

Terrestrial models and global change: challenges for the future

GEORGE C. HURTT, PAUL R. MOORCROFT, STEPHEN W. PACALA and SIMON A. LEVIN

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544–1003, USA

Abstract

A wide variety of models have illustrated the potential importance of terrestrial biological feedbacks on climate and climate change; yet our ability to make precise predictions is severely limited, due to a high degree of uncertainty. In this paper, after briefly reviewing current models, we present challenges for new terrestrial models and introduce a simple mechanistic approach that may complement existing approaches.

Keywords: biodiversity, climate change, ecosystem models, land use

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Introduction

Global climate changes in the past have had dramatic impacts on the land surface. The geological record documents the advance and retreat of glaciers and corresponding changes in sea level (Folland *et al.* 1990). The fossil pollen record illustrates large changes in the geographical distribution of vegetation (Bernabo & Webb 1977). What is less certain, but of little doubt, is that changes to the land surface produce large-scale feedbacks on climate.

Our understanding of the potential importance of terrestrial biological feedbacks on climate comes largely from general circulation models (GCMs). In this regard, atmospheric scientists have made great progress. Including biological details of the land surface in GCMs improves palaeo (Otto-Bliesner & Upchurch 1997) and current climate predictions (Pielke *et al.* 1997; Fennessy & Xue 1997). In addition, several large-scale experiments have shown that the atmospheric models and the way they incorporate details from the land surface are on track (e.g. FIFE and HAPEx).

However, because the biophysical and biogeochemical feedbacks on climate depend on the properties of local vegetation and soil, which in turn respond to climate, predicting these feedbacks depends critically on predicting relevant land surface dynamics. To this end, progress is lagging. Our best global-scale biological models still have serious problems of averaging and scaling, and omit important influences. The biological challenge is both exciting and daunting. The biological feedbacks on climate are potentially large, but we suffer

from an inability to predict relevant long-term community and ecosystem dynamics from models based on physiological principles alone.

This paper is about models for the study of terrestrial biological feedbacks on climate and climate change. We begin by describing briefly two general lessons from the available models. The first is that the potential feedbacks from the land surface on climate are large. However, the second is that the uncertainties in the magnitude and direction of those feedbacks are also large. We then present challenges for future models. The issues that we discuss are widely understood in the global change community. Our purpose here is to provide a summary. We end with an introduction to a nascent approach representing work in progress. This paper is not meant as a review or critique of available models, nor as a complete description of a new approach. While relevant models have produced many accomplishments, there are important challenges ahead. This paper is intended as motivation and perspective for future models that will confront these challenges.

Lessons from available terrestrial models

Terrestrial models that are relevant to feedbacks on climate have been reviewed previously (Heal *et al.* 1993; Malanson 1993). In Heal *et al.* (1993), the models are grouped into seven types: leaf, crop, biogeochemical, stand, landscape, biophysical, and biome. Malanson (1993) groups the models into three types: transfer functions, stand models, and physiological models.

Correspondence: George C. Hurtt, tel +1/609 258-3868, fax +1/609 258-1334, e-mail gchurtt@princeton.edu

Type	Examples
I. Biogeochemical	Miami (Lieth, 1972) TEM (Raich <i>et al.</i> , 1991; Melillo <i>et al.</i> , 1993) CENTURY (Parton <i>et al.</i> , 1988) GTEC (King <i>et al.</i> , 1997) CASA (Potter <i>et al.</i> , 1993)
II. Biophysical	SiB (Sellers <i>et al.</i> , 1986) BATS (Dickinson <i>et al.</i> , 1993) LSM (Bonan, 1994) LSX (Pollard & Tjompson, 1995)
III. Biogeographic	Holdridge (Holdridge, 1967) Biome (Prentice <i>et al.</i> , 1992; Haxeltine <i>et al.</i> , 1996; Haxeltine & Prentice, 1996) MAPSS (Neilson, 1995) DOLY (Woodward, 1987; Woodward <i>et al.</i> , 1995)
I+II	LSM + carbon (Bonan, 1995)
II + III	BATS + Holdridge (Henderson-Sellers & McGuffie, 1995)
I + III	Holdridge + carbon (Smith <i>et al.</i> , 1992) Biome + carbon (Prentice & Sykes, 1995)
I + II + III	IBIS (Foley <i>et al.</i> , 1996)

Table 1 Types and examples of terrestrial models for global change studies. The upper portion of the table lists three basic types of models and gives examples of each type. The lower portion of the table gives examples of models that are hybrids of two or three of the basic types.

Alternatively, the models can be grouped based on their objectives. Biogeochemical models are focused primarily on the air–land balance of carbon and other chemical constituents. Biophysical models are focused on direct physical interactions between the atmosphere and land surface. Biogeographical models are concerned with predicting the distribution of vegetation. Because the total terrestrial response and feedback includes all three of these objectives, models have also been developed with a combination of these objectives. Table 1 provides an example of the use of this classification.

Available terrestrial models have been very successful at illustrating the potential for biological feedbacks on climate and climate change. These models consistently show that biological feedbacks are large, but there is considerable uncertainty.

Biological feedbacks on climate are potentially large

Terrestrial models consistently show that biological feedbacks on climate are potentially large. This result has been demonstrated in numerous studies, and has helped to fuel enormous interest in the study of biological feedbacks on climate and climate change. We briefly summarize a few examples.

In a coupled biophysical–climate model, Shukla *et al.* (Shukla *et al.* 1990) simulated the deforestation of the Amazon and compared the results to control runs with an intact Amazon forest. The result was a decrease in evapotranspiration and precipitation over the region. In addition, there were corresponding increases in runoff, sensible heat flux, and average annual temperature over

the region. The average annual temperature increase ranged from 0° to 3° at the surface over the Amazon.

In a second extreme scenario with a coupled biophysical model, Bonan *et al.* (1992) found that the albedo difference between boreal vegetation and bare ground or tundra had a large effect on surface temperatures. Increased land surface albedo between January and April because of exposed snow caused colder temperatures over much of the northern hemisphere compared to the control simulations with an intact forest. Zonally averaged temperatures decreased as much as 12° in April and as much as 5° in July. The temperature change extended as far south as 10° North latitude, well outside of the perturbed area.

The list of studies that indicate potentially large biological feedbacks on climate is long and includes less extreme scenarios and both biogeographic and biogeochemical effects. For example, Henderson-Sellers & McGuffie (1995) illustrated, using a coupled biogeography and climate model, that changes in the distribution of vegetation during climate change can cause important biophysical feedbacks on climate. Using equilibrium biogeochemical assumptions, Smith *et al.* (1992) estimated that in response to a doubled CO₂ climate, terrestrial carbon storage could increase from 8.5 to 180.5 GtC depending on the climate model used. In a similar study, Prentice and Sykes estimated that terrestrial carbon storage will change from –11 to +103 GtC (Prentice & Sykes 1995). By comparison, the atmosphere currently contains roughly 150 GtC more now than in did in preindustrial times (Siegenthaler & Sarmiento 1993).

The uncertainties in the magnitude of biological feedbacks, while poorly known, are large

A second consistent result from the available terrestrial models is that the uncertainties in the magnitude of biological feedbacks on climate, while poorly known, are also large. The degree of uncertainty is largely unknown because quantifying it in model predictions has not been a significant priority to date. Most studies report predictions without any quantitative estimate of significance or confidence. Others report a range of predictions, such as in the studies of Smith *et al.* (1992) and Prentice & Sykes (1995) cited above. These ranges are often enormous and hard to evaluate. Moreover, in the case of these latter two examples, the ranges are generated solely from the use of different climate models and do not include uncertainty in the biological models.

One way we can get an indication of the level of uncertainty in terrestrial model predictions is by comparing the predictions of different models in carefully organized model intercomparison studies, such as an intercomparison of biogeographical and biogeochemical models that are forced by climate models (VEMAP Members 1995). In this study, a set of biogeochemical and biogeographic models were forced, singly and coupled together, under current CO₂ and climate conditions and the results were compared with those under doubled CO₂ and associated climate conditions. The model predictions diverged substantially when run under the altered conditions. For example, over the range of climate models of doubled CO₂ conditions, the range of coupled terrestrial model (coupled biogeographical and biogeochemical model) predictions for continental U.S. net primary production (NPP) is from a negligible change to an increase by 40%. Total carbon storage could increase by 32% or decrease by 39%. The range of model predictions was nearly as large using any single climate model. Clearly, the biological responses (and corresponding biological feedbacks) predicted by these models are highly uncertain.

Challenges for new models

Take 'fitting' out of the closet

While model predictions diverged under altered climates in the VEMAP model intercomparison study cited above, there was close agreement under current climate and CO₂ conditions. Under current conditions, modelled U.S. NPP ranged from 3.1 to 3.9 PgC y⁻¹ and total carbon storage estimates ranged from 109 to 125 PgC. The agreement of the models under current climate conditions and divergence under predicted future conditions is a

strong indication that they are fit to current patterns, but lack consensus on what is responsible for those patterns.

That the models differ on the mechanisms responsible for the patterns is a point of fact (VEMAP Members 1995). For example among the biogeochemical models, BIOME-BCG relies primarily on the control of water on plant carbon uptake and storage, whereas TEM and CENTURY rely primarily on the control of nitrogen availability. The biogeographical models all use similar thermal and water balance controls to limit the distribution of vegetation types, but differ markedly in their representations of potential evapotranspiration and direct CO₂ effects.

Model fitting is controversial. While fitting (and more generally parameter estimation) can be a valuable part of an overall scheme of model development and evaluation (Edwards 1972), without careful statistical treatment, it can be difficult to determine the extent to which the performance of a model depends on its structure and known constants, as opposed to simply the fitting of even a few parameters to observed patterns. In addition, fit parameter values are not always easily reconcilable with independent field data. Understanding where parameter values (and for that matter functional forms) come from and how well they are known, together with a fuller discussion of model fitting and model evaluation, will help us determine the degree of confidence to place in a given model.

Degree and equitability of detail

One trend in the development of coupled terrestrial models is towards increased physiological detail (Sellers *et al.* 1997). Yet, increasing detail at small scales is no assurance of improved prediction or explanation at larger scales (Levin 1992). While basing terrestrial models on plant physiology makes sense because physiological responses of plants are directly affected by climate and often have direct physical feedbacks on climate (e.g. evapotranspiration), basing these models on detailed physiology presents difficult challenges. To achieve confidence, we must find ways to scale from the physiological performance of cells or leaves to the long-term performance of whole plants and plant populations and, more difficult, to long-term community and ecosystem dynamics. (Levin 1992; Ehleringer & Field 1993; Jarvis 1995; Levin *et al.* 1997).

One important source of uncertainty in scaling up is plant resource allocation. We still do not have a sufficient understanding of plant resource allocation to model long-term plant performance, yet allocation by plants influences both plant performance and biophysical properties relevant to climate. For example, if plants allocate resources preferentially to roots, then they may become

better competitors for nutrients and water at the expense of potentially increased photosynthetic capacity (e.g. leaf area). Alternatively, if plants allocate preferentially to leaves, then they may increase their photosynthetic capacity at the expense of increased water stress and decreased soil water and nutrient acquisition. What makes allocation difficult is that individual plants can be highly plastic, and different species can have different basic allocation strategies (Mooney 1972; Bloom *et al.* 1985; Tilman 1988). Plant allocation is a fundamentally nonlinear process, and nonlinearities can amplify error in models (Deutschman 1996).

Allocation is just one source of uncertainty in scaling up. Population and community effects can occur on the same order as the physiological effects already emphasized in current models. Bolker *et al.* (1995) provide an example of the potential importance of community dynamics to properties of ecosystems. A version of the individual-based forest simulator SORTIE (Pacala *et al.* 1993; Pacala *et al.* 1996) with a single homogeneous average tree species had very different predictions under enhanced CO₂ conditions than a version of SORTIE with the observed biodiversity, even on decadal time scales and even for such quantities as total above-ground carbon storage. In particular, model communities with higher biodiversity showed a roughly 30% increase in total basal area over time scales of 50–100 years.

Recent empirical studies also illustrate large effects of biodiversity on the functioning of systems. Biodiversity may stabilize ecosystems (Naeem *et al.* 1994; Tilman & Downing 1994), lead to higher rates of NPP and greater resource depletion (Tilman *et al.* 1996), and dramatically affect the consequences of nitrogen addition to an ecosystem (Wedin & Tilman 1996). For example, in an experimental grassland communities with more species had greater total plant cover (higher integrated NPP) and less nitrogen available in the soil (Tilman *et al.* 1996).

Finally, even if we had a way to scale up formally from physiology through plant allocation and community dynamics to derive solutions for 'potential' vegetation as a function of environmental variables, we would still be missing the consequences of disturbance and land-use. These consequences are dramatic, and both disturbance and land use are on the rise (Vitousek *et al.* 1986; Skole & Tucker 1993; Vitousek *et al.* 1997; Noble & Dirzo 1997; Dale 1997). Even a small grid cell is typically heterogeneous at smaller scales for a variety of reasons, of which disturbance and land use are increasingly important.

Early successional sites tend to accumulate above-ground carbon relatively quickly compared to late successional sites (Houghton *et al.* 1983), because plants in early successional sites are rapidly growing. Disturbance and land use also interact with processes at smaller scales,

potentially altering the dynamics and outcome of inter-specific competition between plants. Disturbance can also affect community and ecosystem responses to climate change, when, for example, early and late successional species respond differentially to the change (Bolker *et al.* 1995). Converted land that is the product of human land use can have very different ecosystem properties and dynamics than the natural system it replaces. Clearly, prediction and characterization of land use and disturbance represent crucial areas of research.

While coupled global terrestrial models seem to be progressing with ever more detailed plant physiology, there are many important effects at larger scales that are far removed from plant physiology.

Search for macroscopic descriptions

Because there are many sources of uncertainty in our understanding of longterm land surface dynamics, and because we cannot yet accurately scale all of the way up, there may be a tendency to add missing effects to the models of detailed physiology that are already available and coupled to climate models. Yet resulting models can become prohibitively complicated and hold the capacity to amplify errors in multiple directions. It might be tempting to combine the 'best' biogeography, biogeochemistry, and biophysical models; but any resulting model still would lack several important influences such as biodiversity, disturbance and land use, succession, and limited plant dispersal. Given the complexity of the existing component models, let alone the potentially needed additions, is there any hope that we would understand these models or that they would make statistically useful predictions? Are we at an impasse?

One way to progress is by formulating models at intermediate scales of biological detail. In an effort to keep the models simple, important processes at smaller scales could be included through relatively simple expressions that are derived from a detailed understanding of mechanisms operating at those scales. Plant community ecology, for example, is largely proceeding from the scale of a phenomenological understanding of whole plant performance to predict the dynamics of plant communities over long time scales (Shugart, 1984; Pacala *et al.* 1996). The macroscopic properties of gases may be derived from the ensemble behaviour of interacting particle systems.

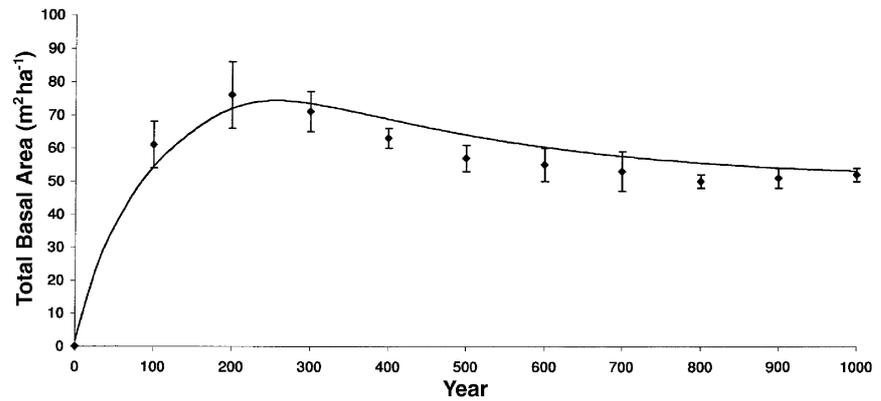
One possible approach

Our work is aimed at developing a relatively simple mechanistic ecosystem model that is equitable in detail and that will run at large scales. One major impediment to this goal been the lack of an economical description of plant population and community dynamics. Stochastic

Table 2 The approximation is comprised of two coupled equations. The first equation describes the local density of plants n (or carbon in plants) of type x , size s , and age a since disturbance. This equation includes the rate of plant growth G , mortality u , and ageing. Plants compete for light L , water W , and nutrient N which differentially affect growth and mortality. The second equation describes the density of patches p of different ages. This equation includes patch ageing and disturbance. There are five boundary conditions. F is plant fecundity, m is the fraction of dispersal that is nonlocal, and γ is plant survivorship following disturbance. In practice, m can be calculated by integrating a species' dispersal kernel over the area outside a patch. Together, these equations generally describe plant dynamics (and carbon in plants) competing on a heterogeneous landscape, including the effects of landscape disturbance.

Governing Equations:	
Plant dynamics	$\frac{\partial}{\partial t}n(x, s, a, t) = -\frac{\partial}{\partial s}[G(x, s, a, t)n(x, s, a, t)] - \mu(x, s, a, t)n(x, s, a, t) - \frac{\partial}{\partial a}n(x, s, a, t)$
Patch dynamics	$\frac{\partial}{\partial t}p(a, t) = -\frac{\partial}{\partial a}p(a, t) - \lambda(a, t)p(a, t)$
Boundary Conditions:	
Initial plant distribution	$n(x, s, a, 0) = n(x_0, s_0, a_0)$
Initial patch distribution	$p(a, 0) = p(a_0)$
Plant reproduction	$n(x, 0, a, t) = \frac{1}{G_0} \{ \int_0^\infty F(x, s, a, t)n(x, s, a, t)[1 - m(x, s, a, t)]ds + 1/p(a, t) \int_0^\infty \int_0^\infty F(x, s, a, t)n(x, s, a, t)p(a, t)m(x, s, a, t)dsda \}$
Plant survival	$n(x, s, 0, t) = \gamma(x, s, a, t)/p(0, t) \int_0^\infty \lambda(a, t)p(a, t)n(x, s, a, t)da$
New patches	$p(0, t) = \int_0^\infty \lambda(a, t)p(a, t)da$

Fig. 1 The accumulation of total plant basal area during succession in a forested region of Connecticut. The points with bars illustrate the ensemble mean predictions plus and minus one standard deviation, of the forest simulator SORTIE (Pacala & Deutschman 1995). The curve depicts a preliminary version of a PDE approximation of SORTIE that accounts for patch age. Note that the approximation, using the same parameter values as the simulator, does an excellent job of predicting the mean behaviour.



individual-based forest models have been highly successful at simulating the course of succession from submodels of plant life history (Botkin *et al.* 1972; Shugart & West 1977; Shugart 1984; Pacala *et al.* 1993; Pacala *et al.* 1996; Shugart and Smith 1996). While some of these models are not well suited to global change studies (Pacala & Hurtt 1993), many of the deficiencies can be overcome by estimating parameters from field data and adding processes at other scales. One basic impediment to their use in large-scale studies, however, has been that they are too complex to run at large scales.

An approximation to the dynamics of a successful individual based model would have the features needed to model vegetation dynamics and would run much faster than the individual-based counterpart. At the core of our approach is the general structure of one such approxi-

ation. Though the derivation of the approximation is beyond the scope of this paper, we summarize it here.

Consider running a stochastic individual based model on a large plane. We overlay a fine 3D grid and consider a cell of the grid to be occupied if the top centre point of a tree's crown is within the cell. We then seek the formal expectation of the stochastic process governing the occupancy of the cells. The general expression for this expectation is very complicated. One simple case is the 'mean-field' case (Pacala & Deutschman 1995), which assumes no horizontal spatial heterogeneity. That case was shown to be grossly inadequate for approximating the mean behaviour of SORTIE (Pacala & Deutschman 1995). The approximation we use here is derived in a similar fashion, but includes horizontal spatial heterogeneity by conditioning on patch successional age.

The resulting approximation is a system of two coupled partial differential equations. The form of the equations is very similar to the model introduced by Levin & Paine (1974) for intertidal communities. In addition, Kohyama has successfully used models of a similar form in other studies of vegetation dynamics (Kohyama 1993; Kohyama & Shigesada 1995). Of the two equations, one describes the demography of patches, and the other describes the dynamics of plants (or the carbon in plants) of different types and sizes in patches of different ages since disturbance. Boundary conditions include initial conditions, plant reproduction, the creation of new patches following disturbance, and the survivorship of plants following disturbance. Table 2 describes the general set of equations and boundary conditions.

Figure 1 illustrates the ability of the approximation to reproduce the ensemble mean behaviour of the forest simulator SORTIE, using the same functions and parameter values. The close agreement between the approximation and the ensemble mean behaviour of SORTIE indicates that the approximation scales up from the individual-level information in the submodels and parameter values of the simulator to larger scale predictions that are of interest in global change studies. The formal derivation explaining why it does so is analogous to other scaling problems in physics (Pacala *et al.* in prep.; Kubo *et al.* in prep.). By using parameter values that can be determined empirically, the approximation will allow us to conduct error analyses by propagating measure parameter uncertainty through the model. Many of the

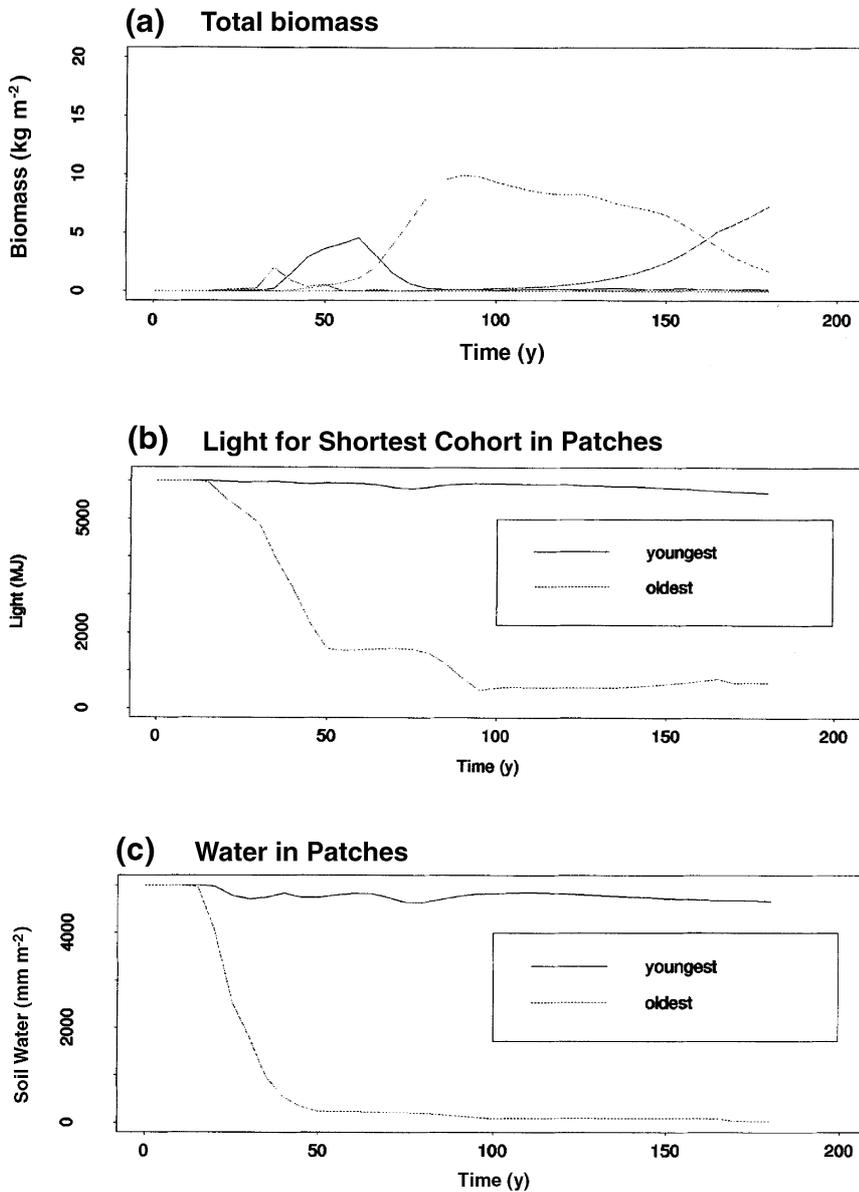


Fig. 2 The five panels in this figure depict the dynamics of demonstration version of a new model (a). This panel shows the community dynamics for the entire model domain during the run. The different curves represent the biomass different species (points along a continuous biodiversity axis). (b): The light availability of the smallest plants in a patch is very different in young and old patches. At the end of the model run, the youngest patches have no tall plants and there is thus a large amount of light hitting the smallest plants. On the other hand, the oldest patches have tall plants which shade the understory. (c): At the end of the model run, soil water availability is also very different on young and old patches. (d): At the end of the model run, the biomass density in patches strongly increases with patch age. (e): This panel shows the frequency of distribution of patches of different ages since disturbance at the end of the run.

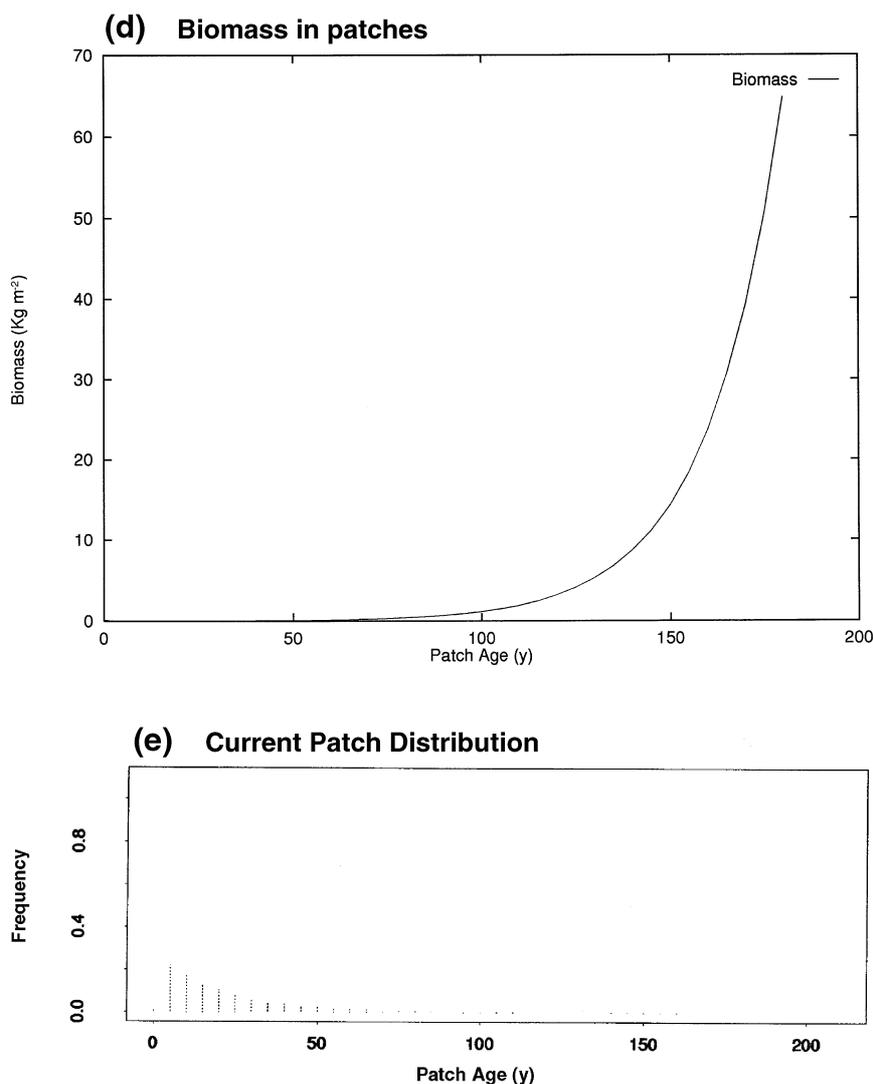
predictions of the individual-based model SORTIE, for example, are robust to formal error propagation (Pacala *et al.* 1996).

Solely for illustrative purposes, we have constructed an extremely simple demonstration version of a new model built around the general structure of this approximation. It is of an area on the scale of a typical grid cell in a GCM (e.g. degree \times degree). A separate set of equations would be needed for each grid cell of a GCM in a large-scale simulation, and the coupling between those grid cells would have to be added. The model is aseasonal and has a constant disturbance rate that removes plants that are taller than a threshold height. There is a simple bucket hydrological model. Plant growth is a function only of light and water availability; plants differ only along a single trade-off axis with root-to-shoot ratio and water-use efficiency trading off against the height at which plants stop growing and switch to

reproduction. Plant mortality is a function of plant growth rate; dispersal is global within the grid cell.

Figure 2(a) summarizes the community dynamics for the entire model domain starting from an initial small population of juveniles of each species (discrete points along a continuous biodiversity axis). Note that the biomass of late successional species increases at the expense of early successional species during the run.

The model tracks a continuum of subgrid-scale patches of different ages since disturbance. Each patch has its own plants and light and water conditions. Figure 2(b) depicts the dynamics of light availability for the shortest plants in the youngest and oldest patches within the grid cell. Figure 2(c) shows the dynamics of soil water availability in the youngest and oldest patches within the grid cell. For the end of the model run, Fig. 2(d) illustrates the biomass in patches as a function of patch age, and Fig. 2(e) depicts the frequency distribution of



patch ages. The youngest patches (most recently disturbed) tend to have the highest soil water availability and the greatest light availability near the ground because plant biomass is low in the youngest patches and there are no tall plants there. The subgrid-scale heterogeneity tracked by this model can be contrasted with the assumption of homogeneous conditions over this scale in other models.

Our work on the development of a new ecosystem model that is built around the general structure of the approximation described above is just beginning. We are not yet wedded to any particular submodels such as the physiology that determines plant performance, particular hydrological or land use models, nor any particular soil carbon and nutrient model. These will all have to be developed and added. The approximation that we have presented provides a template into which these details can be added and refined.

To develop an ecosystem model, we are drawing on other available submodels and data, while working on simplified descriptions of relevant details and processes. Our modelling of soil carbon and nutrient dynamics has already been advanced with a dramatically simplified understanding of the workings of the CENTURY model (Bolker *et al.* in press). Progress in plant physiology will allow us to refine formulations of plant growth and mortality as mechanistic functions of resource concentrations. A new remote sensing instrument SLICER should make measurements of the vertical structure of plant communities over large scales possible. The patch dynamics component of the model will rely heavily on disturbance, land use, and land use change data and model developments.

Discussion

Any evaluation of the currently available terrestrial models depends on one's goals or expectations. Available terrestrial models have proven instructive in many ways. Most importantly, they have taught us about the nature and potential importance of large scale biological feedbacks on climate. However, it would be unrealistic to expect that these models will ever be able to close the anthropogenic carbon budget directly. The uncertainties in the models are likely to remain far greater than what is needed for the foreseeable future. Closing the global carbon budget will have to rely on other methods.

As an alternative to other ongoing model development strategies, we advocate the development of new biological models that are relatively simple, formulated at an intermediate scale of biological detail, and used to make predictions at both larger and smaller scales. Model fitting could be used when necessary, overtly and with statistics, to calibrate these models with a small subset

of data. The testbed of these models will not be limited to data on the scale on which the models are formulated; it could be at both larger and smaller biological and spatio-temporal scales. Indeed, perhaps the most important testbed for relevant models in the future will not be at the global scale under current or modelled future conditions, but in relatively easily verifiable smaller scale predictions.

The approach that we have proposed meets several of the challenges discussed in this paper. Because the model scales, both its parameter values and predictions are easily observable. This should relieve some of the impetus for and concerns with model fitting. Because it is well suited to address issues of biodiversity and land use, while being driven by submodels of plant physiology, it can be mechanistic and equitable in detail. Because it is a good approximation to an underlying individual based model, we are in a position to capitalize on the successes of individual based models without the expense. It will be exciting to see how successful this approximation is for plant community models generally. Our challenge now is to keep the model simple and mechanistic with the additions of other crucial ecosystem model components, as this core develops into a complete ecosystem model.

Future terrestrial models may begin to emphasize some relatively underappreciated effects and make some novel predictions (novel at least for global models). For example, these new models may predict that most of the land surface is accumulating carbon at any given time (through succession) and losing it only catastrophically (through disturbance). Model predictions can be compared to the results of other approaches such as inversion studies that attempt to pinpoint the spatial and temporal distribution of carbon sources and sinks. Legitimate consideration of issues such as plant allocation, interspecific plant competition, finite plant dispersal, biodiversity, disturbance, land use, and other phenomena should help clarify whether models that use equilibrium assumptions are overly alarmist or overly reassuring. Addressing all of these issues with confidence will require simple mechanistic models that scale. Adopting a standard that model predictions be accompanied by quantitative measures of uncertainty would not only help to illustrate this point, but would be beneficial for both the users of these models and the science of improving them.

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