

Potential impacts of climate change on ecosystems: a review of implications for policymakers and conservation biologists

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ABSTRACT: Climate change represents a significant threat to global biodiversity and ecosystem integrity. The UN Framework Convention on Climate Change (UNFCCC), which has been ratified by 118 nations and came into force in 1994, has amongst its aims the protection of ecosystems. This paper reviews the relevant text in the Convention and gives an overview of scientific efforts to provide policymakers with the necessary information on ecosystem impacts. The sensitivity of different types of ecosystem to climatic change is discussed and the concepts of ecological limits and thresholds are addressed and examples given. The paper concludes there is a need for a better understanding of the impacts of climate change on ecosystem resilience in order to maintain biological diversity and respond to the needs of policymakers in implementing the UNFCCC. Recommendations are made for increased research effort, including increased resolution of climate models, better predictive capacity at a regional level for within- and between-year rainfall patterns, seasonality and extreme events. Collaborative monitoring programs, including long-term ecological research along climate gradients, are proposed for 4 biomes: coastal wetlands, montane ecosystems, coral reefs and Arctic ecosystems.

KEY WORDS: Adaptation · Biodiversity · Climate Conservation · Critical levels · Ecosystem impacts · Global warming · Protected areas UNFCCC

INTRODUCTION

Without urgent measures to control carbon dioxide and other greenhouse gas emissions, the global climate may be rapidly and radically changed (Houghton et al. 1990). The consequences of these changes could be negative for many species of wildlife and types of natural ecosystem. Sea level rise, increased risk of fire and storm, changed rainfall patterns and trends towards warming and aridity would be amongst the factors leading to ecosystem impacts. Solving the climate change problem may be one of the most critical environmental challenges of the coming decades. Achievement of a solution that results in reduced emissions of greenhouse gases will depend on the successful implementation and strengthening of the United Nations Framework Convention on Climate Change (UNFCCC).

THE CLIMATE CONVENTION AND THE NEEDS OF POLICYMAKERS

Biodiversity conservation and maintenance is explicitly built into the UNFCCC as a part of the over-arching objective:

The ultimate objective of this Convention and any related legal instruments that the Conference of the Parties may adopt is to achieve, in accordance with the relevant provisions of the Convention, stabilization 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* [my emphasis], to ensure that food production is not threatened and to enable economic development to proceed in a sustainable manner.

This reference to ecosystems in Article 2 of the Convention has been often quoted (e.g. Swart & Vellinga 1994), but there are 2 other key paragraphs that help to put the objective in context. Supporting the 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* [my emphasis] or on the operation of socio-economic systems or on human health and welfare.

And finally, Article 3.3 states that:

The Parties should take precautionary measures to anticipate, prevent or minimize 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* [my emphasis], taking into account that policies and measures to deal with climate change should be cost-effective so as to ensure global benefits at the lowest possible cost.

From these 3 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 yet turn out to be a crucial guide to implementation of the Convention. Arrow et al. (1995) recently defined resilience as 'a measure of the magnitude of disturbances that can be absorbed before a system centered on one locally stable equilibrium flips to another'.

In order for policymakers to determine targets for atmospheric concentrations of greenhouse gases, they will need improved scientific information and advice on the degree of risk posed to biodiversity and ecosystems. A recent study (Bernabo & Eglinton 1992) addressing US policymakers' uncertainties about climate change impacts identified relative sensitivity of different natural ecosystems and geographic regions, and information about adaptability amongst the top 5 priority issues for research. These decisionmakers also agreed that the research community should try to 'provide interim information and iterative assessments while developing long-term answers'

Policymakers need information on time-scales that allow them to use the best available analysis in ongoing decisionmaking and negotiation processes. Expert judgment has emerged as part of the impact and risk assessment process of the Intergovernmental Panel on Climate Change (IPCC) (Carter et al. 1994), and bal-

anced opinions and analysis of existing data should facilitate more effective decisionmaking. The World Wide Fund for Nature (WWF) has recently proposed a 2-track approach for assessment of ecological limits to climate change (WWF 1994a). This would consist of interim target-setting for emissions reductions based on review and assessment of existing knowledge, in parallel with a longer-term, more comprehensive analysis.

In all likelihood, a preliminary climate vulnerability assessment for ecosystems, addressing key systems, regional vulnerabilities and selected thresholds for change, could be prepared within 12 mo (Bernabo & Eglinton 1992). Such an analysis could be expanded in scope and refined in detail over the next 2 to 10 yr, resulting in regular input aimed at reducing decision-maker uncertainty as implementation and strengthening of the climate treaty goes on.

Climate change impacts

Participants in a recent scientific workshop convened by the WWF concluded that 'current greenhouse gas concentrations are already likely to pose serious risks to some species and ecosystems. Carbon dioxide concentrations are 25% above preindustrial levels, and rising, while methane concentrations have doubled since preindustrial times. Recent severe storms, droughts, floods, and forest fires, although they cannot unambiguously be linked to climate change, give an indication of the impacts that could result from human interference with the climate system, even at current greenhouse gas concentrations' (WWF 1994b).

Climatic changes during the quaternary period caused major alterations in biomes and ecosystems across Europe and North America. Yet very few species went totally extinct during this period, other than those restricted to islands or mountain ranges, because the populations of plants and animals were able to migrate according to the changing climatic conditions (Davis 1983). The current situation appears to be very different for 2 reasons. First, the rate of climate change may be unprecedented, and many organisms are unlikely to be able to adapt or migrate fast enough. Second, natural habitats are now patchy and isolated, like islands in a developed landscape, and species are often blocked from successful migration.

Much evidence suggests that the climate may have already begun to change. According to historical temperature records the 1980s was the warmest decade on record, and 1994 the third or fourth warmest year since reliable measurements began in 1850. Some of the strongest supporting evidence for the existence of a warming trend during the last 100 yr comes from

analyses showing that most of the world's mountain glaciers are shrinking and that snow cover is decreasing too (Houghton et al. 1992). Significant reductions in extent of Arctic sea ice have been recorded during the last 15 yr, and an acceleration in the rate of decrease was detected after 1987 (Johannessen et al. 1995). Sea surface temperatures have increased, and in California (USA) at least, this warming is associated with a massive decline in zooplankton populations (Roemmich & McGowan 1995). Bore hole temperature data from North America show a major warming since the mid-19th century (Deming 1995), and tree-ring studies show mean summer temperatures in Siberia to have been higher throughout the present century than at any time in the past 1000 yr (Briffa et al. 1995). Further indications of the warming trend come from research into the underlying cause of the desertification that has taken a grip in the Sahelian countries of sub-Saharan Africa. The Sahel is experiencing a 25 yr period of low rainfall and desiccation at least as severe as anything seen during the past millennium (Hulme & Kelly 1993).

Although it is not yet possible to prove that changes such as these are caused by man-made greenhouse gas emissions, they are consistent with predictions made by global circulation models (GCMs). Most GCMs predict that we can expect global warming during the next century of between 0.15 and 0.33°C decade⁻¹ under the IPCC's mid-range emissions scenario. This warming will not be evenly spread over the globe though, and the greatest changes are expected at higher latitudes. Warming will be accompanied by sea level rise, for which the IPCC scenario suggests a rate of between 2 and 10 cm decade⁻¹ during the next century.

As well as the changes in temperature and sea level, there is major concern about increased variability of weather patterns. Storms and hurricanes may become more frequent, intense and widespread, rainfall patterns will change, and the likelihood of many countries experiencing severe droughts and floods will increase. Some evidence already exists that extreme weather events have become more common in the United States during the last 2 decades (Karl 1995). It has been suggested that, on land, increases in droughts and storms could radically increase the risk of wildfires in temperate and boreal forests. The social and economic costs of these disasters will fall most heavily on the nations least able to afford them.

That human-induced climatic change poses a major threat to biodiversity has been widely known for more than a decade. Several wide-ranging reviews have been published during that time that tried to take stock of the potential impacts (e.g. Dobson et al. 1989, Rose & Hurst 1991, Peters & Lovejoy 1992, Markham et al.

1993). Attempts have also been made to identify those biomes and ecosystems that may be most sensitive to climate change. Sensitivity can be determined in a number of ways. It may be where the first impacts are likely to be seen, where the most serious adverse effects are likely to occur, where there is least political 'tolerance' for ecological damage, or where the least adaptive capacity exists. Vulnerable systems can be organized by biome, region, ecosystem or site, thereby forming a suite of 'critical ecosystems'. Priority for long-term ecological research and monitoring for change could be given to critical ecosystem sites. Specific landscape types are already defined as sensitive in the text of the UNFCCC, and a number of reviewing authors have suggested groups of biomes or ecosystems that may be at highest risk. A representative list is presented in Table 1.

Loss of biodiversity: the background to climate impacts

The earth's biodiversity is undergoing a major, and highly deleterious, simplification as the result of human activities (Wilson 1988). Biological diversity is generally taken to mean the combination of genetic variation, species richness and taxonomic diversity, and ecosystem diversity (IUCN/UNEP/WWF 1991). Landscape diversity is often added to the definition (Noss & Cooperrider 1994). Biodiversity at all levels is currently being lost at an unprecedented rate. Just one measure of this loss is the rate of species extinctions. Background extinction rates through geological time have been roughly estimated at the rate of 1 mammal and 2 birds every 400 yr (Groombridge 1992). Documented extinctions for the last 400 yr already include 58 mammals and 115 birds (WRI 1994). This is undoubtedly a major underestimate.

Highest levels of biodiversity are in the tropics, particularly the tropical forests, and estimates for the total number of species range between 5 and 30 million, less than 2 million of which have been described (Wilson 1988). The top end of this range is based largely on estimates of insect species richness in tropical forests. Current rates of extinction from the tropical forest biome alone have been estimated as between 1 and 11% decade⁻¹ (Groombridge 1992).

There is a tendency for the issue of species extinctions to gain the greatest attention in any public debate about conservation and biodiversity loss. In fact, ecologists are becoming increasingly concerned with maintaining diversity at all levels, from phenotype to community patchiness and landscape heterogeneity. In aiming to reduce the impacts of climate change, a greater understanding of the role of biological diver-

Table 1. Selected references to most sensitive or critical ecosystems

Biome, ecosystem or landscape type	Key climate variables	Source
Mangroves	Relative rate of sea level rise Storm frequency and severity	Rose & Hurst (1991) Markham et al. (1993)
Coral reefs	Relative rate of sea level rise Storm frequency and severity Sea-surface temperature	Rose & Hurst (1991) Markham et al. (1993)
Coastal marshes	Relative rate of sea level rise Storm frequency and severity	Rose & Hurst (1991) Markham et al. (1993)
Tropical montane forest	Cloud cover & sunlight hours Hurricane frequency & severity Drought frequency, annual and inter-annual rainfall distribution	Markham et al. (1993) Hamilton et al. (1993)
Raised peat bogs	Mean summer temperature Mean annual precipitation	Schouten et al. (1992) Markham et al. (1993)
Alpine/mountains	Mean annual temperature Snow fall and melt	Peters & Lovejoy (1992) Nilsson & Pitt (1991) Rose & Hurst (1991) UNEP/WMO (1992) Markham et al. (1993)
Arctic	Mean annual temperature Season length Precipitation	Chapin et al. (1992) Holten (1993) Peters & Lovejoy (1992) Rose & Hurst (1991)
Boreal forest	Mean annual temperature Fire frequency and severity Storm frequency and severity	Shugart et al. (1992) Peters & Lovejoy (1992) Rose & Hurst (1991)
Low-lying islands	Relative sea level rise Storm frequency and severity	UNEP/WMO (1992)
Arid and semi-arid areas	Precipitation patterns Minimum winter temperatures	UNEP/WMO (1992)

sity in ecosystem functioning will be required (Walker 1992).

Human-induced climate change adds another layer to the already complex interplay of forces, natural and anthropogenic, that shape the natural world. Nature has long been regarded as stable, or constant in its make-up. It is, in fact, highly dynamic, with most ecosystems being in some form of transient state (albeit on a range of time scales). The need to prepare for adaptation to climate change is highlighting this issue for the scientific community and the public at large.

Current attempts to understand the importance and functioning of biological diversity and the influence of climate change are hampered by ongoing environmental degradation. Principal causes of biodiversity loss worldwide include habitat destruction, pollution, invasive species, and over-exploitation of resources

such as fisheries and forests. High amongst the driving forces behind these problems are demographic change and population growth, inequitable consumption patterns, inefficient energy use and commodity trade structures. The net result of these many stresses is a loss of biological diversity.

In recent years, biologists have begun to shift their attention from species-based conservation approaches toward strategies that are centered upon the maintenance of the full range of undiminished ecosystem processes and biological diversity (Agardy 1994). The ability of ecosystems to respond to and recover from disturbance is termed resilience, and there is considerable evidence that species diversity strengthens resilience, especially where redundancy or overlap in functional groups of species within ecosystems exists (Tilman & Downing 1994). Where several species are able to perform the same functions in an ecosystem, they will exhibit different tolerances to disturbance. This redundancy provides a buffer against change (Walker 1995). Loss of biodiversity, therefore, will most likely reduce ecological resilience and ability to adapt to climate change. The maintenance of biological diversity, redundancy and resilience is vital for the mitigation of global climate change impacts.

Ecological limits to climate change

Although climate change will add to the stresses causing environmental degradation, the actual impacts of this additional stress factor are hard to predict. It is necessary to try and make some generalizations about the potential ecological limits to climate change in order to set emissions reductions targets under the Convention. Ecological limits may be set using a combination of both scientific data and subjective policy criteria. Within the context of UNFCCC, the policy criteria of most relevance to individual Parties will vary from country to country. Whichever methodologies or forms of ecological risk assessment techniques are used in this process, political and value judgments will still need to be made. Value-laden terms such as

'significant effects', 'serious damage' and 'unacceptable change' are scattered through the defining literature of this debate. Even the phrase 'adapt naturally' presents huge barriers of definition. The role of scientists must be to give as much guidance on these issues as possible.

Several key principles have been identified that can be used in assessing potential ecosystem vulnerability to climate change:

- 'The faster the rate of climatic change, the higher the probability of substantial disruption of ecosystem structure and function and surprise within natural ecosystems, and the greater risk of serious ecosystem degradation' (WWF 1994b);
- Ecosystems will not move wholesale in response to climate change. Rather, each species will react differently. Existing species associations will break up and new communities of plants and animals form in their place (Peters & Darling 1985);
- Ecosystem response to climate change will largely depend on competition among species to maintain themselves in new geographic areas or under changing conditions. Species such as pests, parasites and opportunists will benefit in many cases (Peters & Darling 1985);
- 'Ecosystems already stressed by human activities will be more vulnerable to climatic threats and among the first to show the effects of climate change. However, the multiple factors affecting these ecosystems will complicate the identification of strictly climatic effects' (WWF 1994b);
- 'Species adaptation abilities depend not only on genetic variability but also on dispersal and migration capacity. Genetic variability within populations and ecosystem resilience is being reduced through habitat fragmentation. It will be further reduced by pressures resulting from human-induced climate forcing at any level' (WWF 1994b);
- 'For many ecosystems, increases in the frequency and severity, and changes in the geographic distribution, of extreme weather events including drought, storms and floods will lead to some of the most serious impacts. Changes in seasonal precipitation patterns and weather variability will also be critical. These changes are likely under any climatic change scenario' (WWF 1994b).

It has been proposed that development of the concept of 'critical levels' could be used to facilitate interpretation of Article 2 of the Convention (Swart & Vellinga 1994). This concept and the related one of critical loads was previously developed in most detail for the management of acid deposition problems in Europe. The recently revised Sulphur Protocol of the UN/ECE

Convention on Long-range Transboundary Air Pollution (CLRTAP) uses critical loads of sulphur deposition for soil and water as the basis for determining necessary international reductions in emissions. However, this is a simpler problem than that of climate, as the critical loads for sulphur are based on known dose response relationships for the input of one chemical to the environment.

There have been very few attempts to set critical levels of climate change for ecosystems. Rijsberman & Swart (1990) proposed critical levels for maximum absolute change and maximum rate of change for global average parameters including temperature and sea level rise. These have been widely quoted, but lack practicality because of the inappropriateness of global averages for ecosystem risk analysis. For instance, while 1990 IPCC estimates of global sea level rise were 6 cm decade⁻¹ over the next century (Houghton et al. 1990), actual relative sea level rise for any particular coastal site is determined by a combination of sea level rise, land subsidence and sediment accretion rates, and is further influenced by human coastal management and transient events such as storms. Relative sea level rise rates for 18 sites on the east coast of the USA have been estimated to range from 0.9 to 13.0 mm yr⁻¹ (Reid & Trexler 1991).

Critical thresholds

In identifying severe climate change impacts it may be necessary to speak of critical thresholds. Thresholds of climatic events include:

- Absolute thresholds of a climatic variable which, if exceeded, lead to immediate and significant stress to an exposure unit;
- Preconditioned thresholds, where the threshold value depends on the previous conditioning of the exposure unit;
- Cumulative thresholds, where significant effects are observed on the exposure unit only after a given time has elapsed, due to the accumulated effect of previous climate;
- Coincidental thresholds, where significant effects are felt on the exposure unit due to a critical combination of climatic conditions occurring either simultaneously or consecutively.

Types of climate change threshold include thresholds of mean change, thresholds of variability change and thresholds of rates of change.

Sprengers et al. (1994) have listed examples of thresholds or threshold levels for climatic conditions and climatic change. I review additional examples in Table 2. Large amounts of relevant physiological and

Table 2. Some examples of ecological tolerances and thresholds in relation to climatic variables and global change

Biome	Region, country (Source)	Threshold	Effects	Other factors
Tidal coastal marsh	Connecticut, USA (Warren & Niering 1993)	Relative sea level rise: 10.0 to 12.5 cm century ⁻¹	Change in plant community structure. Replacement of <i>Juncus gerardi-Spartina patens</i> complex	Storms, sediment supply, human alterations
Coastal mangroves	Oceanic islands (Pacific, Indian Ocean, Atlantic) (Ellison & Stoddart 1991)	Relative sea level rise: 9 to 12 cm century ⁻¹	Mangroves not receiving significant levels of sediment input will be stressed, and at rates of sea level rise greater than 12 cm century ⁻¹ will begin to retreat	Sediment supply
Coral reefs	Indo-Pacific (Smith & Buddemeier 1992)	Temperature: 1 to 2 d exposures of 3–4°C above normal maximum. Or several weeks of temperatures 1–2°C above normal	Can cause temperature-induced bleaching. Mortality can be more than 90% at 4°C above normal maximum for even a few hours. Recovery is normal for bleaching induced by changes of less than 2°C	Irradiance (visible and UV). Variable according to taxa. Related to long-term, site-historical mean temperature of warmest month. Other human impacts
Marine	East coast, USA (Ray et al. 1993)	Water temperature: 13 to 18°C	Shad <i>Alosa sapidissima</i> track water temperatures within this range, and spawning peaks at 15°C. Temperature changes could reduce number of repeat spawners and reduce success	Overfishing
Riverine wetlands	Mississippi River, IL, USA (Janzen 1994)	Mean July temperature: increase of 4°C	Elimination of production of male offspring in a population of painted turtles <i>Chrysemys picta</i>	
Bogs	Wales/Germany/Ireland/The Netherlands (Schouten et al. 1992)	Mean annual temperature: 11°C	11°C appears to be the limiting temperature for formation of ombrotrophic bogs in NW Europe	Drought and moisture stress
Heathland	South coast and Lancashire, UK (Gates 1992)	Daily average sunshine hours: not less than 6.5 h through May	The 6.5 h May isohel limits UK distribution of sand lizards	
Alpine	Austrian and Swiss Alps (Grabherr et al. 1994)	Mean annual temperature: increase of 1 to 1.5°C over the last 100 yr	Rates of upslope migration for Alpine plants is between 1 and 4 m decade ⁻¹ , but would need to be 10 m to keep up with rate of warming	Animal movements, CO ₂ concentrations
Alpine	Yellowstone National Park, USA (Romme & Turner 1990)	Summer drought stress: increases may lead to upward shift in lower timberline of 460 m	This scenario would reduce available habitat for whitebark pine in Yellowstone National Park by 90%. Whitebark pine is a key food source for grizzly bears and Clark's nutcrackers	
Tropical montane forest	Luquillo, Puerto Rico (O'Brien et al. 1992)	Hurricane frequency: greater than once every 9 yr	Model experiments for the Tabonoco rain forest predict a trend towards early successional forest types, reduced biomass and declining populations of large commercial species including <i>Dacryodes excelsa</i> and <i>Sloanea berteriana</i>	Increase in destructive potential of hurricanes, size, and possibly in multiple landfalls
Caves	Indiana, USA (Richter et al. 1993)	Mean winter temperature: cave roost sites 5°C higher than normal	Increased winter body mass loss (42% more than control) during hibernation of Indiana bats <i>Myotis sodalis</i> . High mortality. Warm caves may act as metapopulation sinks	

Table 2 (continued)

Biome	Region, country Source	Threshold	Effects	Other factors
Temperate forest	Northern Rocky Mountains, North America (Nilsson & Pitt 1991)	Mean fire return frequency: 40 yr	Rapid decline of whitebark pine stands (over 200 yr)	(Using FRESUM model)
Temperate forest	Southern Appalachia, USA (Clinton et al. 1993)	Drought length: severe, prolonged, drought from 1985 through 1988. Annual precipitation averaged 24 % below normal, peak deficit was 31 % below normal in 1986	66 % of all canopy gaps surveyed in 1988 in a mid-elevational mixed-oak forest were created after 1986. 44 % of gaps were formed by scarlet oak <i>Quercus coccinea</i> . Canopy turnover rate based on 1988 rates would be 8 times faster (66 yr) than in 1985 (526 yr)	Scarlet oak decline can be linked to drought-induced infection with the shoe-string fungus <i>Armillaria mellea</i>
Temperate zone	UK (Dennis 1993)	Ambient temperature: prolonged summer chilling (less than 4°C). Ambient temperature above 33°C	Prolonged chilling is lethal to the small white butterfly <i>Pieris brassicae</i> . Eggs laid at ambient temperatures over 33°C are infertile	
Arctic	Circumpolar (Sveinbjornsson 1992)	Ambient temperature: treeline is correlated with mean temperature of 10°C for the warmest month and a minimum of 30 d with a mean daily temperature above 10°C	Warming would cause northward migration of treeline	
Arctic/alpine	Norway (Holten 1993)	Winter temperature: increases of 4°C or more	Warming threatens the group of Norwegian plant species limited by a January isotherm of -10°C or lower, including <i>Campanula uniflora</i> , <i>Draba alpina</i> , <i>Luzula arctica</i> , <i>Poa arctica</i> , <i>Ranunculus nivalis</i> , <i>Stellaria crassipes</i> , and <i>Carex capitata</i>	
Warm desert	USA (Nobel 1985)	Minimum winter temperature: below freezing	<i>Carnegia gigantea</i> is restricted to regions where freezing temperatures do not exceed 24 h. Four <i>Opuntia</i> spp. die at temperatures below -8°C. Only 3 of the 65 species of arborescent ceroid cacti occurring in the Sonoran desert are found north of the frost line	

ecophysiological information exist that could be reviewed and better integrated with the science informing the climate policy debate. For instance, while Table 2 gives just 1 example of a field study assessing temperature-dependent sex determination for a reptile species, Paukstis & Janzen (1990) have reviewed data from more than 170 laboratory-based temperature/sex ratio studies for 90 reptile species. A quick glance at their data reveals that changes in incubation temperature of between 3 and 5°C can have profound effects on sex determination in many species. However, this example also shows how much more work remains to be undertaken: laboratory studies have been done for only about 15 % of known reptile species, methodolo-

gies lack uniformity, and field studies have so far been rare.

In addition to examining thresholds of change, the question of whether biomes or ecosystems are threatened by climate change also needs to be looked at in the context of spatial scale. The coral reef biome may not be in great danger from climate change on a global scale (it may even expand into new areas), but individual reefs may be severely threatened. Sensitivity of individual reefs is increased by multiple and varying types of anthropogenic stresses (Smith & Buddemeier 1992).

Even if it is possible to identify change thresholds for certain species, communities or systems, it will be nec-

essary to address the issue of 'acceptable change' (Sprengers et al. 1994). There are strong indications that it will not be possible to bring absolute global warming below a level that will have significant serious impacts on at least some species and ecosystems. Therefore, choices will have to be made as to which climate change impacts on ecosystems are politically tolerable. The concept of triage has been suggested as a mechanism for determining conservation priorities (Buddemeier 1990, McIntyre et al. 1992). Hierarchies based on functional groups (guilds) and ecological redundancy have also been proposed (Walker 1992).

More scientifically supportable assessments, that are of use to policymakers, will require a regionally based approach (Swart & Vellinga 1994). Whilst biodiversity conservation is a global goal, and its achievement is to the benefit of humankind, its practice is generally focused on country- and site-specific actions. It makes sense, therefore, to try and identify critical climate change criteria and potential indicator systems and species for different regions.

In addition, radically improved capacity to predict regional climate change will be required in order to quantify threats to biodiversity and conservation at a local scale. Higher resolution models that deal better with inter- and intra-annual rainfall variability, seasonality and extreme events (especially drought) are required in order to assess ecosystem vulnerability to climate change.

A further step towards quantifying ecological limits to climate change is to identify key areas for concentrating biodiversity conservation efforts. Attempts to do this for terrestrial biodiversity have often focused on the identification of centers of endemism for higher plants and birds (Groombridge 1992). Other categories of conservation priority would include species listed under national statutes such as the USA's Endangered Species Act, or sites designated as protected areas, national parks and World Heritage Sites. It is also possible to combine information on species endemism and richness with data on protected areas, legislation, degree of threat and selected socio-economic indicators to produce a conservation potential/threat index which can be used to prioritize conservation investments (Dinerstein & Wikramanayake 1993).

It could reasonably be argued that increased rates of environmental degradation in any ecosystem will lead to further loss of biodiversity. For most threatened species and habitats, climate change does not present the most immediate threat, but it does represent a long-term, ultimate threat (Franklin et al. 1990). The potential impacts of climate change will be an academic question in relation to ecosystems that we are unable to save from current and immediate threats. Many ecosystems are under severe pressure already, and the

addition of climate impacts to existing problems could, in many cases, have severe additive effects.

For some ecosystems, such as coral reefs (Smith & Buddemeier 1992) and tropical forests (Whitmore 1993), climate change is a very low-level threat in comparison to current degradation, but should current conservation efforts be even partially successful, the threat is likely to grow stronger. In coming decades, as habitats decline and become more fragmented and their communities become less diverse, there is every likelihood that the rate of climate change will increase. As natural systems lose their resilience, the threat from climate impacts will become more acute and act as a cumulative stressor in addition to existing problems. Much of today's discussion about climate change centers on predicting what could happen to today's ecosystems in several decades' time. In fact, many of those ecosystems will have already changed radically during the next 10 to 20 yr, and so more attention should be focused on what effects climate will have on even more severely degraded habitats than those present today.

The case of tropical forests

There has also been a tendency to assume that the major impacts of climate change on ecosystems will be felt where the temperature increase is greatest, most likely towards the higher latitudes. This may deflect attention from possible impacts on biodiversity in the tropics, where changes may be influenced more by changes in rainfall distribution within and between years, extreme events such as tropical storms and fires, shifts in seasonality and human land-use feedbacks. The tropical forest regions provide just such an example where temperature changes may be small but other climate related impacts may have very deleterious effects.

For instance, changes in seasonal precipitation, length of seasons and frequency and intensity of extreme events may be highly disruptive of biological diversity in tropical seasonal forests. The vertebrate fauna of these forests can be extremely sensitive to changes in the abundance of food resources during different stages of the annual cycle. Unusual weather conditions can cause severe population declines amongst many species of birds and mammals. If the frequency of such extreme events increases to a level where species are unable to recover to their normal or viable population levels between events, major shifts in ecosystem balance can occur.

Keystone species, such as palms or figs, are critical in providing animals with food resources at times of seasonal scarcity (Hartshorn in press). Seasonal rainfall

fluctuations exacerbated by global change could increase food scarcity. Stiles (1992) reported that severe drought in the Caribbean lowlands of Costa Rica in 1973 affected the flowering of several important food plants for a hummingbird called the long-tailed hermit. In particular, the failure of the food-plant *Heliconia pogonantha* to produce enough flowers to provide sufficient nectar during the first half of the breeding season resulted in severely reduced breeding success for the hermits. Stiles (1992) estimated that a 3 to 4 yr recovery period would be required for hummingbird populations to recover to pre-drought levels.

A different type of seasonal disruption was observed at Barro Colorado Island (BCI) in Panama during 1970. An unusually wet dry season prevented many trees from flowering or fruiting, and resulted in a famine for forest vertebrates, with large numbers of frugivorous animals such as howler monkeys and agoutis dying (Foster 1982). In 1983, BCI experienced an extended dry season, 2 mo longer than normal, that led to much increased tree mortality in the succeeding years. These types of disruptions can have strong knock-on effects in the complex systems of tropical forests where complex and delicate relationships are common amongst plants and their pollinators and agents of seed dispersal including insects, bats, birds and mammals (Hartshorn 1992).

Amphibian populations appear to be undergoing decline worldwide, including in areas of tropical forest habitat largely unaffected by habitat destruction (Blaustein et al. 1994). Climatic influences, especially abnormally low rainfall and high temperature anomalies associated with the 1986-1987 El Niño Southern Oscillation (ENSO) cycle are thought to be significant causal factors in the catastrophic decline of golden toad and harlequin frog populations in Costa Rica's Monteverde cloud forest (Pounds & Crump 1994). The high rates of endemism and narrow niches of neotropical anurans may make them particularly sensitive to drying trends and changes in seasonality (Donnelly pers. comm.). In general, it is likely that increased drought and perturbations in seasonality may be the most significant threats to tropical forests from climate change, and that forest fragmentation and human pressure will exacerbate the problems (Bawa & Markham 1995).

The biodiversity of cloud forest systems may be especially sensitive to climate change. Any lifting of the cloud cap or significant changes in occult precipitation could have severe consequences, particularly for plants of the high canopy such as ferns and orchids (Cheung 1992). Tropical montane dwarf forest may also be sensitive to increased frequency of hurricanes, as recovery from disturbance can be exceptionally long. It has been estimated that this type of forest at

Luquillo in Puerto Rico will take more than 250 yr to recover from the impact of Hurricane Hugo in 1989 (Scatena 1993).

Adaptability as measured by migration and distribution

Central to the resolution of the question of how to define the phrase 'adapt naturally' as contained in Article 2 of the UNFCCC is the question of which climate change impacts species and natural communities can adapt to and how fast. Natural adaptation can take a number of forms, including acclimatization, evolution or migration. There is rather poor information on the first two, but it is possible to make some rough quantifications for migration rates. Paleoecological evidence points to possible maximum migration rates for a number of tree species in the northern hemisphere, and some of these are presented in Table 3.

In the temperate regions, because of a combination of slow migration rates and the temperature shifts that occur when moving between latitudes, some species will be under stress at temperature changes of 0.0015 C yr^{-1} and unable to keep up with change at $0.00075 \text{ C yr}^{-1}$. The threshold of migration stress is exceeded in most IPCC scenarios. Furthermore, the achievement of optimal migration rates depends on factors other than temperature change. Human land-use patterns and the increasingly fragmented nature of temperate forests now present formidable barriers to natural migration (Peters & Darling 1985). Community disruption and inter-specific competition, particularly with weedy species and aliens, will play a major part in migration success. The availability of suitable substrate is also a requirement for movement, and in many cases suitable mycorrhizal fungi and rhizosphere bacteria will need to be present in the newly colonized soils (Perry et al. 1990).

Table 3. Tree species migration rates noted from palaeoecological studies

Tree species	Migration rate (m yr ⁻¹)	Source
Black spruce	2000	Dennis (1993)
White spruce	2000	Dennis (1993)
North American spp.	100-450	Morse et al. (1993)
Engelmann spruce	10-200	Peters & Lovejoy (1992)
Scots pine	40-80	Peters & Lovejoy (1992)
American chestnut	100	Davis (1983)
American beech	50	Davis (1983)

There seems to be little disagreement in the literature that a warming of as little as 1°C would have major implications for the boreal forests, with potentially at least a 25% reduction in global extent. Major dieback would occur at the southern borders of the ranges in North America and Russia (Solomon 1992).

Migration is an issue for fauna as well as for flora. For example, although most birds are extremely mobile, some species will not cross open clearings even as small as tree-fall gaps. Others are associated with specific vegetation species or formations. Required habitat species may fail to migrate, such as Jack pine in the well documented case of Kirtland's warbler (Botkin et al. 1991). Annual migrants depend on the availability of specific habitats for 'refueling' stops on their journeys, require satisfactory conditions for fat build-up and moult prior to setting off, and may migrate in synchrony with the availability of transient food sources. For example, several species of shorebird rely on relatively few coastal refueling stops on the Atlantic and Pacific flyways. Alternative sites with sufficient predictability of timing and supply of food probably do not exist (Skagen & Knopf 1993). Coastal inundation or other climate impacts could seriously affect these species. For example, some populations of shorebirds also depend on synchronous timing of horseshoe crab spawning in Delaware Bay (USA) and on insect emergence at their arrival in the Arctic tundra. Both these events probably are significantly climate controlled.

Insects too may face migration problems. Dennis (1993) has estimated that a north European butterfly with a life span of 5 d would need to migrate at 213 m h⁻¹ for 6 h a day in order for populations to track changes in climatic zones resulting from a 2°C change by 2040. This would be easy for the small white or the small tortoiseshell, but probably impossible for the silver-studded blue, which has a measured maximum migration rate of under 50 m d⁻¹.

Similar considerations apply for freshwater fish, which, despite being highly mobile and, in the case of many species, migratory too, are strongly limited by the physical distribution of rivers and lakes. Most fish have limited tolerances for changes in water temperature, and where water warms as a result of climate change, there will be very significant threats for species that are unable to find their way to cooler waters.

CONCLUSIONS

An inescapable conclusion from the above discussion is that the science of the ecological impacts of climate change should be a fully integrated part of conservation biology. There are many points of contact between the debates about climate change and about

ecosystem management, and yet far too few linkages are currently being made. A number of attempts to draw lessons for conservation from assessments of the potential impacts of climate change have been made (e.g. Peters 1985, McNeely 1990, Parsons 1991, Markham et al. 1993, Turner et al. 1994), but a strong connection has not yet been established. Vitousek (1994) suggested that ecologists need to become more connected with experts in other disciplines and to attempt to cross barriers and help provide a broader understanding of the crucial issues of global change, including climate change, to policymakers and the public.

Conservationists tend to strongly emphasize the importance of species protection (Walker 1992) and protected area management, but managing for climate change will require, in addition, greater attention to ecosystem processes and overall land-use patterns. Current conservation management and strategy tend to be characterized by a form of short-termism which acknowledges driving causes of environmental degradation, but fails to take them adequately into account. An example of this is the general lack of integration of demographic data into the planning of conservation field projects in developing countries (Dompka 1994). Climate change too is often seen as a future problem that is currently insignificant in comparison to more immediate pressures. This results in the development of conservation strategies that will sometimes be in place for decades, but which have not taken future environmental changes, including climate, into account. Corridor systems between reserves, for instance, may be developed in complete ignorance of potential directional impacts of climate change on species distribution (Halpin pers. comm.). Efforts to develop conservation plans and strategies that will be meaningful as the climate changes are, however, severely hampered by the very low confidence with which local climate changes can currently be predicted.

The gradual shift in priorities in recent years from structurally based, species-oriented conservation to an approach rooted in preserving ecological processes and complexity (Agardy 1994) will require increased attention to the climate issue if it is to be successful. Recent advances in the development and management of marine protected areas have been stimulated by the realization that many concepts derived from terrestrial conservation are of little relevance in the marine environment (not least the idea that you can demarcate an area of sea and thereby protect it). And just as the marine conservation debate is now centering on issues of ecosystem process, multiple use and interaction of wide-ranging forms of environmental degradation and stress, so too is the forest management debate changing. An ecosystem management approach is being

proposed to replace current forest management and landscape management approaches. The latter is based on the assumption that intensive management can mimic natural processes and transient events (e.g. clear-cuts mimic windblow and fire), whilst the former seeks to maintain ecological integrity and harmonize human needs with sustainable utilization of natural resources.

'Ecosystem management integrates scientific knowledge of ecological relationships within a complex sociopolitical and values framework toward the general goal of protecting native ecosystems integrity over the long-term' (Grumbine 1994). The long-term goals of ecosystem management will be impossible to achieve if climate change is not considered. Of critical importance, however, is the confluence of interests between the proponents of ecosystem management and those advocating climate change adaptation strategies. Both groups believe it is necessary to create more protected areas, allow for flexible boundary zoning, develop corridor and buffer systems, aim for ecosystem and landscape heterogeneity, reduce human impacts in core zones and pay greater attention to natural succession and transient events (e.g. Peters & Darling 1985, Franklin et al. 1990, McNeely 1990, Markham et al. 1993, Noss & Cooperrider 1994).

The political and scientific importance of understanding ecological responses to climate change underlines the need for radical improvement and expansion of biological monitoring activities. To give a few key examples, a greater emphasis will need to be placed on baseline studies, long-term ecological monitoring (particularly along climate gradients), large-scale field-based experimental manipulations, multiple-stress interactions, response to climate variability, landscape ecology, evolutionary adaptation and population genetics. Several recent reviews have proposed improved climate change research programs with strong monitoring components (e.g. Bernabo & Eglinton 1992, Chapin et al. 1992, Kingsolver et al. 1993), but action to implement such recommendations is slow in coming.

There is a need to develop mechanisms for risk assessment that will allow judgments to be made about strategies to reduce emissions in order to reduce environmental degradation. Cairns & McCormick (1992) have argued strongly that environmental changes such as global warming will require that ecosystem monitoring becomes integral to methodologies for ecological risk assessments. They propose also that indicators of ecological integrity need to have value in assessing compliance with ecosystem protection goals, that they must be able to be used to help diagnose the cause of the change, and that they can be used as an early warning system.

National, regional and global monitoring programs could better meet the needs of climate change research and policy development if existing climate research programs, long-term ecological research site networks and global monitoring systems could be linked more effectively. Identification of priority biomes for global monitoring could be based upon a combination of criteria that might include: (1) global representation; (2) biological importance; (3) existing research network, and; (4) sensitivity to climate change. The choice of biomes should include terrestrial and marine, and provide the opportunity to integrate with monitoring of indicator species or taxonomic groups, such as butterflies or amphibians.

In order to fulfill these criteria, several biomes could be proposed for the development of multi-disciplinary climate and biodiversity monitoring programs, e.g. coral reefs, tundra/taiga ecotone, montane ecosystems, and coastal wetlands. Between them, these biomes are found in virtually every country of the world, they are fully representative of latitudinal and altitudinal scales and they cover biological diversity and biological productivity. Within each biome there is a range of human intervention from high impact to nearly pristine, and all are well-represented amongst global protected areas and existing scientific research programs. Finally, in addition to exhibiting complex responses to climate and interacting effects, these biomes are most likely to show signal impacts from the climate change parameters easiest to measure (temperature, precipitation and sea level rise) and, therefore, can serve an early-warning function.

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