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Authors

Field, Christopher B
Ruimy, Anne
Luo, Yiqi
[et al.](#)

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VEMAP: model shootout at the sub-continental corral

Global change presents grand challenges for ecology. For a science with a rich tradition of description that developed and matured with an emphasis on explaining current patterns in nature, the transition to prediction is exciting but daunting. The VEMAP (Vegetation/Ecosystem Modeling and Analysis Project) members – 26 ecosystem scientists, modelers and biogeographers – have accepted aspects of the challenge of prediction at the sub-continental scale. They are exercising two kinds of ecological models in order to explore the possible consequences of doubled atmospheric CO₂ and altered climate. The first VEMAP product¹ (called VEMAP1, hereafter) strides boldly but guardedly into the landscape of prediction, armed with general circulation model (GCM) scenarios, previously published ecological models, and a philosophy that emphasizes exploring issues, uncovering weaknesses with existing tools, and establishing priorities for future research.

VEMAP is, at its core, about the development of a predictive global ecology. The approach is not comprehensive. It is not yet validated. It is doubtful that the specifics of the predictions are of any use to policy makers. Yet, the first VEMAP product is an important advance. It makes solid progress in demonstrating that different classes of models can fit together and that small differences in model structures and mechanisms do not necessarily explode into uninterpretable results. In addition, it makes interesting and heuristically useful predictions about the future carbon balance and distribution of biomes in the conterminous United States.

VEMAP1 begins with three published scenarios for global equilibrium climate (i.e. temperature and precipitation) in a world with double the present amount of atmospheric CO₂. The three GCM scenarios suggest quite different climate regimes for the conterminous United States – the target area of VEMAP1. Simulated mean temperatures increase from 3.0 to 6.7°C, and precipitation increases by 4 to 21%. This variation introduces another of the objectives of VEMAP1. Previously published model results about future ecosystem structure and function vary greatly. This variability has contributed to the challenge in drawing general conclusions². Until VEMAP1, however, it has not been possible to partition this variation between effects of climate scenario and ecological model. VEMAP1, which concludes that the variation among

GCM and ecological scenarios is comparable, should help modulate any feelings of 'low variance' superiority harbored by students of the physical climate system.

VEMAP1 develops these scenarios (a surprisingly involved and important aspect of the study) and uses them as the climate for experiments with three biogeography models and three biogeochemistry models. The biogeography models [BIOME2 (Ref. 3), DOLY (Ref. 4) and MAPSS (Ref. 5)] simulate the equilibrium distribution of potential natural vegetation. The biogeochemistry models [BIOME-BGC (Ref. 6), CENTURY (Ref. 7) and TEM (Ref. 8)] simulate net primary production (NPP) and ecosystem carbon stocks. The basic VEMAP1 experiment ran each of the six ecological models under (1) current climate, (2) current climate with high CO₂, (3) future climate with current CO₂ for each GCM scenario, and (4) future climate with doubled CO₂ for each GCM scenario. A fifth experiment used the biome distributions output by the biogeography models under increased CO₂, and under future climate, as input for the biogeochemistry models. The multi-stage design provides a basis for assessing the separate and combined effects of climate, CO₂, biome distributions, and ecosystem physiology. It also provides a first estimate of the changes in NPP and carbon storage that might result from redistribution of the major biomes.

VEMAP1 does not present a single answer or 'best' estimate for future biome boundaries and NPP. There is, however, a reassuring similarity and reasonableness among the simulations with different models, especially for current conditions. Yet, even perfect agreement among models is no guarantee of accuracy. Comparisons against experimental data are much stronger tests of accuracy, and these will be essential if the emphasis on prediction increases in the future. For current conditions, all three biogeography models produce similar estimates for the potential area of forests, grasslands, shrublands and savannas, and all three biogeochemistry models simulate similar NPP and total carbon stores. Changing the amount of atmospheric CO₂ has almost no effect on the spread among models. All three biogeochemistry models predict a small increase (5–11%) in NPP. One of the biogeography models predicts an increase in the ratio of C₃ to C₄ grassland as the only CO₂-dependent change. The other two predict modest increases in forest area.

Simulations with GCM climates for double CO₂ yield a diversity of results among models, and reveal the first contrasts in the direction of simulated responses. Especially for the most severe GCM climate [UKMO (Ref. 9)], two biogeochemistry models predict increased NPP, but one model predicts a decrease. Two biogeography models predict an increase in the area of broadleaf forest, but one predicts a decrease. The range in estimated NPP and carbon storage expands still further in simulations with both doubled CO₂ and altered climate. Using the biome distributions simulated by the biogeography models as the vegetation maps for the biogeochemistry models does not further expand the range of results for NPP and carbon storage. For the simulations representing the greatest departures from current conditions (altered climate, doubled CO₂ and redistributed biomes), the range in estimated NPP for a given GCM scenario is hardly negligible, but neither is it overwhelming. For example, the increase in simulated NPP under the GFDL R30 climate (Ref. 10), and doubled CO₂, ranged from 18% for CENTURY with the BIOME2 vegetation to 39% for TEM with the DOLY vegetation. This sensitivity to the ecological models is no greater than the largest difference resulting from a GCM scenario. For BIOME-BGC with the BIOME2 vegetation, simulated NPP under doubled CO₂ increased by 22% under the GFDL climate but by less than 1% under the UKMO climate.

Overall, the variation among results of both classes of models is relatively modest, highlighting one of the most important lessons from VEMAP1. Strong forcing of one or a few processes does not necessarily result in large changes in ecosystem stocks and fluxes. Instead, the fixed or nearly fixed levels of other potentially limiting resources (especially nitrogen and photosynthetically active radiation) tend to constrain the range of responses.

The similarities among model simulations, particularly for the current climate or the current climate with doubled CO₂, suggests that we may, as a community, have a solid grip on the mechanisms that most strongly determine the future shape of the biosphere. But they could also reflect at least three different factors. One, the simulations may be similar because all the models incorporate similar, incomplete suites of mechanisms. Two, the similarities may result from tuning the model responses to the limited body of empirical evidence. And three, it is at least possible that the predicted outcomes are relatively insensitive to a reasonable range of modeled mechanisms. A detailed discussion of these options was beyond the objectives of VEMAP1. But given the range of mechanisms through which the models

responded to increased CO₂, it seems unlikely that the latter two options are completely irrelevant.

Many of the most interesting points in VEMAP1 involve the reasons for the differences among the simulations. This is not the paper's primary focus. Yet, it is likely to be the topic that is most important for the participating modeling groups. For example, sensitivity to drought appears to be critical in driving differences among the models. VEMAP1 strengthens the motivation for careful evaluations of evapotranspiration estimated from equilibrium theory (as in BIOME2) versus aerodynamic theory (as in DOLY and MAPSS). It also highlights the role of factors like TEM's assumption that the vegetation competes more effectively for nutrients when above-ground resources are less limiting. Careful studies combining model comparisons with analysis of empirical data will be a primary basis for the next generation of improved models.

For the research groups involved, some of the lessons from VEMAP1 were cultural. Groups with different perspectives and different techniques learned about alternative approaches, algorithms and areas of emphasis. Contrasts in the management and sharing of model code revealed a range of approaches to the nuts and bolts of doing science with simulation models. Challenges in this area range from the difficulty of evaluating algorithms in models where code is not shared to the issue of attributing origin when an aspect of one model is slightly modified code from another model. Hopefully, the VEMAP process will help establish protocols where code can be shared freely.

VEMAP1 is an important milestone in the development of predictive ecology,

but it is far from definitive. The conditions for the simulation, with potential natural vegetation and equilibrium at doubled CO₂ levels are both very artificial. The mechanisms through which the models simulate responses to increased CO₂ differ greatly among the models and are clearly a subset of the potentially important CO₂ effects. Several components of global change, including nutrient deposition, tropospheric ozone and altered UV-B, are not addressed in VEMAP1. At this stage in the development of global ecology, these factors do not represent weaknesses. It is critical that the infrastructure for global prediction and the evaluation of the tools proceed gradually, with measured steps. VEMAP1 is a spectacularly important first step that should alert the community of ecologists and earth system scientists that predictive ecology is on the way.

Christopher B. Field
Anne Ruimy

Carnegie Institution of Washington, Dept of Plant Biology, 290 Panama Street, Stanford, CA 94305, USA

Yiqi Luo

Bioresources Center, Desert Research Institute, 7010 Dandini Boulevard, Reno, NV 89506, USA

Carolyn M. Malmström
James T. Randerson
Matthew V. Thompson

Dept of Biological Sciences, Stanford University, Stanford, CA 94305, USA, and Carnegie Institution of Washington, Dept of Plant Biology, 290 Panama Street, Stanford, CA 94305, USA

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Exploding species

Amidst all the discussion and disagreement about just how many species exist there used to be two accepted principles. The first is that we are unsure to within an order of magnitude exactly how many species there are in total^{1–3}, and the second is that we know pretty well how many species of birds there are; with a typical figure being about 10 000 (Refs 3,4). Participants at a recent conference have thrown the second principle into question⁴. Results from molecular studies are showing various populations to be quite different genetically from each other, and they should therefore perhaps be reclassified as species. Such reclassifications are debated, because they do not appeal directly to the classic biological species concept, which stakes reproductive isolation as the main criterion for erecting a subspecies to species status⁴. Field researchers directly address this question, and their results are also pointing to a revised estimate of the number of bird species, which is considerably more than was previously thought.

These studies are typified by research on the Old World leaf warblers (genus *Phylloscopus*), a group of small greenish birds living throughout the temperate re-

gions of Eurasia. Many species look extremely similar to each other, and it was only in 1768 that Gilbert White in his book *Natural History of Selbourne*⁵ separated the three British species – the familiar chiffchaff (*P. collybita*), willow warbler (*P. trochilus*) and wood warbler (*P. sibilatrix*) – based on their quite dissimilar songs. Two hundred years on, Alström, Olsson and Colston, working in China, have added three new species using the White approach, which is essentially skilled field observation^{6–8}. The main additional tool they use is song playback. Heterospecifics usually show no interest in other species' songs. At least one of the newly described species had representatives sitting in the drawers of the British Museum but had been lumped with other species similar in plumage and size, raising questions about