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The Greenhouse Effect and Nature Reserves

Global warming would diminish biological diversity by causing extinctions among reserve species

Robert L. Peters and Joan D. S. Darling

As I did stand my watch upon
the hill,
I look'd toward Birnam, and anon,
methought,
The wood began to move.

Macbeth, Act 5, Scene 5

Current human development and population trends suggest to all but the very optimistic that by the next century most other surviving terrestrial species may well be relegated to small patches of their original habitat, patches isolated by vast areas of human-dominated urban or agricultural lands. Without heroic measures of habitat conservation and intelligent management, hundreds of thousands of plant and animal species could become extinct by the end of this century (Myers 1979, Lovejoy 1980), with more to follow in the next. This diminution of biological diversity will have major consequences for human society.

Many species will be lost because no habitat reserves are set aside for them, but even those within reserves will be threatened by a combination of genetic and ecological events (Diamond 1975; see also Soulé and Wilcox 1980). Recent investigation into these events has provided insight into

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Conservation plans should reflect knowledge of climatic effects as soon as it becomes available

how reserves should be designed and managed (see Frankel and Soulé 1981, Schonewald-Cox et al. 1983, Soulé and Wilcox 1980). But although the significance of future climate change to species survival has been independently mentioned by several authors (Ford 1982, Norse and McManus 1980, Wilcox 1980), little attention has been given to the impact on biological diversity of an increasingly likely event: global CO₂-induced climatic change, commonly called the greenhouse effect. If the greenhouse effect occurs, it will pose a new and major threat to species within reserves, species already stressed by the effects of habitat fragmentation.

Our understanding of how atmospheric composition affects global climate is still in its infancy, but an increasing body of knowledge suggests that several types of change affecting the survival of species—including a substantial global increase in temperature, a widespread alteration of rainfall patterns, and perhaps a rise in sea level—may be caused by rising concentrations of CO₂ and other anthropogenic polyatomic gases (Hoffman et al. 1983, Machta 1983, Manabe et al. 1981, National Re-

search Council 1983, Schneider and Londer 1984).

In this paper we will identify problems caused by climate change that affect biological communities, examine the particular difficulties faced by species in biological reserves, and suggest management options. Although we recognize that dealing with short-term extinction threats alone will strain the resources of conservationists, we feel that the possible negative effects of global warming could be so severe that conservation plans should be amended to reflect knowledge of climatic effects as soon as it becomes available. Decisions about the siting and design of reserves and assumptions about how much management will be needed in the future must reflect the increased demands, both economic and biological, of global warming.

Patterns of climatic changes

Continued burning of fossil fuels, with a possible contribution from progressive deforestation, is causing an increase in atmospheric CO₂ concentration that could reach double the concentration in 1880 within the next 100 years (Hansen et al. 1981, NRC 1983, Schneider and Londer 1984). The concentration of additional greenhouse gases, notably methane and fluorochlorocarbons, will also increase significantly as the result of human activities (Machta 1983, Ramanathan et al. 1985). Because these greenhouse gases absorb some of the upward infrared radiation from the ground, preventing its escape into

space, the lower atmosphere will likely grow warmer. There is still a great deal of uncertainty about the greenhouse process, and predictions depend upon assumptions about future trends in fossil fuel use, the precise nature of the carbon cycle, and the complexities of atmospheric interactions. Nonetheless, most experts agree that globally the climatic average could warm by $3 \pm 1.5^\circ\text{C}$ by the end of the next century (NRC 1983). Moreover, this change would likely be greatest at the poles (Schneider and Londer 1984; see Figure 1a for one model's predictions).

A change of this magnitude is large compared with normal fluctuations. For example, an increase of only 2°C over the current average global temperature would make the planet warmer than at any time in the past 100,000 years (Schneider and Londer 1984).

Furthermore, although CO_2 doubling and concomitant temperature increase would probably not be reached for approximately another 100 years, transient increases during the next 50 years might still have significant impact on biological systems. Indeed, if climatic models predicting the greenhouse effect are correct, global warming should be distinguishable from normal climatic variation perhaps within the next 10–15 years (Hansen et al. 1981, Madden and Ramanathan 1980) and may, in fact, already be observable (World Meteorological Organization 1982).

As important to biological communities as temperature change itself is that the projected increases in temperature would cause widespread changes in precipitation patterns (Hansen et al. 1981, Kellogg and Schware 1981, Manabe et al. 1981, Wigley et al. 1980). For many species,

a change in water availability would have greater impact than temperature changes of the order predicted (e.g., Neilson and Wullstein 1983).

Although precise regional predictions of future precipitation patterns are yet to come, some attempts have been made to estimate large-scale changes. For example, in their model of future rainfall patterns, Kellogg and Schware (1981) suggest that the American Great Plains may experience as much as a 40% decrease in rainfall by the year 2040 (Figure 1b). In some areas, increased evaporation caused by increased temperature could exacerbate regional drying (e.g., Manabe et al. 1981).

A rise in sea level resulting from thermal expansion of sea water and melting of glaciers and polar ice caps has been widely discussed as well, although estimates of such a rise vary (Hansen et al. 1981, Hoffman et al. 1983, NRC 1983).¹ NRC (1983) has estimated a possible increase of 70 cm over the next century; another study projects a most likely rise of between 144 and 217 cm by 2100 (Hoffman et al. 1983). If the western Antarctic ice cap melted, which is highly uncertain, rises of up to 5–6 m might occur over the next several hundred years (Hansen et al. 1981, NRC 1983).

In addition, the warming trend may alter the ocean's vertical circulation, causing change in the upwelling patterns that sustain many marine communities (Frye 1983, Kellogg 1983).

Finally, increased atmospheric CO_2 may result in more acidic, nutrient-poor soils (Kellison and Weir 1986). It may also change photosynthetic efficiencies, growth rates, and water requirements of different plant species in different ways (NRC 1983), thereby altering competitive outcomes (Strain and Bazzaz 1983), and possibly destabilizing natural ecosystems.

The special case of biological reserves

Such changes in important environmental parameters that determine the range of species would affect nearly all species, but the consequences would be most dire for those restrict-

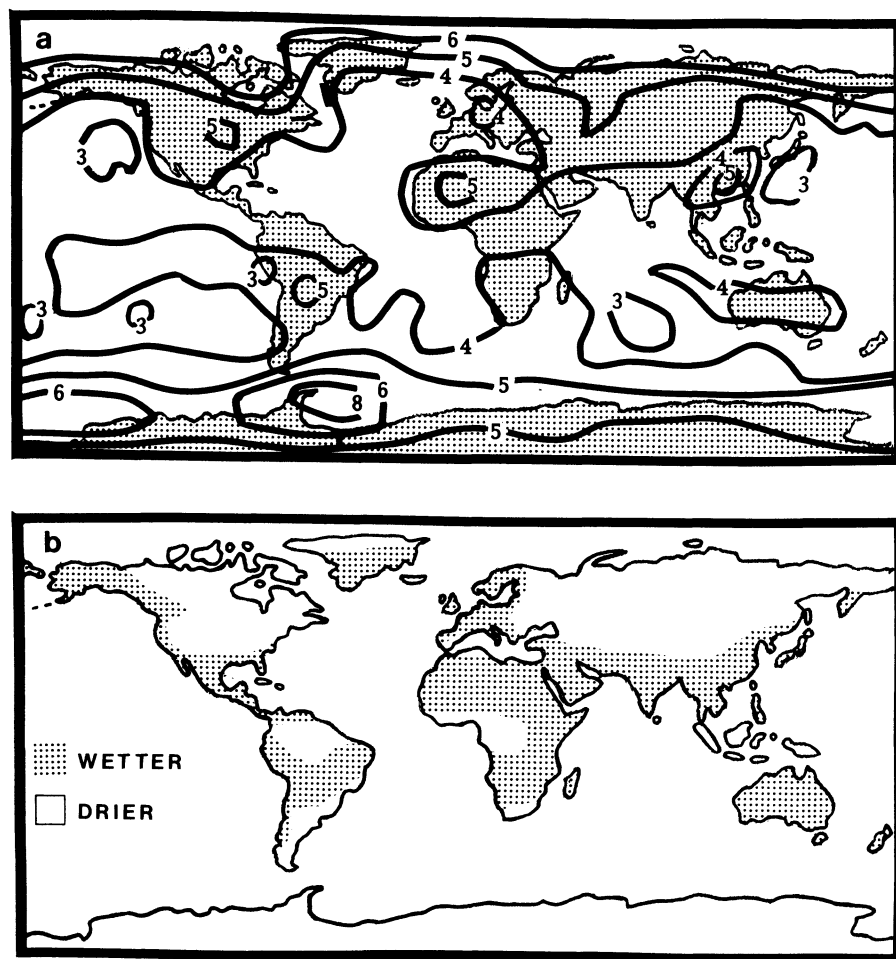


Figure 1. a. Global patterns of surface temperature increase, as predicted by the Goddard Institute for Space Studies (GISS) model (Hansen et al. 1985). Numbers are $^\circ\text{C}$. b. Global changes in moisture patterns. After Kellogg and Schware (1981).

¹It has also been suggested that sea level could drop because of ice and snow buildup in Antarctica; see Hansen et al. (1981).

ed to reserves or sharing characteristics of species restricted to reserves, notably limited range, small populations, and genetic isolation. Populations within reserves, such as national parks, national forests, and wildlife refuges, will typically be remnants of larger original populations reduced through overharvesting or habitat loss and therefore subject to a variety of threats more serious to them than to larger and more widespread populations.

Whenever the area an original community of species occupies is reduced, as when a reserve is created and the land surrounding it developed, some species are lost (Diamond 1975, Terborgh and Winter 1980, Wilcox 1980). Some disappear rapidly because the reserve does not include necessary resources; others are lost because any large-scale environmental change can cause extinction if the population is too localized; some vanish because of inbreeding and genetic drift.

As these environmental and genetic factors combine to cause the loss of some species, readjustment of mutualistic, parasitic, competitive, and predator-prey relationships among the remaining species must take place, most likely causing the loss of still others (e.g., Paine 1966). Climate change thus brings new pressures, including physiological stress and changes in competitive interactions, to bear on reserve species already stressed by a disequilibrated community. A common result of these climate-induced pressures would be further diminution of species' ranges and population sizes, which would in turn accentuate the various environmental and genetic effects associated with small populations, perhaps leading to extinctions.

Not only can the isolation of a population within a reserve surrounded by altered, unsuitable habitat mean it would receive little numerical or genetic augmentation from any populations outside the reserve, but the converse is also true. Isolated reserve populations could not respond to changing climatic conditions within the reserve by colonizing other "islands" of habitat outside the reserve where the climate is suitable.

Reserve species, which would generally be geographically localized,

would be more likely to experience intolerable climatic changes throughout their ranges than would more widespread species. For example, a tree species whose entire range falls in an area due to undergo regional drying is more at risk than one whose larger range includes areas outside the desiccation zone. Further, remnant populations in reserves may represent only a fraction of the gene pool originally present in the species as a whole (Frankel and Soule 1981). Diminution of a species' range could mean the loss of populations adapted to particular climatic conditions, decreasing the genetic material that both nature and humans have to work with.

A climatic change would often improve conditions for a particular species at one margin of its range and worsen conditions at the opposite. Reserve populations located near a margin where conditions are deteriorating would therefore be more threatened than ones at the opposite end of the range (Figure 2).

Communities respond to climate change

In the past, entire biomes have shifted in response to global temperature changes no larger than those that may occur during the next 100 years (Baker 1983, Bernabo and Webb 1977, Butzer 1980, Flohn 1979, Muller 1979, Van Devender and Spaulding 1979). In general, during warming, shifts were poleward; species colonized new habitats toward the poles, often while their ranges contracted away from the equator as conditions there became unsuitable. Equatorial organisms thus expanded their ranges into areas previously tenanted by temperate ones, while temperate organisms did the same in some areas previously the domain of boreal communities.

During several Pleistocene interglacials, for example, the temperature in North America was apparently 2–3° C higher than now. Osage oranges and pawpaws grew near Toronto, several hundred kilometers north of their present distribution; manatees swam in New Jersey; tapirs and peccaries foraged in Pennsylvania; and Cape Cod had a forest like that of present-day North Carolina (Dorf

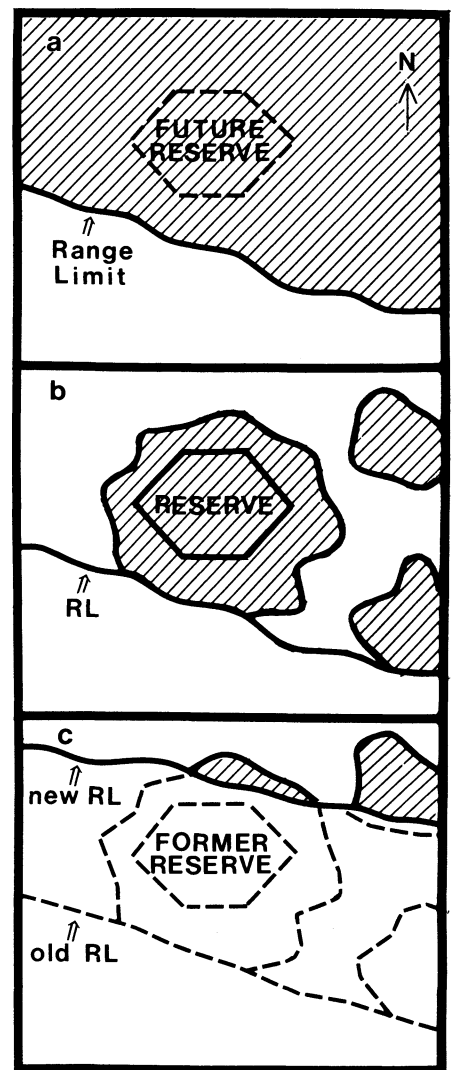


Figure 2. How climatic warming may turn biological reserves into former reserves. Hatching indicates: a. species distribution before human habitation (range limit, RL, indicates southern limit of species range); b. fragmented species distribution after human habitation; c. species distribution after warming.

1976). Other significant changes in species' ranges have been caused by altered precipitation accompanying global warming, including expansion of prairie in the American Midwest during a global warming episode approximately 7000 years ago (Bernabo and Webb 1977).

Although Pleistocene and past Holocene warming periods were probably not due to elevated CO₂ levels, researchers have predicted that, if the proposed CO₂-induced warming occurs, similar species shifts would also occur, and vegetation belts would



South American marsh deer (*Blastocercus dichotomus*). Even organisms physically able to disperse widely may be slow to colonize new habitat because new habitat patches may be rare and behavior may inhibit dispersion. Photo: Andrew Laurie, New York Zoological Society, courtesy World Wildlife Fund-US.

move hundreds of kilometers towards the poles (Frye 1983); 300 km is a reasonable estimate based on models (Miller et al. 1986) and on the positions of vegetation zones during analogous warming periods in the past (Dorf 1976, Furley et al. 1983).

Although both the fossil record and current distributions demonstrate that many species have been able to shift successfully in response to such climate changes, many others have not, either because their rates of migration were too slow or because geographical barriers like oceans, mountains, or areas of inappropriate soil type prevented their reaching suitable habitats.

For example, a large, diverse group of plant genera, including water-shield (*Brassenia*), sweet gum (*Liquidambar*), tulip tree (*Liriodendron*), magnolia (*Magnolia*), moonseed (*Menispermum*), hemlock (*Tsuga*), arbor vitae (*Thuja*), and white cedar

(*Chamaecyparis*), had a circumpolar distribution in the Tertiary. But during the Pleistocene ice ages, all went extinct in Europe while surviving in North America. Presumably, the east-west orientation of such barriers as the Pyrenees, Alps, and the Mediterranean, which blocked southward migration, was partly responsible for their extinction (Tralau 1973). In the case of reserve species, human modification of surrounding habitat will create barriers of agricultural or urban land that will be just as effective as mountains or oceans in preventing colonization of other suitable areas.

If global warming of 2–3° C did occur by the end of the next century, it would be very rapid compared with prehistoric changes of similar magnitude. In contrast, the change to warmer conditions at the end of the last ice age, considered rapid, spanned several thousand years (Da-

vis 1983). The rate of change has profound significance for species survival, for even if suitable land is preserved for a species to shift to, extinction may still occur if present habitat becomes unsuitable faster than new habitat can be colonized.

The fossil record shows that dispersal rates have been crucial to species' ability to colonize suitable habitat during past climate changes. For example, warm-temperate plant species were pushed south out of Great Britain and Ireland by cold during the Pleistocene. As the temperature increased, these plants later moved northward again, but only some dispersed rapidly enough to reach Great Britain before rising sea levels separated it from the European continent, and fewer could colonize Ireland before that island was separated from Britain (Cox et al. 1973). Other species that thrived in Europe during the cold periods, but could not survive

the conditions in postglacial forests, could not extend their ranges northward in time and became extinct except in cold, mountaintop refugia (Seddon 1971).

If estimates of a several-hundred-kilometer poleward shift in temperate biotic belts during the next century are correct, then a localized population now living where temperatures are near its maximum thermal tolerance would have to shift northward at a rate of several kilometers per year to avoid being left behind in areas too warm for survival. Although some species, such as plants propagated by spores or dust seeds, may be able to match these rates (Perring 1965), many species could not disperse fast enough to compensate for the expected climatic change without human assistance. Even wind-assisted dispersal may fall short of the mark for many species. For example, wind scatters seeds of the grass *Agrostis hiemalis*, but 95% fall within 9 m of the parent plant (Willson 1983). In the case of Engelmann spruce, a tree

with light, wind-dispersed seeds, fewer than 5% of the seeds travel even 200 m downwind, leading to an estimated migration rate of between 1 and 20 km per century (Seddon 1971). An extreme case is the double coconut (*Lodoicea maldivica*), whose giant seed can "only fall off the tree, and if the tree grows on a slope, roll downhill" (Willson 1983).

Although animals are mobile, the distribution of some animals is limited by the distributions of particular plants; their dispersal rates would thus largely be determined by those of co-occurring plants. On the other hand, some highly mobile animals, particularly those whose choice of habitat is relatively unrestrictive, may shift rapidly. Several authors (see Edgell 1984) have suggested, for instance, that climate change caused major range shifts in some European migratory waterfowl in this century. On the other hand, even animals physically capable of distant dispersal may often be restricted by behavior. Many tropical deep-forest birds, for

example, simply do not cross even very small unforested areas (Diamond 1975).

Because species shift at different rates in response to climate change, communities may disassociate into their component species. Recent studies of fossil packrat (*Neotoma* spp.) middens in the southwestern United States show that during the wetter, moderate climate of 22,000–12,000 years ago, there was not a concerted shift of communities. Instead, species responded individually to climatic change, forming stable but, by present-day standards, unusual assemblages of plants and animals (Van Devender and Spaulding 1979). In eastern North America, too, post-glacial communities were often ephemeral associations of species, changing as individual ranges changed (Davis 1983).

An alternative to latitudinal shifting, even for species that cannot disperse rapidly, is to change altitude. Generally, a short climb in altitude corresponds to a major shift in lati-

Mountains in the Parque Nacional Los Alerces, Argentina. In previous warming periods, the tree lines on several South American mountain ranges moved upward by some 1000–1500 meters. Photo courtesy World Wildlife Fund-US.



tude: the 3° C cooling of 500 m in elevation equals roughly 250 km in latitude (MacArthur 1972). Thus, during the middle Holocene when temperatures in eastern North America were 2° C warmer than at present, hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*) were found 350 m higher on mountains than they are today (Davis 1983). Similarly, species that could not shift poleward rapidly enough during a future warming trend to track a climatic optimum might be able to find sanctuary on mountains.

Underlying biological mechanisms

Climate change might cause local extinction in two interrelated ways. One is physiological: the climate of a formerly habitable area changes so it no longer corresponds to a species' physiological tolerances. The other is interspecific: climate change alters interactions, such as predation or competition, so that a formerly successful species is eliminated from an area where it could physiologically survive.

There are numerous examples of temperature's directly influencing species distribution and survival. The direct range-limiting effects of excessive warmth include lethality, as in corals (Glynn 1984), and interference with reproduction, as in the large blue butterfly, *Maculinea arion* (Ford 1982). Moisture extremes exceeding physiological tolerances also determine species' distributions. Thus, the European range of the beech tree (*Fagus sylvatica*) ends to the south where rainfall is less than 600 mm annually (Seddon 1971), and dog's mercury (*Mercurialis perennis*), an herb restricted to well-drained sites in Britain, cannot survive a water table less than 10 cm below the soil surface (Ford 1982).

But in many cases, interspecific interactions altered by climatic change will have a major role in determining new species distributions and, concomitantly, the susceptibility of species in reserves to extinction. Temperature can influence predation rates (Rand 1964), parasitism (Aho et al. 1976), and competitive interactions (Beauchamp and Ullyott 1932). For example, although the flatworm *Pla-*

naria gonocephala is physiologically able to live when alone in streams of 6.5–23° C, the presence of a competitor, *P. montenigrina*, excludes it from waters cooler than 13–14° C. Because *P. montenigrina* cannot tolerate waters warmer than 13–14° C, a warming trend would increase the habitat available to *P. gonocephala* (Beauchamp and Ullyott 1932). Similarly, the British plant oxlip (*Primula elatior*) can grow under a variety of moisture regimes, including on dry sites, but it is excluded from dry sites by dog's mercury (Ford 1982).

Species may not only be threatened by competitors naturally occurring within a reserve, but they may also feel pressure from invaders that find the new climatic regime to their liking. For example, *Melaleuca quinquevervia*, a bamboo-like Australian eucalypt, has invaded the Florida Everglades, forming dense monotypic stands where drainage and frequent fires have disturbed the natural marsh community (Courtenay 1978, Myers 1983). Such invasions may become commonplace in response to large-scale climate changes, and controlling them is one of the major concerns of reserve managers (Goigel and Bratton 1983).

The underlying physiological adaptations of most species to climate are conservative, and it is unlikely that most species could evolve significantly new tolerances in the time allotted to them by the coming warming trend. The llama, for example, has water turnover rates as low as those of its relative the camel, even though the llama has lived in cold, wet environments for several million years (MacFarlane 1976). Indeed, the evolutionary conservatism in thermal tolerance of many plant and animal species—beetles, for example (Coope 1977)—is the underlying assumption that allows us to infer past climates from faunal and plant assemblages.

In contrast, some invertebrates have apparently adapted when introduced into new thermal environments. Several species of freshwater tropical invertebrates accidentally introduced into temperate waters survived initially only in artificially heated waters, such as power plant outflows, but were later found spreading into nonheated sites (Aston 1968, Ford 1982).

A reserve scenario

Because the ecological ties binding a species to its environment are so complex, the preceding physiological, interspecific, and genetic factors would combine to affect reserve populations confronted with climatic change.

Imagine a hypothetical situation where a single oxlip population is confined within a British reserve, excluded from the reserve's dry sites by a competitor, dog's mercury. Then, because of global climatic changes, rainfall decreases within the reserve, allowing dog's mercury to displace the oxlip from an increasing number of its traditional sites.

At the same time, the ecological relationships of other species in the reserve are also changing, and some of these affect the oxlip. For example, a previously rare, second competitor of the oxlip undergoes a population explosion following the extinction of its major predator. In addition, a new insect herbivore introduced by humans finds the oxlip to its liking.

As the oxlip population becomes smaller and more fragmented from physiological stress, competitive exclusion, and increased predation, random environmental catastrophes and the genetic deterioration common in small populations take their toll. Because the reserve population has been isolated from those outside the reserve, its genetic composition is relatively homogeneous and may lack the variability to cope with the environmental threats. Moreover, no propagules from outside can bolster or reestablish populations within the reserve.

When the oxlip disappears, other reserve populations, such as insect herbivores, that depend on the oxlip will also decline. Even a decrease in the oxlip population that falls short of extinction may cause extinction of species depending on it for food.

Although this scenario is hypothetical, such complex interplay leading to extinction can be seen today. For example, the two southern subspecies of the northern flying squirrel, *Glaucomys sabrinus fuscus* and *G.s. coloratus*, are confined as glacial relicts to several boreal populations in the Appalachian Mountains. They are increasingly endangered by both human-caused habitat loss and

encroachment into their range by the southern flying squirrel, *Glaucomys volans*, which outcompetes them in the deciduous forests that are replacing the boreal conifers in retreat because of harvesting and climatic warming. The endangered subspecies are further threatened by a nematode parasite, which kills them but not the southern flying squirrel, its primary host (Handley 1979). Additional climatic warming may expand the range of the southern flying squirrel at the expense of the northern subspecies, hastening their decline.

Communities at risk

Although many reserve communities would suffer from changing climates, we theorize that a few types of species and communities may be particularly affected by warming trends over the next 100 years:

1. *Peripheral populations.* Populations located near the edge of a species range that is contracting in response to climate change would be at greater risk than those at the center or on an expanding edge (see Figure 2).

2. *Geographically localized species.* Even if their populations were large, species whose geographic range is small to begin with, such as many reserve species, would be less likely to have any populations in areas of suitable habitat after a climate change than those whose distribution is more widespread (Beardmore 1983). Island species are a special case of geographically restricted species. If the latitudinal migration required of them exceeds the size of the island, a climate change would leave little alternative but extinction. However, climatic changes on oceanic islands might be relatively mild because the sea would moderate the air temperature.

3. *Genetically impoverished species.* Species that are reduced to small populations or whose ranges are severely curtailed may lose the genetic diversity, including ecotypes adapted to particular climatic conditions, needed to successfully respond to climatic change. Thus, projected climate change provides yet another reason to retain as much genetic diversity as possible within a species.

4. *Specialized species.* Such species are generally less tolerant of ecologi-



Migrating wildebeest (*Connochaetes taurinus*) on the Serengeti Plain. These animals must travel hundreds of kilometers in response to present seasonal climatic fluctuations; even small changes in weather patterns may disrupt this closely tuned system. Photo: Norman Myers, courtesy World Wildlife Fund-US.

cal change because, by definition, some aspect of their life requires a narrow range of environmental conditions, conditions that might not exist during the ecological perturbations of a major climatic change. Often the survival of a specialist is tied to the survival of one or a few other species, as in the Everglades kite (*Rostrhamus sociabilis*), which depends on the apple snail (*Pomacea caliginosa*) as its single food source. The snails are themselves localized in range, and a decrease in their abundance due to drying of the Everglades has threat-

ened the kite with extinction in the United States (Bent 1961). Future saltwater incursion into the swamps or decreases in rainfall could further threaten the kite.

5. *Poor dispersers.* During past periods of climatic change, different species expanded their ranges at highly individual rates. For example, sugar maple (*Acer saccharum*), hickories (*Carya spp.*), oaks (*Quercus spp.*), and elms (*Ulmus spp.*) spread northward rapidly in eastern North America during the postglacial early Holocene. Chestnut (*Castanea dentata*)

spread much more slowly, apparently because its self-sterility made it difficult to establish by seed (Davis 1983). The increasingly disjunct distribution of suitable habitat may make it very difficult for species not adapted for colonization to spread to new areas if the climate changes.

6. *Annuals*. Another interesting possibility is that annual and perennial species would differ in their ability to persist in reserves when confronted by climatic change. Complete reproductive failure in a given year by an annual species within a reserve spells local extinction unless propagules either remain dormant until a more favorable year or arrive from sources outside the reserve. Because many annual species are efficient dispersers and colonizers with long-lasting propagules, these strategies may suc-

ceed. A perennial with equal dispersal abilities, however, has an advantage over annuals because the parent population can often survive conditions unsuitable for the establishment of young (e.g., Banus and Kolehmainen 1976), possibly for a number of years, until conditions become favorable for reproduction.

Whatever the case with annuals, some evidence suggests that species depending on annual hosts run a greater risk of local extinction than those depending on perennials. For example, Ehrlich et al. (1980) found that populations of the checkerspot butterfly *Euphydryas editha* relying on annual plant hosts apparently suffered a higher rate of local extinction during climatically unfavorable years than did those relying on a perennial host.

7. *Montane and alpine communities*. Because mountain peaks are smaller than bases, as species shift upward in response to warming, they typically occupy smaller and smaller areas, have smaller populations, and may thus become more vulnerable to genetic and environmental pressures. And because mountain populations are relatively isolated from other populations of the same species on other mountains, recruitment and recolonization would be difficult except for highly mobile species. Species originally situated near mountaintops might have no habitat to move up to and may be entirely replaced by the relatively thermophilous species moving up from below (Figure 3). Examples of past extinctions attributed to upward shifting by communities include alpine plants once living on mountains in Central and South America, where vegetation zones have shifted upward by 1000–1500 m since the last glacial maximum (Flenley 1979, Heusser 1974).

An interesting analogy to alpine species are those living in other types of cold refugia that would also shrink as the climate warmed. For example, the northern Gulf of California contains a fauna distinct from that of the southern gulf. Several endemic isopods survive in the north, apparently because a cold local climate protects them from the tropical fish predators that occur throughout the rest of the gulf (Wallerstein and Brusca 1982). If the climate warms, however, these fish may extend their range into the cold refugium.

8. *Arctic communities*. It is possible that, because temperatures in arctic regions may increase more than in areas closer to the equator (Hansen et al. 1986), arctic species may undergo greater physiological and competitive stress. On the other hand, many arctic species have adapted to withstand very large annual fluctuations in temperature, and so a sizable temperature change may well be tolerated.

9. *Coastal communities*. Many coastal species, like marine mammals and birds, depend on the rich food sources supported by coastal upwelling. The coastal communities they belong to may be disrupted if, as has been suggested (Frye 1983, Kellogg 1983), upwelling patterns are altered by global warming. That changes in

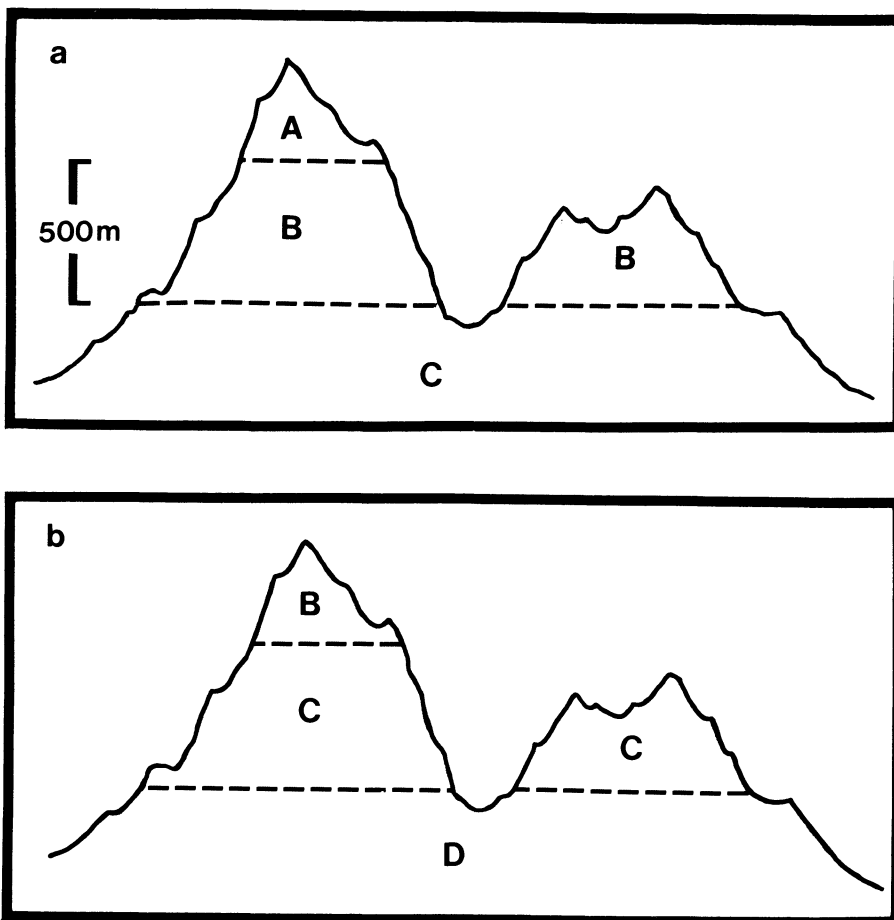


Figure 3. a. Present altitudinal distribution of three species, A, B, and C. b. Species distribution after a 500-m shift in altitude in response to a 3°C rise in temperature (based on Hopkin's bioclimatic law; MacArthur 1972). Species A becomes locally extinct. Species B shifts upward, and the total area it occupies decreases. Species C becomes fragmented and restricted to a smaller area, while species D successfully colonizes the lowest altitude habitats.

upwelling may provoke widespread disruption has been demonstrated by recurrent El Niño events (e.g., Duffy 1983).

If those predicting sea level rise are correct, much coastal habitat, like salt marshes and islets used by nesting birds, may be inundated or eroded. With no development, coastal communities would shift upland as the sea rose, but human development of land above present high water may preclude this. In a study for the EPA, Kana et al. (1984) concluded that losses of wetlands around Charleston, South Carolina, could be severe—40–80%—in the face of a rapidly rising sea level, but they will be even worse—approaching 100%—if bulkheads are built to protect the area that is now highland.

Freshwater lowlands along the coast would also be likely to suffer from the intrusion of salt water. The cypress trees of the US Gulf Coast, for example, do not tolerate salt water, yet they grow only slightly above sea level (Titus et al. 1984).

What this means for management

Preventing global warming would be the most environmentally conservative response. Granted, this would be difficult, not only because fossil fuel use will increase as the world's population grows, but also because effective action would demand a high degree of international cooperation. If efforts to prevent global warming fail, however, and if global temperatures continue to rise, then ameliorating the negative effects of climatic change on biological resources will require substantially increased investment in reserve purchase and management.

To make intelligent plans for siting and managing reserves, we need more knowledge. We must refine our ability to predict future conditions in reserves. We also need to know more about how temperature, precipitation, CO₂ concentrations, and interspecific interactions determine range limits (e.g., Picton 1984, Randall 1982) and, most important, how they can cause local extinctions. Adequately understanding the influences of climate on population dynamics may require long-term studies of reserve populations, studies similar to

Ehrlich's two decades of research on checkerspot butterflies (Ehrlich 1965, Ehrlich et al. 1980).

In addition to basic research, reserves that suffer from the stresses of altered climatic regimes will require carefully planned and increasingly intensive management to minimize species loss. For example, modifying conditions within reserves may be necessary to preserve some species; depending on new moisture patterns, irrigation or drainage may be needed. Because of changes in interspecific interactions, competitors and predators may need to be controlled and invading species weeded out. The goal would be to stabilize existing community composition by forestalling both succession and habitat deterioration, much as the habitat of Kirtland's warbler is periodically burned to maintain pine woods (Leopold 1978).

If such measures are unsuccessful, and old reserves do not retain necessary thermal or moisture characteristics, individuals of disappearing species may have to be transferred to new reserves. For example, warmth-adapted ecotypes or subspecies may have to be transplanted to reserves nearer the poles. Other species may have to be reintroduced in reserves where they have become temporarily extinct. An unusually severe drought, for example, might cause local extinctions in areas where a species ordinarily could survive with minimal management. Such transplantations and reintroductions, particularly involving complexes of species, will often be difficult, but applicable technologies are being developed (Botkin 1977, Lovejoy 1985).

To the extent that we can still establish reserves, pertinent information about changing climate and subsequent ecological response should be used in deciding how to design and locate them to minimize the effects of changing temperature and moisture. In many areas of the Northern Hemisphere, for example, where northward shifts in climatic zones are likely, it makes sense to locate reserves as near the northern limit of a species' range as possible, rather than farther south, where conditions are likely to become unsuitable. Again, plans to reserve certain shallow alkali lakes in the Great Plains for the endangered

pipin plover, *Charadrius melodus* (Chiple 1983), could perhaps incorporate information on potential effects of the future decreases in precipitation that may occur in this area (Kellogg and Schware 1981).

It is often suggested that reserves might best be placed in areas of high species endemism, like the presumed Pleistocene refugia of South America, which are often interpreted as areas where many species successfully survived and diversified during past periods of drying (Terborgh and Winter 1983). Siting reserves in such areas maximizes the number of endemic species saved in each reserve. A similar good argument for cost-effectiveness can be made for areas of high species diversity. In either case, knowing the long-term effects of future local climate would be invaluable in determining whether a species- or endemic-rich reserve is indeed suitable for the long-term survival of the species within.

Locating reserves where topography and soil types are heterogeneous could increase the chance that a species' precise temperature or moisture requirements would be met. Wilcox and Murphy (1985) have shown that populations of a checkerspot butterfly survive longer under normal climatic fluctuations if they inhabit several slopes facing different directions, thus have different moisture characteristics. Altitudinal variability within a reserve would increase the chance that vertical shifting could occur. Fortunately, many reserves have been placed in mountainous land because such areas are generally less suitable for agriculture.

Maximizing the size and number of reserves would enhance the long-term survival of species. In large reserves, species would have a greater chance of finding suitable microclimates or of shifting altitudinally or latitudinally. If we could increase the number of reserves so that each species and community type were represented in more than one reserve, we would increase the chance that if the climate in a reserve became unsuitable, the organisms within it might still survive elsewhere.

Flexible zoning around reserves could preserve an option to shift reserve boundaries in the future, as, for example, by trading pasture land for

reserve land. The multiuse, multi-zoned biosphere reserves now being set up in some countries, such as India (Saharia 1986), provide models of the sort of flexibility needed.

The unique situation of each reserve will challenge managers and planners to produce further ideas for maintaining biological diversity, and their task will be made more difficult by how fast changes are likely to occur. If we wait until we can predict exactly which parts of the world will be wetter or drier, for example, it will be too late—too late to begin the time-consuming task of setting up alternative reserves, too late to begin studying the effects of climate on competitive interactions, too late to identify those species most vulnerable to climatic change.

If we are concerned with setting up reserves and maintaining biological diversity—not just to eke out another 50 years or so of species survival but to preserve some remnants of the natural world for the year 2100 and beyond—we must begin now to incorporate information about global warming, as it becomes available, into the planning process.

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