Using Biotic Interactions to Forecast the Consequences of Global Climate Change

Andrew M. Sugden

DISCUSSIONS OF GLOBAL CLIMATE CHANGE have tended to emphasize physical factors, the physiological responses of individual organisms and the shifting of vegetation and agricultural zones. Although we can predict future changes in atmospheric trace gas composition from industrial outputs, and although the physical principles of the greenhouse effect are well established, General Circulation Models (GCMs) of the atmosphere are not yet sufficiently developed to predict global weather patterns[1]. There has been little attention to the potential contribution of biotic interactions – the dynamics of evolution, population biology and competition. It may be that we cannot anticipate the direction and consequences of global climate change without integrating these interactions into global-change forecasting.

This challenge was the premise for a US National Science Foundation workshop held in September 1991 at Friday Harbor, San Juan Island, WA, USA. Speakers at the workshop considered four main themes: physiological and population responses and contributions to environmental change; evolutionary and genetic consequences; community responses; and landscape change and habitat fragmentation. Subsequently, individual working groups assessed the state of current knowledge and summarized future research needs. The focus was on terrestrial systems.

In summarizing the session on physiological and population ecology, C. Field (Carnegie Institution, Palo Alto, CA, USA) pointed out the feedback loop that connects individual physiology, population ecology, ecosystem ecology and climate – a connection that is obvious enough, but one that neatly draws attention to the relevance of ecological study to the question of climate change. For example, the physiology of individual plants ultimately influences vegetation type and hence surface albedo, which is a key parameter in determining local and regional weather patterns. At one end of the scale, S. Pacala (University of Connecticut, Storrs, USA) argued that models of forest responses to climate change need to take more account of individual species characteristics – especially dispersal ability and the distinction between fundamental and realized niche – before realistic forecasts can be made. A. Ives (University of Wisconsin, Madison, USA) and G. Gilchrist (University of Washington, Seattle, USA) predicted that species with strongly density-dependent growth rates and 'unique' ecological roles in communities would be more resistant to climate change.

At the other end of the scale, S. Schneider (National Center for Atmospheric Research, Boulder, CO, USA) emphasized that one of the biggest uncertainties in GCMs results from the relative lack of land surface parameters: ecological input is required to fill this gap. Ecologists need to tell climatologists what factors really count: for instance, three weeks of low humidity in a particular habitat could increase the risk of fire much more than would an average 2°C warming. D. Schimel (Colorado State University, Boulder, USA) emphasized the importance of the impacts of biota on atmospheric chemistry and regional weather patterns, and pointed out that the effects of land use (or abuse) are orders of magnitude more significant than other changes. M. Pace (Institute of Ecosystem Studies, Millbrook, NY, USA) suggested that the feedback from ecological systems to climate may be more predictable than the other way round. (For a concise discussion of these questions, see Ref. 2.)

To determine the factors limiting species distributions has occupied a central position in ecological and evolutionary investigations for decades. Obviously, this question assumes a new urgency in the context of climate change. Working with North American passerine birds, T. Root (University of Michigan, Ann Arbor, USA) has been investigating metabolic rates at northern winter limits of distribution[3,4]. For the 14 species studied, the metabolic rate at the northern winter limit is approximately 2.5 times higher than the basal metabolic rate. The implication of this work is that to predict changes in bird communities, one might need only to understand the physiological limits placed on each individual species, without worrying about interspecific interactions. Information of this kind is unavailable for most groups of organisms, but it is likely to provide a useful basis for predicting range shifts with temperature shifts. This work also demonstrates how studies of individual physiology might be scaled up to the community level and beyond.

Given the urgency of the climate-change problem, its potential evolutionary effects might seem a rather low priority for research. Moreover, the rate of current climate change is far greater than at any previous time for which we have reliable evidence, and its obvious effects are likely to be movement and extinction, not genetic change. However, some compelling counter-arguments were advanced. M. Geber and T. Dawson (Cornell University, Ithaca, NY, USA) pointed to a wealth of recent studies showing that genetic variation and ecotypic differentiation exist in plant traits that respond to factors such as drought, temperature extremes and phenology. A. Hoffmann (La Trobe University, Bundoora, Australia) reviewed similar studies with animals and cited examples of rapid evolution of stress resistance in insects in response to artificial and natural selection. M. Lynch (University of Oregon, Eugene, USA) presented models that examine the critical rate of environmental change for determining such evolutionary outcomes. In a model in which the optimal value for a character trait moves in one direction, fitness could be maintained even when the mean phenotype shifts on the order of ten standard deviations in 50–60 generations – theory that could be relevant in the context of climate change, at least for species with relatively short generation times. Lynch showed that organisms can compensate for some level of change, but that there is an upper limit; if the rate of environmental change exceeds that limit, extinction is inevitable.

In subsequent working-group discussions, the evolutionary group considered that the central theme around which research should be organized is to discover what determines the potential rate of evolutionary change in a species as a whole. This could be addressed in a variety of ways: examining the history of evolution in a spatial context (i.e. what kind of habitat fragmentation is important?); determining critical rates of habitat

Andrew Sugden is Editor of *TREE*, Elsevier Trends Journals, 68 Hills Road, Cambridge CB2 1LA, UK.

fragmentation; establishing the differences between gene flow and dispersal; gathering currently scattered knowledge on environment-dependent gene expression; and doing transplant experiments to determine the genetic traits involved in failure to adapt to new conditions.

Land use and habitat fragmentation are, of course, already having more immediately severe effects on biodiversity than climate change (D. Wilcove, Environmental Defense Fund, Washington DC, USA). What is important now is the mix of global warming with the other changes that have been under way since the industrial revolution (J. Karr, University of Washington, Seattle, USA). Landscape ecology provides a framework within which population and community responses to change in different regions can be usefully compared (B. Danielson, University of Arizona, Tucson, USA); habitats can, for instance, be classified into source, sink and unusable with respect to particular species. In discussing the effects of habitat fragmentation on the endangered northern spotted owl (*Strix occidentalis caurina*) in the old-growth forests of the northwestern United States, B. Noon (Redwood Sciences Laboratory, Arcata, CA, USA) drew attention to the absence of owls from seemingly suitable habitat patches; to a logger, such patches might seem ripe for clear-cutting, but to a metapopulation biologist or landscape ecologist such patches represent 'vacancies' that are inevitably associated with any species living in a fragmented habitat. Models make it clear that if vacant patches of old growth become too scarce, the population will cross a threshold and plunge toward extinction. Preservation of such vacant patches becomes even more important in the context of climate change – especially when they occur at current range limits.

Throughout the workshop, the need for *forecasting* was frequently stressed. P. Kareiva (University of Washington, Seattle, USA) argued that this is a fundamentally new problem for ecologists, who have mainly been occupied with interpreting past and present patterns. Although predictive modelling has become a cornerstone of ecological progress, the aim is mostly to arrive at ever more refined explanations for existing observable phenomena. Forecasting, on the other hand, entails developing databases and theory to extrapolate current distributions into the future. A key element of effective forecasting, as meteorologists know, is continuous monitoring of the relevant variables. J. Kingsolver (University of Washington, Seattle, USA) and others argued for an expansion of the science of ecological monitoring; we not only need more and better long-term data sets, but also a much better idea of what variables should be monitored to give the most predictive power (for a good recent example see Ref. 5, which deals with the potential effects of climate change on prairie wetland in North America).

Although this workshop drew mainly on US research, its conclusions apply at the global level. How should research be coordinated nationally and internationally to achieve progress that can be communicated effectively to voters and policy makers? In summarizing the discussions, S. Levin (Cornell University, Ithaca, NY, USA) recommended a continuation of a combined top-down and bottom-up approach in which national and international bodies and research initiatives maintain a suitable framework for individual and team-based research. Such a framework can be provided by schemes such as the International Geosphere–Biosphere Program (IGBP)[6] and the Sustainable Biosphere Initiative (SBI)[7] (J. Lubchenco, Oregon State University, Corvallis, USA).

The agenda of ecology and evolutionary biology has always been to understand the factors limiting the distribution and abundance of organisms in space and time. The biological consequences of rapid global climate change constitute a special case within this agenda. In most if not all of the topics discussed at this workshop, the last century of research has provided solid intellectual foundations. What is needed now, therefore, is not a radical theoretical reorientation but a further blending of disciplines. One of the more interesting developments during the 1980s was the blurring of the boundaries between separate traditions such as community ecology, palaeobiology, population genetics and systematics; it's unlikely that a workshop combining most of these elements would have been conceivable a decade ago. However, bridges between ecology and the atmospheric and earth sciences also need to be consolidated, as S. Schneider and D. Schimel frequently emphasized during the workshop. A powerful predictive science of the biosphere will be a vital component of successful political and economic development in the 21st century. Before that, it will be necessary to convince legislators that ecological forecasting is crucial to planet management and that such forecasting is within our grasp.

Correction

Coleman, R.M. and Gross, M.R. *Trends Ecol. Evol.* 6, 404–406 (December 1991)
Errors were introduced during the redrawing of the arrows in Box 2. The correct version is reprinted in its entirety below. I apologise for the mistake. Ed.

Box 2. Possible relationships between past investment (PI), future investment (FI), and future reproductive success (FRS)

(a) No change in resource budget

PI ——► FI
FI ——► FRS
PI —————► FRS

(b) Change in resource budget

PI - - -► FI
FI ——► FRS
PI - - - - - - -► FRS

(c) Other factors influence FRS

PI ——► FI
FI - - -► FRS
PI - - - - - - -► FRS

(d) Change in resource budget and other factors influence FRS

PI - - -► FI
FI - - -► FRS
PI – – – –► FRS

A solid line means 'completely determines', a narrowly dashed line means 'partially determines', and a widely dashed line means 'weakly determines'. In (a), changes in PI directly determine changes in FRS. In (b) and (c), changes in PI only partially determine changes in FRS because of the weakened relationship between PI and FI, and FI and FRS respectively. In (d), changes in PI only weakly determine changes in FRS.

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