percentage lost to sea evaluated (Robertson *et al.* 1988).
- Tidal creek bank erosion. This causes slumping of banks and loss of trees owing to more active tidal currents, particularly rapid ebb currents (Wolanski and Chappell in press). Management responses should enforce prohibition of boats with motor propellers and jet skis from mangrove areas, as wake waves will enhance creek bank erosion.

Sea-level trends can be identified from long-term tide gauge records, such as the UNESCO (Intergovernmental Oceanographic Commission) Global Sea-level Observing System (GLOSS). The establishment of such tide gauges in areas with mangroves should be supported.

For identification of problems related to rising sea-level, the mangrove substrate elevation in different zones should be surveyed with respect to tide gauge datum. Such elevation surveys will indicate the preferred elevations of different mangrove species, which will be of use should replanting become necessary with sea-level rise. They may also identify areas low in the tidal spectrum which may already be experiencing problems with erosion. Over time, elevation surveys combined with the monitoring of sedimentation rates should indicate problem areas. A permanent benchmark should be established close to each mangrove area, to which different surveys can be related for comparison.

Inundation stress

Impoundment of mangroves for mosquito control provides an analogy to the effects of increased inundation. Harrington and Harrington (1982) recorded extensive death of *Avicennia germinans* (black mangrove) and *Rhizophora mangle* (red mangrove) at India River, East Florida, following four months of 30–45 cm depth of flooding of an impoundment. Naidoo (1983) found that prolonged flooding resulted in reduced rates of photosynthesis in *Bruguiera gymnorrhiza* (large-leafed mangrove), and Lahmann (1988) found that rates of litter fall reduced during flooded months of an impounded *Rhizophora mangle* forest in Florida. When lenticels of aerial roots become inundated, oxygen concentrations in the plant fall dramatically (Scholander *et al.* 1955). If inundation is sustained, anoxic conditions and mortalities follow. This is thought to have been the cause of widespread mortality of *Avicennia germinans* stands in Puerto Rico recorded by Jimenez *et al.* (1985), following permanent flooding as a consequence of adjacent dredging.

It is possible that increased inundation with sea-level rise may cause stress in this manner, resulting in reduced net primary production. Park managers can expect the consequences to be reduced growth, reduced litter fall, and reduced production of propagules. Variable tolerances of species to inundation would promote landward migration of species zones by death of older trees and successful seedling establishment in zones of higher elevation. Changes over time in community composition can be monitored by vegetation surveys, described in the section below on climate warming.

Increased salinity

Increase in salinity in mangroves leading to salt stress can result from a number of factors: sea-level rise, groundwater depletion owing to reduced freshwater flux, groundwater extraction, and reduced rainfall. Two major physiological adaptations enable mangrove survival in saline ocean water (Scholander *et al.* 1962), salt exclusion in species such as *Rhizophora* and *Laguncularia* (white mangrove), and salt excretion in species such as *Avicennia* and *Aegiceras*. Salt excluders not only operate ultrafiltration, but also cease or diminish transpiration and photosynthesis when exposed to saline water. Salt secretors can continue photosynthesis utilising ocean water in transpiration, owing to salt glands in the leaves.

Red mangrove seedlings, Australia. Photo: WWF/Ben Cropp.

A number of experiments have shown reduced seedling survival and growth, and decreased photosynthetic capacity with increase of salinity (Ball and Farquhar 1984).

The shallow water table of the Everglades National Park is susceptible to saline intrusion from sea-level rise and groundwater extraction, owing to low topography and porous rock. Alexander and Crook (1974) used evidence of pine stumps in the salt water mangrove areas of Key Largo to show the landward encroachment of mangroves into grasslands and cypress swamps. Loss of freshwater wetlands with saline intrusion is also documented in the Florida Keys by Ross *et al.* (1994), using tide gauge records to attribute the cause to relative sea-level rise.

In the Northern Territory of Australia, Woodroffe and Mulrennan (1993) documented the recent dramatic changes to the Lower Mary River floodplain, adjacent to the Kakadu National Park, with saltwater intrusion and upstream expansion of the tidal creek network. This has caused death of freshwater wetland communities with the loss of 60 km^2 of Melaleuca forest, and upstream invasion of mangroves. There are a number of possible reasons for these events, including relative sea-level rise (Woodroffe 1995). Similar, though less spectacular, extension of creeks has occurred on the Alligator Rivers system within the Kakadu National Park (Woodroffe 1995). Clark and Guppy (1988) showed that sea-level rise of 0.5-1.0 m would destroy the Alligator Rivers freshwater wetlands, and return it to the large mangrove swamp that existed during the mid-Holocene.

Park managers can expect salinity stress in some mangrove species as a result of rising sea-level, indicated by reduced growth, reduced litter production and death. Successful seedling establishment will occur further landward, resulting in the retreat of species zones and the invasion of freshwater wetlands by mangroves. Limitation of groundwater extraction in the catchment, or promotion of sedimentation within the mangroves could mitigate this impact.

Climate warming

Mangrove park managers should expect climate warming to have a beneficial effect on mangrove ecosystems, with increased productivity, and expansion of ranges of species.

Arboraceous mangrove ecosystems border herbaceous salt marsh ecosystems in subtropical latitudes, at the 16=B°C isotherm for air temperature of the coldest month, at the margins of incidence of ground frost, and where water temperatures never exceed 24°C. At these limits species of *Avicennia* occur, *Avicennia marina* (grey mangrove) reaching the highest latitude at Victoria in south-east Australia (38°S), also reaching 33°S in south-west Australia, and 37°S in North Island, New Zealand. In the northern hemisphere, the highest latitude for mangroves is Bermuda at 32°N where *Rhizophora mangle* and *Avicennia germinans* occur. In Florida mangroves reach nearly 30°N, and on the African Red Sea Coast *Avicennia marina* reaches 27°N. The number of mangrove species increases as one moves towards the equator. Higher latitude mangroves are therefore of low diversity, stunted owing to low productivity, and with seasonal phenology.

With climate warming these higher latitude marginal mangroves can be expected to increase in diversity. Warming will also cause expansion of the ranges of other mangrove species into mangrove margins only occupied by *Avicennia* species, and expansion of the ranges of mangroves into salt marsh environments. The heterogeneity of regional sea surface temperature at the limits of mangrove species ranges would indicate regional differences in mangrove response. Variable gradients of sea surface isotherms mean that, for example, the expansion of range in south-east USA will be limited relative to that in south-east Australia or south-east Africa.

Combined with higher atmospheric CO_2 levels (discussed below), climate warming can be expected to increase mangrove productivity, shown by increased growth and litter production at all locations.

Mangroves have been shown to experience thermal stress in areas of waste heat pollution (Banus 1983), where water temperatures in excess of 35°C affected roots of *Rhizophora mangle*, with many rotted off at high tide level, and others became more slender and more numerous. Diversity of invertebrate root communities was much reduced, and seedling establishment prevented over 38°C. In temperature stressed conditions *Rhizophora mangle* produces more numerous but smaller leaves (Lugo and Snedaker 1974). With climate warming, such temperatures may be reached in drier localities where humidity does not moderate temperatures, but widespread thermal stress of mangroves cannot be expected from the climate warming predicted.

Monitoring to identify change in mangrove productivity and diversity should include detailed mapping of the mangrove community, to show location of different mangrove zones, and of seaward and landward fringes of the mangrove area. Older records from the mangrove area should be compiled into a database, and large scale colour air photographs taken. Information on the history of sites should be compiled from climate records, previous studies and records of logging or other activities, which should enable climate change impacts to be distinguished from other changes already underway. There should also be five-yearly measurements of community structure, including tree size, tree density, tree species, and diversity and density of macrofauna. Productivity changes can be identified by the measurement of tree growth through the monitoring of increase in diameter and changes in leaf area index.

Increased CO_2

As well as its climatic effects, increased CO_2 directly affects plant growth and development. Mangroves have a C3 pathway of carbon fixation in photosynthesis (Clough *et al.* 1982), where metabolic responses to increased atmospheric CO_2 have been shown to be increased productivity and more efficient water use due to reduced stomatal conductance (Warrick *et al.* 1987). Hence an increase in atmospheric CO_2 can be expected to improve mangrove tree growth and litter production, which can be identified by long-term monitoring as indicated above under climate warming.

Precipitation changes

Most of the world's mangroves are found in warm humid regions, becoming less extensive on drier coastlines. In equatorial and tropical summer rainfall regions mangroves are tall, dense and floristically diverse. In subtropical dry regions mangroves are low, scattered and sporadic. Mangrove diversity is a function of rainfall patterns, with greatest abundance of species in areas of higher rainfall, owing to the benefits from fluvial runoff of sedimentation and nutrient supply.

This is clearly shown in Australia, where at 20°S there are four species on the drier west coast and 20 species on the wetter east coast (Tomlinson 1986). On the Queensland coast, the tallest mangrove forests, with complete cover and five distinct zones, occur where mean annual rainfall is over 1,500 mm and distributed through the year. Where rainfall is less than 1,500 mm and seasonal, mangroves are shorter, with gaps; halophytic herbs and naked salt flats replace landward zones, and seaward zones are narrower (Macnae 1966).

The reasons for these patterns relate to salt stress. Under humid conditions, mangrove soils are almost continuously leached by heavy rains, and fresh water is available from river discharge and groundwater outflow, which provides nutrients. Under arid conditions, evaporation from the intertidal mangroves at low tide leads to high concentrations of salt, in some cases resulting in unvegetated hypersaline flats around high tide level.

Snedaker (1995) has postulated that changes in rainfall patterns will have a significant effect on mangrove ecosystems. Increased rainfall should result in reduced salinity and exposure to sulphate, and an increase in the delivery of terrigenous nutrients. Mangrove park managers can expect decreased rainfall and increased evaporation to reduce the extent of mangrove areas, particularly with loss of the landward zone to unvegetated hypersaline flats. The number of mangrove zones and the diversity of each zone can be expected to decrease, and growth rates can be expected to decline. In conditions of increased rainfall the extent of mangrove areas can be expected to increase, with colonisation of previously unvegetated areas of the landward fringe. The diversity of mangrove zones and growth rates should also increase.

Monitoring to indicate changes in salinity should take measurements of soil salinity profiles to a depth of 2 metres, and predawn water potential, both of which assess the soil salinity experienced by plants. This is of more ecological significance than the salinity of creek water. Changes in community structure and productivity can be identified by the same techniques as described in monitoring for impacts of climate warming.

Storms

Modelling studies suggest an increase in the frequency and intensity of tropical hurricanes (Emanuel 1987), as a result of increasing sea-surface temperatures. The effects of storms on mangroves can be roughly classified as minor (some defoliation), severe (partial destruction of the mangrove ecosystem) and destructive (almost all mangrove trees killed). Studies have been largely based on observation.

Craighead (1971) reviewed the devastating effects of hurricanes on the Florida mangroves in 1935, 1960 and 1965, when large areas were destroyed. Severe hurricanes have been affecting Florida throughout the Holocene (Davis *et al.* 1989), and the Everglades could have become a hurricane dependant ecosystem, relying on storms for the maintenance of diversity and fresh water input by rainfall and runoff (Vogl 1980). Venkatesan (1966) described the effects of the November 1952 cyclone on the mangroves of the Cauvery in south India, where a surge caused the Muthupet and Chattram forests to be submerged under 2 m of water for a fortnight. As a result of this, *Avicennia* was killed over large areas.

From combinations of the factors of sea-level rise and changes in ecophysiology and community composition with climate change, mangroves may be prone to damage in lesser magnitude storms than has been shown previously. Mangrove park managers should assess areas with respect to storm vulnerability. It may be possible to build up natural barriers to heavy wave action. In Hungry Bay, Bermuda, a mangrove

Buttress-rooted mangroves in Daintree National Park, North Queensland, Australia. Photo: WWF/Frédy Merçay.

nature reserve is increasingly affected by storm surges owing to the natural erosion of a protective peninsula.

In the event of major storm destruction, mangrove park managers should have rehabilitation plans, for the clearance of debris and replanting with seedlings from unaffected areas.

Conclusion

Mangrove ecosystems are expected to show a sensitive response to predicted climate change and sea-level rise. The nature of this response is complex, and subject to factors of environmental setting. Sea-level position is central to the functional ecology of a mangrove swamp, and a rise in sea-level will perturb every aspect of the ecosystem. This combined with effects of climate change, and stresses from storms and human disturbances, will cause mangroves to experience disruption and area losses in the next few decades.

Certain identification of climate change and sea-level rise effects on mangroves requires long-term monitoring of biological and physical parameters at a network of locations using standard techniques. This would allow comparison of data in order to distinguish a regional trend in change from that resulting from local effects. Though aimed at distinguishing climate change effects, the monitoring system would therefore also show local effects and disturbances, which would provide environmental managers with ecological data to allow for informed management of mangrove ecosystems.

Several expert groups have identified the need for a global monitoring system of mangrove response to climate change (IOC 1991, UNEP 1994), but none to date has been implemented. This is the intention of the UNEP-IOC-WMO-IUCN Long-Term Global Monitoring System of Coastal and Near Shore Phenomena Related to Climate Change (IOC 1991), to be established as part of the Global Ocean Observing System. In the South Pacific region, SPREP recently developed a Regional Wetland Action Plan, in which actions 3.3.1 and 3.3.5 are the development of a regional monitoring system for mangrove ecosystem health (Idechong *et al.* 1995). Mangrove park managers should encourage such regional monitoring networks, as this will assist informed management with respect to climate change effects on mangroves.

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Impacts of climate change on selected ecosystems in Europe

DAVID STONE

Protected area managers depend on reliable, up-to-date information in order to plan future development and management activities. To date, the selection of many protected areas has been based on their biological richness or because they are in a particularly scenic landscape. To address the longer term needs of protected areas and society, protected area managers must now take a closer look at existing and planned protected areas with a view to determining how these might cope with future events, one of the most daunting of which is perhaps the predicted change in the Earth's climate. This review examines some of the main issues concerning climate change impacts on priority ecosystems in Europe by drawing on existing studies.

PAST CLIMATIC EVENTS have had a major impact on moulding the shape of present day biotic communities. Current changes in the world's climate do, however, appear different to previous episodes in that these changes are happening at an unprecedented rate. The average global temperature has, for example, increased by about 0.75°C since 1850 and, if current climate models are correct, future warming will proceed at an even faster rate (de Groot and Ketner 1994). As a result there are many uncertainties as to how different species and even entire wildlife communities will react to changes in climate.

A doubling of the global CO_2 concentration would, according to global circulation models, result in annual temperature increases between 1.5 and 4.5°C (Schlesinger 1986, Bolin *et al.* 1986). For Europe, Jäger (1987) has estimated that the greatest changes during the summer months will take place in the Mediterranean region (with a possible range of from +2 to +16°C). During the winter period, both the Mediterranean and northern Europe would be most affected, with a possible temperature fluctuations from -0.5 to 4°C and +5° to +10°C, respectively.

Climate change will affect ecosystems by affecting their components – individual organisms, or species, as well as abiotic features (Sprengers *et al.* 1994). Each species will react in a specific manner to any such changes. While many of these changes may be quite subtle, because of the close linkages between different species in a given ecosystem, it is to be expected that any such changes will become obvious through the reactions of, or possible knock-on effects on, other species as well.

While current models provide support that changes in temperature are likely to take place, this will not be the only factor that species and ecosystems will have to deal with. According to Sprengers *et al.* (1984), other processes that are of particular importance, although to different extents, are:

- annual mean temperature
- mean temperature during the growing season
- inter-annual variances

- duration of growing season
- day/night temperature range
- extreme seasonal temperatures
- seasonal and annual precipitation rates
- the relationship between temperature and precipitation.

Many studies suggest that the rate of climate change and the rate of increase in atmospheric concentration of greenhouse gases will be the major factor in determining the type and degree of impacts, with a variety of responses expected for different regions and for different communities within ecosystems (IPCC 1992). Current climatic projections suggest that the rate of change is likely to be faster than the ability of some species to be able to respond adequately. In addition, the response of some species, groups of species or ecosystems may be sudden and dramatic – a feature that would contribute further to ecosystem degradation and destabilisation. Projected changes in temperature and precipitation suggest that climatic zones could shift several hundred kilometres towards the polar regions during the next 50 years. Few plants and animals would be able to keep pace with this rate and would lag behind these climatic shifts. Many would therefore find themselves in a different climatic regime, which may be more or less favourable to their growth needs. As a result, certain species may thrive, while others may become extinct.

Threatened ecosystems in Europe?

While predictions at the global and regional level have attempted to define some of the possible impacts of climate change on various ecosystems, relatively little attention has been given to determining whether there is any practical evidence that might support such predictions. The following is a first attempt to determine what experience has already been gained for selected priority ecosystems in Europe, with a view to providing future guidelines and indicators to protected area managers and others charged with the development and management of protected areas.

Forests and other vegetation

If the climate continues to get warmer there is likely to be a major alteration in the pattern of forest cover in Europe. The physical location of forests as well as the actual species composition and growth patterns will be determined by an entirely new set of ecological limitations. It is thought that major forest-type zones and species ranges could shift significantly as a result of climate change.

Overall, the greatest changes in Europe's forests are expected to take place at the northern limits of tree growth. The results of several studies show that both high latitude and low latitude boundaries of temperate and northern forests may shift hundreds of kilometres towards the North Pole (IPCC 1992). This may place forests well outside the boundaries of existing protected areas. Both coniferous and broad-leaved thermophilic tree species will find favourable environments much further north than their current limits. In the northern parts of the former USSR, the boundary of the zone is expected to move northward to 40–50 degrees of latitude (a shift of 500–600 km). The tundra zone is expected to disappear from the north of Eurasia (IPCC 1992).

At the same time, expected changes in precipitation will allow certain species to extend their boundaries south towards the equator. Certain broad-leaved species will expand their ranges and these ecosystems will become more maritime in terms of species composition (IPCC 1992). The forest steppe sub-zone of the European former USSR will change, while in southern portions of western Siberia, the forest steppe boundary could move by as much as 200 km.

Pine forest and reindeer moss in Jotunheimen National Park, Norway. Photo: Klein-Hubert/WWF/BIOS.

In addition, it is likely that some forests or woodlands growing on poor, dry soils may become unhealthy or die following a succession of dry summers, despite longer growing seasons and increased CO_2 fertilisation. Were this to happen, they may be replaced by other invasive species. It is also possible that when such land is cleared of forest it may be usurped for other purposes, such as agriculture.

Europe's boreal forests are most vulnerable to further increases in atmospheric temperature. These forests consist of stands of mainly even-aged trees, the growth of which is often temperature limited (IPCC 1992). Changes in evapotranspiration, higher temperatures, greater fire risks, increased pest and disease incidence, and more frequent storms are likely to take place (Dudley 1995). Predictions vary considerably, but one model suggests that as much as 40% of current forest cover could be lost. Even a 1°C rise in average temperature could result in the loss of 25% of the world's boreal forests. Were this to take place, major dieback of forests could be expected at the southern limits of the northern European forests. The transition zone between temperate and boreal forests would probably experience the largest movement as temperate forests move further north (IPCC 1995).

Against such predicted losses, however, climatic models also forecast an increased productivity from such forests as a result of increased growth rates and additional opportunities that arise for growing new species of trees. The economic and ecological consequences of either scenario need to be carefully considered by park managers: greater timber production, for example, may not favour local biodiversity but could receive widespread support for economic reasons.

The biotic community of the broad Mediterranean region is unlikely to be directly affected by a warmer climate, since plant species are already well adapted to periodic water shortages. In the central European and sub-Atlantic biotic communities, however, a degeneration in the extent of native species is forecast with the invasion of heliophytic and xerophytic species such as *Quercus ilex* and *Q. pubescens* (Ministry of Environment 1995). Thus, in Italy for example, the following communities are considered to be especially vulnerable to climate change: high mountain areas; the alpine zone; forests in lowlying plains with *Quercus robur* and *Carpinus betulus*; riparian and riverine basin forests with *Alnus glutinosa* and *Fraxinus oxycarpa*; wetland and marsh vegetation; and moorland vegetation. Species such as *Silene acaulis* of the Alpine tundra and *Kobresia myosuroides* in the Central Appenines, which are characteristic of areas with very low winter temperatures, are therefore probably threatened by invasive species adapted to higher temperatures.

Weakened forests

Another factor which park managers should consider is that many European forests have already been impacted by atmospheric pollution. Such ecosystems are less able to respond to changes in climate, particularly extreme weather conditions such as drought or high winds. Plants are also more susceptible to insect attack. Oak wilt disease in the former USSR, for example, appears to be dependent on the decreased ability of trees to resist leaf-eating insects during periods of drought (Israel *et al.* 1983).

In addition to the adverse effects on tree species, the dynamics and nitrogen balance of meadows and pastures have been affected by air pollution with increases in some species (*Polygonum bisorta*, *Calamagrostis villosa*, *Avenella flexuosa*, *Silene vulgaris*) at the expense of others (*Carex beigelowii*, *Selaginalla selaginoides*, *Paris quadrifolia*). Lichens (*Usnea* and *Cornicularia* spp.) and fungi have decreased significantly. Peat bog vegetation is also threatened by atmospheric pollutants.

Wetlands and freshwater ecosystems

In addition to their considerable social and economic functions, many wetlands play an important role for many wildlife species, especially waterfowl. The wetlands of Coto Doñana, Spain, for example, are of international importance on account of the large number of waterfowl they support. This region has already experienced a number of problems as a result of a lowering of the water table to meet agricultural, domestic and industrial needs. Desiccation of inland wetland sites has already led to the loss of at least 100 plant species from the area in the past 80 years (van Huis and Ketner 1987). Further losses should be anticipated under the predicted climate change scenario.

Wetland in Coto Doñana National Park, Spain. Photo: WWF/Sebastian Ruiz.

Among freshwater communities, species such as fish, amphibians and reptiles are especially vulnerable to changes in water level and quality. Regier and Meisner (1990) have identified three main links between possible climate changes and the loss of freshwater fishes. First, species ranges are likely to shift towards higher latitudes and sites that once supported species assemblages typical of cold waters are likely to be replaced by warm water-loving species. Biota from warmer parts of a river downstream are also expected to penetrate further upriver, leading to a displacement or loss of species towards headwaters.

Lower run-off and reduced river flows should also be expected as a result of higher rates of evaporation and where climate change results in lower precipitation levels. This would provide less habitat for aquatic organisms, lead to reduced levels of groundwater recharge, and concentrate pollutants. For lacustrine species, particularly those of shallow water bodies, the lowering of available habitat for certain species may cause those species to shift their niches to, for example, deeper parts of the lake (Trippel *et al.* 1991).

Species extinctions are unlikely to occur as long as routes remain available for species to disperse to higher altitudes or cooler latitudes. Threatened species would most likely include poor dispersers and/or those which are already living on the margins of their ecological limits. The effects of disturbances and disruptions to natural stream flows, such as those caused by dams and canals, should also be taken into consideration as barriers to dispersal.

Traditional breeding grounds for many species, e.g. salmonids, are located on shallow gravel beds, many of which might become exposed as a result of reduced river flow. Temperature changes may also, of course, affect the timing of emergence, availability and distribution of many aquatic crustaceans and insect larvae upon which the majority of freshwater fish species depend.

Marshes, fens, peatlands and similar bodies of standing water which support complex vegetation communities are likely to experience major changes as a result of any climate change involving higher temperatures and greater evaporation.

Marine and coastal ecosystems

Marine and coastal ecosystems face a wide range of potential consequences from any change in climate. Increasing sea-levels, altered sea water temperatures and mineral concentrations, and changes in the levels of primary productivity are among the major concerns that have been identified.

In Europe, one of the most significant effects would be a rise in sea-level and more widespread flooding. Detailed analyses have been carried in out in many countries, the majority being based on climate models. However, few data were found to support past or potential changes in ecosystem shifts. In the United Kingdom, it has been determined that an increase in sea-level would result in the following:

- An increase frequency of extremely high sea-levels and coastal flooding. Flooding, in particular, would have serious economic and social consequences on local and regional infrastructure.
- A reduced efficiency of groundwater and sewage drainage in low-lying areas.
- Increased salination of groundwater over a long period, with consequent effects on agriculture and water supply.
- Inundation of significant areas of wetlands and salt marshes with the concomitant inshore migration of coastal ecosystems.

Existing and planned protected areas in the coastal zone are therefore likely to be impacted. Coastal dune systems are also at risk from inundation and risk disruption or replacement further inland. In the United Kingdom, 82% of remaining salt marshes are protected but much of this is in narrow strips immediately adjoining agricultural lands (Roberts 1990). In the event of any rise of sea-level, salt marsh plants would not be able to immediately move on to adjoining lands although, in time, these lands may become too saline to support agriculture. The flooding of coastal areas by sea water could lead to the loss of freshwater and brackish marshes, which are important for fisheries, and could also reduce the available area of arable land.

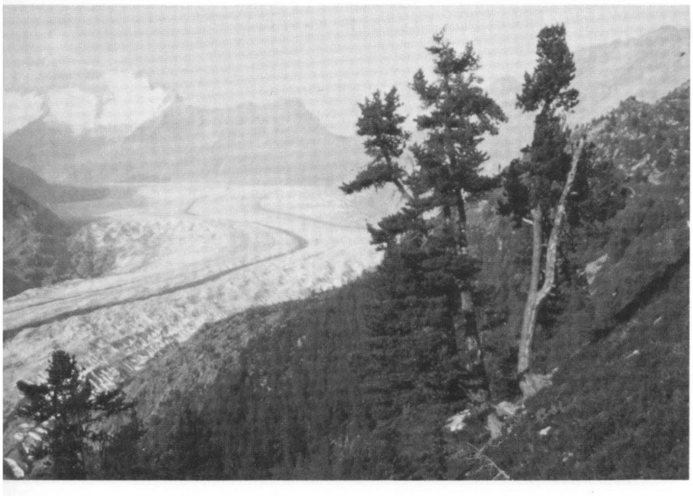
Coastal erosion is also likely to increase in many cases: many of Europe's coastlines are heavily populated, with associated urban developments and amenities. Coastal erosion is already significant at many of these: in Italy for example, just under 50% of the coastline is affected (data from the Department of Earth Sciences, University of Rome), largely as a result of land development (which causes high levels of surface water run-off) and reduced silt deposition along the coast because of canalisation. Finally, in areas subject to subsidence, the relative rise in sea-levels could be much higher, with more serious consequences than elsewhere on the coast. The lower parts of the alluvial plain from Romagna to Friuli would be particularly susceptible to any such modifications.

Concern has already been expressed over potential climate change impacts on the Mediterranean Sea. Water loss due to evaporation is already greater than the gain of freshwater provided by direct precipitation and river discharge. As a result, if the Sea received no additional water sources, the mean sea-level would be lowered by about one metre every year (see Zavatarelli 1988). As it stands, however, the water volume is maintained by inflowing water from the Atlantic Ocean. Climatic changes leading to an increase in sea temperature and an alteration of the winter weather system, causing milder winters, could tip the ocean system towards a reduced deep water formation and lower oxygen concentrations in the bottom waters.

Major emphasis to date has been placed on the potential impacts of sea water temperature increases and, more recently, the consequences of a rise in sea-level. In terms of conservation, however, many other factors need to be taken into consideration, in particular the impact on coastal fisheries.

Mountain areas

Europe's mountains are believed to be among the sites that will be most affected by climate change. A warmer climate will not only affect rainfall and snow levels, but will also influence the duration and extent of snow cover and the timing and level of eventual snow melt and run-off – features that have important consequences for people as well as wildlife.



A retreating glacier at Aletsch Reserve in the Swiss Alps. Photo: WWF/ Hartmut Jungius.

Mountain forests in Europe were long protected from human disturbance by their isolation. This, however, has not protected them from airborne pollutants: more than half of the alpine and Carpathian forests are said to be sick and dying prematurely. The Swiss Forest Institute has estimated that the number of sick trees increased by about 10% in the past 20 years. Acidity and warmer climatic conditions have been attributed to this dieback.

The mountains of Europe play a vital role in supplying freshwater for domestic and industrial purposes, providing about 50% of the water for major river systems such as the Rhine, Rhone, Po and Danube. Predicted climate changes would almost certainly alter current flow rates, with heavier winter flood waters and lower summer flows. Changes in precipitation, perhaps combined with modifications of vegetation cover (loss of forest or changing agricultural practices) could result in accelerated soil erosion, leading to a loss of valuable top soil, organic and nutrient content, as well as increased possibilities of landslides and avalanches in vulnerable regions.

A major problem with interpreting mountain climates is the lack of weather data. A combination of historical indicators and observational data are used in this paper to describe some pertinent features. In the Alps, the altitudinal limit of permanent snow cover is currently (December 1995) 100 m higher than its was 15 years ago (Loh 1995). Previous records illustrate that the permanent snow limit had already risen by 100 m from 1850 to 1980. Valleys of the pre-Alps are now covered in snow for 3–4 weeks less per annum than before.

Data already show that alpine glaciers are retreating and have lost 30% of their overall bulk in recent years. Some glaciers, such as the Rhine, have already shrunk by 50%. (It should also be noted, however, that some small glaciers have spread, but this is alleged to be due more to steep slopes than to the volume of the glaciers themselves.) It is likely that by the end of the next century, between one-third and one-half of remaining mountain glaciers could have disappeared (IPCC 1995).

Ecosystems and communities occurring at higher altitudes are very sensitive to climate warming mainly because the climatic gradients and associated changes in vegetation patterns occur over very short distances (de Groot and Ketner 1994). A temperature rise of 3°C, for example, corresponds with a shift in climate zones and the corresponding snow and tree lines of about 500–600 m. This is more that the average width of a single vegetation belt and could mean the disappearance of many species from higher alpine regions, particularly in ecological communities on mountain summits.

Species and biodiversity

Over much of Europe, plants and animals have adapted to living in an environment that is heavily influenced by human activities. Future changes in species distribution and composition could be influenced as much by socioeconomic or political decisions on land-use as by climate change. Most impacts on the flora and fauna will probably occur as a result of changes in the frequency or magnitude of extreme events such as drought, fire, floods, high winds and unseasonal periods of cool weather.

It is difficult to determine precise long-term impacts on flora and fauna. According to the UK Climate Change Impacts Review Group (1991), the following general features could occur in the UK:

- Where rainfall is plentiful, an increase in CO_2 concentration accompanied by a lengthening of the growing season is likely to increase the productivity of the vegetation.
- There will be significant movement of species northwards and to higher elevations. Insects, birds and plants that have a high fecundity and rapid dispersal rate will be among the first to move. Species which do not extend their ranges will not necessarily be affected adversely – many species will adapt to climate change. The predicted rate of climate change is too rapid for many to adapt genetically.
- Migration of plants is likely to occur in spurts, following extreme events such as drought or fire which permit new species to colonise empty sites.

- There will be an increased probability of invasion and spread of alien weeds, pests, diseases and viruses.
- Many native species and communities will be adversely affected and may disappear from the UK. Particular losses are likely to occur within montane, saltmarsh and coastal communities, confined 'island' habitats, and wetlands and peatlands.
- An increase in sea-level of 20–30 cm would have an impact on about 10% of protected areas and might adversely affect invertebrates and birds which inhabit mudflats.
- There may be an increase in the overall number of species of invertebrates, birds and mammals in much of the UK (following migration and invasion), but the natural flora is likely to be impoverished by the loss of many rare and currently endangered species which occur in isolated, damp, coastal or cool habitats.
- Land-use changes brought about by changes in agricultural and forestry policy in the UK could influence the natural biota as much as climate change itself.

Climate change will almost certainly lead to a loss of biological diversity. While some species will find themselves well placed (both in terms of geographical positioning, as well as their ability to react and adapt to new ecological conditions), others will be unable to cope with new conditions. Examples of such 'winner' and 'loser' species are given in Table 1.

The same report also notes that in addition to changes at the species and community level within ecosystems, entire landscapes are also likely to undergo a major transformation, at least at certain latitudes. Some of the potential changes are given below:

- Heathlands may be subject to more frequent fires if the climate becomes warmer and drier. These ecosystems would then be invaded by new colonising species.
- Fens and beat bogs would dry out a result of increased evaporation and lower ground recharge levels.

Table 1. *Examples of potential 'winners' and 'losers' in the UK fauna and flora (judged by a change in distribution and/or abundance) as a result of climate change (UK Climate Change Impacts Review Group 1991).*

Group	*'Winners'*	*'Losers'*
Plants	Improved seed production in e.g. stemless thistle and small-leaved vine; southern species of disturbed ground e.g. black twitch, wall barley and prickly lettuce	Woodland geophytes such as bluebell and ramsons; northern species such as Jacob's ladder and mossy saxifrage
Invertebrates	Dragonflies; aphids; most butterflies and moths	Midges; alpine sawflies
Birds	Dartford warbler; stonechat	Snow bunting; dotterel
Mammals	Many bat species Mountain hare	
Fish	Salmon; carp	Arctic char; freshwater whitefish

- The area and species composition, as well as chemical composition of the soils, of blanket peatlands would change considerably if rainfall levels decrease and/or if temperatures increase.
- The area and species composition of salt marshes and brackish water habitats would change considerably with any rise in sea-level.
- Many montane plant communities may be lost.
- Permanent pasture may change following reduced precipitation, suitability of grassland species and/or as a result of invasion of new species.

The range of many plant species with 'weed' characteristics has increased in recent decades. This has mainly been attributed to human actions related to changes in land-use, but attention should be drawn to the fact that those species which display a tendency to expand their ranges are predominantly species with high temperature requirements (de Groot and Ketner 1994). For a review on alien invasions, see Macdonald 1994.

Another probable effect of climate change will be a series of phenological events. For plants, these include features such as foliation, flowering time and seed setting, and for insects and certain other groups of animals, the timing of migration. Table 2 highlights some possible changes in the flowering time of several plant species in the Netherlands, United Kingdom and Norway.

Holten and Carey (1992) examined some potential effects of climate change on species distributions in terrestrial ecosystems in Norway. Their findings suggest that species such as *Campanula uniflora* (a rare alpine and continental species) may be threatened by extinction as a result of both climate change and changes in snow cover and run-off. In contrast, temperate and oceanic species, such as *Hypericum pulchrum* (a frost-sensitive coastal species), would be favoured under the altered climate regime, but colonisation by these species could be delayed by natural or man-made barriers.

Keeping apace with change

Species are likely to differ considerably in the speed at which they are able to respond to climate change, notably through migration. Certain woody species such

Table 2. *Number of days of earlier onset of flowering of some European plant species as a result of temperature rise (de Goot and Kenter 1994).*

	Average date of flowering (day/month)			Expected date of flowering (day/month)			Number of days earlier flowering		
Species	*NL*	*UK*	*N*	*NL*	*UK*	*N*	*NL*	*UK*	*N*
Corylus avellana	25/2	1/2	23/3	11/2		11/2	14		37
Tussilago farfara	20/3	27/2	10/4	27/2	13/2	2/3	23	14	39
Anemone nemorosa	7/4	22/3	11/4	11/3	1/3	3/3	27	21	39
Chrysanthemum leucanthemum	22/5	20/5	16/5	26/4	18/4	18/5	26	32	29
Alnus glutinosa	10/3		14/3	10/2		11/2	20		33

NL: Netherlands. UK: United Kingdom. N: Norway.

as holly (*Ilex aquifolium*) and ivy (*Hedera helix*) are now found much further north than during the last period of deglaciation. If temperature is the main factor influencing these species, then holly, whose current distribution is closely linked to the January 0°C zone in north-west Europe, could move as much as 1,000 km to the north-east under doubled CO_2 conditions. At the same time, however, other species are likely to experience a decline in distribution, e.g. *Linnaea borealis*, *Empetrum nigrum* and *Trientalis europaea*. These species are expected to retreat from the southern borders of their ranges or decline in abundance (de Groot and Ketner 1994).

Even at its fastest rate of expansion, palaeological data from the period 9,000 to 6,000 BP show that oak trees took about 500 years to move some 200 km – an average migration speed of 40 km each century (de Groot and Ketner 1994). Such knowledge is essential to park managers and others responsible for planning future protected areas. A summary of migration times for different plant species is shown in Table 3.

Insects, particularly aphids, butterflies and moths, are widely expected to increase their ranges and, perhaps, levels of abundance. Many species of butterflies show levels of peak abundance and distribution during periods of warm weather, for example, the swallowtail (*Papilio machaon*) which reached peak numbers and was recorded over much wider areas in the Netherlands during the warm years of the 1940s before declining again in the colder and wetter 1960s (van Swaay 1990). Similar trends have been noticed for many species of butterflies and moths in the UK (see Burton 1975 for a review), while in Hungary, a northward migration of thermophilous pest insects was observed during the period from 1881–1990 when winter temperatures increased significantly (Stollár *et al.* 1993). (A review of the effects of a series of mild winters and hot summers on different parts of the UK flora and fauna and major ecosystems in the UK for the years 1988–1990 can be found in HMSO 1993.)

Table 3. *Range of observed migration rates in 16 plant taxa in Europe (de Groot and Ketner 1994)*

Taxon	*Range of observed migration rates (m/year)*
Fraxinus	25–200
Abies	40–300
Castanea sativa	200–300
Fagus	200–300
Pistacia	200–300
Juglans	400
Tilia	50–500
Picea	80–500
Fraxinus excelsior	200–500
Quercus	75–500
Carpinus betulus	50–1,000
Ulmus	100–200
Acer	500–1,000
Corylus	500–1,000
Pinus	1,500
Alnus	1,500

Protected areas

The response of biotic communities and populations to greater warmth and uncertain moisture changes will be critical to managers and planners of parks, reserves and other protected areas, worldwide. The vast majority of existing protected areas have been established to protect one or more specific items: national parks have been established for single species or ecosystems, some of which act as glacial refugia for certain species, cultural reserves have been set aside to protect the homes of traditional communities, and other heritage sites have been identified on the basis of natural wonders. Yet for the present purposes, the species and communities on which such protected areas have been based may not be able to function outside of the relatively narrow range of temperature and precipitation, or the interference from other species, that they currently enjoy.

A major concern for park management in all areas is to begin monitoring the appropriate weather variables and biotic populations and communities (Solomon 1994). Current climate change scenarios suggest that the geographic extent of vegetation types may shift through the stationary boundaries of established nature reserves (Urban *et al.* 1994). Any such translocation of vegetation ranges could act to further disrupt and fragment vestiges of protected area habitat leading to local extinctions. In one analysis of this situation, four models were used to examine the percentage of terrestrial land area that might demonstrate a shift in life zones under changed climate. The results suggested that from 39%–55% of the land area may change (Smith *et al.* 1990). Another similar exercise was carried out to evaluate the impact on existing Biosphere Reserves, the majority of which incidentally occur in Europe and North America. According to five different models, as few as 40, or as many as 190 biosphere reserves could be impacted as a result of climate change (Urban *et al.* 1994).

In a similar exercise, Leemans (1990) observed that at least 16% of existing reserves will encounter major difficulties with protecting present communities under changed climate conditions, but that this level could reach as many as 60% of existing reserves. While these and the above figures are rather crude they do nonetheless serve to illustrate that there are substantial consequences for all protected areas as a result of climate changes.

Iberian Lynx, Lynx pardinus, *Coto Doñana National Park, Spain.* Photo: WWF/Fritz Vollmar.

Conclusion

Our understanding of the potential environmental impacts of climate change remains full of uncertainties and there is a great need for additional studies. In particular, much more attention should be given to monitoring current and past changes of species distribution in direct comparison with meteorological data. Particular attention should also be given to monitoring and protecting key species and habitats that are potentially most at risk from climate change. This includes species which are:

- at the edge of (or beyond) their optimal range
- geographically localised species, such as those found on mountain peaks, in isolated habitat patches, etc.
- genetically impoverished species
- poor dispersers
- slow to reproduce
- localised populations of annual species.

Ecosystems most at risk are those for which options for adaptability are already limited. Included are species or communities from montane environments, alpine ecosystems, polar, island and coastal communities, as well as individual sites already degraded, threatened or stressed by human interference.

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Ecosystem resilience, biodiversity and climate change: setting limits

JAY R. MALCOLM AND ADAM MARKHAM

Global warming may lead to an unprecedented re-sorting of the earth's ecosystems. In a general discussion on how this landscape modification might occur, we discuss key concepts in ecosystem change. In particular, we focus on the disproportionate role of keystone species and processes in determining ecosystem change. We suggest that a functional (systems) approach is of less utility in predicting biodiversity impacts that a more species-based (evolutionary) approach and that further gains in predicting ecosystem responses to climate change will be derived from increased efforts to meld the two sub-disciplines. The unpredictable reordering of key ecosystem functions through feedback cascades is proposed to be a worst-case scenario, that should be avoided at all costs. Setting greenhouse gas emission limits to minimise ecological effects will require a careful consideration of the effects of climate/habitat disequilibria on species, particularly those that play a disproportionate role in structuring ecosystems. Finally, we list possible predictions for assessing the vulnerability of ecosystems to radical change.

CONTINUED GREENHOUSE warming has the potential to massively alter the planet's ecosystems on a temporal scale unprecedented in geological history. Over the next century, we may be facing an even greater re-sorting of communities than seen during the last ice ages. For example, Holdridge models coupled with outputs from 2×CO_2 general circulation models (GCMs) suggest an approximately 50% change in the spatial distribution of life zones within North America (Neilson 1993). To obtain a precedent for the 3–5°C global warming anticipated in the coming century, we may need to go back as far as 20 million years to the Miocene (Dobson *et al.* 1989), an epoch when most of the world's current species had not yet made an appearance. Buddemeier (1990) notes that it is the likelihood of this rapid change in interaction with other local and regional land-use changes that represents a worst-case scenario credible enough to be taken seriously as a major threat to biodiversity. Thus, the future maintenance of effective systems of protected areas may depend on a much fuller understanding of species and ecosystem response to climatic change.

The potential for large-scale changes in the spatial distribution of biomes and ecosystems begs the question: in what way will the change come about? Equilibrium models that combine climate change scenarios with eco-climatic indices unfortunately tell us nothing about the mechanisms of change (Neilson 1993). In a sense, they are best-case scenarios: in response to gradual changes in climate, one imagines the orderly movement of ecosystems across the landscape. However, aside from the role that increasing ecosystem fragmentation plays in preventing any such movement, one must consider both the nature of the climate change itself as well as the internal dynamics of ecosystems in assessing the likelihood of such a scenario. For example, directional changes in climate may be accompanied by increased climatic variability and increased frequencies of catastrophic events (Markham 1996). Also, different components of ecosystems will respond differently to climate change and the novel sets of interactions that are created may lead to abrupt change. Neilson (1993) makes a useful distinction in this regard and describes contrasting views of ecosystem change. One is essentially demographic: biogeographic displacement is limited largely by dispersal and establishment rates, and an ecosystem is viewed as an aggregate of more-or-less independently operating species. According to this view, the response to climate change is gradual and essentially additive. The second encompasses a more functional and integrative perspective, and recognises the possibility that ecosystem processes could be disrupted over large areas, leading to altered feedback relationships and possibly to catastrophic change.

These questions concerning mechanisms of change have more than academic interest. Ecosystem change figures prominently in the United Nations Framework Convention on Climate change (Article 2):

> *"The ultimate objective of this Convention and any related legal instruments that the Conference of Parties may adopt is to achieve, in accordance with the relevant provisions of the Convention, stabilisation of greenhouse gas concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system. Such a level should be achieved within a time-frame sufficient to allow ecosystems to adapt naturally to climate change ..."*

Article 1.1 puts this objective in context and further supports the emphasis on ecosystem change:

> *"'Adverse effects of climate change' means changes in the physical environment or biota resulting from climate change which have significant deleterious effects on the composition, resilience, or productivity of natural and managed ecosystems ..."*

Thus, both quantitative and qualitative aspects of ecosystem change are critical standards in implementing the convention and setting emission targets and limits to climate change (Markham 1996).

In this paper, we review some key concepts of ecosystem responses to a changing climate. We were particularly interested in practical applications of these concepts to the conservation of species richness, and we focus in particular on the role of biodiversity in modulating ecosystem behaviour. What properties of an ecosystem predispose it to climate change impacts and the erosion of diversity? From a biodiversity standpoint, how much climate change is too much? Can we define thresholds of ecosystem change?

Ecosystem resilience

Ecosystem resilience serves as a useful starting point because of the focus on responses to disturbance events. Holling (1973, in press) discusses two concepts that he terms "engineering" and "ecological" resilience. The first defines resilience in terms of resistance to disturbance and the speed of return to an equilibrium steady state. An analogy is a ball on surface that reaches a point of local equilibrium in a depression on the surface. Resilience is determined by the steepness of the depression's walls: how easy is it to displace the ball from the low point in the depression?

Directional climate change will lead to a radical re-sorting of the earth's biomes, especially in mountainous areas where eco-climatic zonation is marked. Photo: WWF/Galen Rowell.

The second concept concentrates on conditions relatively far from any local equilibrium/steady state, and the possibility that the system can flip into another regime of behaviour or stability domain. In this case, the measure of resilience is the magnitude of disturbance that the system can absorb before it changes its structure; i.e., before it is pushed into another stability domain. Thus, resilience is a measure of the limits of the local stability of the self-organisation of the system (Perrings *et al.* 1995). To extend the analogy, one can imagine other depressions (stability domains) on the surface, and define resilience as the effort or distance required to move the ball from one until it is 'captured' by another.

In a general discussion of the utility of ecological resilience, Holling (in press), stresses the importance of episodic ecosystem change and notes that irreversible (or nearly so) states exist (desertification being a classic example). He also suggests that system dynamics are partly dependent on spatial and temporal attributes that are neither uniform nor scale invariant (Holling 1992, in press); hence, returning to our analogy, we have good reason to expect a surface with distinct depressions.

Defining a useful notion of resilience will depend of course on the character and the magnitude of the disturbance. Holling's two concepts are most useful when we think about an episodic disturbance; that is, a disturbance that has a distinct beginning and end. A more useful definition of resilience from a climate change perspective must consider not only the possibility of episodic climate change (as for example during extreme weather events), but more importantly the probability of long-term **directional** change. A similar distinction is made in the limnological literature between whole-lake PULSE (episodic) and PRESS (directional) experiments (Frost *et al.* 1995). In the case of long-term directional change, we do not have a baseline against which we can measure resilience (no longer do we have a locally stable equilibrium) and our focus shifts from the rate or likelihood of recovery, to the rate and nature of the change itself.

Mechanisms of change

As part of a general strategy to simplify myriad potential relationships and identify those that are most critical to ecosystem function (Risser 1994), theories of ecosystem change have focused on the possible disproportionate importance of certain key components or dynamics. In reviewing these ideas, it is useful to make a distinction between species and processes as drivers of ecosystem change. Assigning a key role to species has its roots in community ecology, whereas a process-based approach comes from systems analysis. Both ideas have been proposed as methods to prioritise conservation (e.g. Caughley 1993, Paine 1995, Walker 1992). However, as we discuss below, they provide contrasting views on the relationship between species diversity and ecosystem change.

Keystone species

As envisioned by Paine (1969), keystone species influence the structure of their community structure out of proportion to their biomass or abundance. In the classic marine example, through selective predation on a competitively superior prey, starfish indirectly maintained resources for a host of other species (Paine 1969). Similarly, in an example from the tropics, Terborgh (1986) argued for the disproportionate importance of a small group of tropical plants (12 of some 2,000 species), in that they provided critical fruit resources for vertebrate frugivores during the annual dry-season period of scarcity (see also Leighton and Leighton 1983).

Lawton and Jones (1995) extended the keystone species concept to include what they termed "ecosystem engineers": species that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials. In so doing, these species modify, maintain, and/or create habitats and change the availability (quality, quantity, distribution) of resources utilised by other taxa. Their classic example of an engineer is the beaver (*Castor canadensis*), which by alteration of resource flows creates habitats for a host of plant and animal species. As in the case of the keystone species concept, they assume that the loss of the engineer would lead to a host of direct and indirect effects that could cascade through the system. Also included as ecosystem engineers are species that modulate major abiotic controls. A possible example is introduced cheatgrass (*Bromus tectorum*) in south-western Idaho, which, through its interaction with fires, causes widespread changes in shrub/steppe habitats (Knick and Rotenberry 1995, in prep.). In response to Krebs (1985) suggestion that keystone species may be relatively rare in natural communities, or that they may be common but not recognised, Lawton and Jones (1995) proposed that keystone species occur in virtually all habitats. They further proposed that most of the effects of keystone species are due to engineering rather than trophic effects.

Keystone processes

Lawton and Jones (1995) did not confine their assessment to the species level, however, and went on to consider not only the idiosyncratic behaviour of individual species, but the systems-level behaviour of broad classes of species. They noted, for example, the central role of trees in structuring the forest environment, through modifications of hydrology, nutrient cycles, soil stability, humidity, temperature, wind speed, and light levels (see Holling 1992, Chapin 1993). This important role is easily confirmed when one considers the upheaval of forest ecosystems close to edges (e.g. Murcia 1995, Malcolm 1994, in press a). In extending the engineering concept from a species to a life form, however, these authors crossed a subtle but important conceptual boundary. The one-to-one correspondence between a species and its actions in the system is no longer applicable. In the tree example, we can imagine (at least conceptually) replacing some subset of the tree species in a forest with another set, without importantly changing the forest environment. In contrast, finding a replacement for a beaver is quite a different task.

In a similar vein, Walker (1992, 1995) argued that for conservation purposes, it is best to focus on aspects of biodiversity that most influence ecosystem function; for example, where species loss most readily leads to irreversible changes in the inherent structure and function of an ecosystem. He suggested that by maintaining the integrity of ecosystem function, the resilience of the system is also maintained, and the chances of losing the many species that we do not even know about are minimised. According to Walker's thinking, given inadequate understanding and knowledge, the best strategy is to ensure that ecosystem has constant structure (physiognomy) and function (primary productivity, nutrient regimes, trophic pattern, efficiency of water use etc.).

Walker (1995) coined the term "driver" for the species that perform key functions and placed all species that can perform a given function in a "functional guild". According to this definition, resiliency resides not only in the diversity of drivers, but also in the number of species that can potentially substitute for drivers; that is, in the number and breadth of the functional guilds. Note that, with respect to performing the key function, species in the same guild are complementary, or to use a less flattering term, redundant. Greater redundancy within guilds would tend to increase resilience. A straightforward prediction of complementarity would be that if the abundance of a driver is decreased, a compensatory increase of another species in the guild must necessarily occur if the ecosystem process is to be maintained. Without such compensation, the magnitude of the process must decrease (Lawton and Brown 1993, Frost *et al.* 1995). Thus, compensation and redundancy are two sides of the same coin (Frost *et al.* 1995). In support of this prediction, Frost *et al.* (1995) noted that ecosystem processes such as primary productivity and decomposition are sometimes maintained at nearly constant levels despite shifts in species composition, revealing complementarity of ecosystem function. Similarly, Carpenter and Kitchell (1993) found that various compensatory responses at the species, population, and community levels limited the ecosystem-level effects of major perturbations in fish predator communities.

Several palm species in the Neotropics figure prominently in providing food resources during periods of resource scarcity. Photo: Jay Malcolm.

Perhaps the most extreme version of the keystone process concept is Holling's (1992), "Extended Keystone Hypothesis", which holds that "all terrestrial ecosystems are controlled and organised by a small set of key plant, animal, and abiotic processes that structure the landscape at different scales". These keystone processes create discontinuous dynamic spatial and temporal patterns, and create feedbacks that reinforce persistence of temporal and spatial scale domains (Holling 1992 in press). Under this hypothesis, resilience is ecological and measures the likelihood of a shift to another set of keystone processes.

The role of species diversity in ecosystem change

The emphasis on species-specific processes in determining patterns of change on one hand, and functional attributes of species and systems on the other, has important implications for the role assigned to species diversity in influencing ecosystem change. Tilman and Downing (1994) characterise the two alternatives: (1) the "diversity-stability" hypothesis, which holds that species differ in their traits and that diverse ecosystems are more likely to contain some species that can thrive during a particular environmental perturbation and thus compensate for competitors that are reduced by disturbance, and (2) the "species-redundancy" hypothesis which proposes that ecosystem functioning is independent of diversity provided major functional types are present. Again, as in the definitions of resilience, these concepts focus on episodic disturbance instead of directional change; however, they do outline the contrasting roles of species diversity in determining ecosystem change. The former view has its origins in community ecology, and embodies a distinctly evolutionary outlook (see Caughley 1993). In a recent discussion, Paine (1995) characterised this view when he suggested that the chief benefit of the keystone species concept is in conveying a sense of nature's dynamic fragility and an interactive, multispecies perspective. The emphasis is on historical contingency and adaptation: ecosystems are constrained by physical laws, but their characteristics are to a large extent statistical by-products of organismal evolution and historical accident. On the other hand, the species-redundancy idea has its origins in systems theory, attaches lesser importance to historical contingency, and emphasises fundamental and emergent properties of complex systems.

The different emphasis on species in the two views also appears to coincide with alternate definitions of the currency of stability. The multispecies outlook defines stability in terms of species composition (biodiversity), whereas the systems outlook defines stability in terms of ecosystem function. For example, in his description of functional redundancy, Walker (1992) defined ecosystem resilience as the capacity of the system to maintain its characteristic patterns and rates of processes (such as primary productivity, allocation of photosynthate, surface hydrology, energy exchange, nutrient cycling, herbivory etc). A more extreme view is espoused by Perrings *et al.* (1995), who suggested that the fundamental goal of biodiversity conservation is not species conservation *per se*, but protection of the productive potential of ecosystems.

A reduced significance of species composition in determining ecosystem behaviour in the functional approach is especially obvious in the concept of complementarity (redundancy). As noted above, in many cases ecosystem properties such as primary productivity and decomposition are maintained at nearly constant levels despite radical shifts in species composition, as caused for example by invading species (Vitousek 1990) or other disturbances (Frost *et al.* 1995). Thus, different measures of stability are obtained depending on the currency used. However, from a biodiversity perspective, maintenance of ecosystem properties is not particularly relevant if the original complement of species has disappeared.

Holt (1995) argued that a microevolutionary perspective might help sharpen our understanding of factors determining keystone effects, a plea that we echo here. In addition, as suggested by species complementarity, we suggest that a strongly evolutionary and at least partly organismal (as an alternative to function-based) viewpoint is required if the keystone approach is to prove useful in predicting biodiversity change. Examples that demonstrate the utility of an organismal viewpoint in understanding ecosystem behaviour include (references in Holt 1995):

- Studies that show that the effect of grazing on above-ground net primary production declined as the length of the shared evolutionary history increased.
- A game-theory model of the competitive advantage of height *versus* the cost of building and maintaining supporting tissue predicted that optimal height was not the height that maximised the collective biomass production of a stand.
- The high concentration of defensive secondary compounds in the foliage of plants in low nutrient environments reduced energy flow into higher trophic levels, and feedbacks (through low soil decomposition) to lower soil fertility.
- By influencing rates of herbivory, the presence or absence of sea otters may indirectly determine concentrations of secondary compounds in algae, which, as in the example above, could feed back and influence productivity and energy flows in the system. Species richness itself is importantly determined by exogenous factors, such as the length of time an ecosystem has been in existence etc. In the tropics, species richness of vertebrates in human-created secondary habitats may be largely a function of pre-adaptation (Malcolm in press b). As a final example, Terborgh (1986) suggested that it is the lack of good seasonal cues for plants in the tropics that leads to resource variability in the first place, and sets the stage for the importance of keystone resources in the frugivore community.
- An evolutionary perspective is also important in interpreting species compensation. According to the concept of density compensation in ecological theory (MacArthur *et al.* 1972), if two species utilise the same resources, the abundance of one will increase if the other decreases, even if the functional roles of each are quite different. The idea of functional complementarity is very different; in this case, a compensatory response in density maintains a given function. We note that because of a general lack of correspondence between the ecosystem function performed by a species, and the reasons for density compensation, compensation will not necessarily be observed if two species have the same functional role. After all, species are designed to use resources, not to perform ecosystem functions. The fact that a functional role has become available has relatively little to do with whether another species will fill it.

By stressing an evolutionary, species-based viewpoint, we do not mean to imply that functional constraints are not important in understanding ecosystem behaviour. After all, biome-level convergence in ecosystem structure and process requires a perspective that considers biotic evolution in the context of such functional constraints. We do suggest however, that the manner in which one views ecosystem structure will determine how ecosystem change can be measured, and ultimately how the impact of climate change can be judged.

Setting limits to change

How do we measure change and propose limits to the amount of change? Unfortunately, it seems very likely from both evolutionary and systems perspectives that abrupt, non-linear, and unpredictable changes are more likely to occur than those that are gradual, linear, and predictable. Holt (1995) noted that in evolutionary and community dynamics, the mean state of a system is a poor predictor of long-term response to change. Long-term responses often involve magnification of seemingly unimportant alleles, phenotypes, and species. Surprises are the norm when systems are perturbed; for example during the whole-lake experiments conducted by Carpenter and Kitchell (1993) and others. Holling's (1973, in press) concept of "ecosystem" *versus* "engineering" resilience similarly stresses the likelihood of unpredictable, non-linear change. In the gravitational analogy, surfaces are complex with numerous depressions, and as the ball moves about on the surface the surface itself deforms as new feedback relationships (self-organising states) are established (Holling in press).

Thresholds and feedback loops

It is this non-linear change, driven by unanticipated positive and negative feedbacks (Carpenter and Kitchell 1993), that ultimately establishes the scale against which ecosystem responses to climate change are measured. A related concept is a climate change threshold (Markham 1996). Organisms have certain climatic limits within which they occur; climate change outside of these limits defines a threshold for geographic range shifts (Markham 1996). Similarly, in an ecosystem perspective, we can define thresholds of change. However, given the possibility of episodic change, it makes most sense to set thresholds at the boundary of episodic, destructive change and non-episodic, benign change. The problem is defining destructive *versus* benign change, or, as the United Nations Framework Convention terms it, non-natural *versus* natural change.

Neilson (1993) defines various process-based hierarchies (demographic, physiognomic and functional) and supposes that ever-greater climate change will progress further up the hierarchies. For example, a slight change in climate may produce a subtle shift low down on the hierarchy, but not extend further up. A large number of functionally equivalent species may buffer the system against further change and ensure that overall ecosystem-level processes remain unchanged. As phrased by Neilson (1993), our question then becomes: at what point on the hierarchy is change important?

Under the scenario of change that is directional (i.e. inevitable), change will progress further up the Neilson's (1993) hierarchies eventually. However, this change could come about in very different ways, depending on the rate of forcing (i.e. the rate of climate change). We offer no great insights here, except to suggest that episodic shifts in ecosystem function should be avoided at all costs. The possibility of non-linear effects means that policy first should be concerned with changes of lesser magnitude. In a climate change perspective, system-wide changes in structure, such as those observed during trophic and positive feedback cascades, seem to be a worst-case scenario. Modifications in species composition that lead to species endangerment will usually occur far before these largely irreversible revolutions in ecosystem function come into play. Thus, as a standard of climate change, we suggest that climate change must occur at a rate much lower than rates that give rise to abrupt changes in system characteristics. In Holling's surface analogy, change should be such that the ball is always firmly against a plank that pushes the ball across the surface, and does not race ahead of the plank as it is captured in depressions along the way.

An important example is the recent history of the lesser snow goose (*Chen caerulescens caerulescens*) colony at La Pérouse Bay on Hudson's Bay (as summarised in Jefferies *et al.* 1995). Goose populations have been increasing in the recent past, apparently due to increased availability of winter forage and refuges and less hunting pressure. The increasing numbers coupled with a cooling anomaly in the eastern arctic over the last two decades are leading to the destruction of the wetland. Local geese are arriving in greater numbers, and geese on the way north are delayed because of the cool spring. Because of the relative lack of above-ground vegetation, the geese feed extensively by grubbing, and rip up the marsh. Removal of the vegetation leads to increased evaporation, as well as increased salination, and feeds back in a positive way to further destroy the marsh. The result is a trophic cascade, with impacts on other marsh fauna (soil invertebrates and some shorebirds and ducks) and ecosystem processes (including lower nitrogen mineralisation). In this example, the increase in the goose population is linked strongly to human activities, and weather change has acted as a trigger to initiate and exacerbate the feedback cycle. Clearly, the magnitude of the climate change, in concert with more direct human impacts, led to a radical and destructive change in the marsh. In the absence of climate change, the cycle may never have been started.

Disequilibria

If these positive feedback loops and functional shifts are viewed as worst-case scenarios, a lower (more "natural") limit for the rate of climate change must somehow be established. We propose that such a limit ultimately must be organismally, and not functionally based, and it must focus on ecosystem behaviour near the current equilibrium. Shifts that carry the system far from the equilibrium, in our view, are virtually impossible to predict beforehand because they depend on complex feedback relationships and non-linearities.

One possible criterion for establishing limits to climate change would be the disruption of co-evolutionary complexes. Climatic change at a high enough rates to disrupt these systems could result in multiple extinctions. Although co-evolutionary systems are complex, they are simple in comparison to ecosystems. Another possibility would be to consider the negative impacts of novel combinations of habitat/environmental variables on a species or group of species (Davis 1986, Dobson *et al.* 1989, Markham 1996). For example, Thomas E. Martin (in litt.) reports that year-to-year shifts in climate along a moisture gradient led to shifts in the distribution of ground-nesting birds, but the shifts were partially constrained by habitat preferences and incurred demographic costs. The negative effects of this disequilibrium between habitat and climate will be important at high rates of climate change and cannot be escaped by a distributional shift. Martin suggests that it is through disequilibria such as these that the effects of climate

Trees are particularly important in determining ecosystem characteristics, as evidenced by the upheaval in forest ecosystem processes that accompanies the creation of edges. Photo: Jay Malcolm.

change will become manifest. This criterion has the advantage that behaviour of the species at close-to-equilibrium conditions may provide information required for modelling the effects of climate change. These models would require a species-based perspective and the functional attributes of the system would be defined from the perspective of fitness costs and benefits. With appropriate dynamics and lags, these models could be coupled with climate change scenarios to study the extent of possible disequilibria. Models that couple demographic/functional and form/functional perspectives (Neilson 1993) may provide a point from which to begin.

Predicting ecosystem change

Several of the above authors have bravely attempted to predict some general properties of ecosystems that predispose them to radical change; we list several of these here. These predictions in many cases delimit the sorts of system behaviours that should be avoided at all costs.

- Lawton and Jones (1995) proposed that the engineering effect of species will be greatest when species have one or more of the following attributes: (1) large per capita effects, (2) high densities, (3) presence over large areas and long periods of time, (4) give rise to structures that persist for millennia and that influence resource flows. The persistent effects of engineers will greatly slow down rates of ecological change and impose considerable buffering and inertia on ecosystems.
- Walker (1992) suggested that systems most vulnerable to change are those with: (1) functional guilds with few members, (2) guilds where change leads to large alterations in ecosystem processes, and (3) guilds where density compensation is not observed upon removal of a species.
- Neilson (1993) suggests that, at least in warm regions, water balance determines vegetation density, and because mature ecosystems are close to the drought threshold, they are more sensitive to climate change than earlier successional species. The vulnerability of mature systems is further exacerbated by the fact that species that are characteristic of these systems are in general poor colonisers compared to those in earlier successional seres.
- Holling (1986) argues that reducing the variability of critical variables leads to loss of resilience. Walker (1995) similarly suggests that on theoretical and empirical grounds, diversity at the community level (patchiness) is important in long-term stability.
- Systems already experiencing human-impacts are more vulnerable that pristine systems (Markham 1996).
- Terborgh (1986; see also Foster 1982) suggested that in the tropics, the inability to find good cues as to seasonality (such as temperature and photoperiod in temperate regions) created strong links in food webs, such that changes in the abundance of just a few species can cascade through the system.

Conclusion

Questions concerning the qualitative and quantitative responses of ecosystems to climate change are not easily answered. In a hierarchy of ecosystem change, we suggest that limits to change must be based on responses of individual species in addition to co-evolutionary complexes of species, especially those that play disproportionate roles in influencing ecosystem structure. Alterations that result in radical re-ordering of ecosystem interactions and cascading structural and functional changes due to feedback relationships must be avoided. In order to assess the likely impacts of climate change on biodiversity within a given ecosystem, a stronger emphasis on linking the organismal approach of evolutionary ecology and the function approach of ecosystems ecology is required.

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Legal brief

The United Nations Framework Convention on Climate Change (the Climate Convention)

ADAM MARKHAM AND JONATHAN LOH

The signing of the Climate Convention was one of the most important outcomes of the 1992 UNCED meeting or "Earth Summit" in Rio, where developed countries agreed to halt the growth of greenhouse gas emissions into the atmosphere, and reduce their emissions to 1990 levels by the year 2000. The Convention has since been ratified by 155 nations.

Developing countries are not obliged to make any emissions reductions under the Convention, according to the principle of common but differentiated responsibilities. This recognises the historical disparity between the industrialised and the developing countries in their relative contributions to global warming. Also of importance is the precautionary principle, which is built into the treaty to ensure that absolute scientific certainty about the effects of climate change is not a precondition for taking action to prevent it, for then it would be too late.

The Climate Convention is explicitly concerned with biological conservation. Article 2 states:

> *The ultimate objective of this Convention ... is to achieve ... stabilisation of greenhouse gas concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system. Such a level should be achieved within a time-frame sufficient* to allow ecosystems to adapt naturally to climate change, *to ensure that food production is not threatened and to enable economic development to proceed in a sustainable manner.* [Emphasis added.]

Two further statements offer guidance on this matter. Supporting this emphasis on *allowing ecosystems to adapt naturally* is the following definition from Article 1.1:

> *"Adverse effects of climate change" means changes in the physical environment or biota resulting from climate change which have* significant deleterious effects on the composition, resilience or productivity of natural and managed ecosystems ...

And finally, Article 3.3 states that:

> *The Parties should take precautionary measures to anticipate, prevent or minimise the causes of climate change and mitigate its adverse effects.* Where there are threats of serious or irreversible damage, lack of full scientific certainty should not be used as a reason for postponing such measures ...

From these three statements it is clear that the Parties to the Convention must try to prevent negative impacts of climate change on biodiversity as well as on ecosystem structure and process. The reference to ecosystem resilience in Article 1.1 has not yet been widely noted, and may offer crucial guidance to implementation of the Convention. Resilience in scientific terms describes the ability of an ecosystem to absorb changes in variable factors, such as pollution or disturbance, without being destroyed or broken up.

Article 3.3 contains the principle that uncertainty should not be an impediment to action. From the perspective of conservation biology it can be said that uncertainty in ecosystem responses provides a strong argument for taking precautionary measures.

Given the growing scientific consensus that ecological impacts of climate change are a near-term threat, the interpretation of the essence of Article 2 is one of the most important tasks facing the Parties to the Climate Convention. Development of an effective post-2000 regime for the Convention will need to be based on an adequate understanding of the issue of ecological limits to climate change.

Few attempts have been made to define generalised ecosystem limits to climate change since the report *Targets and Indicators of Climatic Change* produced by the Stockholm Environment Institute (SEI) in 1990. Their suite of critical limits of climate change included a decadal rate of sea-level rise of between 20 mm and 50 mm, and a decadal rate of temperature rise of 0.1°C. According to the IPCC's best estimate, projected warming to the end of the next century implies a global average rate of around 0.2°C a decade, twice the rate proposed by SEI as a target threshold for climate change.

WWF has carried out a number of studies and workshops to determine the ecological limits to climate change and believes that even the SEI target is dangerously permissive. The world has warmed by about 0.6°C this century and consequently ecological changes are already taking place. Some boreal and Arctic-alpine ecosystems are already close to their limits and will not be able to adapt naturally to further warming.

Many species and ecosystems will exhibit non-linear responses to climate change. Beyond a certain point large changes in nature may be triggered by small changes in climatic conditions. The vulnerability of certain types of ecosystem is already becoming clearer and a number of ecological limits to climate change can be identified. For instance:

- A 1°C warming at higher latitudes can be expected to have major negative impacts on the distribution and health of boreal forests.
- For some tree species (such as Scots pine and Douglas fir) the migration threshold may be no more than 0.015°C per decade, and long-term warming above this rate will lead to dieback and decline.
- Coral reefs exposed to temperatures of 3–4°C above normal maximum for merely one to two days, or several weeks of temperatures only 1–2°C above normal, can suffer bleaching leading to mortality.
- The maximum rate of sea-level rise tolerated by certain types of coastal mangrove systems is about 12 cm per century.
- Certain alpine plant species respond to warming with a migration rate of only 1–4 metres altitude per decade.

To respect these ecological limits would require large, rapid and immediate reductions in global greenhouse gas emissions. The first Conference of the Parties to the Convention since Rio was held last year in Berlin where a mandate was endorsed to negotiate new emission targets beyond the year 2000 for industrialised countries. At present, however, it appears that only two, the UK and Germany, will be able to honour their original commitment of reducing emissions to 1990 levels by the year 2000, and neither of those for reasons to do with the ultimate objective of the Climate Convention.

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Résumés

Gestion des aires protégées face aux changements climatiques

PETER B. BRIDGEWATER

Les changements climatiques vont avoir un impact important sur les aires protégées et leur gestion. Ces impacts particuliers vont comprendre la perte de certains types de communautés et d'écosystèmes situés à des limites climatiques (par exemple, les communautés des régions montagneuses), un changement du pourcentage des types de communautés résultant des changements du climat et de la topographie (par exemple, les communautés côtières), une plus grande sécheresse et une perte générale de la diversité biologique. Certaines communautés nouvelles pourront sans doute s'établir après un tri des diverses espèces indigènes et l'établissement d'espèces exotiques.

Les gestionnaires de l'environnement devront utiliser une infrastructure écologique des paysages afin de surveiller les changements et de mettre au point des mesures de conservation appropriées. Il faudra prêter une attention toute particulière à certaines zones de l'infrastructure écologique comme les limites, barrières et couloirs. La surveillance des biomes jouera un rôle important dans la détection des changements climatiques, en particulier dans les 20 à 50 prochaines années. Des modèles de comparaison devraient être utilisés pour les espèces considérées menacées. Pour ces dernières, le transfert, ou bien pour les végétaux la préservation du propagule ou du germoplasme pour d'éventuels transferts, représentent un moyen possible de conservation.

Afin d'assurer une adaptation naturelle continue des communautés et des biomes, il sera essentiel de comprendre précisément la nature de la dynamique des terrains et la nécessité de liens appropriés entre les aires protégées. Il faudra peut-être aussi accepter que certaines aires protégées vont s'appauvrir en raison des changements climatiques et que d'autres régions, à présent moins importantes, devront être ajoutées au réseau des aires protégées. Les Agences pour la Gestion des Aires Protégées doivent être prêtes à utiliser toutes les Catégories des Aires Protégées adoptées par l'UICN et la CPNAP et de faire passer au besoin les aires protégées d'une catégorie à une autre. L'avantage de l'utilisation d'une infrastructure écologique des paysages est qu'elle permet une telle approche générale. Une telle souplesse d'approche sera indispensable au gestionnaire des aires protégées face à un régime de changements climatiques.

Impacts possibles des changements climatiques futurs sur les mangroves: implications pour les parcs marins

JOANNA C. ELLISON

Les forêts de mangroves se rencontrent sur les rivages tranquilles et sédimentaires des tropiques et abritent une flore et une faune spécialisées. Les arbres des mangroves répondent par des adaptations physiologiques et morphologiques aux agressions subies par leur biotope intertidal particulier, caractérisé par une haute salinité, une faible teneur en oxygène, une carence en éléments nutritifs et une mobilité du substrat. Une élévation du niveau de la mer (résultant principalement d'une modification des apports sédimentaires), une modification du régime des précipitations, une augmentation de la température et les effets directs de plus fortes concentrations de CO_2 dans l'atmosphère constitueraient les principaux impacts possibles des changements climatiques sur les écosystèmes des mangroves.

Une comparaison avec des cas analogues passés indique que la relation étroite entre les marécages des mangroves et le niveau de la mer les rend tout particulièrement vulnérables aux effets de toute élévation possible du niveau de la mer. Les marécages situés sur les îles océaniques basses seront plus vulnérables en raison des faibles taux de sédimentation. L'élévation du niveau de la mer pourrait entraîner une érosion des sédiments vers le large, et une augmentation du niveau d'inondation et du taux de salinité pourrait causer des symptômes d'agression chez les espèces des mangroves, comme par exemple une diminution de la croissance, une plus faible production de détritus et une moindre résistance aux espèces nuisibles et aux tempêtes.

Une augmentation de la température et les effets directs de concentrations plus élevées de CO_2 devraient entraîner une plus grande productivité des mangroves, une modification des cycles phénologiques et une expansion des mangroves à de plus hautes latitudes.

L'identification certaine des changements climatiques et des effets d'une élévation du niveau de la mer sur les mangroves nécessitent une surveillance continue des paramètres biologiques et physiques,

ceci sur un réseau de sites et utilisant des techniques courantes. Les gestionnaires de l'environnement disposeraient ainsi de données écologiques leur permettant une gestion informée des écosystèmes de mangroves.

Impact des changements climatiques sur certains écosystèmes européens

DAVID STONE

Les gestionnaires des aires protégées dépendent d'informations sûres et très récentes pour planifier leurs développements et activités de gestion futurs. Jusqu'à présent, la sélection de nombreuses aires protégées était basée sur leur richesse biologique ou bien sur leur site remarquable. Afin de répondre aux besoins à long terme des aires protégées et des sociétés, les gestionnaires des aires protégées doivent maintenant examiner de plus près les aires protégées existantes et futures afin de pouvoir prédire comment celles-ci pourront faire face aux événements futurs, l'un des plus alarmants étant la prédiction des changements climatiques de notre planète. Cet article examine, en se référant à des études actuelles, certains des problèmes essentiels liés à l'impact des changements climatiques sur les écosystèmes prioritaires européens.

Résistance des écosystèmes, biodiversité, et changements climatiques: fixation de limites

JAY R. MALCOLM AND ADAM MARKHAM

Le réchauffement général de l'atmosphère pourrait conduire à un ré-arrangement sans précédent des écosystèmes mondiaux. Dans une discussion plus générale sur les raisons de cette modification possible des paysages nous examinons les concepts fondamentaux de la modification des écosystèmes. Nous nous concentrons particulièrement sur le rôle disproportionné joué par certaines espèces et certains processus vitaux dans la détermination de la modification des écosystèmes. Nous suggérons qu'une approche fonctionnelle (systématique) est de moindre valeur pour la prédiction des impacts sur la biodiversité qu'une approche basée plutôt sur les espèces (évolutionniste) et qu'il sera plus facile de prédire les réactions des écosystèmes aux changements climatiques si ces deux disciplines sont réunies. La réorganisation imprévisible des fonctions des principaux écosystèmes par une succession de rétroactions représenterait une des pires hypothèses devant être évitée à tout prix. La fixation de normes d'émissions de gas afin de réduire les effets écologiques devra nécessiter un examen tout particulier des effets du déséquilibre climat/habitat sur les espèces, en particulier sur celles jouant un rôle disproportionné dans la structure des écosystèmes. Nous énumérons enfin les prédictions possibles permettant une évaluation de la vulnérabilité des écosystèmes face à des changements extrêmes.

Resumenes

La administración de áreas protegidas en relación al cambio climático

PETER B. BRIDGEWATER

El cambio climático va a tener un impacto significativo sobre las áreas protegidas y sobre su manejo. En particular, éstos impactos incluirán a la pérdida de tipos de comunidades y ecosistemas que se encuentren en los limites climáticos (e.g. comunidades de montaña), a los cambios en la proporción de tipos de comunidades resultantes de cambios climáticos y cambios en la forma y clasificación de terrenos (e.g. comunidades costeras) y a un aumento en la aridez y en la pérdida general de diversidad biológica. Nuevas comunidades posiblemente se establecerán después del ajuste en la mezcla de especies indígenas y del establecimiento de especies exóticas.

Será esencial que los administradores en conservación tengan en cuenta un escenario ecológico para poder monitorear y diseñar medidas reparadoras. En particular, se le deberá prestar atención a los elementos de infraestructura ecológica como límites, barreras y corredores. El monitoreo de la biota, especialmente dentro de un marco de tiempo de 20 a 50 años, será un aspecto importante en la detección de cambios climáticos. Se deberán usar modelos con varias opciones para aquellas especies que se consideren bajo riesgo. En el caso de las especies en peligro, éstas opciones incluyen translocación (migración natural ó artificial), ó en el caso de plantas, ésto incluiría el almacenamiento de propágulos ó germoplasma para una translocación final.

Para poder asegurar la continuidad de los ajustes naturales de las comunidades y la biota, es vital el entender la naturaleza de la dinámica de manchas aisladas y la necesidad de establecer enlaces apropiados entre las áreas protegidas. Tal vez también sea necesario el aceptar que algunas áreas protegidas terminarán convirtiéndose en áreas empobrecidas durante el proceso de cambio climático. Asimismo, otras áreas menos valiosas actualmente, terminarán siendo incluidas en la red de áreas protegidas en el futuro. Las Agencias de Manejo de Areas Protegidas deben prepararse para usar la gama completa de Categorías para Areas Protegidas de la UICN-CPNAP. También deben de estar preparadas a trasladar a algunas áreas protegidas a otras categorías adecuadas. La ventaja de tener en cuenta un escenario ecológico estriba en que se puede adoptar una amplia visión. Un enfoque flexible de éste tipo podría ser vital para el administrador de áreas protegidas bajo un régimen de cambios climáticos.

El impacto potencial del pronóstico de cambios climáticos sobre manglares: consecuencias para parques marinos

JOANNA C. ELLISON

Los bosques de manglar se localizan en costas sedimentarias de baja energía en los trópicos y proporcionan hábitats para un grupo especializado de flora y fauna. Los manglares presentan adaptaciones fisiológicas y morfológicas a las condiciones ambientales creadas por sus hábitats intermareales, como alta salinidad, bajo oxígeno, disponibilidad pobre de nutrientes y poca movilidad de substrato. Se espera que los impactos más importantes del cambio climático que afectarán a los ecosistemas de manglar serían el aumento en el nivel del mar (principalmente a través de alteraciones en los presupuestos de los sedimentos), cambios en la precipitación, aumentos en la temperatura y los efectos directos de niveles más altos de dióxido de carbono en la atmósfera.

Se ha indicado con pasados análogos, que la estrecha relación entre los manglares y el nivel del mar los coloca en una posición especialmente vulnerable a las interrupciones resultantes de futuros aumentos en el nivel del mar. Es muy probable que como resultado de sus bajas tasas de sedimentación, los manglares de islas oceánicas sean más sensitivos a éstas interrupciones. Los aumentos en el nivel del mar pueden ocasionar erosión de los sedimentos en la margen costera que da hacia el mar. El aumento en las inundaciones y en la salinidad pueden resultar en síntomas de deterioro en las especies de manglar reflejados en una reducción en el crecimiento, en la producción de hojarasca y en su resistencia a pestes y a tormentas.

Es posible que un aumento en la temperatura y los efectos directos de un aumento en los niveles de CO_2 tengan varios resultados como el aumento en la productividad de los manglares, el cambio en los patrones fenológicos y en una extensión en la distribución de los manglares hacia latitudes más elevadas.

La identificación de ciertos efectos de los cambios climáticos sobre los manglares requiere del monitoreo de parámetros biológicos y físicos a largo plazo, mediante una red de localidades y con el uso de técnicas uniformes. Esto les proporcionará datos ecológicos a los administradores ambientales que les permitirá el manejo informado de sus ecosistemas de manglar.

Los impactos de cambio climático sobre una selección de ecosistemas en Europa

DAVID STONE

Los administradores de áreas protegidas dependen de información confiable y actualizada para poder planear futuras actividades de desarrollo y manejo. Hasta ahora, la selección de muchas áreas protegidas se había basado en su riqueza ecológica ó por ser parte de un paisaje particularmente escénico. Para tomar en cuenta las necesidades de las áreas protegidas y de la sociedad a largo plazo, los administradores de áreas protegidas deben observar más de cerca a las áreas protegidas existentes y a las planeadas, con miras a determinar como éstas van a hacerle frente a futuros eventos. Uno de los cambios más difíciles de determinar es quizá el pronosticado cambio en el clima de la Tierra. Este documento, basado en estudios existentes, examina algunos de los puntos más importantes relacionados con los impactos del cambio climático sobre sistemas prioritarios en Europa.

Capacidad de adaptación de los ecosistemas, cambios en biodiversidad y clima: el establecimiento de límites

JAY R. MALCOLM AND ADAM MARKHAM

Es posible que como resultado del calentamiento global ocurra un reajuste imprecedente de los ecosistemas del planeta. Durante una discusión general de las posibilidades de que ésta modificación pudiera ocurrir, se discutieron conceptos importantes sobre cambios en los ecosistemas. En particular, el enfoque se centró en el papel prominente de las especies y procesos claves que determinan cambios en los ecosistemas. Se sugiere que el uso de un enfoque funcional (de ecosistemas) tiene una menor utilidad para predecir impactos sobre biodiversidad, que un enfoque mayormente basado en especies (evolutivo). También se sugiere que los beneficios futuros para pronosticar las respuestas de los ecosistemas hacia los cambios climáticos se derivarán de un aumento de esfuerzos para unir a estas dos sub-disciplinas. Se propone como el peor escenario, el reordenamiento impredecible de las funciones claves de ecosistemas a través de cascadas de retroalimentación, las cuales deben prevenirse a toda costa. Para delimitar la emisión de gases de invernadero a fin de minimizar estos efectos sobre la ecología, se requiere de cuidadosas consideraciones, especialmente en relación con los efectos del desequilibrio del clima o del hábitat sobre las especies. Sobre todo, en relación a las especies prominentes en la estructura de los ecosistemas. Finalmente, se enlistan los posibles pronósticos necesarios para evaluar la vulnerabilidad de los ecosistemas en relación a cambios radicales.

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