

CHAPTER 51

THE EFFECT OF GLOBAL CLIMATIC CHANGE ON NATURAL COMMUNITIES

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Current human population and development pressures are breaking wild biological communities into fragments surrounded by human-dominated urban or agricultural lands. The result is that many wild species, perhaps hundreds of thousands by the end of this century, will be lost because of habitat disturbance (Lovejoy, 1980; Myers, 1979). Recent advances in conservation biology have demonstrated that even some species we thought would be protected within reserves may still be lost because the reserves are too small to maintain viable populations of all the species within them (Frankel and Soulé, 1981; Schonewald-Cox et al., 1983; Soulé, 1986; Soulé and Wilcox, 1980). To this daunting picture must be added a newly recognized threat, one with potentially disastrous consequences for biological diversity. This threat is global warming, commonly called the greenhouse effect.

It now seems very likely that ecologically significant climate change will occur within the next century and that many natural populations of wild organisms will be unable to exist within their present ranges. They will be lost, unless they are able to colonize new habitat where the climate is suitable, either on their own or with human help. Simply because many species survived past natural climate changes does not mean that they will survive this one without aid. The coming change promises to be very big and very fast, and because human activities will increasingly fragment and isolate populations, it will be more difficult for many species to successfully colonize new habitat when the old one becomes unsuitable.

FUTURE CLIMATE

What do we know about the climatic future? In the last several years a virtual consensus has been reached among atmospheric scientists that the planet will warm significantly during the next hundred years as the result of the production of carbon dioxide and other so-called greenhouse gases by humans (NRC, 1983; Schneider and Londer, 1984). Because molecules of these gases absorb infrared radiation, preventing it from radiating into space, increases in their concentration will cause increases in average global temperature. Exactly how large the warming will be and how fast it will come are still uncertain, but best estimates are of a magnitude sufficient to have profound effects on natural biological systems. In 1983 the National Research Council concluded that $3 \pm 1.5^\circ\text{C}$ of warming by the end of the next century was most likely (NRC, 1983), based on effects due to carbon dioxide concentration alone (see [Figure 51-1A](#) for one model's predictions). More recent analyses of the contributions of other greenhouse gases, including methane and the chlorofluorocarbons, suggest that the total greenhouse effect may be double that of carbon dioxide alone—cutting in half the amount of time necessary to reach a particular level of warming (Machta, 1983; Ramanathan et al., 1985). In short, warming of several degrees is likely within the next 100 years, perhaps the next 50 years. While a warming of this amount may seem small, it is not. Even a 2°C change is very large compared to normal fluctuations and would leave us with a planet warmer than at any time in the past 100,000 years (Schneider and Londer, 1984).

In thinking about the effects of climate change on natural communities, it is important to realize that the effects do not suddenly begin at some arbitrary threshold, such as the commonly used benchmark of doubled carbon dioxide concentration. Rather, ecological responses will begin with small amounts of warming and will increase as the warming does. Thus, a species like the dwarf birch (*Betula nana*), which exists in Britain only at sites where the temperature never exceeds 22°C (Ford, 1982), might begin retracting the southernmost portion of its range as soon as the local temperature climbs over 22°C .

In the long term, temperatures may rise above the several degrees predicted for a doubled carbon dioxide scenario, for there is no reason that concentrations of carbon dioxide and other greenhouse gases, and hence warming, should stabilize when the benchmark of doubled carbon dioxide is reached. If people continue to put more gases into the atmosphere, temperatures will continue to climb.

At least as important as temperature rise itself in affecting the distributions of species and the stability of biological communities will be the widespread changes in precipitation it causes (Hansen et al., 1981; Manabe et al., 1981; Wigley et al., 1980). Thus, the southern limit of the European beech tree (*Fagus sylvatica*) is determined by the point at which rainfall is less than 600 millimeters annually (Seddon, 1971), and a change in rainfall would be expected to cause a change in range. Although models of future rainfall distribution based on projected temperature increases are still rough, their implications are cause for concern. One model predicts that global warming will cause rainfall decreases of up to 40% for the American Great Plains by the year 2040 ([Figure 51-1B](#); Kellogg and Schware,

1981). Other factors associated with rising temperatures that have biological implications include the direct physiological effects of rising atmospheric carbon dioxide concentration itself on plants (in Lemon, 1983) and a moderate sea level rise, variously estimated to be between 144 and 217 centimeters by 2100, according to the U.S. Environmental Protection Agency (EPA) (Hoffman et al., 1983). Plants will vary according to the way carbon dioxide concentrations affect their photosynthetic efficiencies and water requirements, thus altering interspecific relationships. In addition, changes in both precipitation and elevated carbon dioxide levels would alter soil chemistry (Emanuel et al., 1985; Kellison and Weir, in press).

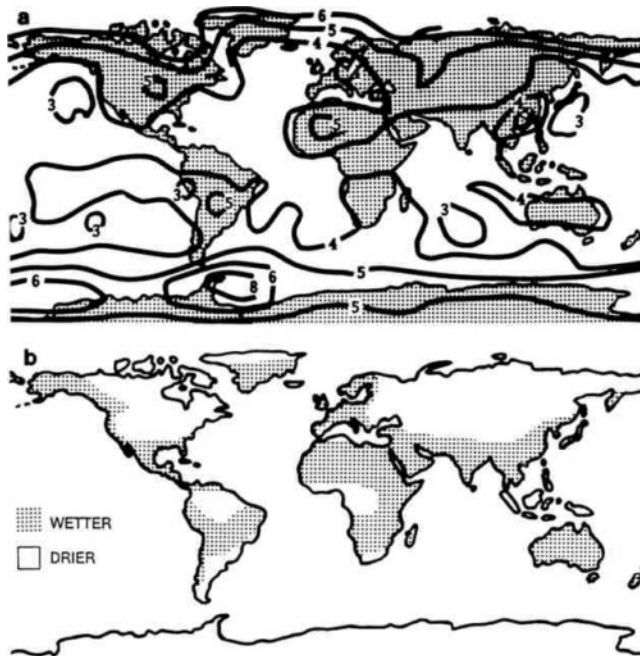


FIGURE 51-1 (a) Global patterns of surface temperature increase, as projected by the Goddard Institute for Space Studies (GISS) model (Hansen et al., in press). Numbers are in degrees Celsius, (b) Global changes in moisture patterns. After Kellogg and Schwarc (1981).

SPECIES RANGES SHIFT IN RESPONSE TO CLIMATE CHANGE

By using the fossil record to study past responses of communities to similar climate changes, we can get some idea of how species ranges might respond to the physiological and competitive stresses imposed by future change. The most important observation is that, not surprisingly, species tend to track their climatic optima, retracting their ranges where conditions become unsuitable while expanding them where conditions improve (Ford, 1982; Peters and Darling, 1985). A general observation is that during past warming trends, species have shifted both toward higher latitudes and higher elevations (Baker, 1983; Bernabo and Webb, 1977; Flohn, 1979; Van Devender and Spaulding, 1979). During several Pleistocene interglacial periods when the temperature in North America was only 2° to 3°C higher than at present, osage oranges (*Maclura* sp.) and pawpaws (*Asimina* sp.) grew near Toronto, several hundred miles north of their present distribution; manatees (*Trichechus* sp.) swam off the New Jersey shore; tapirs (*Tapirus* sp.) and peccaries (*Tayassu* sp.) foraged in Pennsylvania; and Cape Cod had a forest like that of present-day North Carolina (Dorf, 1976). As to altitudinal shifting, 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*), for example, were found 350 meters higher on mountains than they are today (Davis, 1983). In general, a short climb in altitude corresponds to a major shift in latitude, so that 3°C of cooling may be found by traveling either 500 meters up a mountain or 250 kilometers toward a pole (MacArthur, 1972).

Evidence of such range shifts during periods of warming in the past, together with projections of range shifts based on physiological tolerances and computer-modeled future climatic conditions, suggest that in the United States, the oncoming warming trend may shift the area within which a particular species may flourish by as much as several hundred kilometers to the north. A projection for loblolly pine (*Pinus taeda*), for example, suggests that the southern limit of this species in the United States may shift more than 300 kilometers to the north by the year 2080 because of moisture stress (Miller et al., in press). Another simulation indicates that the doubling of atmospheric carbon dioxide concentrations expected by the early part of the next century would result in elimination of Douglas fir (*Pseudotsuga taxifolia*) from the lowlands of California and Oregon, because rising temperatures would preclude the seasonal chilling this species requires for seed germination and shoot growth (Leverenz and Lev, in press). On a larger scale, other simulations indicate that projected temperature changes (exclusive of changes in precipitation and soil characteristics) caused by a doubling of carbon dioxide concentration would result in the shifting of entire ecosystem complexes, including the loss of as much as 37% of boreal forest (Emanuel et al., 1985).

Because each species disperses at a different rate, major climatic changes typically result in a resorting of the species constituting natural communities and the creation of new plant and animal associations (e.g., Van Devender and Spaulding, 1979; see also [Figure 51–2](#)), thereby causing new, sometimes stressful interactions among species.

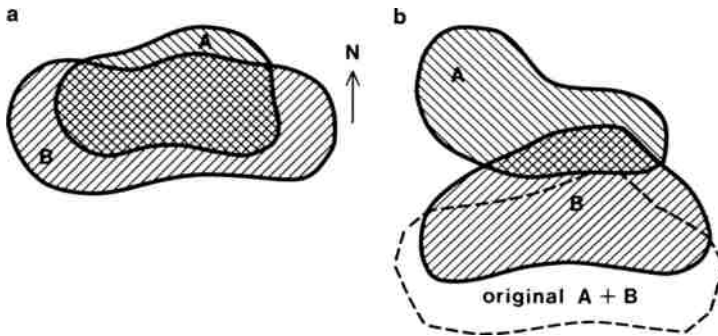


FIGURE 51-2 (a) Initial distribution of two species, A and B, whose ranges largely overlap, (b) In response to climatic change, latitudinal shifting occurs at species-specific rates and the ranges disassociate.

LOCALIZED SPECIES MAY NOT BE ABLE TO COLONIZE NEW HABITAT

If the entire range occupied by a species becomes unsuitable because of climate change, the species must either colonize a new, more suitable habitat or become extinct. The smaller the present range, the more likely it will be that the species will find the entire habitat unsuitable and therefore that extinction will occur. As discussed below, the vulnerability of many species will be increased by human encroachment that restricts them to small areas. Species restricted to reserves, like the one illustrated in [Figure 51-3](#), are good examples.

Imagine a restricted population like that represented in [Figure 51-3](#). What is the chance that colonists, such as seeds or migrating animals, from the original population will find new habitat before the parent population becomes extinct? It will, of course, depend upon a number of factors: how much suitable area there is (i.e., the size of the target the colonists must reach), how far away the suitable area is, how many potential colonists are sent out (which will be a function of how large the original population is and the reproductive strategy of the species), how efficient these colonists are at dispersing themselves, how many physical barriers to dispersal exist, and how long some individuals within the original population can survive to reproduce.

Although the number of colonists produced per parent and their intrinsic dispersal ability are likely to be essentially the same as during past times when species had to respond to climate change, this is not so for the other variables. For many species, the target areas to be reached will be reduced by development, the number of potential colonists will be reduced through reduction of the parent population, the length of time the parent population is allowed to exist may be reduced both through the rapidity of the climate change and development pressures, and, im

portantly, many more barriers to dispersal in the form of agriculture, urbanization, and other types of habitat degradation will be added to the natural physical barriers of mountains, oceans, and deserts. The predicament faced by a species in this situation is illustrated in Figure 51-4 for the Engelmann spruce (*Picea ccengelmanni*).

For a plant, the Engelmann spruce is probably a moderate disperser. It has small, wind-dispersed seeds, and its natural dispersal rate, in the absence of barriers, has been estimated to be between 1 and 20 kilometers per century (Seddon, 1971). If we assume that climate change will cause a several-hundred kilometer shift in the potential range of many species in the United States during the next century, say 30 kilometers per year, a plant with the 1- to 20-kilometer per century rate of the Engelmann spruce would be in trouble. Although some species, such as plants propagated by spores, may be able to match the 30 kilometers per year needed, many other species could not disperse fast enough to compensate for the expected climatic change without human assistance. Even some large animals that are physically capable of rapid dispersal do not travel far for behavioral reasons. Rates for several species of deer, for example, have been observed to be less than 2 kilometers per year (Rapoport, 1982).

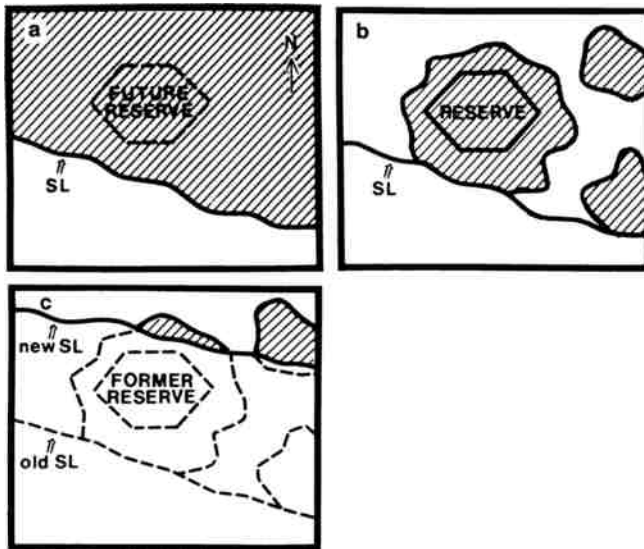


FIGURE 51-3 How climatic warming may turn biological reserves into former reserves. Hatching indicates: (a) species distribution before human habitation; (b) fragmented species distribution after human habitation; (c) species distribution after warming. SL indicates the southern limit of species range.

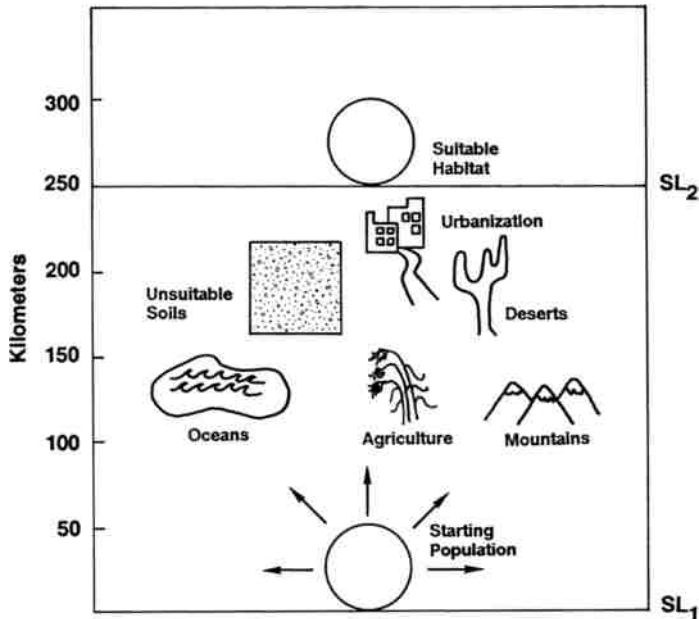


FIGURE 51-4 Obstacle course to be run by species facing climatic change in a human-altered environment. To win, a population must track its shifting climatic optimum and reach suitable habitat north of the new southern limit of the species range. SL_1 is the species southern range limit under initial conditions. SL_2 is the southern limit after climate change. The model assumes a plant population consisting of a single species, whose distribution is determined solely by temperature. After a 3°C rise in temperature, the population must have shifted 250 kilometers to the north to survive, based on Hopkins bioclimatic law (MacArthur, 1972). Shifting will occur by simultaneous range contraction from the south and expansion by dispersion and colonization to the north. Progressive shifting depends upon propagules that can find suitable habitat in which to mature and in turn produce propagules that can colonize more habitat to the north. Propagules must pass around natural and artificial obstacles like mountains, lakes, cities, and farm fields. The Engelmann spruce has an estimated, unimpeded dispersal rate of 20 kilometers/100 years (Seddon, 1971). Therefore, for this species to win by colonizing habitat to the north of the shifted hypothetical limit would require a minimum of 1,250 years.

We know these threats are more than speculation, because the fossil record provides evidence that not only have ranges shifted in response to climate change, but in some cases their total extent was drastically reduced. For example, a large and diverse group of plant genera, including watershield (*Brasenia*), sweetgum (*Liquidambar*), yellow poplar (*Liriodendron*), magnolia (*Magnolia*), moonseed (*Menispermum*), hemlock (*Tsuga*), cedar (*Thuja*), and cypress (*Chamaecyparis*), were

found in both Europe and North America during the Tertiary period. But during the Pleistocene ice ages, these all became extinct in Europe, presumably because the east-west orientation of such barriers as the Pyrenees, the Alps, and the Mediterranean blocked southward migration, while they persisted in North America, which has longitudinally oriented mountain ranges (Tralau, 1973).

MANAGEMENT IMPLICATIONS

How might the threats posed by climatic change to natural communities be mitigated? One basic truth is that the less populations are reduced by development now, the more resilient they will be to climate change. Thus, an excellent way to start planning for climate change would be sound conservation now, in which we try to conserve more than just the minimum number of individuals of a species necessary for present survival.

In terms of responses specifically directed at the effects of climate change, the most environmentally conservative action would be to halt or slow global warming. Granted, this would be difficult, not only because fossil fuel use will probably 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 the purchase and management of reserves.

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, carbon dioxide concentrations, and interspecific interactions determine range limits (see, for example, Picton, 1984, and Randall, 1982) and, most important, how they can cause local extinctions.

Reserves that suffer from the stresses of altered climate will require carefully planned and increasingly intensive management to minimize species loss. To preserve some species, for example, it may be necessary to modify conditions within reserves, such as irrigation or drainage in response to new moisture patterns. 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 the composition of existing communities, much as the habitat of Kirtland's warbler (*Dendroica kirtlandii*) is periodically burned to maintain pine woods (Leopold, 1978).

In attempting to understand how climatically stressed communities may respond and how they might be managed to prevent the gradual depauperization of their constituents, restoration studies, or more properly, community creation experiments can help. Communities may be created outside their normal climatic ranges to mimic the effects of climate change. One such relocation community is the Leopold Pines experimental area at the University of Wisconsin Arboretum in Madison, where there is periodically less rainfall than in the normal pine range several hundred kilometers to the north (W.R. Jordan III, University of Wisconsin, Madison, personal communication, 1985). Researchers have found that although the pines themselves do fairly well once established at the Madison site, many of

the other species that would normally occur in a pine forest, especially the various herbs and small shrubs, have not flourished, despite several attempts to introduce them.

If management measures are unsuccessful, and old reserves do not retain necessary thermal or moisture characteristics, individuals of disappearing species might be transferred to new reserves. For example, warmth-intolerant ecotypes or subspecies might be transplanted to reserves nearer the poles. Other species may have to be periodically reintroduced in reserves that experience occasional climate extremes severe enough to cause extinction, but where the climate would ordinarily allow the species to survive with minimal management. Such transplantations and reintroductions, particularly involving complexes of species, will often be difficult, but some 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. Considerations include:

- The existence of multiple reserves for a given species or community type increases the probability that if one reserve becomes unsuitable for climatic reasons, the organisms may still be represented in another reserve.
- Reserves should be heterogeneous with respect to topography and soil types, so that even given climatic change, remnant populations may be able to survive in suitable microclimatic areas. Species may survive better in reserves with wide variations in altitude, since from a climatic point of view, a small altitudinal shift corresponds to a large latitudinal one. Thus, to compensate for a 2°C rise in temperature, a Northern Hemisphere species can achieve almost the same result by increasing its altitude only some 500 meters as it would by moving 300 kilometers to the north (MacArthur, 1972).
- As models of climate become more refined, pertinent information should be considered in making decisions about where to site reserves in order to minimize the effects of temperature and moisture changes. In the Northern Hemisphere, for example, where a northward shift in climate zones is likely, it makes sense to locate reserves as near the northern limit of a species' or community's range as possible, rather than farther south, where conditions are likely to become unsuitable more rapidly.
- Maximizing the size of reserves will increase long-term persistence of species by increasing the probability that suitable microclimates exist, by increasing the probability of altitudinal variation, and by increasing the latitudinal distance available to shifting populations.
- In the future, flexible zoning around reserves could allow us to move reserve boundaries in response to changing climatic conditions. Also, as habitat inside a reserve becomes unsuitable for the species or communities within, reserve land might be traded for nonreserve land that either remains suitable or becomes so as the climate changes. The success of these strategies, however, would depend on a highly developed restoration technology that is capable of guaranteeing, in effect, the portability of species and whole communities.

ACTIONS THAT CAN BE TAKEN

The best solutions to the ecological upheaval resulting from climatic change are not yet clear. In fact, little attention has been paid to the problem. What is clear, however, is that these changes in climate would have tremendous impact on communities and populations isolated by development and that by the middle of the next century, they may dwarf any other consideration in planning for reserve management. The problem may seem overwhelming. One thing is worth keeping in mind, however: the more fragmented and smaller populations of species will be less resilient to the new stresses brought about by climate change. Thus, one of the best things that can be done in the short term is to minimize further encroachment of development upon existing natural ecosystems. Furthermore, we must refine our climatological predictions and increase our understanding of how climate affects species, both individually and in their interactions with each other. Such studies may allow us to identify those areas where communities will be most stressed as well as alternative areas where they might best be saved. Meanwhile, efforts to improve techniques for managing communities and ecosystems under stress and for restoring them when necessary must be carried forward energetically.

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REFERENCES

- Baker, R.G. 1983. Holocene vegetational history of the western United States. Pp. 109-125 in H. E.Wright, Jr., ed. Late-Quaternary Environments of the United States. Volume 2. The Holocene. University of Minnesota Press, Minneapolis.
- Bernabo, J.C., and T.Webb III. 1977. Changing patterns in the Holocene pollen record of northeastern North America: A mapped summary. *Quat. Res.* 8:64-96.
- Botkin, D.B. 1977. Strategies for the reintroduction of species into damaged ecosystems. Pp. 241-260 in J.Cairns, Jr., K.L.Dickson, and E.E.Herricks, eds. *Recovery and Restoration of Damaged Ecosystems*. University Press of Virginia, Charlottesville, Va.
- Davis, M.B. 1983. Holocene vegetational history of the eastern United States. Pp. 166-181 in H.E.Wright, Jr., ed. Late-Quaternary Environments of the United States. Volume 2. The Holocene. University of Minnesota Press, Minneapolis.
- Dorf, E. 1976. Climatic changes of the past and present. Pp. 384-412 in C.A.Ross, ed. *Paleobiogeography: Benchmark Papers in Geology* 31. Dowden, Hutchinson, and Ross, Stroudsburg, Pa.
- Emanuel, W.R., H.H.Shugart, and M.P.Stevenson. 1985. Response to comment: Climatic change and the broadscale distribution of terrestrial ecosystem complexes. *Clim. Change* 7:457-460.
- Flohn, H. 1979. Can climate history repeat itself? Possible climatic warming and the case of paleoclimatic warm phases. Pp. 15-28 in W.Bach, J.Pankrath, and W.W.Kellogg, eds. *Man's Impact on Climate*. Elsevier Scientific Publishing, Amsterdam.

- Ford, M.J. 1982. *The Changing Climate: Responses of the Natural Fauna and Flora*. George Allen and Unwin, London. 190 pp.
- Frankel, O.H., and M.E.Soulé. 1981. *Conservation and Evolution*. Cambridge University Press, Cambridge. 327 pp.
- Hansen, J., D.Johnson, A.Lacis, S.Lebedeff, P.Lee, D.Rind, and G.Russell. 1981. Climate impact of increasing atmospheric carbon dioxide. *Science* 213:957-966.
- Hansen, J., A.Lacis., D.Rind, G.Russell, I.Fung, and S.Lebedeff. In press. Evidence for future warming: How large and when. In W.E.Shands and J.S.Hoffman, eds. *The Greenhouse Effect, Climate Change, and U.S. Forests*. Conservation Foundation, Washington, D.C.
- Hoffman, J.S., D.Keyes, and J.G.Titus. 1983. Projecting Future Sea Level Rise: Methodology, Estimates to the Year 2100, and Research Needs. Strategic Studies Staff, Office of Policy Analysis, Office of Policy and Resource Management, U.S. Environmental Protection Agency, Washington, D.C. 121 pp.
- Kellison, R.C., and R.J.Weir. In press. Selection and breeding strategies in tree improvement programs for elevated atmospheric carbon dioxide levels. In W.E.Shands and J.S.Hoffman, eds. *The Greenhouse Effect, Climate Change, and U.S. Forests*. Conservation Foundation, Washington, D.C.
- Kellogg, W.W., and R.Schware. 1981. *Climate Change and Society: Consequences of Increasing Atmospheric Carbon Dioxide*. Westview, Boulder, Colo. 178 pp.
- Lemon, E.R. 1983. *CO₂ and Plants: The Response of Plants to Rising Levels of Atmospheric Carbon Dioxide*. Westview, Boulder, Colo. 280 pp.
- Leopold, A.S. 1978. Wildlife and forest practice. Pp. 108-120 in H.P.Brokaw, ed. *Wildlife and America*. Council on Environmental Quality, U.S. Government Printing Office, Washington, D.C.
- Leverenz, J.W., and D.J.Lev. In press. Effects of CO₂-induced climate changes on the natural ranges of six major commercial tree species in the western U.S. In W.E.Shands and J.S.Hoffman, eds. *The Greenhouse Effect, Climate Change, and U.S. Forests*. Conservation Foundation, Washington, D.C.
- Lovejoy, T.E. 1980. A projection of species extinctions. Pp. 328-331 in *The Global 2000 Report to the President: Entering the Twenty-First Century*. Council on Environmental Quality and the U.S. Department of State. U.S. Government Printing Office, Washington, D.C.
- Lovejoy, T.E. 1985. *Rehabilitation of Degraded Tropical Rainforest Lands*. Commission on Ecology Occasional Paper No. 5. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.
- MacArthur, R.H. 1972. *Geographical Ecology*. Harper & Row, New York. 269 pp.
- Machta, L. 1983. Effects of non-CO₂ greenhouse gases. Pp. 285-291 in *Changing Climate: Report of the Carbon Dioxide Assessment Committee*. National Academy Press, Washington, D.C.
- Manabe, S., R.T.Wetherald, and R.J.Stouffer. 1981. Summer dryness due to an increase of atmospheric CO₂ concentration. *Clim. Change* 3:347-386.
- Miller, W.F., P.M.Dougherty, and G.L.Switzer. In press. Effect of rising CO₂ and potential climate change on loblolly pine distribution, growth, survival, and productivity. In W.E.Shands and J.S.Hoffman, eds. *The Greenhouse Effect, Climate Change, and U.S. Forests*. Conservation Foundation, Washington, D.C.
- Myers, N. 1979. *The Sinking Ark*. Pergamon Press, New York. 307 pp.
- NRC (National Research Council). 1983. *Changing Climate: Report of the Carbon Dioxide Assessment Committee*. National Academy Press, Washington, D.C. 496 pp.
- Peters, R.L., II, and J.D.S.Darling. 1985. The greenhouse effect and nature reserves: Global warming would diminish biological diversity by causing extinctions among reserve species. *BioScience* 35(11):707-717.
- Picton, H.D. 1984. Climate and the prediction of reproduction of three ungulate species. *J. Appl. Ecol.* 21:869-879.
- Ramanathan, V., R.J.Cicerone, H.B.Singh, and J.T.Kiehl. 1985. Trace gas trends and their potential role in climate change. *J. Geophys. Res.* 90:5547-5566.
- Randall, M.G.M. 1982. The dynamics of an insect population throughout its altitudinal distribution: *Coleophora alticolella* (Lepidoptera) in northern England. *J. Anim. Ecol.* 51:993-1016.
- Rapoport, E.H. 1982. *Areography. Geographical Strategies of Species*. Pergamon Press, New York. 269 pp.
- Schneider, S.H., and R.Londer. 1984. *The Coevolution of Climate and Life*. Sierra Club Books, San Francisco. 563 pp.

- Schonewald-Cox, C.M., S.M.Chambers, B.MacBryde, and W.L.Thomas. 1983. Genetics and Conservation. A Reference for Managing Wild Animal and Plant Populations. Benjamin-Cummings Publishing, Menlo Park, Calif. 722 pp.
- Seddon, B. 1971. Introduction to Biogeography. Barnes and Noble, New York. 220 pp.
- Soulé, M.E. 1986. Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, Mass. 584 pp.
- Soulé, M.E., and B.A.Wilcox. 1980. Conservation Biology: An Evolutionary-Ecological Perspective. Sinauer Associates, Sunderland, Mass. 395 pp.
- Tralau, H. 1973. Some Quaternary plants. Pp. 499–503 in A.Hallam, ed. Atlas of Palaeobiogeography. Elsevier Scientific Publishing, Amsterdam.
- Van Devender, T.R., and W.G.Spaulding. 1979. Development of vegetation and climate in the southwestern United States. *Science* 204:701–710.
- Wigley, T.M.L., P.D.Jones, and P.M.Kelly. 1980. Scenario for a warm, high CO₂ world. *Nature* 283:17.