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# Forecasting the Effects of Global Warming on Biodiversity

DANIEL B. BOTKIN, HENRIK SAXE, MIGUEL B. ARAÚJO, RICHARD BETTS, RICHARD H. W. BRADSHAW, TOMAS CEDHAGEN, PETER CHESSON, TERRY P. DAWSON, JULIE R. ETTERSON, DANIEL P. FAITH, SIMON FERRIER, ANTOINE GUISAN, ANJA SKJOLDBORG HANSEN, DAVID W. HILBERT, CRAIG LOEHLE, CHRIS MARGULES, MARK NEW, MATTHEW J. SOBEL, AND DAVID R. B. STOCKWELL

*The demand for accurate forecasting of the effects of global warming on biodiversity is growing, but current methods for forecasting have limitations. In this article, we compare and discuss the different uses of four forecasting methods: (1) models that consider species individually, (2) niche-theory models that group species by habitat (more specifically, by environmental conditions under which a species can persist or does persist), (3) general circulation models and coupled ocean–atmosphere–biosphere models, and (4) species–area curve models that consider all species or large aggregates of species. After outlining the different uses and limitations of these methods, we make eight primary suggestions for improving forecasts. We find that greater use of the fossil record and of modern genetic studies would improve forecasting methods. We note a Quaternary conundrum: While current empirical and theoretical ecological results suggest that many species could be at risk from global warming, during the recent ice ages surprisingly few species became extinct. The potential resolution of this conundrum gives insights into the requirements for more accurate and reliable forecasting. Our eight suggestions also point to constructive synergies in the solution to the different problems.*

*Keywords: biodiversity, forecasting, global warming, modeling, Quaternary conundrum*

**Now that it is widely accepted that global warming** is happening, there is a growing demand for accurate forecasts of its effects, and much concern about its effects on biological diversity. Specialists know that theoretical models of these effects are limited—although useful in certain contexts when all the provisions, preconditions, and limitations of a given model are understood—and should not be taken literally. Often, however, the media do not convey these caveats. It is no wonder that policymakers and the general public are confused.

The purpose of an environmental forecast is either to support a decision process or to test a scientific hypothesis. To support a decision process, it must be clear which decisions the forecast expects to improve. To mitigate the effects of

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global warming on biodiversity, two distinct kinds of actions are needed: long-term actions, such as reducing emissions of greenhouse gases, and short-term ones, such as designing an appropriate nature reserve.

Fossil evidence and recent ecological and genetic research, along with specific problems with present forecasting methods, lead us to believe that current projections of extinction rates are overestimates. Previous work has failed to adequately take into account mechanisms of persistence. We note a Quaternary conundrum: While current empirical and theoretical ecological forecasts suggest that many species could be at risk from global warming, during the recent ice ages few extinctions are documented (Willis et al. 2004). The potential resolution of this conundrum gives insights into the requirements for more accurate and reliable forecasting.

## Eight ways to improve biodiversity forecasting

Reliable ways to forecast rates of extinction, both in relation to global warming and in general, still elude us. In the face of growing demand for accurate, timely forecasts, we consider how these forecasts can be improved, and make eight primary suggestions. One suggestion concerns the fundamentals of formal models; two concern the use of the concept of biodiversity; two, the better use of available data; and three, specific modeling types.

**1. Select a specific definition of biodiversity.** Among the many meanings of the term "biodiversity," it is important to select one as the focus for each specific forecast. Most of the existing literature on forecasting the effects of global warming on biodiversity seems to assume that "biodiversity" has some universally accepted meaning, and that readers already know what this is. However, biodiversity is a complex concept, and its meanings are becoming both more complex and more quantitative as greater emphasis is placed on DNA analysis as a determinant of genetically distinct units. As if distinctions among different levels of organization of biodiversity (genes, species, ecosystems, etc.) were not already complex, there are even more fundamental distinctions between different ways of valuing biodiversity: intrinsic value (species' value independent of human use and needs) and use value (the human use of diversity, ranging from the desire to harvest one species to the ability to see and appreciate complex ecosystems).

**2. Evaluate models before using them.** Models that forecast the impacts of climate change on biodiversity are difficult to validate, and it may be many years before anyone can conclude whether a given forecast of the effects of global warming on biodiversity was nearly right or not. However, scientists can and should evaluate a prospective forecasting method before using it to generate forecasts, and there are well-known methods, applied widely in other disciplines, for doing so. The evaluation should include the accuracy of the method (e.g., its ability to reproduce past situations) and sensitivity analyses. For example, if small changes in one parameter in a model lead to large changes in results, one must ask whether the model is sufficiently robust to be used. This principle is widely acknowledged in many applications of forecasting (Diebold 1998, Araújo et al. 2005a), though not often acknowledged or used in forecasts of climate change and extinctions.

Of the modeling papers we have reviewed, only a few were validated. Commonly, these papers simply correlate present distribution of species with climate variables, then replot the climate for the future from a climate model and, finally, use one-to-one mapping to replot the future distribution of the species, without any validation using independent data (Midgley et al. 2002, Travis 2003, Coulston and Riitters 2005, Hannah et al. 2005, Lawler et al. 2006). Although some are clear about some of their assumptions (mainly equilibrium assumptions), readers who are not experts in modeling can easily misinterpret the results as valid and validated. For example, Hitz and Smith (2004) discuss many possible effects of global warming on the basis of a review of modeling papers, and in this kind of analysis the unvalidated assumptions of models would most likely be ignored.

Furthermore, those who have attempted to validate their models have commonly used "resubstitution," whereby data used to calibrate the models are also used to evaluate them, or have left a portion of the original data set apart for model evaluation (e.g., Travis 2003, Thomas et al. 2004, Coulston and Riitters 2005, Hannah et al. 2005, Thuiller et al. 2005, Lawler et al. 2006). A problem with these approaches is that the test data are not independent, or are only partially so, from those used to fit the models, and models evaluated thus are bound to provide overoptimistic assessments of predictive accuracy (Araújo et al. 2005a). More appropriate tests of models for forecasting include using a model fitted to current data to reproduce the past (e.g., Martinez-Meyer et al. 2004), using a model fitted to past data to reproduce the present (Araújo et al. 2005a), and using data from one geographic region to develop and calibrate a model and data from another distinct geographic area to test that model (e.g., Randin et al. 2006).

**3. Account for multiple causes of changes in biodiversity.** Climate change is only one way in which the environment and human activities are affecting biodiversity. Forecasts must integrate other human impacts as well, but generally they do not. Biodiversity is also under pressure from humans' conversion of natural and seminatural habitats, wildlife trade, war, pollution, physical infrastructure (e.g., roads), and introduction of invasive exotic species (including disease organisms), as well as from natural environmental change, including catastrophes. Forecasts should disentangle the effects of climate change from these other sources of change, or at least account for the climate component and its interaction with the other components (e.g., how current landscape fragmentation could affect species migrations, compared with past migrations in more continuous landscapes).

**4. Obtain good information and make better use of it.** The data that scientists and policymakers need most are usually in-adequately available—sometimes no data exist or, more commonly, the available data are sparse, poorly collected, statistically insufficient, and biased. These include basic information on the abundance and geographic patterns of most species, as well as the data necessary to estimate the probability of extinction for a species. For example, scientists have no knowledge at all about the status of more than 40% of marine fauna (every taxonomically identified species ever recorded) within the Swedish parts of Skagerak, Kattegat, and the Baltic Sea, even though these areas are among the most intensively studied marine areas in the world (table 1; Gärdenfors 2005). Furthermore, although table 1 gives the impression that we have enough knowledge about more than half of the fauna to assign a risk of extinction—11% of the species have been red listed, indicating some level of threat, and 46% classified as of "least concern," suggesting that their populations are vigorous and robust—in fact the information is so meager and poor that the evaluations in many cases are merely intelligent guesses (Gärdenfors 2005; Tomas Cedhagen, Aarhus University, Denmark, personal communication, 10 July 2005). Current initiatives to assemble large data sets from natural history collections (see Graham et al. 2004), such as the Global Biodiversity Information Facility (2006), or to assemble knowledge about ecosystems and biodiversity, such as the Millennium Ecosystem Assessment (2006), are among present efforts to obtain the necessary data. Forecasting methods must not only target key information gaps but also make the best possible use of existing data. For example, models of species distribution may combine available environmental layers with data from museum collections, compensating to some extent for the weaknesses of either form of data on its own (Ferrier et al. 2004).

***Table 1. Summary of preliminary results from work with the Swedish Red List on every recorded species within selected marine taxa.***

| Taxon | Red-listed species | Species of least concern | Species for which knowledge is lacking | Total |
|---|---|---|---|---|
| Porifera | 3 | 28 | 114 | 145 |
| Anthozoa (Cnidaria) | 9 | 22 | 22 | 53 |
| Priapulida | 0 | 1 | 1 | 2 |
| Sipuncula | 0 | 4 | 7 | 11 |
| Phoronida | 0 | 2 | 2 | 4 |
| Echiura | 0 | 2 | 1 | 3 |
| Decapoda (Crustacea) | 5 | 45 | 28 | 78 |
| Mollusca | 52 | 218 | 145 | 415 |
| Chaetognatha | 0 | 5 | 3 | 8 |
| Brachiopoda | 1 | 2 | 1 | 4 |
| Echinodermata | 16 | 35 | 20 | 71 |
| Hemichordata | 0 | 1 | 2 | 3 |
| Total (percentage) | 86 (11) | 365 (46) | 346 (43) | 797 (100) |

*Note:* Red-listed species fall into four categories: critically endangered, endangered, near threatened, and vulnerable. Species for which knowledge is lacking fall into two categories: not evaluated (because of lack of knowledge) and data deficient.

*Source:* Gärdenfors (2005) and unpublished working material from the Swedish Species Information Centre (Tomas Cedhagen, Aarhus University, Denmark, personal communication, 10 July 2005).

**5. Use the Quaternary fossil record to understand mechanisms that preserve biodiversity, and use these in forecasting models.** Current forecasting methods suggest that global warming will cause many extinctions, but the fossil record indicates that, in most regions, surprisingly few species went extinct during the Quaternary (from approximately 2.5 million years BCE to the present)—in North America, for example, only one tree species is known to have gone extinct (Bush and Hooghiemstra 2005). Large extinctions were reported mainly for tree species in northern Europe (68% loss of tree genera; Svenning and Skov 2004) and for large mammals (> 44 kg) in the Northern Hemisphere (MacPhee 1999). We refer to this contrast between the implications of modern forecasts and the observed fossil record as the "Quaternary conundrum." The resolution of this conundrum is key to improving forecasts of climate-change effects on biodiversity. Among the possible explanations are that climate change during the Quaternary was greatly different from climate change forecasted for the future; that genetic and ecological mechanisms, not accounted for in formal forecasting methods, allow the persistence of many species even under rapid climate change; and that factors in addition to climate change could decrease rates of extinction.

Some recent ecological genetics research further deepens the puzzle. For example, the risk of extinction for a species in response to climate change depends on the demography and evolution of genetically differentiated populations across their geographic ranges. If populations are locally adapted, climate change will cause conditions to deteriorate across the species' range, rather than just at the margins of the range. Modern reciprocal transplant experiments, in which spatial gradients in climate serve as proxies for temporal climate change in the future, show that these fitness losses can be large (Rehfeldt et al. 1999, Etterson 2004). For example, a reciprocal transplant experiment on lodgepole pine in Canada indicated that global warming would slow tree growth and increase mortality, resulting in a 20% loss of productivity (Rehfeldt et al. 1999). Likewise, a study of a prairie annual in the Great Plains of the United States showed a 30% reduction in seed production in climates similar to those predicted for future decades. Ecological genetic data, in each of these cases, predicted different rates of adaptive evolution in different parts of the species' range (e.g., rear and leading edge; Hampe and Petit 2005) but generally suggested that evolutionary rates would be slower than the anticipated rate of climate change (Etterson and Shaw 2001, Rehfeldt et al. 2002).

Until recently, it was thought that past temperature changes were no more rapid than 1 degree Celsius (°C) per millennium, but recent information from both Greenland and Antarctica, which goes back approximately 400,000 years, indicates that there have been many intervals of very rapid temperature change, as judged by shifts in oxygen isotope ratios. Some of the most dramatic changes (e.g., 7°C to 12°C within approximately 50 years; Macdougall 2006) are actually of greater amplitude than anything projected for the immediate future. Although these changes were probably not equally severe everywhere on the globe, a well-documented rapid warming did occur around the shores of the North Atlantic at the end of the last glaciation, when melting of the ice cover on the ocean suddenly allowed the Gulf Stream to reach the shores of northern Europe. There, temperatures rose rapidly, perhaps as rapidly as anticipated today for the next several decades (Huntley et al. 1997).

What could explain the Quaternary conundrum? One possibility is that migrations were faster than has been thought possible. A large literature examines late-Quaternary range shifts deduced from the pollen record, and recent papers consider models and seed-dispersal mechanisms that may account both for migration across geographic barriers and for rapid invasion of new territory. Sparse populations of several tree species are now known (from genetic and macrofossil evidence, supplemented by detailed analysis of mapped pollen data) to have persisted during the last glacial maximum in regions where very few, if any, pollen grains have been observed—regions that for this reason would be judged well outside the climate envelope for these species (Tomaru et al. 1998, Brubaker et al. 2005, McLachlan et al. 2005, Magri et al. 2006). These populations serve as advance colonists, allowing rapid population growth in newly available habitat.

A second explanation is that low extinction rates during Quaternary climate change may be partially attributable to ongoing adaptive evolution. Theoretical models suggest that adaptive evolution can enhance the persistence of populations in a changing environment even when migration is possible (Bürger and Lynch 1995). And rapid genetic adaptation to climate has already been documented for a few wild organisms for which long-term studies of field populations have been conducted (reviewed in Bradshaw and Holzapfel 2006). Invasive species have also evolved since their arrival in a new habitat in the 20th century, at surprisingly rapid rates of evolution (e.g., Huey et al. 2000).

A long-standing controversy regarding the role of people in Quaternary extinctions of large mammals speaks to the difficulty of quantifying impacts of multiple factors on species loss. The high extinction rate of large mammals has been widely recognized since the 19th century, and extinctions of large mammals and island birds over the past 100,000 years have been the subject of much conjecture. Paul Martin has made the now well-known case that the timing of extinctions followed human dispersal from Afro-Asia to other parts of the globe and that these extinctions resulted from human "blitzkrieg" overkill (Martin and Steadman 1999). But careful analysis of well-documented extinctions in Beringia suggests that human hunting was superimposed on a preexisting trend of diminishing animal population density (Shapiro et al. 2004, Guthrie 2006). These data suggest that the interaction of environmental change and human resource use can have a larger negative impact on biodiversity than either factor alone.

**6. Improve widely used modeling methods.** Theoretical models are essential to quantitative forecasts of effects of global warming on biodiversity. Four methods are in use today for these forecasts: (1) modeling individuals; (2) using groups of species as the units of interest in a model; (3) integrating biodiversity within general circulation models (GCMs); and (4) using species–area models, that is, modeling based on theories of total biodiversity.

Clearly, since there are 1.5 million named species and many more that are as yet undocumented but believed to exist, methods that require specific information on all species for forecasting overall biodiversity are not practical. At the heart of the choice about which method to use is the question of appropriate spatial and temporal scales, a problem common to many disciplines. The larger the scale of the primary units of a model, the simpler it is to estimate effects over large areas and times, but also the cruder the approximation is and the more likely that undesirable assumptions will prevail. The smaller the scale, the greater the detail that can be considered, but the more detailed the information, the greater the number of calculations that must be made. The question boils down to whether it is better to know a lot of detail about fewer points or much less information about much greater areas. At present, it is not clear which approach is more useful for forecasting the effects of global warming on biodiversity, and one of the results is that research is being carried out at multiple scales.

**Models of individuals.** Researchers have considerable experience with models that use the individual as the primary unit with fixed characteristics, forecasting population and species responses from the sum of the responses of individuals. Computer simulations of vegetation responses to climate and habitat have been available since 1970, beginning with the JABOWA forest model, which forecasts the growth and mortality of individual trees and the regeneration of species in small forested areas (Botkin 1993). Such methods have been applied to reconstruct Holocene forest changes (Davis and Botkin 1985) and to forecast possible effects of global warming on forests (Solomon 1986, Botkin 1993). These models have been widely used to forecast changes in tree species composition under expected climate change. They have also been used to make forecasts about how global warming will affect ecological communities and ecosystems. For example, the JABOWA model forecasts that increases in carbon dioxide ($CO_2$) concentrations in the atmosphere will speed up forest succession (Botkin 1993). Individual-based models have also been used to forecast the effects of climate change on individual endangered species: The JABOWA model forecasts that global warming will further threaten the Kirtland's warbler, an endangered bird that nests only in jack pine stands in southern Michigan. With global warming, this region will no longer be suitable for jack pine, and jack pine is unlikely to grow in the sandy soils farther north (Botkin 1993). Curiously, no attempt has been made to validate either the ecosystem forecast or the endangered species forecast.

An advantage of individual-based models is that they do not impose steady-state assumptions about species, the environment, or the relationships between the two. Non-steady-state conditions can easily be integrated, and subspecies can be treated separately. However, the required species-specific empirical data are not always available, and the spatial scale is small, necessitating many separate simulations to form a general picture.

Considerable work has been done to add to the details of plant physiology incorporated in these models. These models might be improved further in several ways. One way is to increase model realism in the areas of dispersal, temperature response, life history trade-offs, and disturbance response. Another is to use shorter time steps (rather than the usual annual time steps), but this would greatly increase the models' computational loads. A third way is to improve the models' empirical basis (Loehle 2000, Norby et al. 2001). Yet another way is to use better methods to represent the effects of changing $CO_2$, ozone, and other environmental factors (e.g., Saxe et al. 2000, Norby et al. 2001). But arguably the most important need is to attempt validation of this class of models against actual temporal changes in forests, because this kind of forecasting has been available for several decades.

**Niche-theory models.** A large group of models considers a species, or a group of species with similar niches, as a single unit with fixed characteristics, which can be viewed as an integrated measure of a set of environmental variables. Thus the set of environmental conditions alone forecasts the distribution of a species or group of species. These models, based on ecological niche theory, are known by various names—niche-theory models, habitat distribution models, and bioclimatic-envelope models—and have been applied to a variety of taxa, most commonly to plants (e.g., Thuiller et al. 2005), but also to animals, including tropical rainforest vertebrates of many kinds (mammals and birds; e.g., Peterson et al. 2002), amphibians and reptiles (e.g., Araújo and New 2007), and butterflies (e.g., Beaumont and Hughes 2002). This approach traces back to G. Evelyn Hutchinson's definition of the realized niche—the set of all environmental conditions within which a species can persist—and to a generalized theory by Box (1981) for predicting biomes or vegetation types. Two advantages of niche-theory models are that only a few variables are necessary to predict ranges for many species, and that even small-scale, patchy museum collections data can be used (Ferrier et al. 2004).

However, niche-theory models have a number of limitations (Guisan and Thuiller 2005). First, they are primarily correlative, using observed statistical relationships between occurrences of a species and its environment. Second, they assume that observed distributions are in equilibrium (or quasi-equilibrium) with their current environment, and that therefore species become extinct outside the region where the environment, including the climate, meets their present or assumed requirements—contradicting the data reviewed earlier, as well as many natural history observations of transplanted species, that show species have survived in small areas of unusual habitat (Pearson 2006), or in habitats that are outside the well-established geographic range but actually meet their requirements. Thus niche-theory models are likely to overestimate extinctions, even when they realistically suggest changes in ranges of many species.

Another problem with niche-theory models, as with most models, is that they are difficult to validate, and few have been adequately validated. For example, Lawler and colleagues (2006) compare six approaches to modeling the effects of global warming on fauna, but do not attempt to validate any of the models independently. Indeed, bioclimatic models vary greatly in their projections of extinction (e.g., Thuiller et al. 2005, Lawler et al. 2006, Pearson et al. 2006).

An additional complication is that the relationship between the occurrence of a species and climatic variables is not always correlated with the mean. For example, amphibian declines due to outbreaks of a pathogenic chytrid fungus (*Batrachochytrium dendrobatidis*) are related to the annual *range* of temperatures, not to the mean temperature (Pounds et al. 2006).

Unknown and untested biases are also problems for these models (e.g., Kadmon et al. 2003). More computationally intensive approaches, using the "consensus" of many models, have been shown to improve the accuracy of models at predicting observed shifts in distribution (Araújo et al. 2005b). On the other hand, differences in forecasts from different niche models can be as large as the change in predicted distributions due to climate change (Thuiller et al. 2005, Lawler et al. 2006, Pearson et al. 2006). Thus, global estimates of extinctions due to climate change (Thomas et al. 2004) may have greatly overestimated the probability of extinction as a result of the inherent variability in niche modeling (e.g., Thuiller et al. 2004). It is a problem when a paper reports on minor uncertainties and does not describe major uncertainties.

Most applications of bioclimatic-envelope models do not consider dispersal and migration rates (as in Iverson et al. 1999), nor do they consider the biotic interactions of symbiosis, competition, and predation—or other dynamic processes, such as fire (Moretti et al. 2006)—all of which could change the future distribution of the species. Some species may be more constrained locally by biotic interactions than by climate per se, with climate operating at broader landscape scales. If some ecosystems display a high degree of inertia and their responses lag behind changes in climate, then at least some of the component species (e.g., understory plants in a forest) could be buffered from climate change, at least in the short term. For example, some clones of the alpine sedge *Carex curvula* in the European Alps could be as old as 2000 years, and possibly older (Steinger et al. 1996). If so, the clone would have passed through a series of climatic variations (e.g., medieval optimum, little ice age) without shifting to lower or higher elevations. Unfortunately, disentangling direct climatic constraints from other habitat constraints requires quite detailed ecological knowledge, which is usually lacking.

Most niche models assume fixed genetic and phenotypic characteristics for the species (Pearson and Dawson 2003) and thus do not discriminate among various genotypes and phenotypes across a species' range. This is in contrast to what geneticists and experimental ecologists believe to be the case (e.g., Bradshaw and Holzapfel 2006). If these attributes were available, they could be integrated in niche models by fitting a different model for each genotype or phenotype.

One promising use of niche models is to identify gaps in nature reserve systems that will occur as the climate changes. For flora of the Cape of Good Hope, South Africa, Hannah and colleagues (2005) applied a niche model to forecast whether the climate where existing nature reserves are located would be adequate, under global warming, for the species that each reserve is intended to conserve.

**7. Improve ecological principles embedded in general atmosphere–ocean–biotic coupled circulation models.** Niche-theory modeling has been used both by ecologists and by those involved with coupling the biosphere to ocean–atmosphere GCMs (Bergengren et al. 2001). Curiously, these two activities have gone on relatively independently, with the GCMs historically using a simpler and more static kind of niche theory than the models applied directly by ecologists. In part this independence is the result of different goals. Climate modelers have primarily been interested in the influence of vegetation on climate through albedo, surface roughness, water evaporation, and exchange of greenhouse gases and aerosols.

Recently, GCMs have been extended in dynamic global vegetation models, or DGVMs (e.g., Cramer et al. 2001), to consider vegetation and ecosystem dynamics, and therefore the effects of land-use change in a dynamic climate (Betts 2005). These models have led to further refinements in forecasts of atmospheric greenhouse gas concentrations and climate change (e.g., Cox et al. 2000, Friedlingstein et al. 2006). But again the interest has been primarily in the feedbacks of changes in vegetation, and in biogeochemical and biophysical processes, on $CO_2$ concentrations and climate dynamics rather than on biodiversity. Thus biodiversity has not been the primary interest of researchers employing DGVMs; their focus has been less on what happens to vegetation per se than on the effects on climate dynamics.

Meanwhile, those concerned primarily with the effects of global warming on biodiversity have developed the other kinds of models discussed in this article. These two modeling communities need to communicate better in order to improve modeling and understanding on both sides.

In favor of the simplest Box modeling approach (Box 1981) is that only a few climate variables seem necessary to predict ranges for many plant species. Also in favor of this approach is that some applications are mechanistic, based on first principles. For example, some simulate photosynthetic processes, albeit in a conceptual or quasi-biochemical way. However, the rate coefficients for many of the processes, while empirically based, are often poorly quantified. Therefore, although these dynamic vegetation models can simulate the response of plant functional types to climate and other environmental drivers, and show how biomes may shift, they cannot predict biodiversity changes within or between biomes, or the genetic variations discussed earlier. Also, there are large uncertainties at these scales about the data, so these models may have significant biases, particularly in simulating the margins of current biome distributions.

There is a need for continued evaluation of the appropriate level of diversity that must be represented. Ways of incorporating the non-steady-state characteristics of vegetation and the relationship between climate and vegetation need to be developed as the models mature so they can be used to forecast changes in vegetation. Comparison of model output with Quaternary vegetation data is validating the models and providing insight into drivers of vegetation change (Sitch et al. 2003, Giesecke et al. 2006).

**8. Develop better models for forecasting total biodiversity.** One of the simplest and most straightforward methods of forecasting the effects of global warming on total biodiversity is based on the species–area curve. In simplest terms, the number of species is correlated with area. There are many species–area curves, but most commonly such curves are given by the two-parameter curve with the formula $S = cA^z$, where $S$ is the number of species, $A$ is the area, $c$ is the number of species on one unit of area, and $z$ is the rate at which log $S$ increases with log $A$.

This empirical relationship works quite well, provided some care is taken in its application. Most often, it is an equilibrium relationship applying to areas that have existed in their present circumstances for a long time. Rosenzweig (2003) points out that the power law is only approximate, with the power (exponent $z$) changing in accordance with the circumstances (e.g., type of area, such as island, subarea in a continent, or whole continent) and scale. Rosenzweig (2003) and others argue that this relationship has a fundamental ecological basis in the number of species actually present on a contiguous area of size $A$. Another kind of relationship, sometimes called a species–area relationship, is used in sampling to extrapolate to the total number of species on a defined piece of land as the sample size ("area") increases. It is commonly applied to diversity of broad taxa, such as birds, vascular plants, and mammals.

The species–area method of forecasting changes in biodiversity under global warming has six limitations (most summarized by Lewis 2006). First, it assumes an equilibrium (or very slowly changing) relationship between species number and area. Second, the future climate probably will not be an exact analog of the current one, so "moving" a bioclimatic zone for an ecological type may not be accurate (Malcolm et al. 2006). Third, topographic variation, which affects the species–area curve shape, may be greater or less in the future zone. Fourth, factors relating to the shape of areas and the amount of their fragmentation suggest that an alternative "endemics–area curve" may enable more accurate predictions (Harte et al. 2004). Fifth, the correct $z$ value must be chosen: It must apply to the entire area under consideration, and it must also consider the type of area and timescale applicable (Rosenzweig 1995). Sixth, many species are not confined to a particular vegetation zone or type. For the species–area relationship to predict species extinctions, the area must be for closed communities. Thomas and colleagues (2004) used individual species distributions as the basis for their analysis. They examined changes in realized niches without taking into account the likelihood of changed interactions and adaptation, and thus the new areas that they predicted were probably too small. How these area changes relate to changes in area of closed communities is unclear.

These problems need to be overcome and the method tested, perhaps with historical data, before too much weight can be placed on this method. But even if the species–area curve is a correct causal relationship, the required data are limited, so the quantitative estimations may have little value. For example, Thomas and colleagues (2004) used the species–area curve to predict diversity changes by estimating the change in area that species would experience after climate change. In one case they concluded that the area of the boreal forest would decline from 13 "undisturbed" units to 12.5 units globally—a loss of about 4%. But a study of the biomass stored in the boreal forest of North America showed that botanical maps of the North American forests led to the possibility that the area defined as boreal forest differed by a factor of two—200%—eclipsing the forecast loss of 4% (Botkin and Simpson 1990). If scientists cannot agree within a factor of two on the size of the boreal forest, then the forecast loss of 4% means little.

Although in theory one can separate the use of the species–area curve for estimating total species present from an attempted use of this relationship as some kind of causal basis for biodiversity, it is not always clear which is behind an application. If applying this curve to changes in biodiversity simply reverses the sampling operation, so that a decrease in area is assumed to lead to a decline in species number that follows back down the asymptotic curve, then this reverse operation is illogical. Because removing area over an ecological timescale is not a direct reversal of the processes that have added species over evolutionary time (Lewis 2006), there is no a priori reason to expect that the change in species number corresponding to a change in area will track a species–area curve, although there are indications that a power law with a lower $z$ value would apply to predictions for short time horizons (Rosenzweig 2003).

A solution to these problems is suggested by tackling the reason for the observed correlation between species and area. Rosenzweig (1995) and Connor and McCoy (2001) summarize a variety of evidence suggesting that the primary, though not the only, cause of increases in species with increased area is that larger areas tend to have a greater variety of habitats, and thus a greater variety of niche opportunities. If the relative habitat diversity of different-sized areas can be measured directly, this information can be used as a causative predictor of diversity, whereas area is mostly correlative, which brings us back to the basis of the niche-theory models discussed earlier. If changes in habitat diversity can be predicted, they should predict changes in species diversity more accurately than would changes in area.

The limitations of the species–area curve may be corrected by using different subsets of areas to generate a species–area curve that is linked to the habitat heterogeneity captured by a given subset (Faith et al. 1996). Scenarios of climate change are then interpreted as shifts in patterns of habitat heterogeneity, rather than simply as changes in habitat area. This approach allows the use of a range of available biotic and abiotic information, and also may help address shape and fragmentation issues, providing a link between endemics–area and species–area curves so that these can be used in concert. Further, such an approach may allow for assessment not just of climate-change "losers" but also of "winners." The species–area curve offers the simplest theoretical model to link biodiversity to climate change and perhaps, with the modifications suggested here, might be useful in predicting the effects of climate change on biodiversity.

## Recommendations

In this article we point out eight ways to improve forecasts of the effects of global warming on biodiversity. We have considered four kinds of models used to forecast the effects of global warming on biodiversity. Three share a foundation in ecological niche theory. The first group of models, represented by JABOWA-type vegetation models, makes forecasts for individuals and species and has the flexibility to involve non-steady-state relationships between a species and its environment, but requires species-specific data that are not always available.

The second group, ecological niche-theory models, makes forecasts based on the environmental conditions that are possible for a set of species or a single species. Traditionally, these have been applied primarily with climate change taken into account as a driver, but some recent studies expand this approach to include other habitat characteristics. Also traditionally, these models assume equilibrium relationships between species and the environment, and among environmental variables, which limits their utility. Recent advances are making these models more flexible, with the result that this kind of model has broad appeal among scientists and is likely to remain an important and useful approach.

The third group, used by climatologists, consists of bioclimatic-envelope models in even simpler forms than those in use by ecologists. These models have necessarily been simple because of the complexity of all climate models. Although advances have been made, they remain crude from a biological point of view, and static (especially in the relationship between climate and vegetation). They are used to model the feedback between climate and vegetation.

The fourth group comprises models based on species–area theory. These models are appealing in the abstract because they do not require detailed knowledge of species or habitats, but they have often been applied inappropriately for forecasts of the effects of global warming on biodiversity. One promising approach is to focus on links between the species–area curve and models of habitat heterogeneity. Such models build on a combination of available habitat and species data as surrogate information for overall biodiversity patterns.

The effectiveness of these four useful classes of models will depend on the extent to which our recommendations are adopted, especially with respect to obtaining necessary data. Curiously, although three of the approaches—JABOWA-based models, niche-theory models, and models used by climatologists—make use of similar niche-theory ideas about the relationship between a species and its environment, scientists using each of those approaches tend not to communicate with each other or read each other's literature.

We suggest that there is now much scope for an integrated framework for forecasting the impacts of global change on biodiversity. Such a framework could integrate models for species persistence and consider multiple causes of biodiversity change. This emerging framework awaits more of the important evaluation steps, including case studies.

What, then, is the answer to the Quaternary conundrum? The answer appears to lie in part with the ability of species to survive in local "cryptic" refugia, that is, to exist in a patchy, disturbed environment whose complexity allows faster migration than forecast for a continuous landscape, within which species move only at a single rate. The answer also lies in part with greater genetic heterogeneity within species, including local adaptations, which allows rapid evolution. For example, populations close to latitudinal borders are likely to be better adapted to some environmental changes than the average genotype. However, the conundrum is not completely solved, and some important genetic research suggests that species are more vulnerable than the fossil record indicates. A fuller solution to the conundrum will be important for improving forecasts of climate change effects on biodiversity.

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## References cited

Araújo MB, New M. 2007. Ensemble forecasting of species distribution. Trends in Ecology and Evolution 22: 42–47. doi:10.1016/j.tree.2006.09.010

Araújo MB, Pearson RG, Thuiller W, Erhard M. 2005a. Validation of species–climate impact models under climate change. Global Change Biology 11: 1504–1513.

Araújo MB, Whittaker RJ, Ladle R, Erhard M. 2005b. Reducing uncertainty in projections of extinction risk from climate change. Global Ecology and Biogeography 14: 529–538.

Beaumont LJ, Hughes L. 2002. Potential changes in the distributions of latitudinally restricted Australian butterfly species in response to climate change. Global Change Biology 8: 954–971.

Bergengren JC, Thompson SL, Deconto RM. 2001. Modeling global climate–vegetation interactions in a doubled $CO_2$ world. Climatic Change 50: 31–75.

Betts RA. 2005. Integrated approaches to climate–crop modelling: Needs and challenges. Philosophical Transactions of the Royal Society B 360: 2049–2065.

Botkin DB. 1993. Forest Dynamics: An Ecological Model. New York: Oxford University Press.

Botkin DB, Simpson L. 1990. Biomass of the North American boreal forest: A step toward accurate global measures. Biogeochemistry 9: 161–174.

Box EO. 1981. Macroclimate and Plant Forms: An Introduction to Predictive Modeling in Phytogeography. The Hague: Junk.

Bradshaw WE, Holzapfel CM. 2006. Evolutionary response to rapid climate change. Science 312: 1477–1478.

Brubaker LB, Anderson PM, Edwards ME, Lozhkin AV. 2005. Beringia as a glacial refugium for boreal trees and shrubs: New perspectives from mapped pollen data. Journal of Biogeography 32: 833–848.

Bürger R, Lynch M. 1995. Evolution and extinction in a changing environment: A quantitative-genetic analysis. Evolution 49: 151–163.

Bush MB, Hooghiemstra H. 2005. Tropical biotic responses to climate change. Pages 151–163 in Lovejoy TE, Hannah L, eds. Climate Change and Biodiversity. New Haven (CT): Yale University Press.

Connor EF, McCoy ED. 2001. Species–area relationships. Pages 397–411 in Levin SA, ed. Encyclopedia of Biodiversity, vol. 5. New York: Academic Press.

Coulston JW, Riitters KH. 2005. Preserving biodiversity under current and future climates: A case study. Global Ecology and Biogeography Letters 14: 31–38.

Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408: 184–187.

Cramer W, et al. 2001. Global response of terrestrial ecosystem structure and function to $CO_2$ and climate change: Results from six dynamic global vegetation models. Global Change Biology 7: 357–374.

Davis MB, Botkin DB. 1985. Sensitivity of the cool–temperate forests and their fossil pollen to rapid climatic change. Quaternary Research 23: 327–340.

Diebold FX. 1998. Elements of Forecasting. Cincinnati (OH): South-Western College Publishing.

Etterson JR. 2004. Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change, I: Clinal patterns of selection along an environmental gradient in the Great Plains. Evolution 58: 1446–1458.

Etterson JR, Shaw RG. 2001. Constraints to adaptive evolution in response to global warming. Science 294: 151–154.

Faith DP, Walker PA, Ive J, Belbin L. 1996. Integrating conservation and forestry production: Exploring trade-offs between biodiversity and production in regional land-use assessment. Forest Ecology and Management 85: 251–260.

Ferrier S, et al. 2004. Mapping more of terrestrial biodiversity for global conservation assessment. BioScience 54: 1101–1109.

Friedlingstein P, et al. 2006. Climate–carbon cycle feedback analysis: Results from the C4MIP model intercomparison. Journal of Climate 19: 3337–3353.

Gärdenfors U. 2005. The 2005 Red List of Swedish Species. Uppsala (Sweden): Swedish Species Information Centre, Swedish Environmental Protection Agency.

Giesecke T, Hickler T, Kunkel, T, Sykes MT, Bradshaw RHW. 2006. Towards an understanding of the Holocene distribution of *Fagus sylvatica* L. Journal of Biogeography 34: 118–131. doi:10.1111/j.1365-2699.2006.01580.x

Global Biodiversity Information Facility. 2006. Prototype data portal. (15 January 2007; *www.secretariat.gbif.net/portal/index.jsp*)

Graham CH, Ferrier S, Huettman F, Moritz C, Peterson AT. 2004. New developments in museum-based informatics and applications in biodiversity analysis. Trends in Ecology and Evolution 19: 497–503.

Guisan A, Thuiller W. 2005. Predicting species distribution: Offering more than simple habitat models. Ecology Letters 8: 993–1009.

Guthrie D. 2006. New carbon dates link climatic change with human colonization and Pleistocene extinctions. Nature 441: 207–209.

Hampe A, Petit RJ. 2005. Conserving biodiversity under climate change: The rear edge matters. Ecology Letters 8: 461–467.

Hannah L, Midgley G, Hughes G, Bomhard B. 2005. The view from the Cape: Extinction risk, protected areas, and climate change. BioScience 55: 231–242.

Harte J, Ostling A, Green JL, Kinzig A. 2004. Biodiversity conservation: Climate change and extinction risk. Nature 430: 33. doi:10.1038/nature02718

Hitz S, Smith J. 2004. Estimating global impacts from climate change. Global Environmental Change 14: 201–208.

Huey RB, Gilchrist GW, Carlson ML, Berrigan D, Serra L. 2000. Rapid evolution of a geographic cline in size in an introduced fly. Science 287: 308–309.

Huntley B, Cramer W, Morgan AV, Prentice HC, Allen JRM. 1997. Predicting the response of terrestrial biota to future environmental changes. Pages 487–504 in Huntley B, Cramer W, Morgan AV, Prentice HC, Allen JRM, eds. Past and Future Rapid Environmental Changes. Berlin: Springer. NATO ASI Series, vol. 47.

Iverson LR, Prasad AM, Schwartz MW. 1999. Modeling potential future individual tree-species distributions in the eastern United States under a climate change scenario: A case study with *Pinus virginiana.* Ecological Modelling 115: 77–93.

Kadmon R, Farber O, Danin A. 2003. A systematic analysis of factors affecting the performance of climatic envelope models. Ecological Applications 13: 853–867.

Lawler JJ, White D, Neilson RP, Blaustein AR. 2006. Predicting climate-induced range shifts: Mode differences and model reliability. Global Change Biology 12: 1568–1584.

Lewis OT. 2006. Climate change: Species–area curves and the extinction crisis. Philosophical Transactions of the Royal Society B 361: 163–171.

Loehle C. 2000. Forest ecotone response to climate change: Sensitivity to temperature response functional forms. Canadian Journal of Forest Research 30: 1632–1645.

Macdougall D. 2006. Frozen Earth: The Once and Future Story of Ice Ages. Berkeley: University of California Press.

MacPhee RDE. 1999. Extinctions in Near Time: Causes, Contexts, and Consequences. New York: Kluwer Academic/Plenum.

Magri D, et al. 2006. A new scenario for the Quaternary history of European beech populations: Palaeobotanical and genetic consequences. New Phytologist 171: 199–221.

Malcolm JR, Liu C, Neilson RP, Hansen L, Hannah L. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. Conservation Biology 20: 538–548.

Martin PS, Steadman DW. 1999. Prehistoric extinctions on islands and continents. Pages 17–56 in MacPhee RDE, ed. Extinctions in Near Time: Causes, Contexts, and Consequences. New York: Kluwer Academic/Plenum.

Martinez-Meyer E, Townsend Peterson A, Hargrove WW. 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. Global Ecology and Biogeography 13: 305–314.

McLachlan JS, Clark JS, Manos PS. 2005. Molecular indicators of tree migration capacity under rapid climate change. Ecology 86: 2088–2098.

Midgley GF, Hannah L, Millar D, Rutherford MC, Powrie LW. 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. Global Ecology and Biogeography 11: 445–451.

Millennium Ecosystem Assessment. 2006. Ecosystems and Human Well-being: Biodiversity Synthesis. Washington (DC): World Resources Institute. (15 January 2007; *www.maweb.org/en/Products.Synthesis.aspx*)

Moretti M, Conedera M, Moresi R, Guisan A. 2006. Modelling the influence of change in fire regime on the local distribution of a Mediterranean pyrophytic plant species (*Cistus salviifolius* L.) at its northern range limit. Journal of Biogeography 33: 1492–1502.

Norby RJ, Ogle K, Curtis PS, Badeck FW, Huth A, Hurtt GC, Kohyama T, Peñuelas J. 2001. Aboveground growth and competition in forest gap models: An analysis for studies of climatic change. Climatic Change 51: 415–447.

Pearson RG. 2006. Climate change and the migration capacity of species. Trends in Ecology and Evolution 21: 111–113.

Pearson RG, Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? Global Ecology and Biogeography 12: 361–371.

Pearson RG, Thuiller W, Araújo MB, Martinez-Meyer E, Brotons L, McClean C, Miles LJ, Segurado P, Dawson TE, Lees DC. 2006. Model-based uncertainty in species' range prediction. Journal of Biogeography 33: 1704–1711. doi:10.1111/j.1365-2699.2006.01460

Peterson AT, Ortega-Huerta MA, Bartley J, Sanchez-Cordero V, Soberon J, Buddemeier RH, Stockwell DRB. 2002. Future projections for Mexican faunas under global climate change scenarios. Nature 416: 626–629.

Pounds JA, et al. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439: 161–167.

Randin CF, Dirnböck T, Dullinger S, Zimmerman NE, Zappa M, Guisan A. 2006. Are niche-based species distribution models transferable in space? Journal of Biogeography 33: 1689–1703.

Rehfeldt GE, Ying CC, Spittlehouse DL, Hamilton DA Jr. 1999. Genetic responses to climate in *Pinus contorta:* Niche breadth, climate change, and reforestation. Ecological Monographs 69: 375–407.

Rehfeldt GE, Tchebakova JM, Parfenova YI, Wykoff WR, Kuzmina NA, Milyiutin LI. 2002. Intraspecific response to climate change in *Pinus sylvestris.* Global Change Biology 8: 1–18.

Rosenzweig ML. 1995. Species Diversity in Space and Time. Cambridge (United Kingdom): Cambridge University Press.

———. 2003. Reconciliation ecology and the future of species diversity. Oryx 37: 194–205.

Saxe H, Cannell MGR, Johnsen Ø, Ryan MG, Vourlitis G. 2000. Tree and forest functioning in response to global warming. New Phytologist 149: 369–399.

Shapiro B, et al. 2004. Rise and fall of the Beringian steppe bison. Science 306: 1561–1565.

Sitch S, et al. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Global Change Biology 9: 161–185.

Solomon AM. 1986. Transient response of forests to $CO_2$-induced climatic change: Simulation modeling experiments in eastern North America. Oecologia 68: 567–580.

Steinger T, Körner C, Schmid B. 1996. Long-term persistence in a changing climate: DNA analysis suggests very old ages of clones of alpine *Carex curvula.* Oecologia 105: 94–99.

Svenning J-C, Skov F. 2004. Potential and actual ranges of plant species in response to climate change—implications for the impact of 21st century global warming on biodiversity. Paper presented at Copenhagen Meeting on Biodiversity and Climate Change, Environmental Assessment Institute; 28–29 August 2004, Copenhagen, Denmark.

Thomas CD, et al. 2004. Extinction risk from climate change. Nature 427: 145–148.

Thuiller W, Araújo MB, Pearson RG, Whittaker RJ, Brotons L, Lavorel S. 2004. Uncertainty in predictions of extinction risk. Nature 430: 34.

Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC. 2005. Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences 102: 8245–8250.

Tomaru N, Takahashi M, Tsumura Y, Ohba K. 1998. Intraspecific variation and phylogeographic patterns of *Fagus crenata* (*Fagaceae*) mitochondrial DNA. American Journal of Botany 85: 629–636.

Travis JMJ. 2003. Climate change and habitat destruction: A deadly anthropogenic cocktail. Proceedings of the Royal Society B 270: 467–473.

Willis KJ, Bennett KD, Walker D. 2004. The evolutionary legacy of the ice ages. Philosophical Transactions of the Royal Society B 359: 155–303.

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