Global Change has been the theme of this 1989 AIBS meeting in Toronto. The influence of the human species on our environment has become so pervasive that the effects must now be considered on a global scale. The chemistry of the atmosphere has been changed, and with it the interactions between the atmosphere and hydrosphere, the geosphere and the biosphere. Global changes such as destruction of tropical forest, species extinction, loss of stratospheric ozone, and changes in the chemistry of precipitation are already a fact. Additional, more serious changes loom in the future. The greenhouse gases added to the atmosphere have apparently been buffered so far by the workings of the global system as a whole, but they will eventually alter global climate, causing warming at unprecedented rates.

Paleoecologists study the way in which biological communities and systems have responded to environmental changes during the Quaternary. What insights have been gained from studies of the past that are useful to ecologists predicting the future? Four insights from Quaternary studies seem particularly important to research on global change.

The first lesson from the past is that species respond to climate individually. The fossil record documents the adjustments of range limits according to the unique sensitivities of each species to climate. These individual range shifts have caused changes in the composition of plant and animal communities through time. Different combinations of tree species than we see together today occurred in the past (Davis 1981, Webb 1987). Mammal species whose ranges do not overlap today were found together during the full-glacial (Graham 1985). Most of the familiar forest communities in north temperate latitudes acquired their present species composition recently—some forest communities within the last 2000 years (Davis 1981). Even in regions where modern forests are similar, the order of entry of species has been different. For example, beech arrived several thousand years before hemlock in hardwood forests in Michigan’s Lower Peninsula, several thousand years after hemlock in the north (Davis et al. 1986).

This result from the past means that species can be expected to respond individually to climatic changes in the future. We must not build models that predict the future by shifting existing communities or biomes around on the surface of the globe. If we do, we will make mistakes in predicting interactions with other components of the global system, because in the future new and different ecosystems are likely to come into existence.

The evidence for past changes in community and biome structure is very clear. Maps are now available that display pollen percentages at 1000-year intervals from hundreds of fossil profiles across eastern North America (COHMAP 1988, Webb 1988). These maps reveal changes in population size for dominant trees in response to climate. For example, 18,000 years ago, when ice sheets reached their maximum extent, spruce was abundant in the center of the continent, but as a component of vegetation quite different from the modern Boreal Forest. Pine and birch were absent, and many prairie plants were present (Kutzbach and Wright 1985, Wright 1987). As the ice sheet retreated, spruce spread northward. But for a period of several thousand years, centered around 8000 years ago, spruce was rare everywhere, even in regions of Canada where there is Boreal Forest today. The Boreal Forest came into existence about 5000 years ago as spruce increased in response to late-Holocene changes in climate (Webb 1988). Thirty-five years ago we used to think of modern biomes shifting southward ahead of the ice, and moving northward again in its wake; new data like these show that even major landscape units like the North American Boreal Forest can be of very recent origin.

Changes in species composition are important not only from a floristic point of view,
but also because individual species affect ecosystem properties that feed back to the global system, such as albedo, surface roughness, snow cover, and ground frost. All of these variables are influenced by the presence or absence of a coniferous species like spruce. Of course it would be convenient for modelling purposes to classify vegetation in simple terms that are meaningful in interactions with the atmosphere. But even the physiogony of major vegetation units does not remain constant through time. During the warmest part of the Holocene 8000–3000 years ago, for example, the forest margin retreated eastward about 50 km in Minnesota. It was replaced not by prairie, but by an oak savanna or oak scrub vegetation (McAndrews 1967, E. J. Cushing, personal communication). Oak savanna exists today only in a narrow band along the ecotone between prairie and forest (Fig. 1), but for several thousand years it was so extensive that it constituted a new vegetation type appropriately mapped separately from prairie or forest. In this manner new physiognomic vegetation units may come into existence in the future.

A second lesson from the past is that biological responses to climatic change often occur with time lags. Each species and ecosystem component has its own time constant of change. If the climate changes rapidly, as it did at the beginning of the present interglacial 10,000 years ago, for example, species with long time constants of change lag decades or even centuries behind others. Fig. 2 shows the result of a study designed to compare the time course of responses of animals and plants

![Fig. 2: Paleoecological records from the same sediment core plotted against the radiocarbon age of the sediments. The dotted line represents the minimum summer temperature tolerated by species in the beetle assemblage; the solid line is the deposition rate for birch pollen. The steep rise in pollen deposition marking the local establishment of subarctic birch forest occurred about 500 years after beetles indicated summer temperatures adequate for the growth of trees. After the late-glacial cold interval between 11,000 and 10,000 years ago, temperatures rose again; this time beetles and birch trees responded synchronously. From W. Pennington 1986.](image)
to climatic events between 15,000 and 10,000 years ago. In northern Europe temperatures rose steeply throughout this interval except for a brief reversal just before 10,000 years ago. According to the record provided by water beetles found in the sediments of Lake Windermere (dotted line on graph), temperatures rose 5°C in 500 years, about 0.1°C per decade. But the deposition rate of birch pollen in the same sediment core (solid line) lagged behind. Its steep rise, indicating the development of birch woodland, occurred about 500 years after the beetle communities registered a climate warm enough to permit the growth of trees (Pennington 1986).

For many years the lag in late-glacial and early Holocene forest development in northern Europe was attributed to dispersal limitations (Iversen 1954). Although animals such as beetles could disperse rapidly onto the warming landscape to colonize newly formed lakes, dispersal of seed would be more limited. Recently evidence has come to light implicating ecosystem processes rather than seed dispersal: delayed accumulation of organic matter in soil profiles may have been responsible for the slow development of forest (Pennington 1986). Whatever the factor, beetles and forest development responded synchronously as temperatures continued their rise 10,000 years ago, during the rapid warming that ushered in the beginning of the present interglacial (Fig. 2).

Lags of decades or centuries, as demonstrated in the fossil record, become a critical issue because of the extraordinary rate of change we expect in the future. At temperate latitudes even conservative predictions project changes of 0.5° to 1°C per decade (Dickinson 1988). If all organisms were tracking climatic change, then they would all change synchronously, and communities and systems would remain intact. But the extraordinary rates of change expected in the future will overwhelm the capacity of most species to disperse and establish new populations in suitable climatic regions (Davis and Zabinski 1990). With all species lagging the climate, the differences between species in their rates of change (Davis 1986) will become apparent, as some pull ahead of others and form new communities different from those around us today.

A third insight from paleoecology is that disturbance regimes are an aspect of climate that changes as climate changes. In the White Mountains of New Hampshire, for example, wind has always been the most important source of disturbance near treeline (Spear 1989). But at low elevations, charcoal preserved in lake sediment indicates that fire was an important source of disturbance prior to 7000 years ago (Davis 1985, Spear et al. 1989). As the climate has become more mesic fire has become less important. Changes in general atmospheric circulation brought more warm air from the south, reaching a maximum 5000 years ago; this change increased the importance of windstorms.

Evidence of past changes in disturbance regimes from many parts of the world leads to the expectation that rates of disturbance will change in the future as greenhouse warming begins. Paleoecological evidence demonstrates further that a change in disturbance regime can amplify the results of climatic changes, producing a much larger change in vegetation than would have resulted from the direct effects of climate alone. Along the prairie–forest border in Minnesota, for example, oak savanna (Fig. 1) changed to maple forest over a large area as the result of a decline in fire frequency accompanying small changes in climate during the ‘‘Little Ice Age’’ 400 years ago (Grimm 1983, 1984).

Disturbance has been a research focus in recent years, and as a result we are in a stronger position predicting effects of changes in disturbance frequency, than we are predicting the direct effects of changes in climate. Furthermore, general circulation models (GCM’s) do generate information that can be translated into probabilities of extreme events (Rind et al. 1989).

A fourth insight is that multiple impacts will be important, producing effects that are different from any we see around us today. If we search the geography of the earth we can find analogs to many of the fossil assemblages in Quaternary sediments. We use this similarity for interpretation, reconstructing the past by analogy with the present. But as we go back in time, analogs are harder and harder to find. In particular, as we go back into the glacial period itself, 18,000 years ago, we find plant and animal assemblages without modern analogs. In the central plains of North America, for example, there existed vegetation variously described as spruce woodland, spruce forest, prairie, spruce–oak woodland, black ash tundra. This full-glacial vegetation
produced assemblages of spruce, oak, ash, and grass pollen that we find nowhere today (Wright 1987). Large amounts of dust are found in glacial ice that formed at that time (still preserved at depth in the ice sheets of Antarctica and Greenland) suggesting sparse vegetation in many parts of the world, perhaps because of widespread aridity (Peterson et al. 1979, Paterson and Hammer 1987).

We have tried to understand the full-glacial vegetation in terms of climate, but perhaps the explanation lies in the combination of climate and altered atmospheric chemistry of that time. Recently it has become possible to study samples of the ancient atmosphere, preserved as bubbles in ancient glacial ice recovered in ice cores. These reveal that atmospheric carbon dioxide levels fell to less than 200 ppm during the last glacial maximum, well below the preindustrial levels of 270 ppm and the present level of 350 ppm (Paterson and Hammer 1987). It stands to reason, from what we know about direct effects of elevated CO$_2$ (Strain and Cure 1985), that under lower-than-ambient CO$_2$ plants would experience increased moisture stress. The boundary between grassland and forest, to take an example, might have shifted to a higher moisture value along the moisture gradient, resulting in extensive grassland that exaggerated the true extent of areas of low rainfall.

Fig. 3 is a cartoon depicting the relationship I am hypothesizing between vegetation and moisture under three concentrations of atmospheric CO$_2$. The cartoon goes a step further in depicting two kinds of trees (shaded vs. open) with different sensitivities to CO$_2$ concentration (Strain and Cure 1985). At low CO$_2$ levels (200 ppm) one species forms the border with grassland, while under enriched CO$_2$ (540 ppm) the other species becomes dominant. Thus I am suggesting that simultaneous changes in two environmental factors, climate and atmospheric chemistry, could change the response functions of vegetation to climate. Further, response functions might change differentially, resulting in different plant communities than occur in any climatic regime under ambient CO$_2$ concentrations. The unusual animal communities of the full-glacial may reflect not only unusual patterns of vegetation (Graham 1985), but also changes in the nutritive value of foliage that result from low CO$_2$ (Fajer et al. 1989). The important point is that changes of multiple environmental factors, all of them components of global change, can produce ecosystems that have no modern counterpart.

The message from paleoecology is clear. We cannot rely on analogy with the present to predict the future. To predict the future we need functional understanding of the responses of individual species to multiple impacts. Larger scale models will have to build on the reactions of individual species to make accurate predictions of communities, ecosystems, and finally landscape-scale biological systems.

I was eager to speak about this subject at the ESA banquet, where many ecologists with different research interests are present. I am convinced that global change can only be understood if we coordinate research at all levels of ecological organization. Ecosystem ecologists are of course involved; they are challenged to apply their understanding at very large scales and to extrapolate beyond known conditions. Community ecologists must understand the interactions among organisms sufficiently well to be able to predict what will happen if one of a competing species pair is absent, or if competing species are joined by...
a third or fourth species with which they have no contact today. How much will competition and predation be affected by a change in climate? by a change in CO₂ concentration? How important is the loss of species? Are some species more important than others, and if so, which ones?

Population biologists, who have been relatively little involved in global ecology to date, are equally challenged by the research questions raised by global change. We must have a better understanding of the reaction of individual organisms to the environment before we can possibly develop models that scale upwards to predict the reactions of biota on a global scale. How much do we know about environmental physiology, not just for a few species, but for many? Almost nothing is known about ecotypic variation in common species of trees that grow in unmanaged forests. For example, I know of only one prove­

nance orchard for sugar maple, the dominant tree in forests throughout the northeastern United States. This tree is so common now that no one plants it in managed forests. But precisely because it is so abundant, we need to know more about it, so that we can predict how it will react to future environments. Stand-simulation models assume that all individual trees within a species are genetically identical, and that local populations possess the full range of environmental tolerance possessed by the species as a whole. This is obviously simplistic, but do we know enough to specify alternative assumptions?

Given our present knowledge of the genetic architecture of common plants and animals, can we predict the extent to which populations may adapt in situ, instead of shifting geographical range? Evolutionary theory has tended to emphasize an equilibrial environment that suddenly changes to a new state and then remains constant once again. New theory needs to consider environments with a trajectory of rapid change that continues indefinitely into the future. How will genetic variation be affected by a large change in population size or by a rapid shift of geographical range? Even those few species that are able to disperse quickly enough to track the climate (i.e., to extend ranges as much as 500 km per century [Davis and Zabinski 1990]), and thus remain in a similar climatic environment, will face changes in day length, changes in community context, changes in the chemistry of foliage, nutrient availability in soils, pollution load, etc.

It is fortunate that the intellectual challenge posed by global change comes to ecology at a time when a certain rapprochement has come about between population biologists and ecosystem ecologists. That rapprochement is not complete, by any means, but the divisions among us are not so deep as they were even 15 years ago, when many students were trained narrowly in only one subdiscipline. Ecology has matured in the past decade, with ecosystem ecologists acknowledging the impact of individual species on ecosystems, and population biologists acknowledging the impact of disturbance events, unusual years and other manifestations of the physical environment. Whether we can overcome the remaining divisions enough to coordinate research into a multilevel attack on the problems posed by global change remains to be seen.

Global change has been thrust upon us by the success of the human species. The very survival of natural biological systems is threatened. I have tried to emphasize that the scientific problems of global change touch every subfield of the discipline and present the most exciting intellectual challenge that has confronted ecologists in decades. Global change taxes all our understanding of the dynamics of organisms and of their interactions with the environment, in order to synthesize that knowledge into models that can predict ecological responses to combinations of environmental factors and rates of change that have never before impinged on the earth’s biota.

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Margaret B. Davis
Department of Ecology and Behavioral Biology
University of Minnesota
Minneapolis, MN 55455-0302