



Predictive Models of Forest Dynamics

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PERSPECTIVE

Predictive Models of Forest Dynamics

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Dynamic global vegetation models (DGVMs) have shown that forest dynamics could dramatically alter the response of the global climate system to increased atmospheric carbon dioxide over the next century. But there is little agreement between different DGVMs, making forest dynamics one of the greatest sources of uncertainty in predicting future climate. DGVM predictions could be strengthened by integrating the ecological realities of biodiversity and height-structured competition for light, facilitated by recent advances in the mathematics of forest modeling, ecological understanding of diverse forest communities, and the availability of forest inventory data.

There are approximately a trillion canopy trees on Earth (1) from around 100,000 species (2). The trees store approximately as much carbon as is currently in the atmosphere, and forest ecosystems harbor two-thirds of terrestrial biodiversity (3). The challenge of predictive forest modeling is to forecast how this collection of trees will develop in the future, in response to the many perturbations to which it is being subjected, including deforestation, logging, pollution, nitrogen deposition, the loss of pollinating and seed-dispersing animals, and the effects of increased atmospheric CO₂, both direct (the job of a leaf is to convert CO₂ into plant material) and indirect (altered climate).

The most exciting recent advance in forest modeling has been the appearance of dynamic global vegetation models (DGVMs), which simulate the distribution, physiology, and biogeochemistry of forests and other vegetation at global scales, under present, historic, or simulated future climates (4). DGVMs have shown that future changes in global forest carbon storage could greatly affect the response of Earth's climate system to anthropogenic CO₂ emissions over the next century (5). However, because DGVMs were developed recently, with limited information, their predictions are currently highly uncertain (Fig. 1), making vegetation dynamics one of the largest sources of uncertainty in Earth system models. Reducing this uncertainty requires

work on several fronts. For example, physiological parameters need to be better constrained with data (6), and we need better models of disturbances, including fire (7) and land-use change (8). But more fundamental improvements could be achieved by incorporating the ecological realities of biodiversity and competition for light. A recent explosion in forest inventory data might make this possible.

The only reason to build a trunk—to become a tree—is to overtop your neighbors and capture light before they do. This game-theoretic competition for resources is responsible for the enormous amounts of carbon stored in living trees and in undecomposed organic matter and fossil fuels, most of which began as wood. Foresters and forest ecologists have developed individual-based, height-structured models that can accurately predict productivity (9) and species composition (10). At every turn, these have revealed nonlinearities in forest dynamics caused by competition for light. For example, increased growth leads to increased overtopping, which increases mortality, which increases forest carbon loss; with the functions at each stage being nonlinear. In contrast, current DGVMs reduce whole forested regions to the total biomass in compartments (such as leaves, roots, and trunks), with simple phenomenological rules for how the carbon generated from photosynthesis is allocated to, and lost from, these compartments. Moreover, competition among species [or at least among plant functional types (PFTs)], which needs to be represented to predict biome boundaries, follows rules with weak empirical support that differ among models (11).

Therefore, DGVMs could be substantially improved by basing them on the height-structured models developed by foresters and forest ecologists. But because these models are individual-based, this would require simulating every tree on Earth, which would be immensely computationally demanding. A more efficient approach would be to derive so-called macroscopic equations to scale correctly from the parameters governing individual trees to the dynamics of forested regions, in the same way that the Navier Stokes equations scale correctly from molecular motion to fluid dynamics. Recent progress implies that macroscopic equations will soon form the basis of DGVMs. Moorcroft *et al.* (12) introduced a demographic method to scale up individual-based forest models, which has since been used to provide tractable macroscopic equations to scale from trees to stands and to scale from stands to forests (13).

Macroscopic equations will allow global simulations of individual-based forest models, but here arises the problem of biodiversity. The (approximately) 100,000 tree species vary hugely in properties that drive the carbon cycle, such as growth, mortality, decomposition of dead wood, and their dependency on climate. Because of a lack of appropriate data or theory, current DGVMs reduce biodiversity to a small number of PFTs, within which all parameters are constant. The PFTs represent simple morphological and biogeographical aggregations, such as broadleaf versus needleleaf or tropical versus temperate. But these aggregations are unlikely to be optimal for capturing the effects of biodiversity on dynamics, because the among-species differences within PFTs dwarf the average difference between them. For example, the PFT temperate deciduous broadleaf contains the northernmost tree species (Arctic birch) along with subtropical oaks; and evergreen needleleaf contains cold-adapted spruces and firs and heat-adapted pines. Even within a forest composed of a single PFT, species parameters typically vary by an order of magnitude (14). Moreover, the mix of species, and hence parameters, found at a given location is strongly correlated with climate (15), with obvious implications for modeling the climate dependency of forest dynamics. By ignoring most biodiversity, DGVMs could be overestimating the strength of some climate responses because they fail to account for the fact that deleterious effects can be mitigated by increases in those species best

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adapted to the new conditions (16). But they could be underestimating other responses; for example, increased temperature could both increase the growth of extant trees and select for warm-adapted species, which have higher growth rates (17). Therefore, there is a need for a substantial increase in the amount of biodiversity represented in DGVMs.

However, adding biodiversity and height-structured competition into DGVMs would increase the complexity of models that are already severely underconstrained. DGVMs contain large numbers of parameters, which are hand-selected from literature values in order to qualitatively match model predictions to sparse observations of ecosystem fluxes (such as productivity) and states (such as biome boundaries). Physiological parameters are beginning to be objectively estimated with measurements from flask networks and eddy-covariance flux towers (6). But these data contain almost no information about the long-term dynamics of individuals, populations, or communities. Luckily, these dynamics are recorded in a kind of data that has become much more available recently. Forest inventories consist of sample plots within which trees are measured regularly (about every 5 to 10 years). The measurements are low-tech: for example, stem diameter, species, alive or dead. But the sample sizes are large, running into millions of trees in some cases (18, 19). The few published biogeochemical analyses of forest inventory data have yielded results with major implications for our understanding of the global carbon cycle (18–20).

To constrain DGVMs, the tree-level measurements in forest inventories could simply be summed to provide long-term average carbon dynamics to compare with DGVM predictions. But this approach discards most of the information in the data. In contrast, if DGVMs were based around models of individual trees, the individual growth and mortality records could be used to directly estimate key tree-level parameters; although few if any inventories contain sufficient information to estimate all parameters, because they lack measurements of (for example) light, belowground carbon, nutrients, and seed dispersal. In the low-diversity boreal and temperate zones, the abundance of inventory data might be sufficient to estimate parameters for every dominant tree species. In addition to improving predictions for the carbon cycle, this might allow realistic predictions for particular species; for example, climate-induced shifts in species ranges,

which to date have been predicted using only correlative methods (21).

In high-diversity forests, species-specific parameterization is not feasible. Instead, species need

the continuous approach extends naturally to include parameter variation within species. These approaches correspond closely to the discrete and continuous lumping techniques used to model heterogeneous systems of chemical reactions (23).

All of the above add up to a major scientific challenge. We have proven individual-based, height-structured models which, using new scaling methodologies, could be implemented at global scales. We are beginning to understand the trade-off structure of forest communities sufficiently to capture the effects of biodiversity on forest function. And for the first time, we have millions of observations of individual trees with which to constrain the structure and parameters of global models. If these pieces could be put together properly, the result could be a new generation of ecologically realistic, better-constrained DGVMs. A benchmark of success for this endeavor might be that forest dynamics are no longer one of the major sources of uncertainty in predicting the future of Earth's climate.

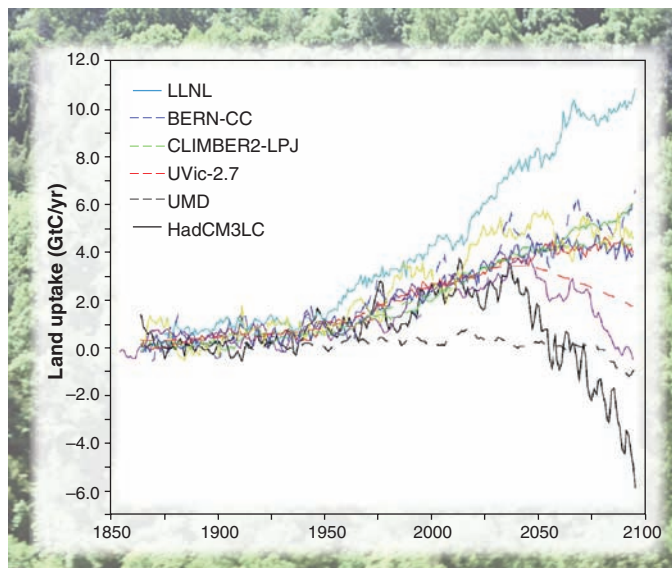


Fig. 1. DGVMs have shown that the terrestrial biosphere could be crucial in determining the future of Earth's climate. But this figure [from (5)] shows how divergent the predictions of DGVMs currently are. For comparison, current anthropogenic CO₂ emissions are 7.6 ± 0.6 Gt of carbon/year. True DGVMs, with a responsive global distribution of PFTs, are labeled (5). The remainder have a dynamic carbon cycle but a fixed distribution of PFTs. Some of the variation in Fig. 1 results from different climate models, but a large spread was also seen when different DGVMs were run uncoupled from global climate models under a common, fixed climate trajectory (11). LLNL, Lawrence Livermore National Laboratory climate model; BERN-CC, Bern carbon-cycle climate model; CLIMBER2-LPJ, Climate-Biosphere model, coupled to the Lund-Potsdam-Jena DGVM; UVic-2.7, University of Victoria Earth system climate model, version 2.7; UMD, University of Maryland coupled carbon-climate model; HadCM3LC, Hadley Centre coupled climate-carbon cycle model.

to be aggregated to reduce the number of parameters to be estimated. And although any such aggregation must result in a loss of biological information, evidence suggests that, with the correct aggregation, this loss could be minimal. This is because wherever parameters have been estimated for different tree species, they have been found to be subject to life history tradeoffs: strategic axes appearing as among-species correlations in parameters (22). Moreover, similar tradeoffs appear to be structuring different forest communities, such as the shade-tolerance spectrum from fast-growing, short-lived pioneers to slow-growing, long-lived species (22). These tradeoffs imply that most of the effects of biodiversity would be retained in models that reduced the state of a forest to the distribution of individual trees along tradeoff axes, regardless of taxonomic identity. Such models could capture the effects of biodiversity on select aspects of forest function (such as carbon dynamics), either by defining a new set of PFTs spread optimally along the axes or by treating the distribution of species as a continuum. Either approach would require fewer data than species-specific parameterization (14), and

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