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INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS
I.C.T.P., P.O. BOX 586, 34100 TRIESTE, ITALY, CABLE: CENTRATOM TRIESTE

UNITED NATIONS INDUSTRIAL DEVELOPMENT ORGANIZATION

INTERNATIONAL CENTRE FOR SCIENCE AND HIGH TECHNOLOGY
c/o INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS 34100 TRIESTE (ITALY) VIA GRIGNANO, 9 (ADRIATICO PALACE) P.O. BOX 586 TELEPHONE 040-224572 TELEFAX 040-224575 TELEX 460449 APH I

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"Can Large-Scale Climatic Models be Linked with Multi-Scale Ecological Studies"

S. Schneider
National Center for Atmospheric Research
P.O. Box 3000
Boulder, Colorado 80307-3000
U.S.A.

CAN LARGE-SCALE CLIMATIC MODELS
BE LINKED WITH MULTI-SCALE ECOLOGICAL STUDIES?*

Terry L. Root**
School of Natural Resources and Environment
University of Michigan
Ann Arbor, Michigan

Stephen H. Schneider**
National Center for Atmospheric Research***
Boulder, Colorado
and
Department of Biological Sciences and
Institute for International Studies
Stanford University
Stanford, California

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INTRODUCTION

No disagreement exists in the scientific community about the existence of the greenhouse effect. Greenhouse-gas injections over the past 150 years have resulted in a 25% increase in CO_2, a 100% increase in CH_4, and the introduction of heat-trapping synthetic chemicals such as chlorofluorocarbons (CFCs) and halons. These emissions are responsible for some 2-3 W/m^2 of additional infrared radiative heat trapping at the earth's surface (IPCC 1990). The debate arises over how to translate several additional W/m^2 of heating into degrees of temperature change. Many physical, biological and chemical "feedback mechanisms" will be interacting, and the lack of detailed experimental control over the processes that force our global climate, including temperature, to vary prevents scientists from knowing precisely how the climate will be affected. The observed $0.5 \pm 0.2^{\circ}C$ 20th century warming trend, however, is indeed consistent with a CO_2-doubling equilibrium sensitivity of anywhere from 0.6 to 5.0°C (Wigley and Raper 1990), which are in agreement with the two extreme scenarios constructed earlier by an international assessment team (Jaeger 1988).

On the low end, the overall change in global temperature is projected to rise only 0.6°C by the end of the next century, whereas the high estimate is a dramatic 5.0°C change. At least on a local or regional scale, the biological consequences of even the low scenario could be significant enough to precipitate measurable distribution changes in some species and probably facilitate some extinctions (e.g., McDonald and Brown 1992). Forecasts of possible biological consequences for the entire range

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*Portions Adapted from Root 1992 and Schneider 1992a

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of projected rise in global temperature will be helpful in providing the guidance needed to avert (hopefully), or at least to help plan for disruptions of communities and ecosystems.

The possible biological changes would not only be due to increased temperature per se, but, probably more importantly, to the rate of the increase. The very rapid rate of change would force transient variations in both mean and extreme climatic statistics. Any alterations to the character of extreme weather events could be quite biologically significant (e.g., massive die offs of Eastern Bluebirds, House Wrens, Eastern Phoebe, Hermit Thrush during severe cold snaps [James 1962]). Additionally, the anticipated changes in global climate are expected to occur at a rate most biologists acknowledge as simply too fast for evolutionary processes, such as natural selection, to keep pace (but see Lynch and Lande 1992 for alternative view). Such constraints on species' abilities to adapt to their rapidly changing habitats could substantially enhance the probability of extinction of numerous species. Indeed, the importance in the difference between evolutionary and ecological time scale was noted by Davis (1990): "The fossil record shows that most forest trees were able to disperse rapidly enough to keep up with most of the climatic changes that took place in recent millennia. These changes were much more gradual than the climatic changes projected for the future. Even so, there were occasional periods of disequilibrium between plant distributions or abundances, soils, and climate that lasted a century or more. The most rapid dispersal rates known from the fossil record, however, are an order of magnitude too slow to keep up with the temperature rise expected in the coming century." Quite simply, tree

species generally take hundreds, even thousands of years for substantial dispersal, while significant temperature rise is forecast to be an order of magnitude faster than that. Additionally, land-use by humans has fragmented the natural environment in such a way that dispersal of individuals and expansion of ranges will be limited without substantial human intervention (Main 1988; Arnold 1988; Wilcove et al 1986). Hence, the biological consequences of the impending warming event could easily be significantly more severe than any comparable event in pre-historic times. Many more species could go extinct and the reshaping of ranges could be more extreme.

Such biological disruption could greatly influence the functioning of ecosystems. Indeed, a tearing apart of species' communities quite possibly would occur, with the ranges of some species moving farther and faster than others. Each species has its own unique ecological and physiological needs (Whittaker 1970) and as a result differential responses to environmental changes will be exhibited by each species (Strain 1987, Cohn 1989). Consequently, species-specific studies are needed to help us understand the ecology, behavior, evolution, physiology, and the like of as many species as possible, particularly those that could be viewed as keystones in various communities. Additionally, studies are needed at a local scale to help us understand interactions of species within communities, and at a regional scale to allow investigation of entire ecosystems. Even though we do not know what the exact increase in the global temperature will be or how regional climates will change, various models exists that can help us predict possible changes (e.g., IPCC 1990, 1992). Using these models coupled with our knowledge of species, communities and ecosystems, we will be able to make more reliable projections of the potential biological consequences of those changes.

The mismatch of scales between the models and the biological studies, however, detracts significantly from our ability to forecast reliably the effect global climate change will have on living organisms. For instance, most ecological studies are carried out in areas roughly the size of a tennis court (Kareiva and Andersen 1988), while the resolution of most climate models is approximately the size of the state of Colorado. A hand full of studies do exist that attempt to bridge this scale "gulf" (e.g., Root 1988 a,b; Gates 1985, Brown and Maurer 1989, Terborgh 1971), but certainly more needs to be done to help us understand the complexities of how living organisms will react to climate change. The purpose of this paper is to discuss approaches that will hopefully reduce the mismatch. We also provide examples of successful "bridging" studies that examine and suggest avenues for future work. These also provide examples of how such studies can be used as a foundation upon which the relatively small-scale biological studies and large-scale climatic studies can be coupled to clarify further the possible biological consequences of global climate change.

GLOBAL WARMING SCENARIOS RELEVANT TO ECOSYSTEM STUDIES

Scientists estimating future climatic changes have focused on large-scale models of the climate--general circulation models (GCMs)--that attempt to represent mathematically the complex physical and chemical interactions among the atmosphere, oceans, ice, biota, and land. As these models have evolved, more and more information has become available and

more comprehensive simulations have been performed. Nevertheless, the complexities of the real climate system still vastly exceed the comprehensiveness of today's GCMs and the capabilities of today's computers (see IPCC 1990, 1992 for a state-of-the-art review and Schneider 1991 for a review of the IPCC process). Simulating one year of weather in 30-minute "time steps" with the crude resolution of 4.5° latitude by 7.5° longitude and ten vertical layers (nearly 20,000 "grid boxes" around the globe) takes approximately 10 hours of Cray Y-MP time. Such a grid cannot resolve the Sierras and Rocky Mountains as separate mountain chains. Refining the resolution to 50x50 km grid squares would so dramatically increase the number of computations that it would take on the order of 1 year of current-generation computer time to calculate 1 year's weather statistics! Obviously, many important imponderables in the models are, thus, unlikely to be resolved before significant climatic changes are felt, and certainly not before we are committed to potentially significant long-term environmental and societal effects. Therefore, we will not have the luxury of solving every significant detail before having to apply the existing models to help avert potentially serious crises involving the degradation of ecosystems. Using the existing models, however, to help guide such preventative applications should hopefully buy some time, thereby allowing us the opportunity to pursue disciplinary and interdisciplinary research on the basic interactions and finer details.

What is most needed to evaluate potential biological effects of temperature change is a regional projection of climatic changes that can be applied to ecosystems. Analyses of large, prehistoric climatic changes (e.g., Berger et al. 1984, Barron and Hecht 1985, Budyko et al. 1987, Schneider 1987, COHMAP 1988) and historical weather analogues (Pittock and Salinger 1982, Jager and Kellogg 1983, Lough et al. 1983) provide some insights to such changes. These methods, however, are also based on climatic cause-and-effect processes that probably are different from future greenhouse-gas radiative effects (Schneider 1984, Mearns et al. 1990a, Crowley 1992).

GCM forecasts at the regional scale are known to be more uncertain than those at larger scales (e.g., IPCC 1992). Regional temperature changes can be much more extreme than the global average, with some regions even showing a negative change (e.g., Schlesinger and Mitchell 1987, IPCC 1990). For example, surface-temperature increases projected for the higher northern latitudes are up to several times larger than the projected global-average response, at least in equilibrium. This could imply sea level changes from changes in ocean volume or snow balance, but estimates (typically 0.5m ± 0.5m sea level rise by 2100) are controversial (e.g., see Schneider 1992b).

Even more uncertain than regional details, but perhaps more important to long-term ecosystem responses, are estimates of climatic variability during the transition to a new equilibrium particularly at the original scale. These include such events as frequency and magnitude of severe storms, enhanced heat waves, temperature extremes or reduced frost probabilities (Parry and Carter 1985; Mearns et al. 1984, 1990b; Wigley 1985). For example, the physical principle which notes that evaporation increases exponentially with surface-water temperature implies that hurricane intensities and length of the hurricane season could increase with warming of the oceans (Emanuel 1987). This obviously would have

significant impact on the ecosystems, both terrestrial and marine, in the paths of such hurricanes (O'Brien et al 1992, Doyle 1981).

GCMs are capable of providing estimates of hourly, daily, monthly or interannual variability for various climatic variables. Climatic variables of central importance to ecologists (e.g., the probability of three weeks of high temperatures over 30° C with relative humidity below 25% is a major correlate with forest fire likelihood [Torn and Fried, 1992]), however, are rarely considered by climate modelers. Thus, ecologists and climatologists must discuss the need for non-traditional measures of climatic variability to facilitate the type of interdisciplinary research needed. Such collaborations are in their infancy and the vast majority are based on so-called "equilibrium" climate-model results in which CO_2 is doubled and held fixed over time. Because the actual greenhouse-gas increases are time-evolving and exponentially growing, these studies will, of course, have to be expanded to include realistic transient cases before they can be of maximum value to ecologists or other impact assessors.

NARROWING THE MISMATCH BETWEEN ECOLOGICAL STUDIES AND CLIMATIC MODEL SCALES

As noted earlier, even the highest-resolution three-dimensional GCMs will not have a grid with nodes much less than 100 km apart within the foreseeable future; individual clouds and most ecological research (to say nothing of cloud microphysics or microclimatic or microphysiological research), for example, occur on scales far smaller than that. GCMs will not, therefore, be able to resolve weather impacting most local biological communities or the importance of local and mesoscale effects of hills, coastlines, lakes, vegetation boundaries, and heterogeneous soil. For regions, however, that have relatively uniform surface characteristics, such as a thousand-kilometer savannah or a tropical forest with little elevation change, GCM grid-scale parametric representations of surface albedo, soil type, and evapotranspiration could be used to estimate local changes. Alterations in climate predicted within one grid square would likely apply fairly uniformly across such homogeneous areas, but steep topography or lakes smaller than GCM grids, both of which can mediate real climate, are not resolved in the models. Therefore, the GCM predictions are only infrequently accurate at a regional or smaller scale.

Large-scale observed climatic anomalies can be mapped to local variations. For instance, Gates (1985) analyzed the local climatic variability for the state of Oregon using a technique known as empirical orthogonal functions (figure 1). A GCM run that produces altered temperatures that are resolved on the western slope of the Cascades could be applied to the climatic-anomaly map of Oregon to determine the climatic effects on local areas on the eastern slopes of the Cascades (which are not resolved in the model). Such a map, constructed from variations of climate observed over several years, may seem an ideal way to translate the GCM grid-scale averaged data to the local or mesoscale. Because empirical data have been used, however, such a relation would be valid only where the causes of recent climatic variations or oscillations carry forward and include the effect of climatic changes forced by trace gases. The north-south Cascade Mountains translate a simple change in the frequency or intensity of westerly winds into a characteristic climatic signature of either cooler and wetter on the west slope and warmer and drier on the east or vice versa. Thus, the signature of climatic change from increases in trace gases may not be the same as from past vacillations, many of which could have been internal oscillations within the climate system, not the result of external climatic forcing (any process that can force the climate to change is known as "climatic forcing"), such as changes in trace gases. For example, an increase in temperature on the western slopes of the Cascades will not necessarily (despite figure 1) imply a decrease in temperature on the eastern slopes if the western-slope temperature rise were forced by greenhouse gas heating; however, eastern-slope cooling might well hold if the western-slope warming were a result of weakened westerlies. Thus, other translations of scale need to be considered to map large-scale global change projections to smaller scales that account for the causes of the large-scale changes.

One might embed a high-resolution mesoscale model within a few grid squares of a GCM, using as boundary conditions for the mesoscale model the wind, temperature, and so forth predicted by the GCM at the squares' boundaries (e.g., Dickinson et al. 1989). A mesoscale model, with grid-square scale typically 50x50 km, could then account for regional topography, soil type, and vegetation cover and could map GCM forecasts to this scale of regional topography. Figure 2 is an example for the western United States. For such a method to have any reasonable hope of success, however, the GCM must produce reasonably accurate grid-scale climatic statistics for the special limited grid area. To return to the Oregon case in figure 1, if the climatic average of the GCM's winds in the unperturbed case (the control case) has the wrong westerly component, the local climate change will probably be misrepresented in a region where topography amplifies any such error in the wind direction. A likely prerequisite for that kind of cross scale mapping, therefore, is a sufficiently accurate control climate for the important variables. Only then does it makes sense to take the next step of imposing a scenario of trace-gas increase on the GCM to estimate how the regional/local-scale climate might change. Although this technique has shown considerable promise for winter-time climate situations in mid-latitudes, how embedding would work in the summer or in the tropics where thunderstorms (smaller in scale than even the mesoscale grid boxes) dominate precipitating systems is yet to be determined.

UNPREDICTABILITY OF TIME-EVOLVING, TRANSIENT CLIMATES IN REGIONAL AREAS

Neither the IPCC (1990, 1992), nor other assessments (for example, NAS 1987, or Schneider 1990) indicate that a strong consensus exists among scientists regarding time-evolving, regionally specific climatic changes. For example, the world is undergoing a steady increase in greenhouse-gas forcing which is heating the earth reasonably uniformly. One might, consequently, superficially expect a uniform global response, but this is far from likely. The centers of continents have relatively low heat-retaining capacity, and thus, their new equilibrium climate would be reached relatively more rapidly when compared to the centers of oceans, which are thermally more stable. Tropical oceans, however, have a thin (on the order of 50 meters) surface layer of well mixed waters. The temperature of that mixed layer changes substantially over ten-year time

scales, which is much slower than the response time of the middle of continents, but again much faster than the rate at which the surface temperatures change at high-latitude oceans, where waters can mix down to the floor of the ocean. Therefore, during the transient phase of climate change, middle of continents, middle of oceans, tropical oceans and high-latitude oceans all are approaching their new equilibrium temperatures at different rates (Schneider and Thompson 1981). This means the temperature differences from land-to-sea and equator-to-pole will change over time, which suggests that regional climatic anomalies associated with global warming will not necessarily be uniformly increasing over time, but could have a transient character very different from the long-term equilibrium character (Stouffer et al. 1989 and Washington and Meehl 1989).

The lack of credible predictability through time on a regional scale has implications for evaluating the adaptability of various ecosystems. The anomalous weather at one time, for example, may be extreme enough to dramatically restrict the genetic variability by killing off maladapted individuals and then when the weather rapidly changes to the other extreme the previously adapted individuals are now themselves maladapted (Watt 1992). The result could easily be extinction. A rapidly changing regional climate would be particularly difficult for natural ecosystems, because the vast majority of habitats cannot be artificially protected from the transient effects (e.g., seeding or transplanting hardier species into the area, or providing needed soil nutrients by applying fertilizers, etc.). Moreover, the less predictable regional climatic changes are the more difficult it will be to maintain sound conservation practices. Additionally, the more rapidly the climate is forced to change by, say, growing greenhouse-gas emissions, the less predictable regional changes will become (Thompson and Schneider 1982).

FORECASTING LARGE-SCALE VEGETATIONAL RESPONSES TO RAPID CLIMATE CHANGE

Despite the difficulties in providing precise, regional projections of climatic changes, plausible scenarios (such as those in IPCC 1990) can be postulated and used to drive ecosystem-response models (e.g., Pastor and Post 1988). Before, however, the consequences of any global warming scenario on ecosystems can be accurately forecast, a rudimentary understanding is needed about the influence climate change will have on the various representative biological components. For example, essential characteristics of ecosystems are shaped by vegetation (Graetz et al. 1988), and many studies have shown that climate strongly affects both the distributions of plants and the compositions of vegetational communities (e.g., Woodward 1987 and references therein, COHMAP 1988, Gates 1980). Even small changes in ambient temperature can cause dramatic effects owing to changes in the physiological demands of the plants. Lower energy demands due to warmer temperatures could easily change the delicate dominance structure that is assumed to be maintained by competition (Strain 1987). Moreover, species disperse at different rates (Cohn 1989), which will result in dramatic alterations of the species composition of basically all biological communities.

Estimates of transient-forest response have been made using so-called "gap" models, first developed by (Botkin et al 1972) and then modified, expanded, and applied by many others (e.g., Pastor and Post 1988, Bonan et al. 1990, Botkin and Nisbet 1991). One such later-generation model

(Martin 1990) was used to predict the vegetation composition for 400 years at a Minnesota site, assuming a "normal" climate. Then, after 400 years a 3^{o}C per century warming-trend scenario was imposed, and the vegetational response was quite significant: the forest disappeared (Martin 1990). The simulated disappearance, Martin notes, is quite dependent on internal model assumptions, such as air humidity and bio-physical parameterization of leaf temperatures. Therefore, we should not take any one scenario or response projection literally. Martin's results, however, should be taken seriously in as much as they indicate that major shifts in forest-species abundances could certainly occur with a few degrees warming and that these shifts would take decades to centuries to unfold--or repair.

A species-specific example has been provided by Davis and Zabinski (1992) for the Sugar Maple. Significant shifts in its range are projected when equilibrium CO_2 doubling is assumed (figure 3). The extent of the predicted distributional shift is less extreme when the Goddard Institute for Space Studies climate model scenario is used (figure 3a) than when the climate change is predicted by the Geophysical Fluid Dynamics Laboratory model (figure 3b). In both cases, however, Sugar Maple not only expands farther North, but massive local die-outs could occur in the South (Davis and Zabinski 1992). Consequently, even though the details of the equilibrium ranges are not the same, both models indicate significant range changes, which in turn will most certainly cause the structure of both northern and southern communities to change dramatically. And as stated earlier, both the climatic change scenarios and ecological response model are for equilibrium conditions, whereas actual changes will be transient in character in both climatic and ecological systems.

THE IMPORTANCE OF TRIANGLE LINKAGES BETWEEN PLANTS, ANIMALS AND CLIMATE AT A LARGE SCALE

The anticipated changes in the ranges of plants will likely have dramatic effects on animals, both on the large, biogeographic scale and on the local, regional scale. The ranges of many animals have been found to be strongly linked to vegetation. For example, Red-cockaded Woodpeckers are endemic to mature pine and pine-oak forests (Mengel and Jackson 1977), or the winter range of Sprague's Pipit is coincident with Andropogon grass (Root 1988c). Consequently, the ranges of various animals that are reliant on vegetation will change as the ranges of plants shift, assuming, of course, that some other factor is not limiting them. If the climate changes more rapidly than the dispersal rate of the plants, resulting in extensive die-offs in the South before individuals can disperse and become established in the North, then the ranges of animals relying on these plants could become compressed. Indeed, in some cases extinction could occur both to the animals and the plants. For instance, the Red-cockaded Woodpecker needs mature living trees for nesting sites (Jackson 1974). If the rising temperature causes a large majority of mature trees to die before the newly established dispensing individuals reached maturity, then this rare woodpecker could easily go extinct.

Many species of animals have ranges that are not directly limited by vegetation, but instead are restricted by temperature. This is true for most ectotherms (e.g., insects and amphibians) as well as some endotherms, such as the Eastern Phoebe, which winters in areas warmer than 4^{o}C (figure 4; Root 1988b). As the globe warms, those species directly limited by

temperature will be able to expand northward as rapidly as their dispersal mechanisms will allow, again assuming other factors are not limiting. The animals limited by vegetation will be only able to expand their ranges as rapidly as the vegetation changes. Consequently, the potential for significant disruption among communities is quite high. For instance, some animals may no longer be able to coexist because an invading species disrupts the "balance" between competing species or between predator and prey species. Therefore, to understand the ecological consequences of global warming on animals in general and birds in specific, the triangle linkages between animals, plants and climate need to be understood. The triangle closes when the effects of altered surface vegetation, for example, are considered because midcontinental summer precipitation is significantly influenced by evapotranspired water vapor.

One representative case, which has been described by Botkin and coworkers (1991), is that of the Kirtland's Warbler in Northern Michigan. Its range is restricted to a narrow area of Jack Pine trees that grow in sandy soils in that region. Models of growth and decline of Jack Pine forests suggest that even a small climate change would be enough to devastate that habitat. The Jack Pines will move North, but the warbler will not be able to survive in the more northerly areas. This bird nests on the ground under relatively young pines. The soil to the North is not generally sandy enough to allow sufficient drainage for successful fledging of young (Cohn 1989). This scenario almost certainly dooms the warbler to extinction in 30-60 years. This potential extinction is indicative of how the already high rate of extinctions around the world will be substantially exacerbated by climate changes occurring more rapidly than species can adapt (e.g., Wilson 1989; Peters and Lovejoy 1992).

SPECIFIC EXAMPLE USING WINTERING NORTH AMERICAN BIRDS

Although climatic factors have long been thought to govern broad biogeographic patterns of animals (Andrewartha and Birch 1954), rarely has this hypothesis been rigorously quantified (Brown and Gibson 1983). To help redress this gap Root (1988a) undertook a massive study of the biogeographic patterns of all wintering North American birds. She found strong statistical correlations between the distribution and abundance of a majority of the 148 land bird and six large-scale environmental factors, which included average minimum January temperature, mean length of frost-free period, potential vegetation, mean annual precipitation, average humidity, and elevation (Root 1988 a,b; 1989). Figure 4 depicts the striking association between the average minimum January temperature and the northern range limit of the Eastern Phoebe. Associations were quantified by finding the area between the range boundary and an environmental isopleth (e.g., figure 4) and then dividing by the length of the range boundary. Less than 1% of the possible associations between the species' ranges and environmental factors are expected to occur by chance. Certainly, other methods can be used to quantify the association between birds' northern boundaries and environmental isopleths, such as examining the range of temperatures spanned across a given boundary or the standard deviation of temperatures along the boundary (Repasky 1991). Such one-dimensional, heuristic measures may be easier to calculate than the two-dimensional average-area deviation method of Root (1988b), but

they cannot provide the same level of detail and focus necessary for certain large-scale questions. The relevance of this for our discussion is that the methods used to associate temperature and range limits can lead to differing inferences, and, thus, a method must be chosen that is the most appropriate to specific scientific questions, such as quantifying the extent of association between birds' northern boundaries and temperature, without introducing complicating extraneous factors such as packed isotherms or edge effects that would accompany the above-mentioned one-dimensional method.

Associations with species' southern boundaries in North America are ignored because a large majority of the species have range limits abutting the edge of the study area (Root 1988b). The comparisons along the northern, eastern and western boundaries of species' ranges reveal that environmental factors show frequent associations (figure 5). Indeed, more than one factor often associates with a given range limit, which is expected because the factors are not independent. With such a large number of range boundaries of wintering birds associated with various climatic and vegetation variables (see Root 1988a for details), changes in global climate could easily facilitate the reshaping and relocation of a significant number of these ranges.

POSSIBLE PHYSIOLOGICAL CONSTRAINTS FACILITATING THE BIRD-CLIMATE LINKAGE

Physiological constraints quite possibly are driving the much-better-than-chance associations between average January minimum temperature and northern range limits for a number of species (Root 1988b). Of the 51 species of songbirds (passeriformes) found to have their northern range limits strongly associated with ambient temperature (Root 1988a), winter physiology studies had been reported in the literature on 14. From these studies she obtained lower critical temperature (*TCRIT*, the ambient temperature at which if it gets colder an individual must increase its metabolic rate to maintain thermal homostasis), the basal metabolic rate (*BMR*, the metabolic rate of a night-resting individual at an ambient temperature a few degrees above its *TCRIT*), and conductance (*COND*, the heat loss of an individual as the ambient temperature drops below *TCRIT*).

Figure 6 depicts the relationship between the measured physiological values, temperature at the northern boundary of the distribution, and the value for the metabolic rate at the northern boundary of the distribution (*NBMR*). The equation used to derive *NBMR* is

$$NBMR = [(TDIST - TCRIT) * COND] + BMR, \qquad (1)$$

with *TDIST* and *TCRIT* measured in degrees C, *BMR* and *NBMR* in kilojoules per day, and *COND* in kilojoules per day per bird per degree C. For all the birds examined, Root found that the metabolic rate at their northern boundaries was nearly a constant multiple of their basal rate. The relationship between these two metabolic rates is

$$NBMR \simeq 2.5\ BMR. \qquad (2)$$

The ratio of *NBMR* to *BMR* shows little variation among species; the mean of this ratio is 2.49 with a standard error of ±0.07. The 95% confidence limit around the regression line defining the *NBMR* and *BMR* relationship provides values that range from 1.95 to 2.93 (Root 1989).

Basal metabolic rate is strongly related to body mass (Achoff and Pohl 1970; Root 1988b). Consequently, the relationship stated in equation 2 suggests, as Repasky (1991) correctly points out, that large species should occur farther north than smaller species. This is exactly what is found for species with their northern range boundary associated with temperature isotherms (Root and Price, in preparation). Small-bodied birds that do not have their northern range boundary limited by temperature do, of course, occur in the North. These appear to be exceptions (Repasky 1991), but they actually help "prove" the rule, because they all have adopted energy-saving mechanisms that allow them to extend their ranges farther north than expected from equation 2. For instance, some of the more northerly small-bodied birds have developed physiological mechanisms, such as hypothermia in the Black-capped Chickadee (Reinertsen 1983), or behavioral mechanisms, such as roosting in cavities as in the Brown Creeper (Ehrlich et al 1988).

The calculated metabolic rates at edges of species' distributions (Root 1988b) are based on resting metabolic rates, and they do not account for extra heat generated, for example, during digestion or activity. One of the assumptions of these calculations is that ambient temperature is an adequate index of an individual's thermal environment. Certainly, microhabitats and wind conditions have great influence on the energy expended to keep warm (Buttemer 1985). Nevertheless, average minimum January temperature appears to describe, to the first order, the wide-scale thermal environment of many species, but certainly more study is needed. Further investigations will help determine if a connection exists between the seemingly ubiquitous value of about 2.5 *BMR* for the night time metabolic rate at the northern edge of winter distributions and daily energy expenditures expounded by other workers (e.g. Walsburg 1980, Drent and Daan 1980, Peterson et al. 1990) or if the similar values are just an unusual coincidence.

What this type of analysis implies is that as climate changes, the physiological tolerance of some birds could cause them--habitat permitting--to change their ranges as rapidly as the climate changes. The range changes in those species for which the habitat is not permitting will probably not be as extreme or as rapid, and those species with ranges not associated with ambient temperature will probably not exhibit an immediate change in range--unless some limiting factor or competitor is climate sensitive. Such differential movements of species will certainly cause a tearing apart of communities, thereby forcing potentially dramatic restructurings and reorganizations. The important point we wish to reiterate is that analyses at large-scales (so-called "top-down" studies) can indicate which smaller-scale (e.g., "bottom-up" community level or single species) studies are most likely to help assess the ecological implications of global changes and to help design conservation measures in response.

FORECASTING POTENTIAL CHANGES IN SPECIES COMMUNITIES: INTEGRATING FIELD AND LARGE-SCALE STUDIES

Three major research activities are needed before we will be able to forecast reliably the potential effects that global climate change will have on species' communities throughout North America. First, much can be learned about the effects of global warming by studying pre-historic species communities that underwent a similar magnitude of warming event from the glacial to the interglacial time. However, important differences between pre-historic and forecasted climate changes, such as the presence of glaciers and the average rate of temperature change being an order of magnitude slower in ancient times, certainly prevent direct comparisons. Consequently, generalities rather than specifics will be the most helpful. For instance, Graham and Mead (1987) note that environmental changes associated with the last deglaciation (so called "Termination 1" in the marine record) had profound effects on the restructuring of biotic communities in North America. Vertebrate species, especially mammals, are particularly useful proxies for these changes, so they provide excellent documentation of the climatic fluctuations of the late Quaternary.

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In general, mammalia fauna responded to the last deglaciation in North America by shifting their ranges relatively quickly (Graham and Mead 1987). Graham and Grimm (1990), however, caution against extensive reliance of past conditions to forecast future patterns. They argue that predicting community response to greenhouse warming becomes particularly hazardous as the typically forecasted temperature increase exceeds that of any period of the last 120,000 years, a conclusion reflecting the results of Davis' (1990) study concerning forest-species response. Future climates may lie outside not only the existing climatic domain, but also outside our paleoclimate database and outside the climate to which existing species are evolutionarily adapted. Therefore, changes inferred by past changes can only be taken as a heuristic guide to possible future changes. However, if such past changes are used to calibrate and validate models of climate-mammal interactions, then such models may provide more credible projections of the effects of climate change on mammalian distributions and abundances (Schneider 1992c).

Second, more research is obviously needed on the ecology, behavior and physiology of individual species, but it needs to be designed and coordinated with larger-scale studies to increase our understanding of how biogeographic patterns may change as the climate changes. Certainly, large-scale studies need to be encouraged, as they currently constitute only a small fraction of ecological research efforts. Such studies can be used to indicate the types of small-scale studies needed. For example, large-scale studies can indicate which species have patterns that suggest their ranges may be temperature limited. In-depth studies on the species' ecology, behavior, physiology and the like, are then needed to understand possible mechanisms that are acting to shape the broader patterns. Community studies are also needed to investigate how species interactions might be influenced by changes in climate. Species compositions of communities may be forced into flux, and, as a result, significant climatic fluctuations will cause major biotic reorganizations.

To fully understand the effects of global warming on species' communities, biogeographical, ecological, behavioral and physiological studies need to be done not only on birds, but on all organisms occurring within various communities. For example, the prey base of birds in a community may be strongly affected by changing climate. Indeed, Coope (1977) has shown a high sensitivity of both individual species and assemblages of beetles to climatic change. More similar in-depth studies are needed not only on the invertebrates present, but also on the other vertebrate members of various communities.

Third, the scientific community needs to foster interdisciplinary work, or, at a bare minimum, multidisciplinary work, that will combine information from a broad spectrum of research: climatology, hydrology, limnology, soil science, chemistry, entomology, mammalogy, ornithology, botany, etc. By integrating relevant information from all these fields, a more comprehensive model can be built that should forecast more reliably the spectrum of consequences that continued release of greenhouse-effect gases will have on ecosystems. This will require actively opening communications among scientists in different fields. This can be a time consuming activity, not only because the jargon varies significantly among fields but also the groups within the scientific community are structured primarily around disciplines rather than around problems (e.g., Chen 1981; Schneider 1988; Bella and King 1989).

Additionally, the reward system within the scientific community is typically such that interdisciplinary work is not valued as highly as disciplinary work (i.e., single-authored papers "count" more toward promotion than multi-authored ones, and granting agencies are set up to fund disciplinary work more easily than interdisciplinary work). Such barriers are common at the cutting edge of problem solving, but they must be breached before the complex problems caused by global climate change can be adequately addressed (e.g., Schneider 1992d).

OUTREACH

The possible biological consequences of global warming range from mild to catastrophic. The best guess of knowledgeable scientists is a 60% chance that the world will warm 1.5 to 4.5°C in the next century (i.e., IPCC 1990, as explained by Schneider 1992a, from which part of earlier sections were modified). On the one hand, some people may say that the odds of significant damage are too low or uncertainty is too high to act now. The problem with this argument is that the concern should not only be over the value of the probability. People also need to be concerned about the potential magnitude of the consequences of global warming. A good analogy is that of a person having a 60% chance of getting a cold if a certain activity is performed, then the cost of that action (i.e., a cold) is often low enough that a probability as "low" as 60% does not modify the person's behavior. However, if the cost of a given activity is contracting a dread disease, then a 60% probability--even a 6% chance--would be of major concern, and dramatic steps would be taken to avoid the activity. This is the principle behind insurance investments or risk averse deterrence expenditures (e.g., see Schwing and Albers 1980).

The scientific community has the ability to determine a range of probable consequences of global warming. As these consequences (whether they are mild or catastrophic) are as clearly identified and understood as possible, policy makers will be able to use this information to structure the type of actions that are needed. Without providing an outreach to policy makers and the general public, we as a scientific community abdicate our responsibility of providing or interpreting scientific information to people who often have specific agendas or selfish interests. Hence, the scientific community as a whole needs to acknowledge the importance of providing in clear language research results needed by decision makers and to participate in the dissemination of our information. Finally, there must be incentives to encourage those in the scientific community to competently fill this role.

IMPLICATIONS FOR POLICY

Climate change is not necessarily a threat to the viability of all climate-sensitive species. However, the transient nature of most projected human-induced climate change is on a scale of decades while the adaptability of many species--or species upon which faster-responding species depend--is on a timescale of centuries. This implies that substantial disequilibrium within ecosystems could be created owing to maladaptions, significant shifts in species ranges, and inevitable extinctions. Consequently the only outcome that can be predicted with virtual certainty is major surprises. The only forecast that seems certain is that the more rapidly the climate changes the higher the probability of substantial disruption and surprise within natural systems. Consequently, dramatic disruption of communities can be expected to occur in the next century. To be able to forecast possible consequences of the projected warming, single-species studies need to be guided by the overall effects that climate may have on the large-scale biogeographic patterns and on the ecology, behavior and physiology of all species (e.g., Root 1988 a,b) including plants and animals. Coupling results together with information from climatologists, geologists, and others, models that will allow us to forecast more reliably the possible biological consequences of scenarios of global warming need to be designed and validated. These forecasts can then be used by policy makers and the general public to determine what types of actions are needed to impede the rapid increase in the global temperature or to ameliorate their impacts on natural systems.

These possibilities have led to a debate as to whether humans need to intervene as "ecological engineers" deliberately removing soon-to-be maladapted species and holding them in captive breeding programs for reintroductions later, or translocating wild individuals into potentially more hospitable environments (Peters and Lovejoy 1992; Soule 1989; Roberts 1988). Rapid global warming will certainly increase the number of species that are maladapted to their climatically-changed habitats. This rapid change, the effects of which may need to be artificially mediated by humans, is created by the increasing use of energy and materials demanded by growing populations insisting on using the cheapest and most readily available technologies to increase their standards of living (e.g., Ehrlich and Holdren 1971).

The most politically acceptable strategy is to accelerate the implementation of already cost-effective activities that also slow down the emissions of greenhouse gases into the atmosphere. Such activities, which have been called the "tie-in" principle, include more efficient production and uses of fossil fuel energy, curtailing the production and use of CFCs, more effective use of nitrogen fertilizer, etc. Although how to act always involves value judgments, we believe humans must invest more present resources as a hedge against potential change. Those actions that are already cost effective (using and producing energy more efficiently is the most important example), should be vigorously pursued now and political obstacles slowing the penetration of such already cost-effective actions be removed and incentives to speed such action be created (e.g., OTA 1991, NAS 1991).

Even though IPCC (1990) has shown that it would take a dramatic 60% or so reduction in CO_2 emissions to stabilize CO_2 concentrations in the atmosphere in the decades ahead, less dramatic emissions reductions would reduce the rate at which climatic changes would proceed. And, as it has been argued here and elsewhere, it is likely the rate of change of climate that most threatens ecosystem disruptions. Therefore, we believe that slowing down the rate of global change is a priority item for the world's environment/development policy agenda.

These high leverage or tie-in strategies (e.g., see Schneider 1990a) are, in our value systems, long overdue for a higher place on the world's action agenda--with or without global warming. Because of the urgency of needing to slow down global climate change, and thereby buying time for humans to assess and the rest of nature to adapt to whatever changes will take place, accelerating the implementation of such actions seem self-evidently the most appropriate immediate policy response to the prospect of unprecedented rapid climatic changes.

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We would like to thank Philippe Martin and *Conservation Biology* reviewers Charles Hall and J. S. Turner for helpful criticisms on earlier drafts of this paper. This work was partially funded by grants from the Winslow Foundation, the USFWS Cooperative Research Center, and the National Science Foundation (BSR-9058031).

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FIGURE CAPTIONS

Figure 1: The distribution of the relationship between large-scale (area-averaged) and local variations of the monthly mean surface air temperature (above) and precipitation (below), as given by the first empirical orthogonal function determined from thirty years' observational monthly means at 49 stations in Oregon in comparison with the state-wide average. Source: Gates, 1985.

Figure 2: Average January total precipitation (centimeters): a) observations; b) R15 general circulation model (i.e., 4.5° latitude X 7.5° longitude); c) mesoscale model driven by output of R15 model. Source: Giorgi, 1990.

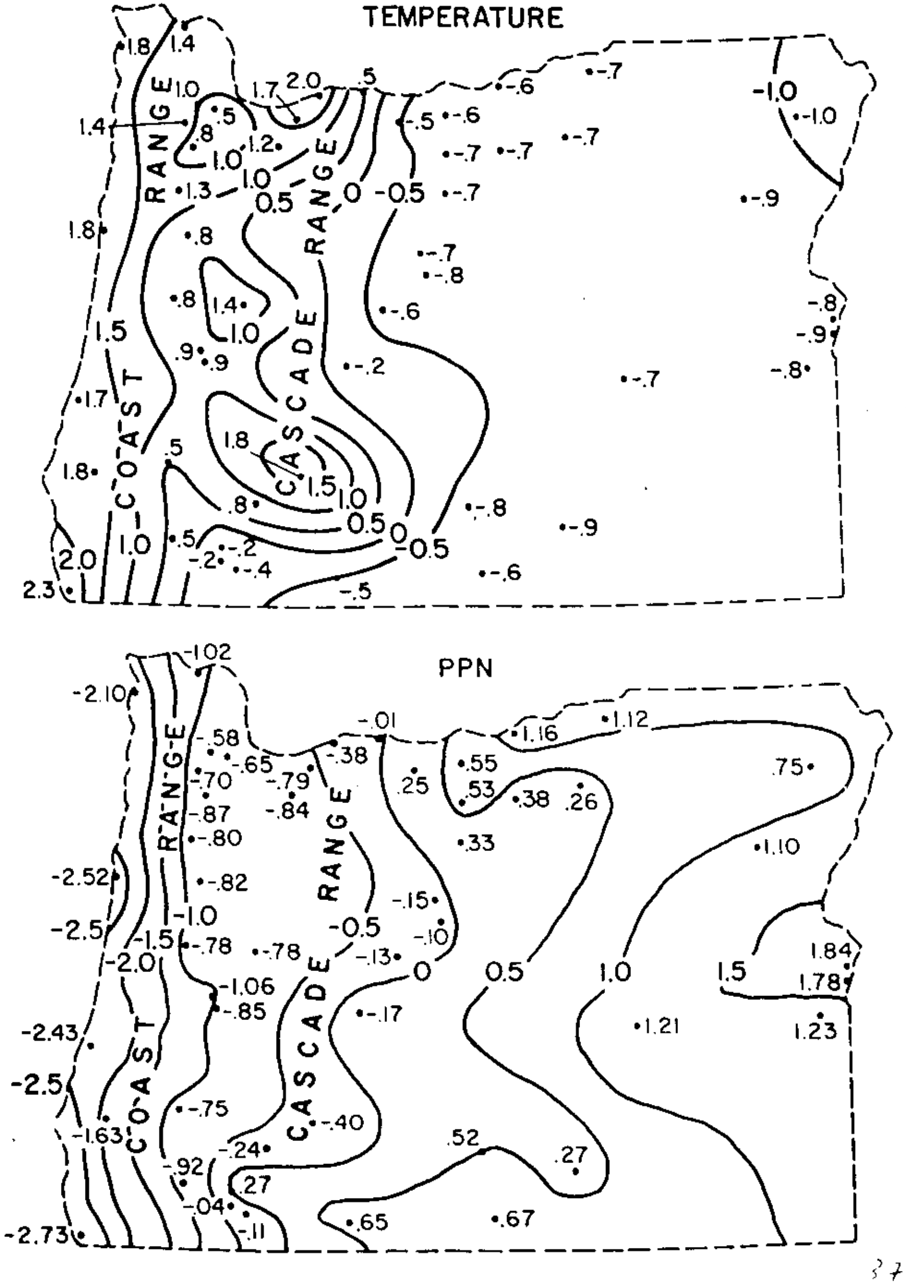
Figure 3: Present geographical range of sugar maple (horizontal lines) and potentially suitable range under doubled CO_2 (vertical lines). Cross-hatching indicates the region of overlap. A: predictions using climate scenario derived from the Goddard Institute for Space Studies general circulation model. B: predictions using climate scenario derived from the Goddard Fluid Dynamics Laboratory model. Gridpoints are sites of climatic data output for each model. Source: Davis and Zabinski, 1992.

Figure 4: The distribution and abundance of the winter range of the Eastern Phoebe. The northern boundary lies very close to the -4 degree C isotherm of January minimum temperature (heavy solid line). Source: T. Root, 1988a.

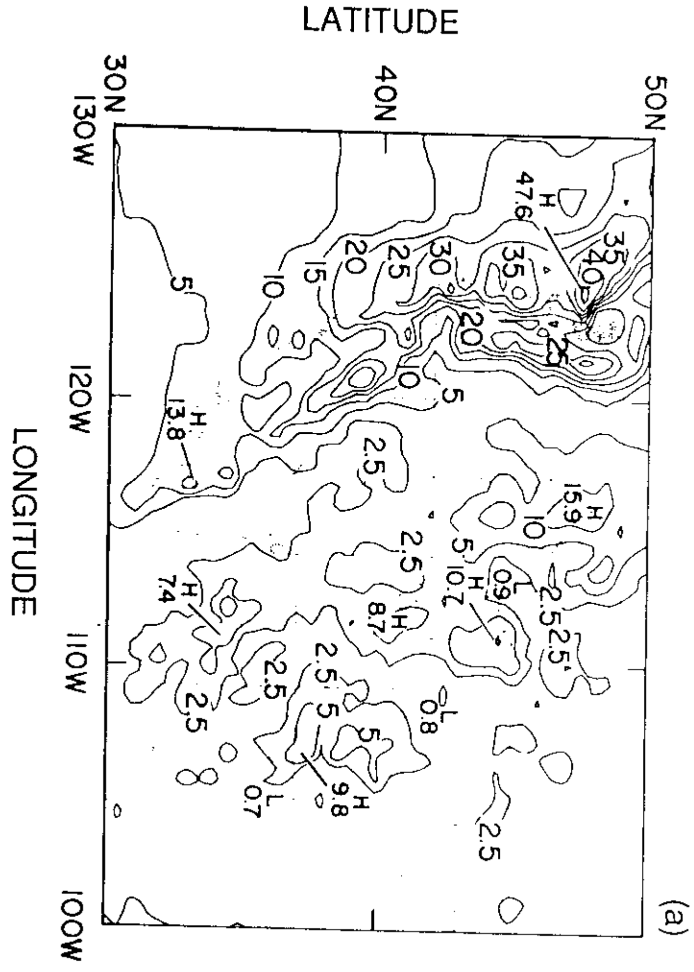
Figure 5: Plot of the percentage of species'northern, eastern and western range boundaries associated with six environmental factors. See text for explanation of terms. After: T. Root, 1988a.

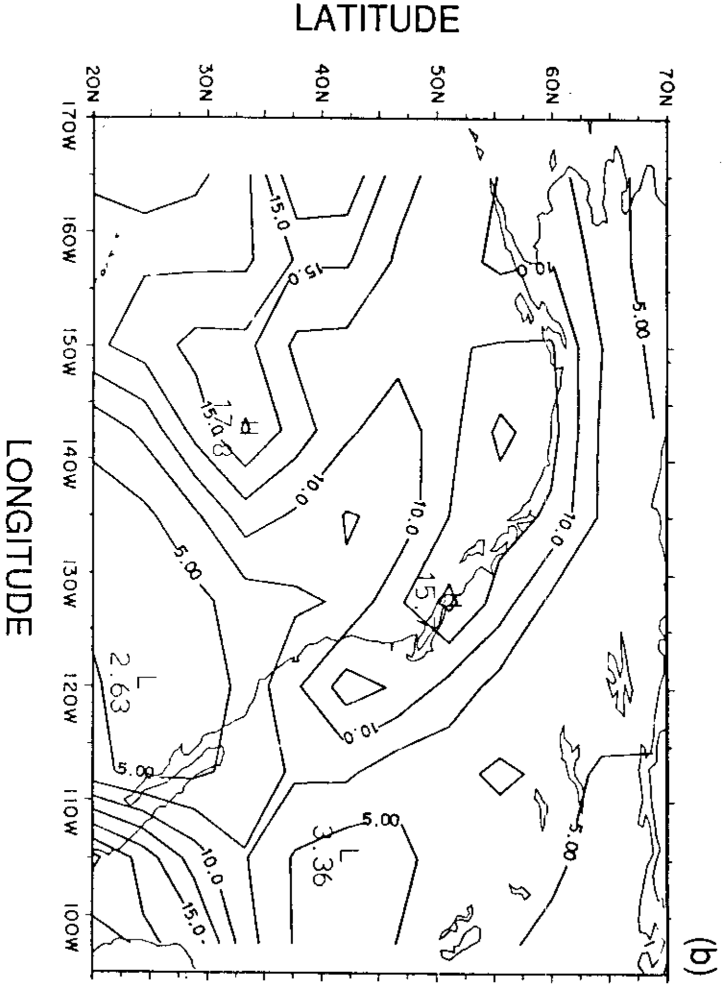
Figure 6: A schematic representation of the relationship between metabolic rate and ambient temperature. The abbreviations are as follows: *BMR*, basal metabolic rate; *COND*, conductance; *TCRIT*, lower critical temperature; *NBMR*, northern boundary metabolic rate; *TDIST*, average minimum January temperature at the northern distribution edge. Source: T. Root, 1988b.

Figure 1



Figure

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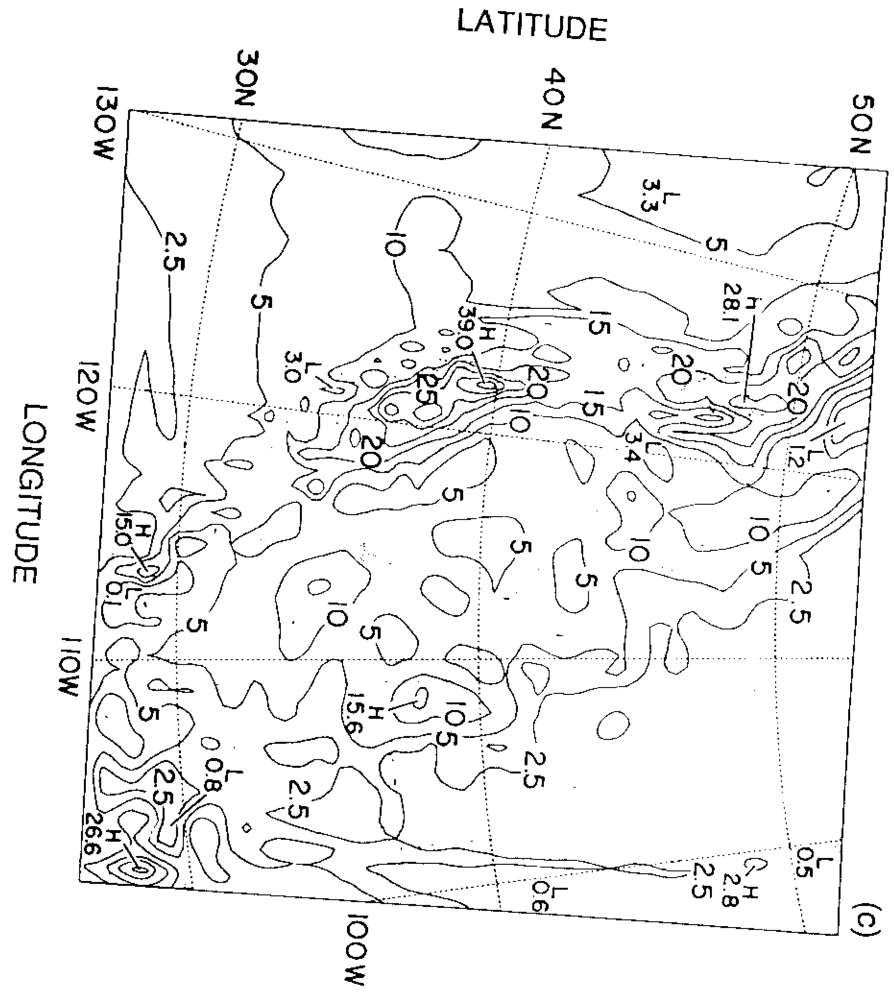
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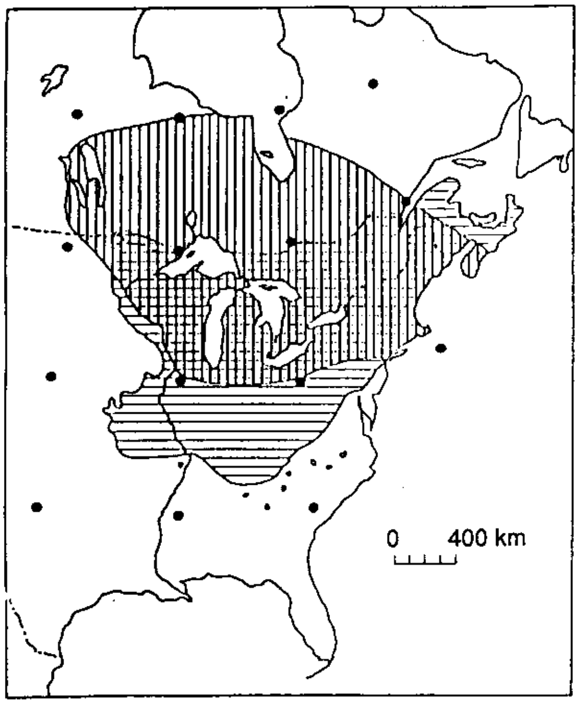
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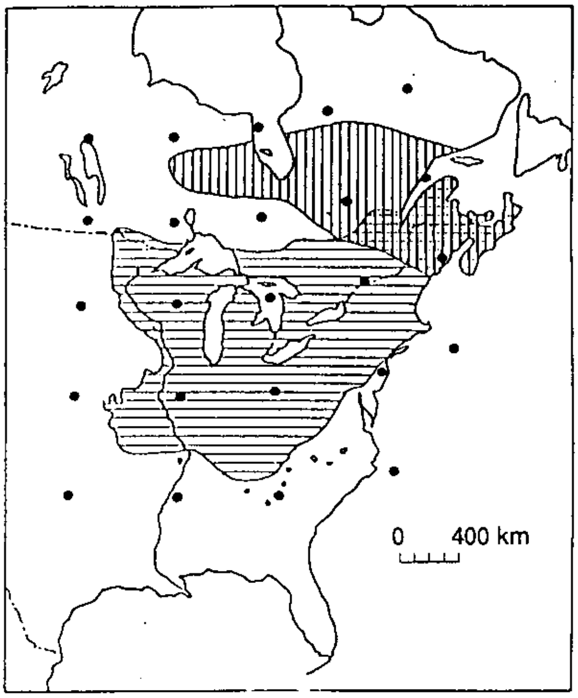
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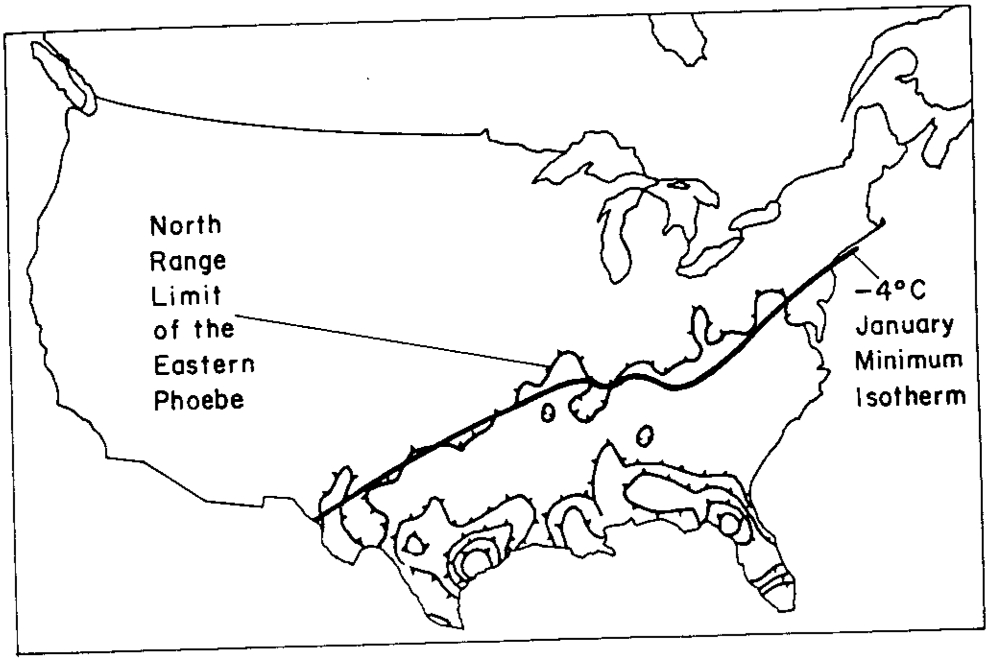
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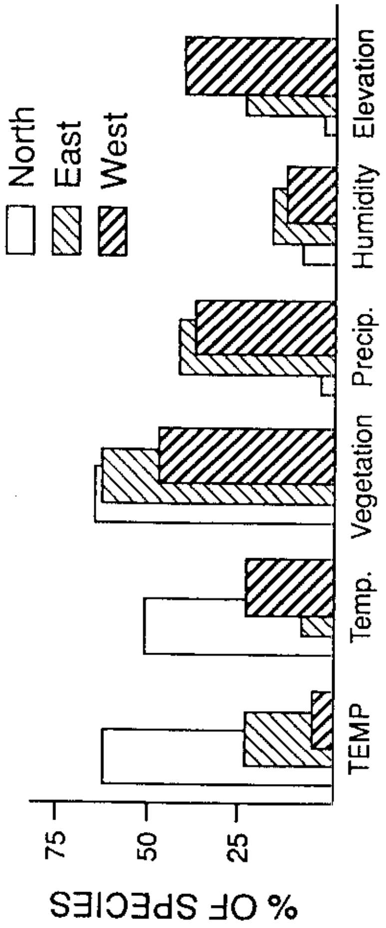
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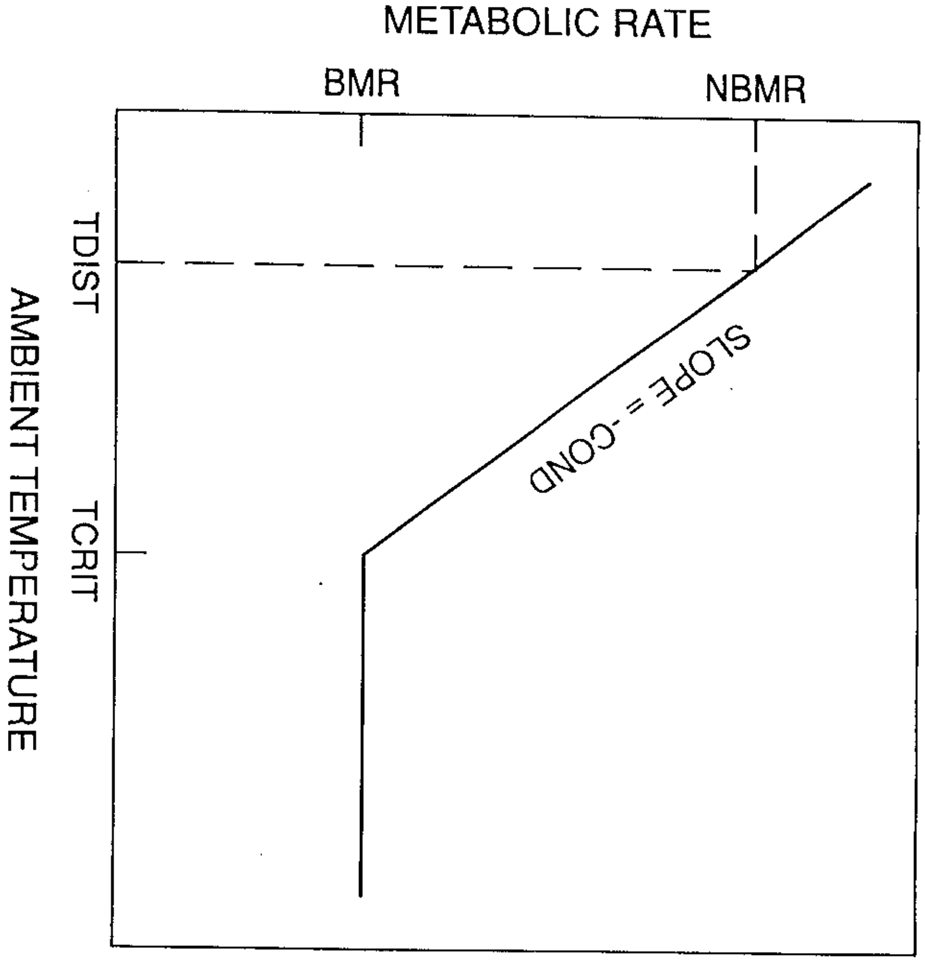
West

11930, 8/92, LF


METABOLIC RATE
BMR
NBMR
TDIST
TCRIT
AMBIENT TEMPERATURE
SLOPE = -COND