Implications of Climate Change for Species Conservation

Briefing paper

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Aims and Scope

The aim of this paper is to provide a review of some of the issues we think are relevant to climate change and species conservation, and to provide a stimulus for discussion. It does not claim to be exhaustive, and makes only limited reference to the numerous experiments on the effects of CO_2 or temperature increase in microcosms; their relevance to natural systems where there may be a multitude of interacting factors has yet to be demonstrated. We have tried to identify current gaps in our understanding and to generate a working set of ideas for future research. This list is sure to be greatly modified during the workshop, and we hope the ideas will become more focused.

The paper reflects our biases and ignorance. We hope the participants at the workshop will help point out the worst examples!

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Climate Change and Species Conservation

Introduction

Traditional threats to species conservation have principally been the effects of habitat loss or fragmentation, introductions of alien species, hunting and pollution. Increasing concentrations of greenhouse gases in the atmosphere are expected to have significant effects on global climate in the coming decades and centuries, and the impact of this has already been detected in biological systems (Hughes 2000). The effects of climate change are pervasive and transnational, whereas most threats are relatively localised and establishment of well-policed reserves can do much to alleviate the problems. The potential consequences of climate change are sufficiently great and immediate for them now to be of central importance to conservation planning (Orlando & Smeardon 1999).

Scenarios for the potential human impact on the biodiversity of terrestrial and freshwater biomes have been developed by Sala et al. (2000). They model the consequences of predicted changes in land use, climate, nitrogen deposition, biotic exchange (species introductions and invasions), and CO_2 concentration on the biodiversity of different biomes, making assumptions about the sensitivity of each biome to each of these main drivers of change. Across all biomes, changes in land use are predicted to have the greatest effect on biodiversity (Fig 1). However, there is considerable variation among biomes, with, for example, Arctic biomes being most sensitive to climate change, tropical forests most sensitive to land use, and lakes most sensitive to biotic exchange (Fig 2). These drivers may or may not interact, and the interactions may be synergistic or antagonistic. Under the scenarios of no interaction or synergistic interaction of drivers, Mediterranean ecosystems, savannahs and grasslands are predicted to experience the greatest biodiversity loss, because they are sensitive to all drivers (see Fig 2). Under a scenario of antagonistic interactions, tropical forests, southern temperate forests and the Arctic are predicted to suffer greatest biodiversity loss because a single driver dominates their response.
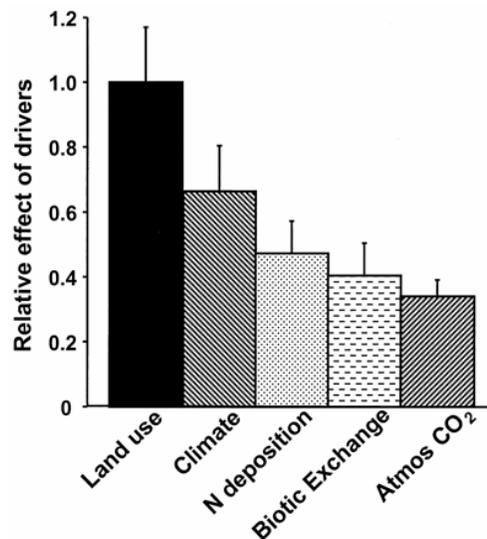
Figure 1. Relative effect of major drivers of changes on biodiversity. Expected biodiversity change for each biome for the year 2100 was calculated as the product of the expected change in drivers times the impact of each driver on biodiversity for each biome. Values are averages of the estimates for each biome and they are made relative to the maximum change, which resulted from change in land use. Thin bars are standard errors and represent variability among biomes. (Sala et al. 2000)

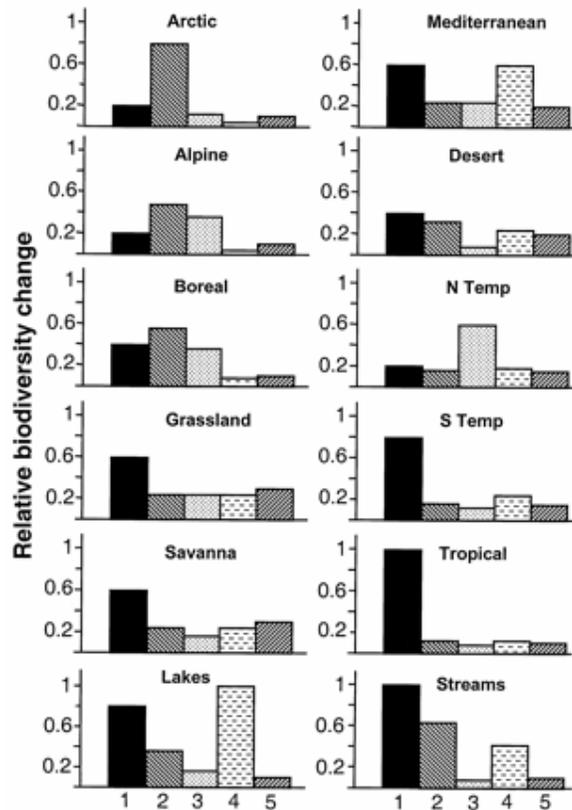Figure 2. Effect of each driver on biodiversity change for each terrestrial biome and freshwater ecosystem type calculated as the product of the expected change of each driver times its impact for each terrestrial biome or freshwater ecosystem. Values are relative to the maximum possible value. Bars: 1, land use; 2, climate; 3, nitrogen deposition; 4, biotic exchange; 5, atmospheric CO2. (from Sala et al. 2000)

The authors acknowledge the many uncertainties in this type of analysis, but nevertheless present clear evidence for the potential importance of climate change for biodiversity loss. Many of the biological and conservation "surprises" of the next century are likely to stem from the interaction of climate change with these other factors.

Climate Change
(Note: this information is largely based on the1996 IPCC results, which are in the process of being superseded. The most recent scenarios should be available at the workshop).

Change in temperature
Mean global temperatures increased by 0.25°C per decade over the latter part of the 20th century. The warming trend is significantly greater than that of the early part of the century when data are corrected for ENSO (El Niño Southern Oscillation) events and volcanic activity (Wigley 2000). The latter 20th century is anomalous in the context of at least the past millennium. The 1990s was the warmest decade, and 1998 the warmest year, at moderately high levels of confidence. The 20th century warming counters a millennial-scale cooling trend which is consistent with long-term astronomical forcing (Mann et al. 1999). Current GCMs (General Circulation Models) predict that future temperature change will range from 0.1°C per decade at the equator to 0.8°C per decade at the Poles. To put this rate of change in context, since the end of the last glacial period 18,000

years BP (Before Present), global temperatures have risen by $\approx 5 \pm 1°C$, corresponding to a mean increase of approximately $0.003°C$ per decade (although most of this increase took place over a relatively short period). There is some evidence from Greenland ice cores of large, rapid changes in climate in the Northern Hemisphere (Grootes et al. 1993), with changes of 6 or 7° occurring over a few decades. Predicting such extreme climate anomalies and their effects on the biota remains a challenge.

Change in precipitation

GCMs generally predict an increase of 5-10% in global mean evaporation from the oceans and a corresponding increase in global mean precipitation. The general increase is not likely to be uniform however, and simulations suggest stronger intensity of monsoons, storms and daily precipitation, even in areas where total number of rainfall days decreases (Harvey 2000). The moisture content of soil is an important component of climate change and if levels of soil moisture were maintained the effects of climate change would be less severe. However soils are in general predicted to become dryer as a result of increased evapotranspiration, and exacerbated in part by the trend of increased number of rain-free days and heavy storms, where water is lost due to surface runoff. These changes will strongly affect the soil which in many cases already has reduced fertility, organic matter content and structure as a result of inappropriate land management (Rosenzweig & Hillel 2000).

Frequency of extreme events

Changes in the frequency and intensity of extreme events may be at least as important for biota as changes in mean temperature or precipitation (Parmesan et al. 2000, Easterling et al. 2000b). Estimating whether the climate in general has become more variable or extreme is hampered by access to high-quality, long-term data which are required to detect trends in rare events (Easterling et al. 2000a). For some areas, there have been significant changes in extreme temperature or precipitation, although the frequency of others, such as landfalling Atlantic hurricanes, may not have changed (Easterling et al. 2000a, b).

ENSO events can have profound consequences at the population, community and ecosystem level (Holmgren et al. 2001). They are often associated with increased precipitation in arid areas, and drought in moist habitats. These may lead to episodic recruitment of trees and shrubs, or canopy tree mortality and fire, respectively. ENSO events occur at irregular intervals, typically every 3-6 years, although recent models have predicted that the frequency of these events will increase over the coming decades as a consequence of global warming (Timmermann et al. 1999).

At a more local scale, unseasonal frosts can have catastrophic consequences for populations of animals, either directly or through death of all or part of their food plants, and may influence the geographical distribution of species (Inouye 2000).

Sea-level rise

As a consequence of melting polar ice-caps and glaciers, and particularly of the thermal expansion of the sea, the last IPCC assessment (1996) forecast maximum sea level rise of between 1.5 and 3 meters after about 500 years (25-70 cm by the year 2100). More recent calculations suggest that the rise may be as much as 7-13 m over the next millennium (IPCC unpublished). Even more modest increases in sea level will affect large areas of land and human populations in low-latitude, species-rich countries (Table 1). There will be direct consequences for the conservation of species in coastal areas, plus the effects of human migration inland. In Europe, there is predicted to be almost complete loss of current wetlands in the Baltic and Mediterranean due to sea level rise by 2080, although new areas will also be created (Parry 2000).

Table 1. Potential impacts of a 1 m sea level rise on selected low latitude countries (from McMichael et al. 1996)

Country	People affected		Land lost	
	1000s	% total	km^2	% total
Bangladesh	71000	60	25000	17.5
Belize	70	35	1900	8.4
Guyana	600	80	2400	1.1
India	7100	1	5800	0.4
Kiribati	100	4	12.5	?
Malaysia	-	-	7000	2.1
Marshall Is.	20	100	9	80.0
Nigeria	3200	4	18600	2.0
Senegal	110	>1	6100	3.1
Tonga	30	47	7	2.9

Remedial action
Action to halt or reduce climate change, most obviously by reducing CO_2 emissions from fossil fuel burning, has been proposed, although the recent failure of governments to ratify the Kyoto protocol suggests that this is not imminent. Furthermore, even if CO_2 emissions were to stop immediately an average warming of 1-2°C would still occur. Mitigation strategies such as the possible widespread planting of forests to sequester carbon would be of more immediate interest to conservation planning. Generalisations about the impact on biodiversity are difficult. Much will depend on where forests are planted (whether in existing degraded forest, or via conversion of grassland or agricultural land), what types of trees are planted (mixed stands of native trees may be expected to have greater conservation value than monoculture plantations of exotics) and the intensity of management. Action to halt the decline of old-growth forests would produce the greatest immediate benefit to conservation.

Research priorities
For conservation biologists to incorporate climate change into planning, the following would be useful
- Climate change scenarios at the regional/ecosystem/biome scale (recognising that finer scale scenarios are unlikely)
- Reduced uncertainty among models
- Data on climate variation over the last 10^2 10^3 10^4 10^5 10^6 years at the above scales, in particular for areas of high conservation importance ("hotspots" – see later). Understanding the variation in climate experienced by species in an assemblage in the past will help predict their response to future change
- Improved predictions of the frequency and magnitude of extreme events
- How will the spatial patterns of climate change during the transition to a warmer climate differ from those once a new set of climatic conditions stabilise (if they do).

Species response to climate change
The response of species to atmospheric and climate change may be grouped into effects on distribution, physiology, phenology and interactions.

Distribution
Responses to previous climate change
In the face of environmental conditions changing beyond their physiological tolerance, organisms may move, adapt or become locally extinct. Evidence from the Pleistocene glaciation suggests that

all these processes occurred. Despite the individualistic responses of many species, many communities were resilient to change and ultimately came to closely resemble the original communities (Davis & Zabinski 1992, Graham & Grimm 1990), with few global extinctions (Coope 1995, Cronin 1985, Potts & Garthwaite 1991, Paulay 1991). However, community reconstruction often takes many millennia, suggesting that projected climate change may lead to continuous changes in biological communities for the next few centuries at least.

Recent changes
A growing body of evidence suggests that species' ranges have moved polewards and upward in altitude in response to warming in the late 20th century, including arctic foxes (Hersteinsson & MacDonald 1992), mountain plants (Grabbherr et al. 1994), intertidal organisms (Barry et al. 1995, Sagarin et al. 1999), northern temperate butterflies (Parmesan 1996, Parmesan et al. 1999), tropical amphibians and birds (Pounds et al. 1999) and British birds (Thomas & Lennon 1999). When there is detailed knowledge of the biology and habitat requirements of a species, these data can be combined with known climate changes to explain shifts in the distribution of species (e.g. Hill, Thomas & Huntley 1999).

None of the observed shifts in distribution can be unequivocally attributed to the effects of climate change, and invoking climate change as the primary cause of observed results has attracted criticism. These at least in part reflect the difficulty of measuring the biological responses to climate change, as
    (a) there is likely to be a significant time-lag in responses,
    (b) responses are measured in different ways in different places (measurements of physical parameters are more standardised),
    (c) climate change is expected to affect different organisms in the same place in different ways, and
    (d) organisms also respond to other types of environmental change (the severity of which is often likely to be correlated with climatic gradients).

We think the widespread acceptance (or rejection) of the biological impact of climate change is likely to take at least another decade of accumulating evidence and analyses. There are five criteria which would need to be met to genuinely demonstrate distribution changes as a response to climate change:
    (a) all species in an assemblage are observed over a substantial area, preferably including all range margins of many of the species,
    (b) showing that their changes correlate finely with climate fluctuations over a long time period,
    (c) species respond in different ways to climate AS PREDICTED by differences in their biology,
    (d) that they respond in different quantitative ways in different areas, correlated with differences in the climate in different parts of their range, whilst
    (e) controlling for changes in abundance in different regions (which may be spuriously correlated with climate gradients because of differences in land use).

Therefore, as things stand we can only conclude that widespread changing distribution patterns are *consistent* with the predicted responses to climate change. But this clearly an area where the precautionary principal should apply, and the conservation implications should be addressed now, rather than after the damage has been done.

Future changes
Predicting future changes in the distribution of species has typically been attempted by measuring a range of climatic variables (sometimes also including other biotic, topographical and historical data) within the known range of an organism, generating a 'bioclimatic range'. The future presence or absence of these conditions under climate change scenarios can then be used to predict the ensuing amount of suitable habitat. One example is the BIOCLIM model (Lindenmayer et al. 1991) which uses 24 variables to characterise average conditions, extremes and seasonality of climate.

This has been used to predict a significant reduction in bioclimatic range for 41 of the 42 species of animals selected in south-eastern Australia, including the 'extinction' of a bioclimatic range (Brereton et al. 1995). Increased confidence may be placed in this sort of prediction if the models can successfully predict the current occurrence of species outside their known range, and this has been achieved with the BIOCLIM model for an Australian shrimp (Tyler et al. 1996). The method has been criticised as it fails to incorporate interactions among species, such as competition, predation and parasitism (Davis et al. 1998a, b, Lawton 1998), although the criticisms largely stem from work on laboratory microcosms of *Drosophila*. Nevertheless, this ecophysiological approach has been successfully used to predict species' distributions (Hodkinson 1999), and in practice it may be the only approach available (Baker et al. 2000). The utility of this approach is likely to be greatest where species' ranges are largely determined by climate, e.g. at northern or altitudinal limits, or dry margins, rather than through their interactions with other species or human activities.

Physiology

Rates of photosynthesis and the growth and productivity of plants respond to increased atmospheric CO_2 concentration and temperature. Elevated CO_2 can stimulate carbon assimilation, changing the C:N ratio of tissues, alter patterns of carbon allocation and increase growth. While animals may use CO_2 concentration as a stimulus for maintaining homeostasis, or during host location in biting flies for example, they are unlikely to be affected by the predicted changes in atmospheric CO_2 concentration. Humans live in submarines at 9,000 ppm CO_2, beehives are maintained at 30,000 ppm CO_2, and soil cavities, termite nests and mammal burrows may contain 50,000 ppm CO_2, so changes from 350 to 700 ppm CO_2 are unlikely to be significant (Graves & Reavey 1996). The indirect effects through their food plants are far more important.

Effects of temperature and moisture availability are likely to have extremely important physiological effects on virtually all species, especially in climatically marginal areas. While there may be particular effects on some species, e.g. those with temperature-dependent sex determination (Janzen 1994), the primary importance for conservation is via their effects on abundance and distribution.

Phenology

There are numerous reports of advanced phenology over recent years in a range of organisms. These include earlier flight times in insects (Fleming & Tatchell 1995, Ellis et al. 1997, Woiwod 1997), earlier egg-laying in birds (Crick et al. 1997, Crick & Sparks 1999, Brown et al. 1999), breeding in amphibians (Beebee 1995) and flowering of trees (Walkovsky 1998). Organisms use different cues to trigger phenological events, and some of these will respond to climate change (e.g. temperature) while others will not (e.g. daylength). These changes, and a *relative* change in timing, may be particularly important where there are tightly coupled relationships among species (e.g. plant-herbivore), or for migrating species. Adult butterflies emerging before flowering may starve (e.g. Singer & Thomas 1996, Thomas et al. 1996), and migratory species using climate cues for migration in their starting area may not find food available at their destination (Inouye et al. 2000).

Interactions

Changes in interactions among species will be a consequence of differential responses to climate in the preceding categories. Assemblages are unlikely to shift *en masse* owing to differences in co-occurring species' sensitivity to temperature (e.g. Willott & Hassall 1998) and their potential migration rates (e.g. Malcolm & Markham 2000). The complexity of the interactions among species in an assemblage can lead to large, unexpected responses to climate change. In the Chihuahuan desert, regional climate change since the mid 1970s has resulted in a 3-fold increase in shrub density, while populations of granivorous rodents and ants have fluctuated widely, with local extinction of some previously abundant species and population increases of the previously rare (Brown et al. 1997).

There has been particular interest in the potential for pests and pathogens to shift their distribution or increase in virulence as a consequence of climate change. This has predominantly focused on agricultural crops (Baker et al. 2000, Chakraborty et al. 1998, Coakley, Scherm & Chakraborty 1999), forests (Ayres & Lombardero 2000) or human diseases (Pascual et al. 2000, Rogers & Randolph 2000). There is also evidence for changes in the nature and frequency of diseases in wild populations of amphibians (Alford & Richards 1999, Carey 2000) and marine organisms (Harvell et al. 1999).

Research agenda

Monitoring changes in species distribution as a result of climate change requires an international approach, and co-ordination of effort. A more efficient use of resources would be achieved if monitoring was at least in part attached to existing projects, such as the IGBP/GCTE global transects which are being developed as a tool for global change research (Steffen *et al.,* 1999). The transects comprise a set of sites around 1000 km long and large enough to contain several grid cells of global vegetation and climate models. Each transect has been designed to sample variation of a major environmental factor as it influences terrestrial ecosystem structure and functioning (e.g. carbon and nutrient cycling, biosphere-atmosphere interactions, hydrological cycling). Fifteen transects have been established so far (Figure 3), and approximately half are actively being used to acquire data along environmental and land-use gradients. Further utilisation of these transects would add enormous synergy to global studies on the impact of climate change on biodiversity, and the data acquired would greatly assist in the further development of vegetation and climate models. Such an approach would be consistent with the goals and objectives of the Convention on Biological Diversity and the United Nations Framework Convention on Climate Change. Clearly, not all these transects will be in optimal locations and it is likely that additional, smaller, transects or modifications of existing IGBP transects may be needed.
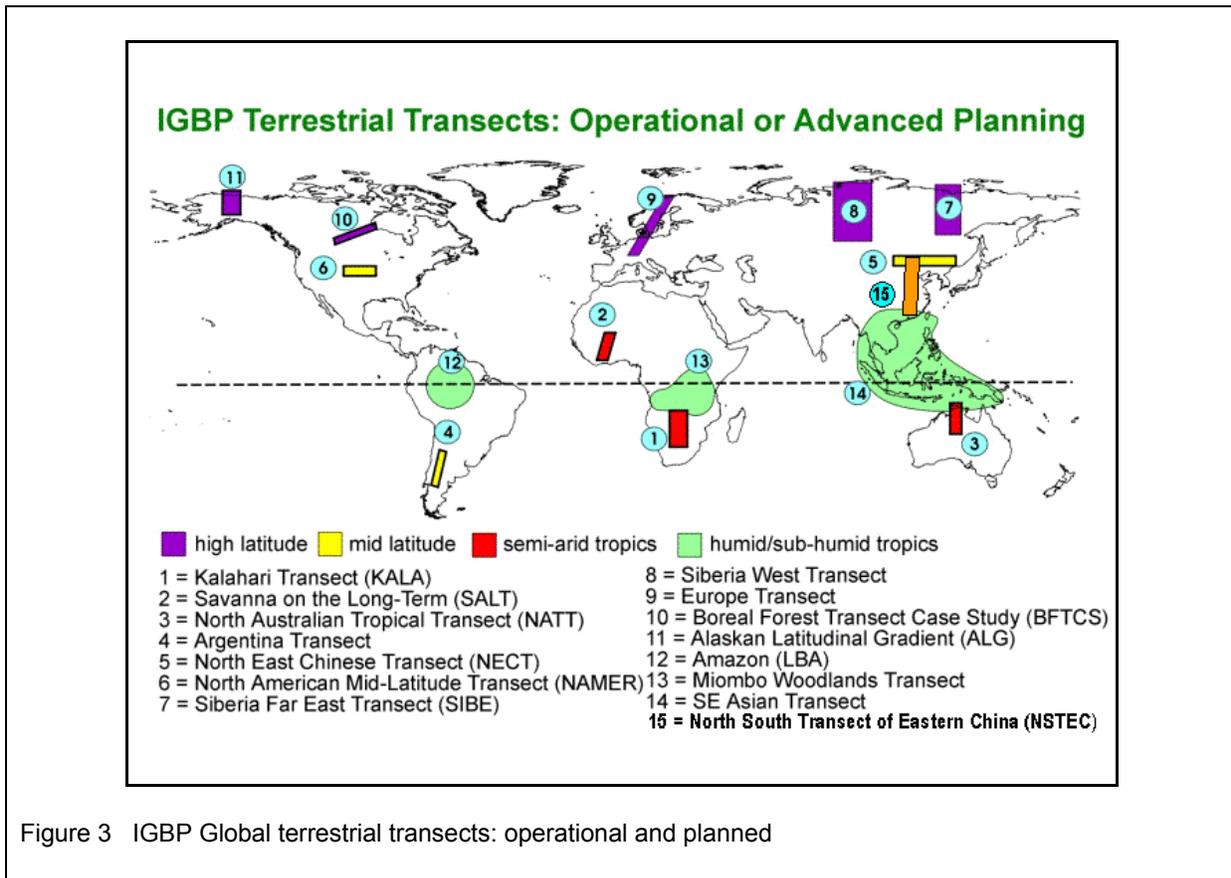

Figure 3   IGBP Global terrestrial transects: operational and planned

Centres of endemism (hotspots)

Biological diversity is not evenly distributed across the Earth. In general, species richness per unit area increases from high latitudes to the equator, although there are exceptions to this rule within certain taxa, and the pattern may be considerably disrupted by a range of environmental and historical variables (Gaston 2000). Additionally, there are areas with particularly high concentrations of endemic species which are also suffering large rates of habitat loss. Given limited resources, these biological 'hotspots' have been proposed as conservation priorities (Fig. 4; Myers et al. 2000).
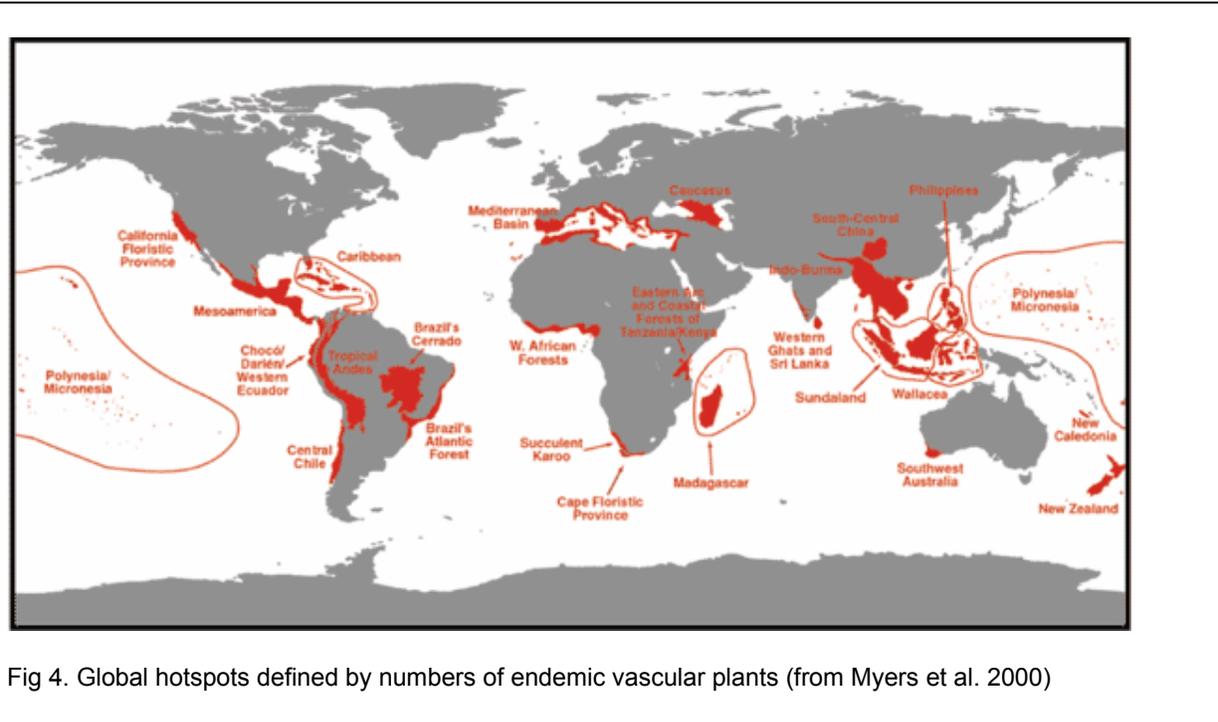

Fig 4. Global hotspots defined by numbers of endemic vascular plants (from Myers et al. 2000)

These 25 hotspots encompass 44% of vascular plants and 35% of vertebrates (excluding fish) in 1.4% of the land surface of the Earth (the areas of endemism are subsets of the areas shown in red). While exceptionally rich in endemics, some areas have not been included in the list of hotspots as they are currently under less human pressure. These include areas of tropical forest in the Amazon, Congo and New Guinea. The use of endemic plants to define hotspots results in somewhat different (and fewer, larger) areas than if, for example, endemic birds are used (Stattersfield et al. 1998). Tropical areas tend to be similarly rich in taxa, whereas semi-arid Mediterranean-type ecosystems have high plant diversity and endemism but low numbers of endemic vertebrates. While other patterns may be generated using different taxa, or by estimating numbers of rare, endangered or taxonomically distinct species, hotspot analysis could be a useful approach to setting conservation priorities at broad geographical scales (Reid 1998). At smaller scales, correlations among richness, rarity or endemism of different taxa may break down, and these scales are those typically used by conservation planners (Prendergast et al. 1993, Reid 1998, Mace et al. 2000). However, for the purpose of this analysis, a broader geographical scale is appropriate as reliable climate change scenarios are unlikely to be developed for localised areas.

There are several hypotheses for the evolution and maintenance of centres of endemism (reviewed in Haffer 1997). These include historical causes and current environmental conditions, although the relative importance of each is difficult to establish. Recent research on the endemic bird areas (EBAs) of East Africa used surrogates of climate derived from satellite data to predict EBAs with an accuracy of 89%, strongly suggesting that current environmental conditions account for a large part of the variation in distribution of these EBAs (Johnson et al. 1998). Modelling studies also suggest climate, rather than history, as the primary driver of plant diversity at regional

and global scales (Kleidon & Mooney 2000, O'Brien et al. 2000). Thus, relatively small centres of endemism hold a substantial portion of the Earth's biodiversity, are suffering high rates of habitat loss and they may to a large extent owe their existence to prevailing climatic conditions. Furthermore, most of these hotspots are in areas affected by El Niño events (see Fig.1 of Holmgren et al. 2001). Their vulnerability and response to climate change is therefore of paramount conservation importance.

In view of their concentrations of endemic species and threat of habitat loss (Myers et al. 2000, Stattersfield et al. 1998), and sensitivity to other anthropogenic disturbance (Sala et al. 2000), three biomes perhaps merit particular attention.

Tropical forests

Tropical forests (including cloud forests) are the most species rich terrestrial ecosystems. They contain the 'hottest hotspots' (Myers et al. 2000), and of the 218 Endemic Bird Areas, 83% are in forest habitat, mostly in the tropics (Stattersfield et al. 1998). There are predicted to be small increases in temperature over much of the tropics, whereas rainfall patterns will vary. However, any slight increase in total precipitation masks the crucial point that there is likely to be an increase in heavy storms coupled with more rain-free days and drought. A trend of increased drought frequency in recent decades has already been detected in Borneo (Walsh & Newbery 1999) and Panama (Condit 1998a). Primary forests vary in their susceptibility to drought (e.g. Condit et al. 1999), and drought is an entirely natural phenomenon which, in conjunction with natural fires, has shaped the structure of many tropical forests (Walsh & Newbery 1999). However, although primary forest is generally resistant to fire, selectively logged forest is more open and fire-prone (Woods 1989). Wood and litter in large gaps dries more quickly and is then susceptible to fire (Holdsworth & Uhl 1997). Increased drought frequency and intensity, as well as higher temperature, is likely to increase the probability of fires starting or spreading, with severe consequences for biological diversity (Taylor et al. 1999). Furthermore, tropical forests are already under intense pressure from logging, fragmentation and hunting, and the projected effects of climate change will add to this (Bawa & Markham 1995, Laurance 1998).

There is now a network of relatively large (up to 50 ha) enumerated plots in tropical forests (Condit 1998b). While they are not large enough to cover ecotones, or to record widespread movement or loss of species, they will provide an opportunity for comparing the demographic responses to climate change, or particular El Niño events for example, in a range of forest types. There are operational or planned transects across gradients in land-use intensity in the humid tropics (Steffen et al. 1999), but there are fewer across natural ecotones, and the work in Monteverde, Costa Rica may be a useful model for the development of these (see Pounds et al. 1999).

Mediterranean ecosystems

The mediterranean-type ecosystems of the Mediterranean basin, California, Chile, South Africa and Australia harbour almost 20% of vascular plant species, including over 26,000 endemic species, hundreds of endemic genera and several endemic families (Cowling et al. 1996). These transitional climate regions are predicted to be strongly affected by climate change, in particular drought and fire, and in addition are subject to intense pressure from human land-use and invasive species (Lavorel et al. 1998, Sala et al. 2000). Aside from these pressing conservation problems, a global monitoring network in these areas would be highly feasible as there is a great deal of previous research in these systems (e.g. see Moreno & Oechel 1995, Cowling et al. 1996, Lavorel et al. 1998). The regions are relatively accessible (part of the problem!), taxonomically well known and in effect provide replicates for global research.

Coral reefs

Coral reefs have been resilient to climate change on a scale of millennia (Wilkinson 1996), and as sea-levels have been relatively stable for the past 6000 years, coral reefs have grown fairly consistently. In recent years, there has been an increase in damage to and mortality of reefs due to

an increase in both the incidence and severity of coral bleaching events. Coral bleaching occurs as a result of the disassociation of coral and their photosynthetic symbionts (zooxanthellae), predominantly as a result of high temperatures (1-2°C above normal summer maxima). While corals can recover from short-term bleaching by the remaining symbionts regenerating or by acquiring new populations, severe or prolonged bleaching causes the coral animals to die.

The latest assessment of the status of coral reefs is that, as of late 2000, 27% of the world's reefs have been effectively lost, with the largest single cause being the massive climate-related coral bleaching event of 1998. This destroyed about 16% of reefs in 9 months during the largest El Niño and La Niña events ever recorded. While there is a good chance that many of the 16% of damaged reefs will recover slowly, probably half of these reefs will never adequately recover. These will add to the 11% of the reefs already lost due to human impacts such as sediment deposition, nutrient pollution, destructive over-fishing, mining of sand and rock and engineering work (Wilkinson1999, in press). Simulation models suggest that under current climate change scenarios, thermal tolerances of reef-building corals are likely to be exceeded every year, and severe events, such as happened in 1998, are likely to become more common (Hoegh-Guldberg 1999). Regeneration may also be hindered due to reduced coral calcification as a result of changed seawater chemistry with increased CO_2 concentrations (Kleypas et al. 1999).

The long-term consequences for biodiversity of these bleaching events are unclear. Many reef taxa are long-lived and clonal. Thus there may be low genetic diversity among populations, making adaptation unlikely, and the response to disturbance may be masked as individuals survive but with no recruitment (Lasker & Coffroth 1999). While further research and monitoring is required (Reaser et al. 2000), coral reef researchers have perhaps been the most successful in establishing global monitoring programmes (e.g. the Global Coral Reef Monitoring Network), and this may be a useful model for comparable programmes in other biomes.

Genetic diversity

Genetic diversity is required for evolutionary change, and the preservation of genetic diversity is of fundamental concern to conservation biology (e.g. Falk & Holsinger 1991). In a changing climate, organisms may need to adapt to changing temperature and rainfall patterns, and to a suite of novel pathogens. Fragmentation and reduction in population size are expected to reduce genetic diversity. This guides conservation action, especially genetic management of captive populations of endangered species, but is also applicable to landscape-scale predictions of change (e.g. Ledig et al. 1997, Gunter et al. 2000). Loss of heterozygosity is predicted to be inversely related to effective population size, and this has been demonstrated for *Drosophila melanogaster*, where allozyme genetic diversity (heterozygosity, percent polymorphism and allelic diversity), inversions and morphological mutations were all lost at greater rates in smaller than larger populations (Montgomery et al. 2000). Chromosomal diversity may be lost as a direct consequence of environmental change (Rodriguez-Trelles & Rodriguez 1998).

In temperate regions subject to glacial histories, there have been retreats and recolonisation of species, and this has left a genetic 'fingerprint' of these events (Hewitt 2000). Most species of terrestrial animals and plants show highest genetic diversity (i.e. most subspecies and most genetic variation within populations) close to their glacial refugia, and least at high latitudes that have been colonised through repeated genetic bottlenecks (e.g. Taberlet 1998, Pamilo & Savolainen, 1999). These refugia are close to the current warm range margins of many species, and therefore lie in regions in which many species are likely to be most susceptible to extinction. Meanwhile, expanding margins are expected to show low genetic variation within populations and low genetic diversity between them.

The situation is much less clear in the tropics, and this is an area where further research is likely to be needed (Bawa & Dayanandan 1998). Nonetheless, it is clear that subspecies of tropical organisms are also concentrated in areas of endemism, and thereby face the same threats. Moreover, because subspecies have narrower ranges than full species, many more subspecies

than species are likely to be threatened with extinction by climate change. A case has been made for the *ex situ* conservation of genetic stocks of agriculturally or commercially important plants as a guard against environmental change (Rosenberg 1988, Neefjes 1996).

Land use

In the short term, changes in land use due to an increasing human population and demand for resources could heavily outweigh the changes due to climate change *per se*, although this balance may shift. Just as the global distributions of biodiversity and biomes are very strongly affected by patterns of rainfall and temperature interacting with geology, so are distributions of human populations and agricultural activity. The effects of climate change on agricultural and forestry practices may equal or outweigh the direct effects on species. This is particularly true for intensively managed and/or densely populated areas where species occur in, and may depend upon, a highly modified landscape (e.g. Andrews & Rebane 1994, Guo 2000).

Predictions of the effects of climate change in Europe suggest that there will be an increase in productivity of agricultural and natural ecosystems, while forestry productivity will increase in northern Europe and decrease in southern Europe. There will be exacerbation of pressures on water resources, deterioration in soil quality, increased vulnerability of coastal areas to flooding, erosion and wetland loss, change in freshwater and marine fish and shellfish biodiversity and a shift in biotic and cryospheric zones in mountain regions (Parry 2000).

Invasions

Human activity has caused the accidental or deliberate movement of species across geographical boundaries, such that many of the ecologically important organisms within some ecosystems have been introduced in historic time (Vitousek et al. 1997). Some introductions may have catastrophic effects. Of recent species extinctions for which there is a known cause, 39% have been attributable to the effects of introduced species (Groombridge 1992). Nevertheless, there is considerable variation in the success and impact of introduced species, and many remain in isolated patches or at low density. Of the species introduced deliberately or accidentally to new regions, an approximate rule-of-thumb seems to be that only about 10% become established in the new region, and of these only about 10% become common and widespread, potentially threatening the native biota (Williamson 1996). However, it is reasonable to presume that native communities are well adapted to the interaction between local edaphic conditions and current climate. Altered environmental conditions driven by climate change may result in the 'ecological release' of many of these latent species, with consequences for the native community. In the deserts of western North America, elevated CO_2 concentration enhances the productivity of introduced *Bromus* grasses relative to native species. This could further increase the success of a group of highly invasive species, exposing the deserts to an accelerated fire-cycle to which they are not adapted, and converting large areas of diverse shrubland into annual grassland dominated by exotics (Smith et al. 2000). A further example could be the Mediterranean Sea, where many species have come through the Suez canal, but have not so far invaded the entire Mediterranean-Black Sea basin.

It seems highly probable that changing climate will cause a new wave of aliens to establish, even in the absence of other human interference. However, predicting the likelihood of success of invasive species remains elusive (Gilpin 1990, Williamson & Fitter 1996), although some progress has been made in determining the attributes which make some plant species more invasive than others (Rejmánek & Richardson 1996). Research on the spread of malaria under changing climate scenarios suggest that the type of models used to predict future spread may be critical and lead to widely varying estimates (Rogers & Randolph 2000).

Protected areas

The future viability of existing protected areas subject to environmental change is a crucial issue for conservation biologists and planners. The concern is that the areas of suitable climate space

occupied by species may move, shrink or even disappear (although some species will prosper, experiencing an increasing area of suitable climate space). Managers of protected areas will need to decide whether they wish to maintain the existing suite of species in the area, or to allow ecological (and evolutionary) change in the ecosystems represented within them (Hunter, Jacobson & Webb 1988). The problem is particularly acute for endemic or restricted-range species which are largely confined to single reserves which may comprise only one major climate zone.

Shifts from one climate zone to another could occur in 39-58% of reserves (Leemans & Halpin 1992, Halpin 1997), with the effects more pronounced in reserves at higher latitudes. A pervasive view is that organisms will move along altitudinal gradients in response to climate change (Peters & Darling 1985), and this has indeed occurred in some instances (e.g. Parmesan 1996). This has led to the general view that reserves with major topographical relief and altitudinal gradients will offer the greatest security. However, modelling scenarios on mountains at different latitudes suggest that vegetation zones do not simply shift upslope; some may expand, while others contract or disappear (Halpin 1997). That apparent 'escape routes' to higher altitude within a reserve may not guarantee species' survival is illustrated by the recent extinction of the golden toad on a tropical mountain in Costa Rica (Pounds et al. 1999). Several recommendations for research to better understand the consequences of climate change for protected areas have been outlined by Halpin (1997), summarised as follows:

(a) Model the sensitivity of ecosystems to climate change at small scales, which may be particularly useful for identifying the thresholds to change
(b) Determine key aspects of the biology (physiological tolerances, dispersal mechanisms etc.) of key species
(c) Understand of local disturbance regimes (fire, drought, pests etc.)
(d) Analyses of the interaction between landscape fragmentation and population dynamics, including changes in human land use
(e) Cost-benefit analyses of management intervention, including ecosystem restoration, assisted species movement, *ex situ* conservation etc.

Research priorities
Below are some general questions which we think are relevant to assessing how climate change will affect species conservation. We hope that they will provide a stimulus for discussion.

The IUCN Species Survival Commission identified the need to "…evaluate the importance of climate change as a threatening process for particular species in particular areas…". We believe that this is currently premature because it depends on the individualistic responses of species to climate (and other) changes in specific and often very small areas (and therefore not very well predicted by models). Rather, we think that more generic issues should be considered first:

i. how does climate change rank among the other widely-recognised threats to biodiversity
ii. what is the predicted effect of climate change on average species richness (and global patterns of richness)
iii. as for ii), but for genetic diversity
iv. what numbers of species might be predicted to become extinct under climate change predictions
v. as for iv), but for subspecies
vi. what parts of the world / biome types are expected to show greatest changes in species richness and loss of endemics

Even approximate answers to these questions would tell us whether the conservation community should regard climate change as the greatest threat to species over the next 300 years, a threat on a par with the other major threats, or a relatively minor issue involving range and management changes. If we cannot make specific predictions for individual species yet, we can at least ask what types of organisms / regions might be most threatened, and therefore what monitoring

programmes to put in place (e.g. along moisture/temperature gradients into/out of areas of endemism; gradients of elevation/depth; oceanic islands; N and S facing slopes; ridges-slopes-valley bottoms etc).

Other fundamental questions that need to be considered are:

vii. what difference is there between the consequences of business-as-usual scenarios, and the best possible scenario of greenhouse gas increases? In other words, would political action to reduce greenhouse gas emissions, sequester carbon or encourage other adaptive strategies make any material difference to threats to biodiversity?
viii. How influential would the maximum temperature reached be?
ix. What is the impact of the duration for which greenhouse gasses/global temperatures are increased (many extinctions may be lagged by decades/centuries after climate change)
x. Would the (rapid) reversion to early 20th century climate in, say, 250 years be better or worse than stabilising the climate at the new temperature?

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