Ecology and Climate: Research Strategies and Implications

Terry L. Root; Stephen H. Schneider

Science, New Series, Volume 269, Issue 5222 (Jul. 21, 1995), 334-341.

ogy has produced some additional insights. Primary among these is the knowledge that the spatial heterogeneity in ecological systems at various scales often influences important functions, ranging from population structure through community composition to ecosystem processes, and that traditional within-patch explanations were incomplete. Landscape ecology has begun to determine the mechanisms behind the relations of spatial pattern and ecological processes. The heterogeneity of entire matrices as well as the structures of specific boundaries in landscapes have been shown to govern the movement of organisms, materials, and energy. Landscape ecology has become a major stimulus for clarifying the fundamental problem of scale in ecology by showing how processes at various scales interact to shape ecological phenomena and by exposing regularities that have wide explanatory potential. Finally, landscape ecology has focused the attention of ecologists on scales and systems in which human impacts, even subtle and distant ones, are necessary ingredients in ecological models. Together, these advances have brought spatial heterogeneity into ecology to perform valuable explanatory and predictive functions, rather than excluding it as a troublesome source of error.

REFERENCES

1. M. G. Turner, *Annu. Rev. Ecol. Syst.* 20, 171 (1989).
2. R. T. T. Forman and M. Godron, *Landscape Ecology* (Wiley, New York, 1986).
3. T. F. H. Allen and T. W. Hoekstra, *Towards a Unified Ecology* (Columbia Univ. Press, New York, 1992).
4. R. O. Bierregaard Jr. *et al.*, *Bioscience* 42, 859 (1992).
5. R. S. Ostfeld, in *Effects of Resource Distribution on Animal-Plant Interactions*, M. D. Hunter, T. Ohgushi, P. W. Price, Eds. (Academic Press, Orlando, FL, 1992), pp. 43–74.
6. K. J. Gurtzweiler and S. H. Anderson, *Landscape Ecol.* 6, 293 (1992).
7. M. Cantwell and R. T. T. Forman, *ibid.* 8, 239 (1993).
8. M. G. Turner and W. H. Romme, *ibid.* 9, 59 (1994).
9. F. H. Bormann and G. E. Likens, *Am. Sci.* 67, 660 (1979).
10. J. Kolasa and S. T. A. Pickett, Eds., *Ecological Heterogeneity* (Springer-Verlag, New York, 1991).
11. C. A. Johnston, in (32), pp. 57–80.
12. R. B. Jackson and M. M. Caldwell, *Ecology* 74, 612 (1993).
13. G. P. Malanson, *Riparian Landscapes* (Cambridge Univ. Press, New York, 1993).
14. M. M. Holland, P. G. Risser, R. J. Naiman, Eds., *Ecotones: The Role of Landscape Boundaries in the Management and Restoration of Changing Environments* (Chapman & Hall, New York, 1991).
15. S. W. Beatty, *J. Biogeogr.* 18, 553 (1991).
16. H. Andrén, in (32), pp. 225–255.
17. C. Murcia, *Trends Ecol. Evol.* 10, 58 (1995).
18. R. T. T. Forman and P. N. Moore, in *Landscape Boundaries, Consequences for Biotic Diversity and Ecological Flows*, A. J. Hansen and F. di Castri, Eds. (Springer-Verlag, New York, 1992), vol. 92, pp. 236–258.
19. V. H. Dale, in *Effects of Land Use Change on Atmospheric CO_2 Concentrations: Southeast Asia as a Case Study*, V. H. Dale, Ed. (Springer-Verlag, New York, 1994), pp. 1–14.
20. P. M. Groffman *et al.*, *Ecology* 74, 1579 (1993).
21. D. J. Futuyma, *Evolutionary Biology* (Sinauer Associates, Sunderland, MA, ed. 2, 1986).
22. A. Young, in (32), pp. 153–177.
23. P. Opdam, *Landscape Ecol.* 5, 93 (1991).
24. S. Harrison, in *Large-Scale Ecology and Conservation Biology*, P. J. Edwards, R. M. May, N. R. Webb, Eds. (Blackwell Scientific, Boston, 1994), pp. 111–128.
25. I. Hanski, in (32), pp. 203–224.
26. S. A. Levin, *Ecology* 73, 1943 (1993).
27. R. P. Neilson and L. H. Wullstein, *J. Biogeogr.* 10, 275 (1983).
28. C. S. Holling, *Ecol. Monogr.* 62, 447 (1992).
29. M. J. McDonnell and S. T. A. Pickett, Eds., *Humans as Components of Ecosystems: The Ecology of Subtle Human Effects and Populated Areas* (Springer-Verlag, New York, 1993).
30. P. M. Groffman and G. E. Likens, Eds., *Integrated Regional Models: Interactions Between Humans and Their Environment* (Chapman & Hall, New York, 1994).
31. G. E. Likens, *Bioscience* 41, 130 (1991).
32. L. Hansson, L. Fahrig, G. Merriam, Eds., *Mosaic Landscapes and Ecological Processes* (Chapman & Hall, New York, 1995).

Ecology and Climate: Research Strategies and Implications

Terry L. Root and Stephen H. Schneider

Natural and anthropogenic global changes are associated with substantial ecological disturbances. Multiscale interconnections among disciplines studying the biotic and abiotic effects of such disturbances are needed. Three research paradigms traditionally have been used and are reviewed here: scale-up, scale-down, and scale-up with embedded scale-down components. None of these approaches by themselves can provide the most reliable ecological assessments. A fourth research paradigm, called strategic cyclical scaling (SCS), is relatively more effective. SCS involves continuous cycling between large- and small-scale studies, thereby offering improved understanding of the behavior of complex environmental systems and allowing more reliable forecast capabilities for analyzing the ecological consequences of global changes.

As they increase in numbers, humans are using technology to achieve higher standards of living (*1*). As a consequence, we continue to modify atmospheric composition, water quality, and land surfaces, as well as introduce a host of novel chemicals into the environment. In addition, we have transported species beyond their natural boundaries, creating exotic invasions (*2*). When such changes occur on a global scale (for example, climate change caused by an enhanced greenhouse effect), or regionally but with sufficient frequency as to be global in scope (for example, habitat fragmentations), they are defined as "global changes." The potential severity of these changes has motivated substantial efforts to understand their ecological implications (*3–9*).

The ecological implications of any global change are difficult to predict for several reasons. First, the rates of human-induced change are often an order of magnitude faster than those related to natural causes, which limits the reliable application of historic analogs (*10–12*). Second, the scales at which different research disciplines operate [climate modelers typically use grid squares 500 by 500 km (*13*), whereas ecologists primarily use tennis-court–sized field plots (*14*)] make interdisciplinary connections difficult and necessitate devising methods for bridging scale gaps (*15, 16*). Third, many disciplines must be integrated. Fourth, uncertainties exist in virtually every aspect of the analyses [for example, baseline data (*17, 18*)]. Furthermore, actions to mitigate potential ecological implications are controversial, because policy options often involve substantial investments that, even if macroeconomically efficient, may dramatically alter regional economic, social, or demographic status quos (*19, 20*), and because diverse audiences require education about uncertainties and potential risks.

The urgency of global change issues demands bold attempts to overcome these obstacles. From a public policy perspective, more reliable predictive power could help society mitigate potential impacts by reducing the factors that force global changes (*21*) [for instance, reducing greenhouse gas emissions through fees on carbon releases (*22*)]. In addition, investigation of possible ecological responses may indicate how humans could facilitate the adaptation of managed and unmanaged ecosystems to global changes (*23*), thereby minimizing plausible damages and maximizing potential opportunities. Examples of such "insurance policies" include accelerating development of less-polluting energy systems (*24*) and

T. L. Root is in the School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI 48109, USA. S. H. Schneider is in the Department of Biological Sciences and Institute for International Studies, Stanford University, Stanford, CA 94305, USA, and at the National Center for Atmospheric Research, Post Office Box 3000, Boulder, CO 80307, USA.

building migration corridors among reserves to facilitate the preservation of species (*25*). All of these efforts require integration of biological, physical, and social information about environmental systems (*26*).

A vast array of studies have contributed to the understanding of ecological responses to global change disturbances (*27–29*). Here, we examine three traditional research strategies for assessing the ecological consequences of global climatic change and discuss the limitations of each. We then describe an emerging, more integrated paradigm that we call strategic cyclical scaling (SCS), which may provide more reliable forecast models. Finally, we discuss the importance of interdisciplinary efforts in predicting the ecological consequences of climatic change.

Scale-Up Paradigm

The "scale-up" or "bottom-up" paradigm is the idealized "first principles" approach attempted by most natural science studies. Empirical observations made at small scales are used to determine possible mechanistic associations or "laws of nature" that are then extrapolated to predict larger scale responses. Some of the most conspicuous features observable at smaller scales, however, may not reveal dominant processes that generate large-scale patterns. Mechanisms creating larger-scale responses can easily be obscured in noisy or unrelated local variations. This often leads to an inability to detect at small scales a coherent pattern of associations among variables needed for ecological impact assessments at large scales (*30*).

Small-scale ecological studies are logistically easier to conduct than are large-scale studies (*15, 16*). At small scales, species interactions usually are more readily observable than are other factors, such as environmental forces. Thus, the predominance of published studies on biotic interactions says relatively little about the ecological importance of large-scale factors.

Consider an ecological example for plants, in which extrapolation may not hold. Increasing atmospheric CO_2 is likely to enhance the photosynthetic activity of plants, because the higher CO_2 concentration outside the leaves results in a higher partial pressure of CO_2 inside the leaves. Additionally, the efficiency of plants' water use will probably improve because the same amount of photosynthate can be produced while stomates remain open for a shorter period of time (thereby reducing transpiration) (*31*).

To quantify such potential effects, agricultural researchers have "fertilized" isolated food plants in growth chambers with increased CO_2 and have reported higher yields and more efficient water use (*32*). Although those results are appropriate at the scale and for the conditions of the tests, the extrapolation of those results first to canopy scale and then to whole ecosystems (*33*) is questionable (*34*). With regard to ecosystem effects, plants do not respond uniformly to increased concentrations of CO_2 (*35*). Consequently, CO_2 fertilization in an ecosystem will confer advantages on some species, which in turn could easily alter interactions among species. In addition, carbon/nitrogen ratios may change, which would affect the nutrient quality of leaves and, in turn, herbivory patterns (*35*).

To what extent is it valid to extrapolate inferences from small-scale experiments to more complex or larger scale environmental systems (*36*)? This depends on whether external large-scale processes can be easily observed at smaller scales. For example, forest ecosystem models driven by global warming scenarios with doubled concentrations of CO_2 project dramatic alterations in the current geographic patterns of global biomes (*37, 38*). When such models are extended to account for some of the direct effects of doubled CO_2 on water use due to decreased stomatal conductance, however, they rely on results extrapolated from single-plant studies to the scale of whole forests. This scale-up method dramatically alters the percentage of area predicted to experience biome change (*39*). Prentice and co-workers (*40*), however, exclude such extrapolations, arguing that at the scale of a forest, relative humidity within the canopy, which significantly influences evapotranspiration, is itself regulated by the plants. In other words, there is a feedback process external to the leaf scale that operates at the ecosystem scale: If CO_2 fertilization decreased the transpiration from each plant, the aggregate forest effect would be to lower the relative humidity of the canopy. This, in turn, would increase transpiration, a negative feedback offsetting the direct CO_2 fertilization effect observed at a small scale. This example, although not definitive, nonetheless implies that the scale-up paradigm may be appropriate at some scales (particularly when it incorporates first principles that fit the situation under study), but it is not reliable for all scales without testing at the scales of the system.

A major limitation of the scale-up paradigm occurs in forecasting the behavior of complex systems. A forecasting model is most credible if it solves analytically a well-tested process-based set of equations that account for the interacting phenomena of interest. The classical reductionist philosophy in science indicates that the laws of physics, for example, apply to phenomena at all scales. Thus, in principle, if such laws can be found (usually at small scales), then the exact solutions of the equations that represent such laws will provide reliable forecasts at all scales. This assumes that all significant phenomena are treated by the laws used in making the forecast. However, this is rarely possible in practice, and thus, although most forecasting models are predominantly scale-up, they must explicitly or implicitly include some scale-down assumptions.

Scale-Down Paradigm

In the "scale-down" or "top-down" paradigm, observed large-scale patterns are correlated with other large-scale patterns in order to identify possible causal relations. This approach suffers because the discovered associations may be statistical artifacts that do not reflect the causal mechanisms needed for reliable forecasting (*41*).

Scale-down techniques have long been used to delineate biogeographic boundaries of biomes (regions characterized by similar species and climates). For example, the Holdridge life-zone classification distinguishes biomes (such as tropical moist forest) by means of two empirical predictors: temperature and precipitation (*42*). Other scale-down empirical formulas predict potential vegetation on the basis of a variety of large-scale factors, such as seasonal temperatures or soil moisture (*43*). Criticisms have been aimed at the static nature of such approaches because they often predict that changes in vegetation appear instantaneously with climate changes, thereby neglecting transient dynamics (*44*). In reality, a succession of vegetation types emerges over a period of decades to centuries after a disturbance, even if the climate does not change after that disturbance.

Sound motivations exist for incorporating transient dynamics into models, as was shown by a large interdisciplinary effort by a team of ecologists, palynologists, paleontologists, climatologists, and geologists who formed a loose research consortium known as the Cooperative Holocene Mapping Project (COHMAP) (*45, 46*). One group of these researchers used proxy indicators to reconstruct vegetation patterns over the past 18,000 years for a significant fraction of the land area of the earth. Spruce, now the dominant pollen type in the boreal zone in central Canada, was a predominant pollen type during the last ice age (15,000 to 20,000 years ago), in what are now the mixed hardwood and corn belt regions of the United States. At that time, Canada was largely under ice, and as the ice receded, spruce moved northward. Early interpretations, including that of Darwin himself (*47*), suggested that biological communities had moved with changing climate.

If this were so and communities moved

as units, then the principal ecological concern over the prospect of future climate change would be that habitat alteration might block the previously free-ranging movement of natural communities in response to climate change. Davis (*48*) reported, however, that species exhibited individualistic behavior in response to climatic changes. COHMAP corroborated this using multiple pollen types from the last ice age to the present interglacial period. Global average temperatures increased roughly 5°C during this 10,000-year transition period, and during the most rapid portion of the transition, the distribution of pollen types showed no analog associations to present-day plant communities (*49*). This information and our knowledge of the differentiated tolerances of individual species for climate changes suggest that present-day species assemblages will not move as units given almost any scenario of anthropogenic climate change and underscore the importance of transient dynamics.

Scale-Down Embedded in Scale-Up Paradigm

Scientists strive to base their simulation models on first principles. However, small-scale phenomena must either be neglected or treated implicitly in scale-up models by embedding a scale-down parametric representation (or "parameterization") of the effects of small-scale processes on large-scale variables.

Ecological models. To include processes that contribute to transient dynamics, approaches such as forest "gap" models have been developed (*50*). These models typically assume a random establishment of tree seedlings from various species. Whether these trees grow well depends on several different environmental factors such as soil nutrients, shading, and solar radiation. Individual tree species usually are assigned a sigmoid curve for growth in trunk diameter under ideal conditions.

This approach may appear to be a process-based scale-up technique, because a small spatial scale (such as 0.1 hectares) is normally assumed. The actual growth rate in the simulation model for each species, however, is usually determined by multiplication of the ideal growth rate by a series of growth-modifying functions that attempt to account for the limiting effects of the various environmental factors. For temperature, the growth-modifying function is determined empirically at a large scale by fitting a parabola with a maximum at the value midway between the extremes (temperatures at each species' northern and southern range limits). This embedding of scale-down empiricism into a scale-up approach has been criticized on the grounds that such large-scale curve-fitting exercises are not based on species physiology (*44*). A remedy would be to use population dynamics models with species-specific parameters that are experimentally derived and include factors such as seed dispersal, so that recruitment is related to the preexisting population of plants, not simply a random number generator (*51*). Such experiments could provide data at more appropriate scales for parameterizations of population dynamics models, but it is unclear to what extent even this extra element of empiricism could provide reliable estimates for all relevant model parameters—at least not in less than the several decades it would take to perform the experiments. Furthermore, other factors such as changing pest communities associated with climatic and land use changes could individually or synergistically confuse interpretations of the proposed medium- to large-scale experiments designed to obtain better parameterizations. Certainly, more than one cycle of scale-up–scale-down interactions is needed.

Climate modeling. Most climate models are developed with the philosophy that solutions to energy, momentum, and mass conservation equations should provide a credible forecasting tool. This first-principles scale-up approach suffers from the fundamental practical limitation that the coupled nonlinear equations that describe the physics of the air, land surfaces, seas, and ice are far too complex to be solved by analytic techniques (*52, 53*). Therefore, approximation techniques are applied (*54*). The resulting grid cells, which are the smallest resolved spatial element of such models, are larger than important small-scale phenomena, such as clouds or the influence of a tall mountain on wind flow. Small-scale phenomena can only be incorporated implicitly into a model by techniques in which a mix of scale-down empiricism and fine-resolution scale-up submodels is applied. This defines a parameterization of the influence of subgrid scale processes as a function of variables that are resolved at the grid scale. Finding and testing parameterizations has occupied climate modelers for decades (*52, 53*).

Scale Transition Techniques

Ecologists building scale-up models must use scale-down parameterizations to treat unresolved phenomena. However, the scales typically addressed by climate models and ecological observations differ by orders of magnitude, which is why some ecologists have sought to increase the number of large-scale ecological studies, and some climatologists are trying to shrink the grid size of climate models. We argue that both are required, along with techniques to bridge the scale gaps (*15*).

To estimate the ecological consequences at small scales of forecast climate change, a researcher must first translate the large-scale climate change forecast to a region of smaller scale. This could mean translating climate information at a 500-by-500-km grid scale to a 50-by-50-m field plot—a 10,000-fold interpolation! Such climate models, also known as general circulation models (GCMs), use this coarse resolution because of the practical limitations of computer hardware resources (*55*).

If a mesoscale grid of 50-by-50-km resolution for a climate model were applied over the entire earth, then computation time on a single processor of a supercomputer to run a year's worth of weather would be on the order of 1 year. Still, 50 km is roughly two orders of magnitude larger than the size of a typical cloud (*13*) and three orders of magnitude larger than the typical scale of an ecological study plot (*14*). Therefore, in the foreseeable future, climate models will be unable to transcend the problem of unresolved subgrid-scale phenomena such as cloudiness or evapotranspiration from plants; nor will climate change information be produced directly from the climate models at the same scale at which most ecological information is gathered.

Indirect methods associating empirical large- and small-scale climate data can translate grid-scale averages to smaller scale patterns needed for ecological assessments. For example, the Sierras or the Cascades in the United States are subgrid-scale mountain chains in a typical GCM, but in the actual climate system, onshore winds would produce cool and rainy conditions on the western side and a high probability of warmer and drier conditions on the downslope or eastern side (*15*). This would suggest that when the grid-scale average temperatures were warmer on the eastern slope, the western slope should be cooler and wetter. If, however, 50 years from now warming on the eastern slope were, for example, a result of a doubled concentration of CO_2 causing an enhanced downward infrared radiation flux, then both eastern and western slopes would likely experience warming. Although the degree of warming and associated precipitation anomalies would not necessarily be uniform, an entirely different pattern would likely occur than that obtained empirically using today's weather conditions. Therefore, downscaling techniques that use regional distributions of environmental variables at local scales and correlate them to the large-scale regional patterns will not necessarily provide good guidelines for how large-scale patterns might be distributed locally if the causes of the future change are different from the causes of the historic fluctuations.

Another more mechanistic technique is

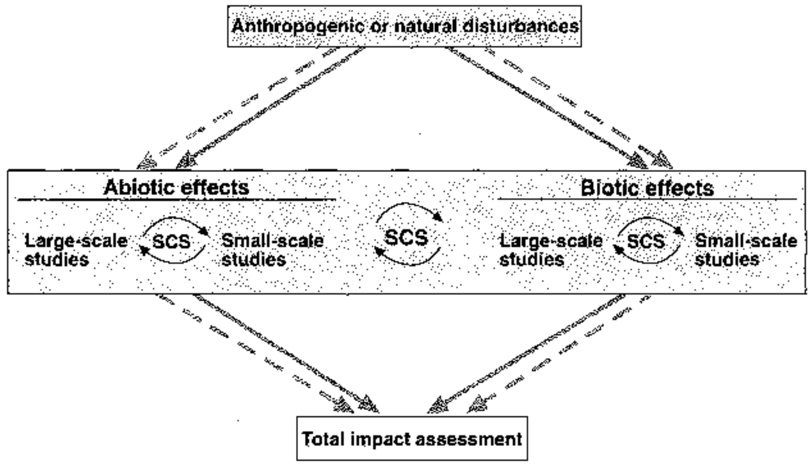

Fig. 1. Investigations across scales of the interactions within and between the biotic and abiotic effects of disturbances are now both possible and required for system-level understanding and for impact assessment. These may be best accomplished by research based on the SCS paradigm, which is a conscious attempt to cycle back and forth between large- and small-scale studies both within and between abiotic and biotic disciplines. Ecological impact assessments can be used as input to overall integrated assessment of global changes. This assessment, in turn, helps with the strategic need to forecast the effectiveness of different policy options. (See Fig. 3 for explanations of this process and color scheme.)

available to translate large-scale patterns: embedding in a particular region a high-resolution model that is driven by large-scale information from a GCM. In essence, this approach uses a predominantly scale-up model based on physical laws to translate GCM grid-scale averages into a smaller scale pattern. This embedding technique translates GCM grid-scale information into mesoscale patterns, which brings climate-model and ecological-response scales much closer (*56*).

Even this technique has several serious problems. First, these models are computer intensive. Second, the model's performance depends on the validity of the GCMs climate statistics in the region of the embedding. For example, if the GCM predicts prevailing winds reasonably well, then the embedded mesoscale model will more faithfully translate the large-scale GCM patterns down to regional detail. If, however, the GCM's simulated wind pattern is not very accurate in the region of embedding, then the mesoscale model will translate the error in its boundary conditions into a higher resolution erroneous pattern. Finally, even a mesoscale grid of 50 by 50 km is coarse relative to the scale of many phenomena such as thunderstorms. Thus, in some regions of the world and in some seasons when such storms are the dominant forms of precipitation, the ability of the mesoscale model to provide a regional pattern of precipitation will only be as good as its scale-down parameterization of thunderstorms.

A scale transition technique developed by Stamm and Gettelman (*57*), called a local climate model (LCM), translates GCM grid-scale predictions of climate changes caused by doubled concentrations of CO_2 to smaller scales. These authors use the statistical technique of canonical regression to compute a 10-by-10-km grid of temperature and precipitation from predictor variables for terrain, sea-surface temperature (SST), wind fields, CO_2 concentration, and solar radiation. Wind fields and SSTs are taken from a doubled-CO_2 GCM run, and a highly simplified energy-balance model is used to evaluate the infrared radiation changes caused by CO_2 concentration changes. This new technique appears promising but has several unsolved problems (*58*).

Strategic Cyclical Scaling Paradigm

We advocate the use of a fourth paradigm, SCS, in which scale-down and scale-up approaches are cyclically applied and strategically designed to address practical problems (Fig. 1). Large-scale associations are used to focus small-scale investigations to ensure that tested causal mechanisms are generating the large-scale relations (*59*). Such mechanisms become the systems-scale "laws" that allow more credible forecasts of the consequences of global change disturbances. SCS is not intended as only a two-step process, but rather as a continuous cycling between strategically designed large- and small-scale studies, with each successive investigation building on previous insights obtained from all scales (*60*).

In our view, the SCS paradigm provides a more scientifically viable and cost-effective means of improving the credibility of ecological assessment than does the isolated pursuit of either the scale-up or scale-down method. It offers a better explanatory potential for complex, multiscale environmental systems (*26*) and more reliable ecological impact assessments and predictive capabilities. Below, we provide two examples of research efforts that followed this paradigm.

Bird case study. One of us (T.L.R.) has applied SCS to the study of wintering North American birds (*61*). With the use of the National Audubon Society's Christmas Bird Count data, average distribution and abundance patterns of a large proportion of wintering birds were found to be associated with environmental factors, such as northern range limits and average minimum January temperature. The scaling question is: What mechanisms at small scales (for example, competition or thermal stress) may have given rise to the large-scale associations? The hypothesis that local physiological constraints caused the particular large-scale temperature and range-boundary associations was tested first. Published small-scale studies on the wintering physiology of key species were used to estimate the northern range boundaries of the birds that exhibited temperature and range-boundary associations (roughly 50% of all songbirds). These birds apparently extend their ranges no farther than to locations where they need not raise their metabolic rates more than ~2.5 times their basal metabolic rate (*61*). This appears to be the maximum metabolic rate these birds can sustain, on average, throughout winter nights to maintain their body temperatures.

At several small field sites along a longitudinal transect running from Michigan to Alabama, it was found that the amount of stored body fat may be restricting the northern range boundary for some birds (*62*). To determine the relative importance of colder temperatures and longer nights (with fewer hours of daylight thus available for foraging), another longitudinal transect, running from Iowa to Louisiana, was incorporated into the study (*63*). This larger-scale design was selected on the basis of previous small-scale studies because it allowed a decoupling of the effects of day length and temperature. The decoupling, in turn, was important to the strategic problem of forecasting potential effects of global warming. Preliminary results suggest that temperatures are more important than day length in explaining the physical constraints that shape bird ranges (*64*). This, in turn, suggests that global temperature changes could cause rapid range and abundance shifts by many bird species, and that the identification of underlying physiological mechanisms can lead to formulas needed for forecasting such changes.

The possibility of rapid biogeographic

shifts by many birds led to an investigation of associations in the year-to-year variations (rather than average limits or abundances as before) between large-scale distribution and abundance patterns of birds and climate variables. Significant annual shifts in the winter ranges of selected species (for example, see Fig. 2) were quantified (65). Preliminary analyses suggest that in warmer years, the winter abundance is significantly higher farther north than it is in colder years (66).

If this research approach works for birds, might it also be appropriate for other taxa? The sex determination of some reptiles is known to be temperature dependent (67), and it has been suggested that the northern range limits of some reptiles and amphibians are determined by ambient temperatures (68). In preliminary investigations, the range limits of several such species have been found to exhibit apparently strong associations with various environmental factors, which suggests that the SCS paradigm may be a powerful research approach for these taxa too. Additionally, the long-term strategic goal is to combine information from various taxa to enhance forecasts of possible ecological consequences of climatic change.

Fig. 2. The range in the United States of the Myrtle race of the yellow-rumped warbler (*Dendroica coronata*) shifted significantly from the winter of 1969 to 1970 (blue solid line) to the winter of 1970 to 1971 (red long-dashed line) to the winter of 1971 to 1972 (yellow short-dashed line) [after (65)].

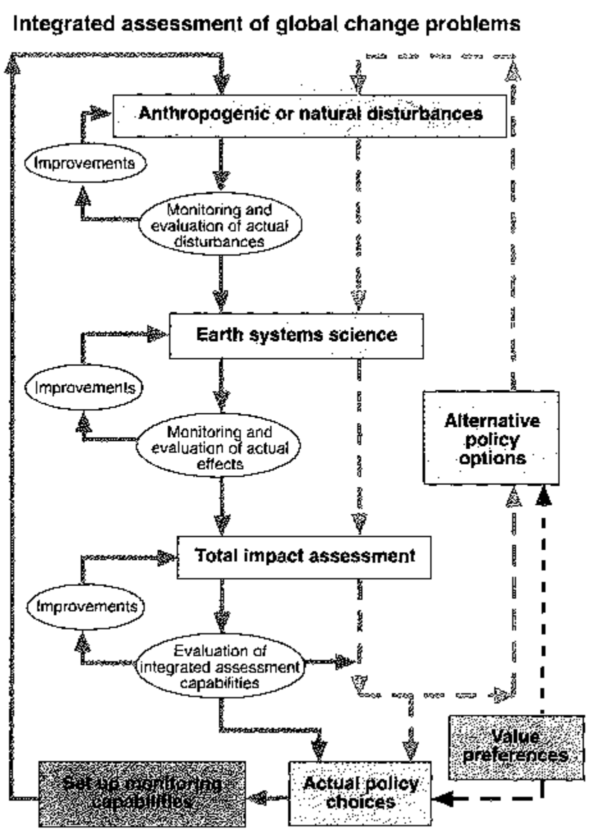

Fig. 3. Framework for the "end-to-end" or integrated assessment (*72*) of global change problems. Two information-flow pathways are distinguished: (i) hypothetical disturbances, effects, and impacts of hypothetical alternative policies (dashed green lines) and (ii) actual disturbances, effects, and impacts arising from actual policy choices (solid red lines). To evaluate (light yellow ovals) and improve (dark yellow ovals) scientific tools and concepts at each level of assessment (blue rectangles), we suggest that the capability to monitor the disturbances, effects, and impacts of actual policy choices (or natural disturbances) be enhanced as rapidly as possible (dark red rectangle). Scientific analyses include assessments of natural and anthropogenic disturbances (dark blue rectangle) and the response of Earth systems (see also Fig. 1) and their implications (medium blue rectangle). These multidisciplinary assessments also need to be integrated (light blue rectangle). Alternative policy options (green rectangle) can be proposed to mitigate impacts or ease adaptations, and the potential efficacy of these options can be tested by the overall integrated assessment process. Value preferences (purple rectangle) influence both actual policy choices (light red rectangle) and hypothetical, alternative policy options (green rectangle), but their influence on the former is usually stronger (purple long-dashed line) than it is on the latter (purple short-dashed line).

COHMAP case study. A second example of SCS-like research is the COHMAP study (69), a team effort cited above, in which strategically designed field and lab work complemented large-scale climatic modeling studies using GCMs. Accepting the premise that atmospheric changes starting 18,000 years ago were forced by changes in the Earth's orbital geometry, greenhouse gas concentrations, and SST, and knowing that such changes can be applied as boundary-forcing conditions for atmospheric GCMs, the COHMAP team used a GCM to produce maps of changing climate at 3000-year intervals. They used scale-down regression models to associate pollen percentages from field data with current climatic variables (January and July temperatures and annual precipitation) (70). The resulting formulas, using fossil pollen data, predicted how climate had changed. These paleoclimate maps were then compared with GCM maps to assess the causes of climatic and ecological changes and to evaluate the regional forecasts of GCMs driven by specified large-scale external boundary forcings. The latter is a practical problem of strategic significance, because the credibility of GCMs' regional climatic anomaly forecasts is controversial. The investigation did not end there, but cycled between large- and small-scale studies, which led to further predictions using GCMs.

To enhance this testing exercise, Kutzbach and Street-Perrott (*71*) developed a regional-scale hydrological model to predict paleolake levels in Africa. They used this model to compare lake levels over the past 18,000 years as computed from GCM climates driving the hydrology model, with paleolake shore changes inferred from fossil field data. The SCS-like COHMAP effort produced comparisons between coupled GCM-hydrological models and paleolake data that were broadly consistent. When combined with vegetation-change map comparisons between GCM-produced pollen abundances and field data on pollen abundances, these comparisons both enhanced our understanding and boosted the credibility of GCM regional projections of forced climate changes.

Integrated Assessments

The overall process for studying global change problems is known as integrated assessment (72) (Fig. 3). The SCS approach (Fig. 1) is an integral part of the Earth systems science subcomponent of this assessment process (Fig 3). The integrated assessment framework (Fig. 3) provides decision-makers at all levels an opportunity to formulate and select better policy choices (72). For example, one strategy for mitigating a typical forecast of global warming of several degrees centigrade by the year 2050 (73) is for policymakers to implement one of a suite of possible abatement policies. Such policies, of course, could be economically damaging to some sectors and perhaps beneficial to others (19–22). Before most policy-makers would be willing to endorse a particular policy, they would likely require estimates of the possible consequences (21, 74). Although the selection of particular alternative policy options is not an entirely value-free process, the integrated assessment processes are not nearly as value-laden as the making of actual policy choices.

The information flows and feedbacks associated with the actual disturbances are distinguished from those associated with the hypothetical disturbances (Fig. 3). Although many of the same scientists, observing systems, models, and paradigms may be applied for both actual and hypothetical integrated assessments, we distinguish these (solid and dashed lines, respectively, in Fig. 3) to emphasize the urgency of setting up, in advance, monitoring capabilities to determine the impact of actual policy choices on the environment and society. In this manner, the effectiveness of state-of-the-art scientific practices can be continuously reevaluated. Baseline data for this feedback process are shown to be needed before the implementation of actual policy choices, which allows the consequences of those choices to become part of the overall integrated assessment improvement process.

To assess how climate change, for example, is affecting ecosystems, baseline data are needed on the status and trends (17, 18) of a vast array of species across all taxa. Not only are such data necessary for studying and monitoring change, but also for devising priorities and practical strategies for biological conservation. This is particularly true, given political and economic constraints that render a "save all species" policy politically intractable. In addition, baseline data are necessary for the development and later evaluation of complex models of ecological systems. Realistic models and baseline data must be applied in order to determine the extent to which various observed changes arise from natural or anthropogenic effects. Besides the intrinsic scientific merit that emerges from understanding the extent to which any observed changes are internally or externally driven, this knowledge is the key to putting policymaking on a firmer factual basis, thereby optimizing the limited resources available for environmental protection.

To conduct such integrated assessments will require addressing issues across many scales and disciplines, necessitating the removal of constraints imposed by disciplinary organization charts or inflexible traditions at existing institutions. We cited the COHMAP effort as a model of cooperative SCS-like research. Not only do the participants deserve credit for experimenting with such a progressive, strategic research design, but credits should also go to the many institutions that cooperated and the foundations that funded this nontraditional SCS-like effort. We believe that as long as most research institutions and funding agencies remain organized in disciplinary subunits, the number of studies using the SCS-like paradigm will be limited. Thus, fundamental, structural institutional changes to foster interdisciplinary multiinstitutional research are long overdue (75).

REFERENCES AND NOTES

1. J. Bongaarts, *Popul. Dev. Rev.* **18**, 299 (1992); J. P. Holdren, *Popul. Environ.* **12**, 231 (1991).
2. S.A. Levin, in *Biological Invasions: A Global Perspective*, J. A. Drake *et al.*, Eds. (Wiley, New York, 1989), pp. 425–435.
3. Intergovernmental Panel on Climate Change (IPCC), *Impact Assessment*, report prepared for IPCC by Working Group II, World Meteorological Organization and United Nations Environment Programme, Geneva, Switzerland, in preparation.
4. R. L. Peters and T. E. Lovejoy, Eds., *Global Warming and Biological Diversity* (Yale Univ. Press, New Haven, CT, 1992).
5. P. M. Kareiva, J. G. Kingsolver, R. B. Huey, Eds., *Biotic Interactions and Global Change* (Sinauer, Sunderland, MA, 1993).
6. T. F. Malone and J. G. Roederer, *Global Change* (Cambridge Univ. Press, Cambridge, 1985).
7. W. C. Clark and R. E. Munn, Eds., *Sustainable Development of the Biosphere* (Cambridge Univ. Press, Cambridge, 1986).
8. F. I. Woodward, Ed., *Global Climate Change: The Ecological Consequences* (Academic Press, New York, 1992).
9. W. B. Meyer and B. L. Turner II, Eds., *Changes in Land Use and Land Cover: A Global Perspective* (Cambridge Univ. Press, Cambridge, 1994).
10. M. B. Davis, in *The Earth in Transition: Patterns and Processes of Biotic Impoverishment*, G. M. Woodwell, Ed. (Cambridge Univ. Press, Cambridge, 1990), pp. 99–110.
11. R. W. Graham and E. C. Grimm, *Trends Ecol. Evol.* **5**, 289 (1990).
12. J. T. Overpeck, R. S. Webb, T. Webb III, *Geology* **20**, 1071 (1992).
13. W. M. Washington and C. L. Parkinson, *An Introduction to Three-Dimensional Climate Modeling* (Oxford Univ. Press, New York, 1986).
14. P. Kareiva and M. Andersen, in *Community Ecology: Workshop Held at Davis, California, April 1986*, A. Hastings, Ed. (Springer-Verlag, New York, 1988), pp. 35–50.
15. T. L. Root and S. H. Schneider, *Conserv. Biol.* **7**, 256 (1993).
16. J. R. Ehleringer and C. B. Field, Eds., *Scaling Physiological Processes: Leaf to Globe* (Academic Press, New York, 1993).
17. E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, M. T. Mac, Eds., *Our Living Resources: A Report to the Nation on the Distribution, Abundance and Health of U.S. Plants, Animals and Ecosystems* (U.S. National Biological Service, Washington, DC, in press).
18. M. Mac *et al.*, Eds., in preparation.
19. Abatement costs will prevent mitigation policies according to T. Schelling, in *Changing Climate: Report of the Carbon Dioxide Assessment Committee* (National Academy Press, Washington, DC, 1983).
20. Abatement costs have been overestimated according to M. Grubb, M. H. Duong, and T. Chapius, in *Integrative Assessment of Mitigation, Impacts and Adaptation to Climate Change*, N. Nakićenović, W. D. Nordhaus, R. Richels, F. L. Toth, Eds. (International Institute of Systems Analysis, Laxenberg, Austria, 1994), pp. 513–533; and L. H. Goulder and S. H. Schneider, in preparation.
21. National Academy of Sciences, *Policy Implications of Greenhouse Warming* (National Academy Press, Washington, DC, 1991).
22. D. Gaskins and J. Weyant, *Am. Econ. Rev.* **83**, 318 (1993); IPCC, *Policy Options*, report prepared for IPCC by Working Group III, World Meteorological Organization and United Nations Environment Programme, Geneva, Switzerland, in preparation.
23. See (21), adaptation section. N. J. Rosenberg, Ed., *Towards an Integrated Impact Assessment of Climate Change: The MINK Study* (Kluwer Academic, Dordrecht, Netherlands, 1993). In addition to passive adaptation, anticipatory adaptations hedge against significant global change impacts [S. H. Schneider and S. L. Thompson, in *The Global Possible*, R. Repetto, Ed. (Yale Univ. Press, New Haven, CT, 1985), pp. 397–430].
24. T. B. Johansson, H. Kelly, A. K. N. Reddy, R. H. Williams, Eds., *Renewable Energy: Sources for Fuels and Electricity* (Island Press, Washington, DC, 1993).
25. R. L. Peters and J. D. Darling, *Bioscience* **35**, 707 (1985); R. L. Peters, in (4), pp. 15–30.
26. F. P. Bretherton, *Proc. IEEE* **73**, 118 (1985).
27. See the recommendations of assessment groups charged with analysis of the ecological implications of global changes. These include: Committee on Global Change of the Commission on Geosciences, Environment, and Resources, National Research Council, *Research Strategies for the U.S. Global Change Research Program* (National Academy Press, Washington, DC, 1990); P. Bourdeau, J. A. Haines, W. Klein, C. R. Krishna Murti, *Ecotoxicology and Climate* (Wiley, New York, 1989); Committee on Environmental Research, *Research to Protect, Restore, and Manage the Environment* (National Academy Press, Washington, DC, 1993); and (8). The following citations of the ecological implications literature provide only a representative cross-section of the scope of research. We emphasize works that contain extensive references to an array of published materials. In addition, we reference materials from a variety of scientific communities that do not normally cite each other's work. For discussion of global change and marine systems, see S. V. Smith and R. W. Buddemeier, *Annu. Rev. Ecol. Syst.* **23**, 89 (1992); J. Lubchenco, S. A. Navarrete, J. C. Castilla, in *Earth System Responses to Global Change*, H. A. Mooney, E. R. Fuentes, B. I. Kronberg, Eds. (Academic Press, New York, 1993); T. E. Bigford, *Coastal Manage.* **19**, 417 (1991); D. Roemmich and J. McGowan, *Science* **267**, 1324 (1995); W. V. Reid and M. C. Trexler, *Coastal Manage.* **20**, 117 (1992); and S. R. Carpenter, S. G. Fisher, N. B. Grimm, J. F. Kitchell, *Annu. Rev. Ecol. Syst.* **23**, 119 (1992). For discussion of global change and freshwater systems, see C. K. Minns and J. E. Moore, *Clim. Change* **22**, 327 (1992); K. A. Poiani and W. C. Johnson, *Bioscience* **41**, 611 (1991); D. W. Schindler *et al.*, *Science* **250**, 967 (1990); R. A. Assel, *Clim. Change* **18**, 377 (1991); and W. R. Rouse, D. W. Carlson, E. J. Weick, *ibid.* **22**, 305 (1992). For discussion of global change and terrestrial vegetation, see (3, 16); J. Harte and R. Shaw, *Science* **267**, 876 (1995); E. Salati and C. A. Nobre, *Clim. Change* **19**, 177 (1991); J. H. C. Gash and W. J. Shuttleworth, *ibid.*, p. 123; P. J. Crutzen and J. G. Goldammer, *Fire in the Environment: The Ecological, Atmospheric, and Climatic Importance of Vegetation Fires* (Wiley,

New York, 1993); C. Price and D. Rind, *J. Clim.* **7**, 1484 (1994); G. M. MacDonald *et al.*, *Nature* **361**, 243 (1993); E. R. Cook and J. Cole, *Clim. Change* **19**, 271 (1991); and S. W. Running and R. R. Nemani, *ibid.*, p. 349. For discussion of global change and biophysical feedback, see A. Henderson-Sellers, *ibid.* **23**, 337 (1993); J. Shukla and Y. Mintz, *Science* **215**, 1498 (1982); J. Lean and D. A. Warrilow, *Nature* **342**, 411 (1989); J. A. Foley, J. E. Kutzbach, S. Levis, *ibid.* **371**, 52 (1994); and G. B. Bonan, D. Pollard, S. L. Thompson, *ibid.* **359**, 716 (1992). For discussion of global change and terrestrial animals, see (*11*); K. A. McDonald and J. H. Brown, *Conserv. Biol.* **6**, 409 (1992); D. M. Gates, *Biophysical Ecology* (Springer-Verlag, New York, 1980); G. R. Coope, *Philos. Trans. R. Soc. London B* **280**, 313 (1977); T. L. Root, in (*5*), pp. 280–292; M. V. Lomolino, *J. Mammal.* **75**, 39 (1994); W. R. Dawson, in (*4*), pp. 158–170; N. L. Rodenhouse, *Conserv. Biol.* **6**, 263 (1991); and T. J. C. Beebee, *Nature* **374**, 219 (1995). For discussion of global change and biogeochemical cycling, see W. H. Schlesinger, *Biogeochemistry: An Analysis of Global Change* (Academic Press, New York, 1991); D. S. Schimel *et al.*, *Global Biogeochem. Cycles* **8**, 279 (1994); D. W. Schindler and S. E. Bayley, *ibid.* **7**, 717 (1993); A. R. Townsend, P. M. Vitousek, E. A. Holland, *Clim. Change* **22**, 293 (1992); A. R. Longhurst, *Limnol. Oceanogr.* **36**, 1507 (1991); and J. L. Sarmiento and J. C. Orr, *ibid.*, p. 1928. For discussion of global change and agricultural ecosystems, see C. Rosenzweig and M. Parry, *Nature* **367**, 133 (1994); S. K. Sinha, *Clim. Change* **19**, 201 (1991); N. J. Rosenberg, *ibid.* **21**, 385 (1992); M. E. Cammell and J. D. Knight, in (*8*), pp. 117–162; and P. L. Klinedinst, D. A. Wilhite, K. G. Hubbard, *Clim. Change* **23**, 21 (1993). For discussion of global change and "surprises," see C. S. Holling, in (*7*), pp. 292–317; W. S. Broecker, *Nature* **328**, 123 (1987); and S. H. Schneider, in *Climate Change and World Food Security*, T. E. Downing, R. S. Chen, R. W. Kates, M. L. Parry, Eds. (Springer-Verlag, New York, in press).

28. J. B. Smith and D. A. Tirpak, Eds., *The Potential Effects of Global Climate Change on the United States* (Hemisphere, New York, 1990).
29. S. J. Morreale, G. J. Ruiz, J. R. Spotila, E. A. Standora, *Science* **216**, 1245 (1982).
30. As T. E. Dawson and F. S. Chapin [in (*16*), p. 318], note, too much "information about detailed mechanisms may be inefficient, incorporating excessive detail and ignoring other aspects that are critical to understanding processes at the higher levels."
31. F. A. Bazzaz, *Annu. Rev. Ecol. Syst.* **21**, 167 (1990).
32. S. B. Idso and B. A. Kimball, *Global Biogeochem. Cycles* **7**, 537 (1993).
33. S. B. Idso and A. J. Brazel, *Nature* **312**, 51 (1984); H. W. Ellsaesser, *Atmósfera* **3**, 3 (1990).
34. C. B. Field, *Nature* **371**, 472 (1994); (*3*); W.C. Oechel *et al.*, *Nature* **371**, 500 (1994).
35. F. A. Bazzaz and E. D. Fajer, *Sci. Am.* **266**, 68 (January 1992).
36. Extrapolating to spatially larger but comparably complex ecosystems is logically different from extrapolating a much less complex system to an ecosystem, even if both have the same physical dimensions. For further discussion, see S. A. Levin, *Ecology* **73**, 1943 (1992).
37. T. M. Smith, H. H. Shugart, G. B. Bonan, J. B. Smith, in (*8*), pp. 93–116; J. M. Melillo *et al.*, *Nature* **363**, 234 (1993); R. P. Neilson, *Ecol. Appl.* **3**, 385 (1993).
38. I. C. Prentice *et al.*, *J. Biogeogr.* **19**, 117 (1992).
39. R. P. Neilson, *Ecol. Appl.* **5**, 362 (1995); Vegetation Ecosystem Model Analysis Project participants, in preparation.
40. The BIOME2 model of I. C. Prentice and colleagues (*38*) includes direct CO_2 effects on C_3/C_4 plant competition but excludes direct CO_2 effects on water-use efficiency [based on K. G. McNaughton and P. G. Jarvis, *Agric. For. Meteorol.* **54**, 279 (1991)].
41. As P. G. Jarvis [in (*16*), p. 121] states, "A major disadvantage of a top-down model is that predictions cannot be made safely outside the range of the variables encountered in the derivation of the lumped parameter function."
42. L. R. Holdridge, *Life Zone Ecology* (Tropical Science Center, San Jose, Costa Rica, 1967). See (*37–40*) for more complex biome models.
43. M. B. Davis and C. Zabinski, in (*4*), pp. 297–308; P. J. Bartlein, I. C. Prentice, T. Webb III, *J. Biogeogr.* **13**, 35 (1986); E. O. Box, *Macroclimate and Plant Forms: An Introduction to Predictive Modeling in Phytogeography* (Junk, Hague, Netherlands, 1981); H. Lieth and E. O. Box, *Publ. Clim.* **25**, 37 (1972).
44. J. Pastor and W. M. Post, *Clim. Change* **23**, 111 (1993); G. B. Bonan, *ibid.* **24**, 281 (1993).
45. COHMAP members, *Science* **241**, 1043 (1988).
46. H. E. Wright *et al.*, Eds., *Global Climates Since the Last Glacial Maximum* (Univ. of Minnesota Press, Minneapolis, MN, 1993).
47. C. Darwin [*On the Origin of Species by Means of Natural Selection* (John Murray, London, 1859)] stated: "As the arctic forms moved first southward and afterward backward to the north, in unison with the changing climate, they will not have been exposed during their long migrations to any great diversity of temperature; and as they all migrated in a body together, their mutual relations will not have been much disturbed. Hence, in accordance with the principles inculcated in this volume, these forms will not have been liable to much modification."
48. M. B. Davis, *Geosci. Man* **13**, 13 (1976).
49. J. T. Overpeck, T. Webb III, I. C. Prentice, *Quat. Res.* **23**, 87 (1985).
50. D. B. Botkin, J. F. Janak, J. R. Wallis, *J. Ecol.* **60**, 849 (1972); J. Pastor and W. M. Post, *Nature* **334**, 55 (1988); H. H. Shugart and T. M. Smith, in (*4*), pp. 147–157.
51. S. W. Pacala and G. C. Hurtt, in (*5*), pp. 57–74; H. A. Mooney, B. G. Drake, R. J. Luxmoore, W. C. Oeschel, L.F. Pitelka, *Bioscience* **41**, 96 (1991).
52. Study of Man's Impact on Climate (SMIC), *Inadvertent Climate Modification* (MIT Press, Cambridge, MA, 1972).
53. IPCC, *Second Scientific Assessment*, report prepared for IPCC by Working Group I, World Meteorological Organization, Geneva, Switzerland, in preparation.
54. Continuous differential equations are replaced with discrete, numerical finite difference equations. See (*13*).
55. See, for example, K. E. Trenberth, Ed., *Climate System Modeling* (Cambridge Univ. Press, Cambridge, 1992); and (*13*). At a resolution of 500 by 500 km, a simulation for 100 years (still a short time from the perspective of ecological changes) would involve 1000 hours of supercomputer time—a nontrivial resource commitment. Moreover, because the original differential equations are discretized into such large grid boxes, sub-grid-scale processes such as cloudiness, which are critical to the energy balance of the climate model, cannot be treated explicitly. Rather they are, as noted, included implicitly by semi-empirical "parameterizations" that relate the grid-box averaged effects of clouds to grid-box averaged variables such as relative humidity or vertical stability. For a nonspecialized treatment, see S. H. Schneider and R. Londer, *The Coevolution of Climate and Life* (Sierra Club Books, San Francisco, CA, 1984), chap. 6.)
56. F. Giorgi, *J. Clim.* **3**, 941 (1990).
57. J. F. Stamm and A. Gettelman, *Clim. Change* **30**, 295 (1995).
58. Although encouraging results were obtained for local climate deviations in the high, topographically varying, western United States, Stamm and Gettelman found that "the LCM has difficulty with estimating extreme (high or low) temperatures." Likewise, they found that "the LCM estimates of January precipitation are biased toward the median." Whether this bias is a result of too few empirical records or a fundamental obstacle based on the high degree of empiricism inherent in the technique (or both) is not yet clear.
59. S. A. Levin [in (*16*), p. 14] notes that, "Although it is well understood that correlations are no substitute for mechanistic understanding of relationships, correlations can play an invaluable role in suggesting candidate mechanisms for (small-scale) investigation."
60. J. Harte, D. Jensen, M. Torn [in (*4*), p. 338] emphasized "the benefits of the combined use of correlations and simple mechanistic models because of the enormous value of this strategy in the resolution of past environmental dilemmas." The need to make inferences across scales in the context of a strategic assessment (global problem solving) also is succinctly stated by Vitousek [in (*16*), p. 173]: "just as ecosystem ecology has advanced in large part through the use of ecosystem-level measurements and experiments [that is, scale-down], the science of global ecology is likely to develop most efficiently if it is driven by regional and global measurements designed to answer globally significant research questions."
61. T. L. Root, *Atlas of Wintering North American Birds* (Univ. of Chicago Press, Chicago, IL, 1988); *J. Biogeogr.* **15**, 489 (1988); *Ecology* **69**, 330 (1988); *ibid.* **70**, 1183 (1989), but see G. Castro, *ibid.*, p. 1181. See criticisms in R. R. Repasky, *ibid.* **72**, 2274 (1991) and rebuttal in T. L. Root, in (*5*), pp. 280–292. J. Diamond [*Nature* **337**, 692 (1989)] coined the "2.5 rule" phrase.
62. T. L. Root, *Proc. 20th Int. Ornithol. Congr.* **2**, 817 (1991). Most birds do not store fat in the same manner as mammals do. Usually in the fall, mammals store fat that will be used throughout the winter. Instead, birds undergo a daily fat-storage cycle, storing fat during the day and using a large percentage of that fat throughout the night. Therefore, they go to roost at dusk with a significant amount of stored fat, use the fat to fuel their metabolism throughout the night, and awake at dawn with significantly less body fat [C. Blem, *Am. Zool.* **16**, 671 (1976)].
63. Four field sites are paired with four sites on the more eastern transect so that each pair occurs at the same latitude (sites in Michigan and Iowa, Indiana and Missouri, Tennessee and Arkansas, and Alabama and Louisiana have the same day length). Because average winter isotherms run at an angle to latitude in this area of the continent, three of the sites along each transect were paired by temperature (sites in Missouri and Michigan, Arkansas and Indiana, and Louisiana and Tennessee have roughly the same average nightly January temperature).
64. T. L. Root, in preparation.
65. ———, *Proc. Am. Philos. Soc.* **138**, 377 (1994).
66. S. H. Schneider and T. L. Root, in (*18*).
67. (*29*), R. L. Burke, *Copiea* **1993**, 854 (1993); F. J. Janzen, *Proc. Natl. Acad. Sci. U.S.A.* **91**, 7487 (1994).
68. J. W. Gibbons, *Herpetologica* **39**, 254 (1983); A. W. Pinder, K. B. Storey, G. R. Ultsch, in *Environmental Physiology of the Amphibians*, M. E. Feder and W. W. Burggren, Eds. (Univ. of Chicago Press, Chicago, IL, 1991), pp. 250–274; T. R. VanDevender, C. H. Lowe, H.E. Lawler, *Herpetol. Nat. Hist.* **2**, 25 (1994).
69. H. E. Wright *et al.* (*46*) note the large-scale nature of climatic change and describe their strategic research design: "We therefore have used climate models and a general understanding of the global controls (e.g., variations in insolation, ice volume, and related glacial-age boundary conditions) in an attempt to repeat nature's experiments and to illustrate the linkages between the varying regional climate patterns and the global controls. We also assembled large sets of data to describe the natural experiments and to evaluate the model results. Similarities between data and models increase confidence in the models and encourage use of the model results in explaining the patterns in the data. Discrepancies indicate where improvements are needed in the boundary conditions, models, and data. A key result of our study is the demonstration of how data and models can interact for the improvement of both. With continued improvements in the data and models, we anticipate that certain of our current explanations for the observed changes will be modified."
70. I. C. Prentice, P. J. Bartlein, T. Webb III, *Ecology* **72**, 2038 (1991).
71. J. E. Kutzbach and F. A. Street-Perrott, *Nature* **317**, 130 (1985).
72. Integrated assessment refers to the "end-to-end" assessment of physical, biological, and social causes of global changes and their implications for environment and society. It involves coupling scenarios of population, land use, affluence, and technology changes over time to biogeochemical models driving climate models driving ecological models, all used to

provide global change scenarios for economic models. Policy options for mitigation and adaptation can be investigated with the use of integrated assessment techniques. For further details and many additional references see N. Nakićenović in (20); E. A. Parsons, *Energy Policy*, in press; and J. Alcamo, Ed., *IMAGE 2.0: Integrated Modeling of Global Climate Change* (Kluwer Academic, Dordrecht, Netherlands, 1994).
73. (53); M. G. Morgan and D. W. Keith, *Environ. Sci. Technol.*, in press.
74. (3, 28); U.S. Congress, Office of Technology Assessment, *Preparing for an Uncertain Climate*, Volume II, OTA-O-568 (U.S. Government Printing Office, Washington, DC, 1993).
75. The National Research Council's Committee on Environmental Research [*Research to Protect, Restore, and Manage the Environment* (National Academy Press, Washington, DC, 1993)] addressed this issue, concluding "The current strength of disciplinary research must be maintained, but more research must be multiscale and multidisciplinary to match the characteristics of the phenomena that we seek to understand. Research must cross the boundaries of mission agencies for the same reason." See also S. H. Schneider, in *Proceedings of the NATO Advanced Research Workshop on Training Global Change Scientists*, D. J. Waddington, Ed. (Springer-Verlag, New York, 1995), pp. 9–40.
76. T.L.R. acknowledges partial support for this work from NSF (IBN-9058031), the U.S. Fish and Wildlife Service Global Change Program, and the Pew Scholars Program in Conservation and the Environment. S.H.S. acknowledges support from the U.S. Department of Agriculture (grant 94-G-237) to the National Center for Atmospheric Research, which is sponsored by NSF. Opinions are those of the authors and do not necessarily reflect the views of the sponsoring agencies. We appreciate the programming help from L. McDaniel and the many useful comments on draft manuscripts by E. J. Brennan, M. Burger, R. Burke, B. Fahey, J. Harte, A. Matton, C. Still, and T. Webb III, as well as the useful suggestions from I. C. Prentice.

Population Growth and Earth's Human Carrying Capacity

Joel E. Cohen

Earth's capacity to support people is determined both by natural constraints and by human choices concerning economics, environment, culture (including values and politics), and demography. Human carrying capacity is therefore dynamic and uncertain. Human choice is not captured by ecological notions of carrying capacity that are appropriate for nonhuman populations. Simple mathematical models of the relation between human population growth and human carrying capacity can account for faster-than-exponential population growth followed by a slowing population growth rate, as observed in recent human history.

Scientific uncertainty about whether and how Earth will support its projected human population has led to public controversy: will humankind live amid scarcity or abundance or a mixture of both (*1*, *2*)? This article surveys the past, the present, and some possible futures of the global human population; compares plausible United Nations population projections with numerical estimates of how many people Earth can support; presents simplified models of the interaction of human population size and human carrying capacity; and identifies some issues for the future.

The Past and Some Possible Futures

Over the last 2000 years, the annual rate of increase of global population grew about 50-fold from an average of 0.04% per year between A.D. 1 and 1650 to its all-time peak of 2.1% per year around 1965 to 1970 (*3*). The growth rate has since declined haltingly to about 1.6% per year (*4*) (Fig. 1). Human influence on the planet has increased faster than the human population. For example, while the human population more than quadrupled from 1860 to 1991, human use of inanimate energy increased from 10^9 (1 billion) megawatt · hours/year (MW · hours/year) to 93 billion MW · hours/year (Fig. 2). For many people, human action is linked to an unprecedented litany of environmental problems (*5*), some of which affect human well-being directly. As more humans contact the viruses and other pathogens of previously remote forests and grasslands, dense urban populations and global travel increase opportunities for infections to spread (*6*): The wild beasts of this century and the next are microbial, not carnivorous.

Along with human population, the inequality in the distribution of global income has grown in recent decades (*7*). In 1992, 15% of people in the world's richest countries enjoyed 79% of the world's income (*8*). In every continent, in giant city systems, people increasingly come into direct contact with others who vary in culture, language, religion, values, ethnicity, and socially defined race and who share the same space for social, political, and economic activities (*9*). The resulting frictions are evident in all parts of the world.

Today, the world has about 5.7 billion people. The population would double in 43 years if it continued to grow at its present rate of 1.6% per year, though that is not likely. The population of less developed regions is growing at 1.9% per year, while that of more developed regions grows at 0.3 to 0.4% per year (*10*). The future of the human population, like the futures of its economies, environments, and cultures, is highly unpredictable. The United Nations (UN) regularly publishes projections that range from high to low (Fig. 1). A high projection published in 1992 assumed that the worldwide average number of children born to a woman during her lifetime at current birthrates (the total fertility rate, or TFR) would fall to 2.5 children per woman in the 21st century; in this scenario, the population would grow to 12.5 billion by

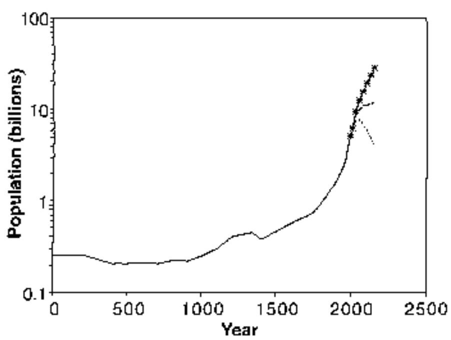

Fig. 1. Recent world population history A.D. 1 to 1990 (solid line) (*53*) and 1992 population projections of the UN (*11*) from 1990 to 2150: high (solid line with asterisks); medium (dashed line); and low (dotted line). Population growth was faster than exponential from about 1400 to 1970.

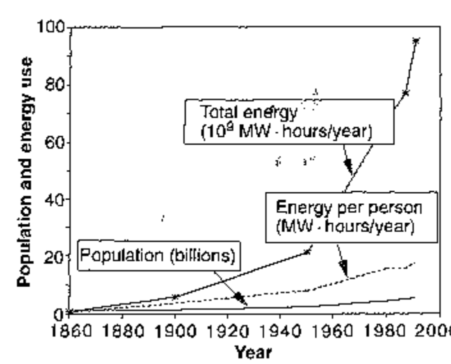

Fig. 2. Inanimate energy use from all sources from 1860 to 1991: aggregate (solid line with asterisks) (*54*) and per person (dashed line). Global population size is indicated by the solid line.

The author is in the Laboratory of Populations, Rockefeller University, 1230 York Avenue, New York, NY 10021, USA.