How close are we to a predictive science of the biosphere?

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In just 20 years, the field of biosphere-atmosphere interactions has gone from a nascent discipline to a central area of modern climate change research. The development of terrestrial biosphere models that predict the responses of ecosystems to climate and increasing CO₂ levels has highlighted several mechanisms by which changes in ecosystem composition and function might alter regional and global climate. However, results from empirical studies suggest that ecosystem responses can differ markedly from the predictions of terrestrial biosphere models. As I discuss here, the challenge now is to connect terrestrial biosphere models to empirical ecosystem measurements. Only by systematically evaluating the predictions of terrestrial biosphere models against suites of ecosystem observations and experiments measurements will a true predictive science of the biosphere be achieved.

Introduction

When the first issue of *TREE* was published in 1986, the study of biosphere–atmosphere interactions was still in its infancy. In 1975, Charney [1] used an analytical model of the interaction between the land-surface and the atmosphere to show how the high albedo (surface reflectance) of the land surface associated with the arid climate of the Sahara reinforces the lack of vegetation in the region. In 1982, Shukla and Mintz identified a second potential feedback mechanism that arises because plant evapotranspiration is a source of moisture for the atmosphere and, consequently, that vegetation affects precipitation and surface temperatures, particularly over continental regions [2].

This recognition of the importance of terrestrial ecosystems for climate led to the development of terrestrial biosphere models designed to capture the bidirectional interaction between vegetation and the atmosphere. Over the past two decades, results from increasingly sophisticated versions of these models (Box 1) have lead to remarkable progress in our understanding of how terrestrial ecosystems might feed back and affect regional and even global climate.

The field of biosphere-atmosphere interactions is dominated by the results of model simulations. There are, of course, good reasons for this: the effects of terrestrial ecosystems on the atmosphere occur at regional and global scales, and predicted changes in ecosystem composition, structure and function play out over decades and centuries, making direct experimentation impossible and empirical observation challenging. Thus, like many areas of climate change science, but unlike most areas of ecology, the understanding of biosphere–atmosphere interactions fundamentally relies on the predictions of large, complex models whose parameters are difficult to

Glossary

Atmospheric General Circulation Model (AGCM): a global-scale model of atmospheric dynamics.

Atmosphere–Ocean General Circulation Model (AOGCM): a global-scale model of atmospheric dynamics coupled to a global-scale model of ocean dynamics. Earth System Model (ESM): a DGVM that is bidirectionally coupled to an AOGCM.

Dynamic Global Vegetation Model (DGVM): a terrestrial biosphere model, which in addition to calculating the fast timescale exchanges of CO_2 , water and energy between the land-surface and the atmosphere, integrates the carbon fluxes into long-term changes in above- and belowground ecosystem structure and composition. They also track the fate of dead plant material entering the soil, and thus yield predictions for the fluxes of CO_2 to the atmosphere arising from the decomposition of plant material (Box 1).

Eddy flux towers: instrumented towers that provide nondestructive measurements of the net exchange of CO_2 , water vapor and other gases between an ecosystem and the atmosphere. The net exchange (vertical flux) is computed by instruments that measure simultaneously the three-dimensional motion of the wind and the concentration of the relevant gas above the top of the plant canopy. Fluxes are typically calculated at 30-min intervals or less, which are then summed to yield daily, monthly and annual estimates of carbon uptake and water loss.

Evapotranspiration: the sum of evaporation and transpiration. In terrestrial ecosystems, evaporation arises from the evaporation of moisture from the soil and from the evaporation of moisture on the surfaces of leaves in the canopy. Transpiration is the loss of water from plants, primarily by moisture lost through the stomata of the leaves. Water for transpiration is acquired by the plant's roots and transferred to the leaves by its vascular system. When converted into energy units, evapotranspiration represents the latent heat flux between the land surface and the atmosphere.

Offline model: a terrestrial biosphere model that is being forced with climatalogical observations rather than running interactively with an atmospheric model.

Online model: a terrestrial biosphere model that is running interactively with an atmospheric model.

Plant functional types: a functional rather than taxonomic classification of plant diversity based on physiological and morphological attributes, and used to represent different forms of vegetation within terrestrial biosphere models. Common characteristics used to subdivide plant species into functional groups include: photosynthetic pathway (e.g. C3 versus C4), leaf type (e.g. coniferous versus broad-leaved), leaf phenology (e.g. deciduous versus evergreen) and structural type (e.g. trees versus shrubs versus herbaceous vegetation).

Potential vegetation: vegetation that would exist in a region in the absence of humans.

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Stomatal conductance: a measure of the ease with which water vapor leaves and carbon dioxide flux enters through the stomata of a plant.

Top-down constraints: metrics of terrestrial biosphere model performance that assess their performance at large scales. Examples include regional- or global-scale estimates of CO_2 and water vapor exchange between terrestrial ecosystems and the atmosphere.

Box 1. Terrestrial biosphere models

The first generation of terrestrial biosphere models [18] consisted of a leaf photosynthesis scheme [74-78] that predicted leaf carbon assimilation and evapotranspiration rates as a function of climate, atmospheric CO2 concentrations, soil hydrological conditions, and leaf physiological traits and phenology (Figure I, blue boxes). Coupling this quantitative description to atmospheric models enabled a 'greening' of the formerly 'bare Earth' representation of the terrestrial land surface within AGCMs, and led to two important predictions regarding potential feedbacks between terrestrial ecosystems and the atmosphere: (i) increasing atmospheric CO2 levels enhance leaf photosynthetic rates, which, in the absence of any acclimatory response, would result in increased terrestrial carbon storage, giving rise to a negative terrestrial biogeochemical feedback that slows the rate at which CO₂ accumulates in the atmosphere and, as a result, the rate of CO2-induced warming; and (ii) the enhancement of leaf photosynthetic rates would be accompanied by a CO₂-induced decline in stomatal conductance, which could decrease the magnitude of the



Figure I.

measure, and that make predictions at scales far larger than we are typically able to make measurements. As a result, the findings of terrestrial biosphere modeling studies are usually appropriately couched in terms of 'potential feedback mechanisms' [3–5]. Indeed, a harsh, but not entirely unwarranted, view would be that our current understanding of biosphere–atmosphere feedbacks is a collection of interesting, but largely untested, hypotheses for the future state of terrestrial ecosystems and climate.

For both scientific and policy reasons, there is urgent need to move beyond discussion of 'potential feedback mechanisms' to a more rigorous assessment of the long-term biosphere-atmosphere feedbacks expected to result from human activities over the next century. How might this be achieved? After describing some of the principal feedback mechanisms identified over the past 20 years, I review here two key findings of empirical ecosystem studies that have important implications for the expected magnitude of terrestrial ecosystem feedbacks onto the atmosphere. I then propose a framework for achieving a more predictive science of the biosphere.

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evapotranspiration feedback, increasing the rate of surface warming, particularly in areas such as Amazonia [18]. The dashed arrows on the left-hand side of Figure I indicate the feedbacks between terrestrial ecosystems and the atmosphere captured in these models.

It was soon recognized that leaf-level physiological responses to near-term atmospheric conditions were likely to be just the beginning of the response of the terrestrial biosphere to changing climate and increasing atmospheric CO₂. Over long timescales, the fast-timescale physiological responses of vegetation to changes in the environment would ultimately translate into longer term changes in ecosystem structure, composition and function. This led to calls for consideration of not only fast-timescale physiological responses of plants to changes in environmental conditions, but also long-term ecological dynamics [73].

In the subsequent DGVM generation of terrestrial biosphere models, the original photosynthesis scheme (Figure I, blue boxes) was used as a driver for terrestrial ecosystem models, which integrate short-term carbon fluxes into long-term changes in above- and belowground ecosystem structure and composition (Figure I, green boxes). Initially developed as 'offline' models' [41,79], coupled descendents soon followed [65,66].

As seen in the Hadley Centre simulation, in contrast to the earlier terrestrial biosphere models that had static patterns of vegetation [18], this new generation of coupled DGVMs makes predictions for the long-term consequences of ecosystem-atmosphere interactions, including long-term biophysical feedbacks arising from changes in ecosystem structure and composition, and the long-term biogeochemical CO2 feedback mechanisms by which decadal-centennial-scale changes in above- and belowground terrestrial carbon stocks influence atmospheric CO2 concentrations (Figure 1, main text). These include the negative biogeochemical feedback that arises if CO2-induced photosynthetic enhancement occurs, and the positive feedback arising from the effects of increased temperature on rates of carbon decomposition and the subsequent release of CO2 into the atmosphere (Figure I, dashed arrow on right-hand side). There are also several more complex terms, whose sign and magnitude depend on how changes in climate and CO2 give rise to changes in aboveground ecosystem composition (Figure 1b, main text), alter plant-canopy phenology, and alter rates of belowground decomposition as a result of changes in soil moisture.

From potential feedback mechanisms to a predictive science of the biosphere

A recent landmark study by the UK Hadley Centre^{*} coupled one of the latest generation of terrestrial biosphere models - a dynamic global vegetation model (DGVM; see Glossary) - to a coupled Atmosphere-Ocean General Circulation Model (AOGCM), forming the first 'Earth system model' [3,6]. This model was then used to examine the role of terrestrial biosphere feedbacks in the climatological response to continuing anthropogenic CO_2 emissions [3,6]. Simulations for the period 1860–2100, in which the atmosphere is forced (driven) with a standard CO_2 emissions scenario, indicate that terrestrial ecosystems will initially take up a significant fraction of the excess anthropogenic carbon, thereby slowing the rate at which CO_2 builds up in the atmosphere (Figure 1a). This occurs primarily as a result of a CO₂-induced enhancement of plant growth (Box 1). However, from 2010 onward, the rate of terrestrial carbon accumulation slows and, by 2050, the land surface becomes a net source of CO_2 to the atmosphere (Figure 1a). Two main feedbacks are responsible for this carbon loss: a collapse of the Amazon forests

^{*} http://www.metoffice.com/research/hadleycentre/

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Figure 1. Ecosystem-atmosphere feedbacks in the climatological response to continuing global anthropogenic CO_2 emissions predicted by the Hadley Centre simulation [3,6]. (a) Cumulative carbon budget during the fully coupled simulation. The thick line shows the simulated cumulative increase in atmospheric CO_2 concentrations; the thinner lines show the cumulative contributions of emissions, land fluxes and ocean fluxes to the pattern of atmospheric CO_2 build-up, with negative slopes implying CO_2 uptake. The terrestrial biosphere takes up CO_2 at a decreasing rate from ~2010 onwards, becoming a net source by ~2050. By 2100, this source almost balances the oceanic sink, so that atmospheric carbon content is increasing at a similar rate as the integrated emissions. Changes in vegetation carbon (b), and soil carbon (c), in units of kg C m⁻², that occur by the end of the simulation, indicating the collapse of the Amazon forests and large-scale losses of soil carbon worldwide. Reproduced with permission from [3,6].

in response to surface warming, resulting from a CO_2 induced decline in evapotranspiration rates over the Amazon Basin (Figure 1b), and a global loss of soil carbon owing to increased soil temperatures (Figure 1c). The combined effect of these feedbacks is a substantial increase in the rate of CO_2 build-up in the atmosphere. By 2100, CO_2 concentrations are 33% higher and mean temperatures over the land surface 2°C higher than in the absence of the vegetation-atmosphere interaction [3,6].

The existence of a regional-scale evapotranspiration feedback over Amazonia had been implied from early biosphere-atmosphere studies that explored the potential effects of deforestation on Amazonian climate by changing the lower boundary conditions for the atmosphere over continents within Atmospheric General Circulation Models (AGCMs). Results from these earlier analyses indicated that a significant fraction of the moisture for precipitation comes from evapotranspiration across the basin and, as a result, changing the land surface from forest to grassland causes significant increases in surface temperatures of 2–5°C, and up to a 30% decrease in annual rainfall over the basin [7,8].

Interestingly, in the Hadley Centre simulation, the transition of Amazonia from tropical forest to grassland does not arise as a result of imposed deforestation, but as a result of a CO_2 -induced decline in evapotranspiration rates that shuts off a key source of moisture for precipitation over the region. This causes a climatologically driven dynamical change in ecosystem composition from forest to tropical

grassland. The physiological response mechanism that initiates this feedback had been previously identified in an earlier coupled terrestrial biosphere model that had predicted leaf-level physiological responses of plants to climate and CO_2 (Box 1). What was new in the Hadley Centre simulation was the embedding of these physiological responses into a DGVM, in which short-term leaf-level physiological responses to environmental conditions can translate into long-term changes in ecosystem structure and composition (Box 1). DGVMs also track the fate of dead plant material entering the soil, thereby incorporating the biogeochemical feedback that arises from changes in soil temperature and moisture altering rates of soil decomposition and the resulting fluxes of CO_2 to the atmosphere (Box 1).

Contemplating the future

Just how seriously should we take the results of the Hadley Centre simulation? Is the Amazon forest really going to collapse by 2050 if CO_2 emissions continue and increasing temperatures cause a widespread loss of soil carbon in the manner predicted? The answer, of course, depends on our confidence in the abilities of coupled DGVMs to simulate accurately the dynamics of the interaction between the climate and terrestrial ecosystems. That is, how many of the potential feedback mechanisms identified by biosphere–atmosphere modeling studies [3–5,9–11] will be realized over the coming decades? Here, I review two key findings from empirical



Figure 2. Comparison of annual woody carbon increment observed in a young loblolly *Pinus taeda* plantation at Duke Forest, North Carolina USA, under elevated atmospheric CO₂ concentrations initiated in 1994 and ambient CO₂ concentrations, in the absence of nutrient addition. The figure shows a plot-level comparison between the free-air CO₂ enrichment prototype (FACEP; green dots) and a nearby untreated, ambient CO₂ plot (open dots). In 1999, the number of untreated plots increased to five. Data for 1993 are the mean carbon increment during the first ten years of the life of the stand prior to CO₂ treatment (open bar, ambient CO₂; green bar, elevated CO₂). Redrawn with permission from [20].

observations, which imply that terrestrial ecosystem responses to climate and CO_2 will be considerably different from current terrestrial biosphere model predictions.

Plant acclimation

The plant functional types represented within coupled DGVMs have fixed traits, such as their maximum photosynthetic rate and their patterns of carbon allocation between leaves, stem and root tissues. By contrast, empirical studies of terrestrial ecosystem responses to climate change have documented widespread evidence of plant acclimation to elevated levels of CO_2 [12–14]. In particular, field-based CO_2 enrichment studies in temperate forests indicate that, although leaf-level photosynthetic rates appear to increase when CO_2 concentrations are increased, there is little or no increase in net carbon storage in the absence of high levels of nitrogen fertilization (Figure 2) [14,20,22].

These observations have important implications for the magnitude of the biophysical and biogeochemical terrestrial feedbacks expected to occur in response to climate and increasing levels of atmospheric CO_2 [15–17]. If widespread acclimation occurs as suggested by the above observations, this will decrease the negative biogeochemical CO_2 feedback that is a significant feature in current terrestrial biosphere model predictions, including the Hadley Centre simulation (Figures 1, 3), causing levels of atmospheric CO_2 to increase at a faster rate than is currently predicted.

Interestingly, the observed plant acclimation responses do not appear to be resulting from a leaf-level downregulation of photosynthesis as originally conceived in early modeling studies of the response of the terrestrial biosphere to increasing CO_2 [18]. Instead, acclimation is arising from plant-level shifts in patterns of carbon allocation toward increased allocation to pools that have high rates of turnover, such as fine-roots, seed production



Figure 3. Comparison of the predicted effects of anthropogenic carbon emissions on global carbon fluxes (a) and global mean temperature (b) predicted by the Hadley Centre (red line) [3] and IPSL (blue line) [5] coupled ('online') terrestrial biosphere models. (a) In both simulations, the terrestrial biosphere acts initially as net carbon sink, taking carbon out of the atmosphere. However, by ~2050, the terrestrial biosphere switches from being a net carbon sink to a net carbon source in the Hadley Centre simulation, whereas the terrestrial biosphere remains a net carbon sink in the IPSL simulation. (b) Changes in global mean temperature in the Hadley Centre and IPSL simulations. The diverging temperature trajectories in the two simulations are primarily due to the different patterns of terrestrial carbon fluxes plotted in (a), indicating that terrestrial ecosystem feedbacks are among the largest sources of uncertainty for predicting future climate [33]. Reproduced with permission from [3,5].

and non-structural carbohydrates [13-14,19-21]. This difference in mechanism has important consequences, because the absence of increased CO₂ uptake will not be accompanied by the larger decrease in the biophysical evapotranspiration feedback that would occur as a result of leaf-level acclimation [18].

Going underground

A significant component of the biogeochemical CO_2 feedback that occurs in the Hadley Centre study arises from a temperature-driven release of soil carbon to the atmosphere, highlighting the need for an improved understanding of the long-term responses of belowground ecosystems to climate change. Recent empirical analyses emphasize the importance of explicitly separating those soil carbon pools with fast intrinsic rates of turnover from more recalcitrant pools [17,22,23], particularly in boreal regions [24]. There is also continuing debate regarding the sensitivity of belowground decomposition to changes in soil temperature and moisture, because these have a dominant role in determining the amount of carbon stored in belowground ecosystems worldwide and, thus, the magnitude of the biogeochemical CO_2 feedback that arises from climate changes [17,24–28].

Current parameterizations of the temperature and moisture dependencies of decomposition within coupled DGVMs are derived from empirical measurements of daily-yearly variability in belowground respiration rates (e.g. [25–27]). The ability of these parameterizations to characterize correctly the response of belowground ecosystems to more secular changes in environmental conditions over decadal and century timescales is, however, largely unknown. Results from at least some soil-warming and soil transplantation experiments suggest that, similar to the plant communities above them, belowground communities are likely to adjust to longer term changes in soil temperature and moisture regimes through a combination of physiological adaptation and longer term compositional changes in the belowground flora and fauna [16,17,25,29].

The advent of new molecular techniques for quantifying the distribution and abundance of soil microorganisms promises to enable the replacement of the current 'blackbox' biogeochemical decomposition models with dynamical models that predict compositional changes in belowground communities in response to climate change, and the resulting effects on soil carbon stocks and fluxes [30]. The observed importance of nitrogen in limiting plant responses to increasing CO_2 levels and the significant additions of nitrogen into terrestrial ecosystems by humans also emphasize the need to develop global-scale models of soil nitrogen dynamics [15,17].

Achieving a predictive science of the biosphere

The current disconnect between terrestrial biosphere models and measurements of ecosystem responses to changes in climate and CO_2 presents a real challenge to moving beyond discussion of 'potential feedback mechanisms' and achieving a more predictive science of the biosphere. Drawing upon several recent developments, I propose a way to bridge this gap.

Model testing and parameterization

The difficulties of evaluating the dynamics of terrestrial biosphere models at their global decadal-century scales of prediction argues strongly for engaging rigorous testing at the spatial and temporal scales at which the models can be compared with observations. Common criteria currently used to assess the predictive abilities of terrestrial biosphere models include the capacity to reproduce patterns of 'potential' (i.e. inferred pre-human settlement) vegetation and seasonal-interannual patterns of carbon fluxes in and out of the terrestrial biosphere inferred from CO₂ measurements at flask monitoring stations. However, as results from 'off-line' model intercomparisons and 'online' model intercomparisons indicate [31-33], although most models can replicate inferred patterns of potential vegetation and seasonal to interannual patterns of productivity, they diverge from each other significantly in their predictions of ecosystem composition, structure and functioning under novel climates (Figure 3). This implies that, although relevant, these criteria are insufficient constraints for developing robust predictions for the long-term coupled dynamics of the biosphere and atmosphere and, thus, a more rigorous terrestrial biosphere model evaluation framework is needed.

A useful blueprint for such a framework is the approach used to assess climate and weather forecasting models, in which models are assigned 'skill-scores' based on their ability to predict a variety of relevant metrics of model performance, such as observed patterns of interannual variability in the strength of the Asian monsoon [34–36]. Adopting such an evaluation framework for terrestrial biosphere models accords with the growing calls for ecologists to engage in ecological forecasting [37].

The evaluation framework needs to be designed explicitly to encompass the range of spatial and temporal scales at which observations of terrestrial ecosystem dynamics are made. The global eddy-flux tower network[†] provides site-level measurements of CO2 and evapotranspiration fluxes in different ecosystems that can be used to test the hourly-yearly dynamics of carbon, water and energy exchange between plant canopies and the atmosphere [38]; satellite measurements provide information about seasonal-interannual patterns of global leaf cover [39]; tall towers, aircraft measurements and the global CO2 flask monitoring network provide additional 'topdown' constraints on the large-scale carbon fluxes between terrestrial ecosystems and the atmosphere [40]; river gauge networks can be used to constrain regional-scale hydrological budgets [36,41]; regional plot-based forest inventories yield information about yearly-decadal vegetation dynamics [42]; and paleobotanical studies yield insight into changes in large-scale ecosystem composition in relation to past climatic events [43]. The large number of unconstrained parameters in terrestrial biosphere models means that a similar cross-scale approach will also be vital for adequate model calibration.

Subgrid scale heterogeneity:

Connecting the current generation of coupled DGVMs to a broader array of observations of ecosystem composition, structure and function places new emphasis on the ability to scale accurately between the smaller spatial and temporal scales at which most ecosystem measurements are made, and the global, decadal-century scales of prediction and inference. The conventional approach to scaling has been a simple 'canopy as big-leaf' scaling, in which the response of the different plant functional types within each climatological grid cell (typically between 10⁴ and 10^5 km^2) is assumed to be that of a single plant writ large experiencing spatially averaged resource conditions [44]. The improvements in weather forecasting that have followed the incorporation of static vegetation 'big-leaf' models into numerical weather forecasting models [45,46] imply that the 'canopy as big-leaf' simplification is not unreasonable when predicting the short-term dynamics of the biosphere-atmosphere interaction[‡]. However, the 'big-

[†] http://www.fluxnet.ornl.gov/fluxnet/index.cfm

[‡] An important exception might be biosphere–atmosphere feedbacks in Amazonia. High-resolution atmospheric modeling studies suggest that sub-grid-scale landsurface heterogeneities arising from the contrasting biophysical properties of forest and agricultural areas being created by deforestation is affecting convective cloud formation, altering the spatial distribution and reducing the total amount of precipitation that falls over the region [73].

leaf' approach poses serious difficulties when predicting long-term biosphere–atmosphere dynamics.

From a theoretical perspective, the spatially localized nature of plant competition for resources, combined with the nonlinear nature of plant growth, mortality and recruitment (the processes that drive long-term changes in vegetation structure and composition) means that knowing the dynamics of an average plant sitting in an average environment is insufficient information for predicting the long-term mean dynamics of heterogeneous plant canopy [47]. A telling manifestation of this is the canopy composition that arises in coupled 'big-leaf' DGVMs. As would be expected from the competitive exclusion principle [48], the single, spatially averaged resource conditions represented within each grid cell of 'big-leaf' dynamic vegetation models naturally tend to yield ecosystems comprised of single plant functional types. This lack of functional diversity is troubling given the large number of empirical and theoretical studies that indicate that functional diversity is a key component of ecosystem resilience to environmental perturbation [49–51], and bears directly on the predictions of the coupled modeling studies: for example, is the collapse of the Amazon forest that occurs in the Hadley Centre model simulations (Figure 1) a robust prediction, or simply an artifact of there being a single type of tropical forest tree across the entire region?

Incorporating abiotic heterogeneities, such as soil type, slope and aspect, into terrestrial biosphere models is relatively straightforward because, over the relevant timescales, these forms of heterogeneity are static, and thus can be represented by subdividing grid cells into fixed fractional areas corresponding to the different landscape types (e.g. [52]). However, incorporating biotic forms of heterogeneity, arising from disturbance processes such as wind-throw, fire and human land-use practices, is more challenging, because these forms of heterogeneity are dynamic in nature over the decadal-century timescales over which anthropogenic climate change is occurring.

Recent work has shown that subgrid scale heterogeneity can be incorporated by developing structured ecosystem models (SEMs) [53-55] that draw upon techniques developed in the ecological literature to account for dynamics of heterogeneous populations [56-58]. This SEM-based approach is currently being implemented in several new earth system models. In contrast to traditional 'big leaf' formulations, SEMs formally scale from individual-level plant dynamics [59-64] to the long-term, large-scale dynamics of ecosystems accounting for the effects of subgrid scale heterogeneity on plant growth, mortality and recruitment dynamics that are crucial for the formation and maintenance of functionally diverse ecosystems [53-55]. Moreover, because their underlying formulation is not at the scale of climatological grid cells, but rather at the scale of individual plants, SEMs facilitate the parameterization and testing of terrestrial biosphere against empirical observations of ecosystem composition structure and function that are collected at scales smaller than the grid-cell scale at which the current 'big-leaf' model formulations are defined.

Plant functional diversity

A key component of any coupled terrestrial biosphere model is its representation of plant functional diversity. In current 'big-leaf' model formulations, the number of plant functional types is small (typically between five and 15 plant functional types for the entire globe). As a result of this, and the absence of subgrid heterogeneity described earlier, biomes comprise single plant functional types [3,65,66].

Recent empirical analyses have begun to quantify dominant axes of global-scale diversity in plant functional traits, including maximum photosynthetic rates, leaf longevities and foliar nitrogen concentrations [67,68]), and large-scale correlates of tree growth and mortality rates that are a major determinant of aboveground carbon storage [69–72]. Interestingly, whereas some of the variability is linked to biome-scale differences in climate, substantial amounts of trait variability occur within biomes and single environments, again re-emphasizing the need for terrestrial biosphere models to embrace subgrid scale ecosystem heterogeneity that is crucial for the formation and maintenance of functionally diverse ecosystems. This is also likely to be an important additional source of ecosystem resilience to environmental change.

Conclusions

The development of DGVMs that make predictions for the short- and long-term responses of ecosystems to climate and increasing CO_2 levels has been a major milestone towards a developing predictive science of the biosphere [73]. These models have identified several key mechanisms by which changes in ecosystem composition, structure and function can influence regional and global climates: however, the significance of their predictions remains uncertain.

Over the same 20-year period, empirical measurements indicate that ecosystem responses to changes in climate and CO₂ concentrations are considerably different from the responses predicted by current terrestrial biosphere models. In particular, there is increasing evidence that, in both above- and belowground communities, physiological adaptation and changes in ecosystem composition are likely to act as sources of ecosystem resilience over some envelope of changing climate and atmospheric CO2 concentrations. The widespread evidence of whole-plant level acclimation responses to elevated CO₂ is a key component of this because it implies that a previously assumed negative biogeochemical feedback of terrestrial ecosystems to the rate of atmospheric CO_2 increase is not occurring and, as a result, the rate of at which CO_2 will accumulate in the atmosphere over the coming century will be larger than expected.

Two further key issues that have emerged from empirical and theoretical studies are the extent to which belowground acclimation and compositional change will alter the temperature and moisture dependencies of decomposition over decadal-centennial timescales, and the significance of subgrid-scale ecosystem heterogeneity and plant diversity when predicting long-term vegetation dynamics and assessing ecosystem resilience to climatological perturbation. Implementing a framework for parameterizing and, above all, testing coupled DGVMs against multiple data sources spanning the range of spatial and temporal scales at which terrestrial ecosystem observations are made will provide much-needed empirical evaluation of the ways in which long-term changes in terrestrial ecosystems might occur, and feed back to the atmosphere over the coming decades. Only by connecting the predictions of terrestrial biosphere models to a broad array of observational constraints collected over the past two decades will our goal of a true 'predictive science of the biosphere' [72] be fulfilled.

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References

- 1 Charney, J.G. (1975) Dynamics of deserts and droughts in the Sahel. Q. J. R. Meteorol. Soc. 101, 193–202
- 2 Shukla, J. and Mintz, Y. (1982) Influence of land-surface evapotranspiration on the Earth's climate. *Science* 215, 498–1501
- 3 Cox, P.M. et al. (2000) Acceleration of global warming due to carboncycle feedbacks in a coupled climate model. *Nature* 408, 184–187
- 4 Levis, S. et al. (1999) Potential high-latitude vegetation feedbacks on CO₂-induced climate change. Geophys. Res. Lett. 26, 747–750
- 5 Friedlingstein, P. et al. (2003) How positive is the feedback between climate change and the carbon cycle? Tellus 55B, 692-700
- 6 Cox, P.M. et al. (2001) Modeling vegetation and the carbon cycle as interactive elements of the climate system. Hadley Cent. Tech. Notes 23, 1–28
- 7 Lean, J. and Warrilow, D.A. (1989) Simulation of the regional climatic impact of Amazon deforestation. *Nature* 342, 411–413
- 8 Shukla, J. et al. (1990) Amazon deforestation and climate change. Science 247, 1322–1325
- 9 Wang, G. and Eltahir, E.B. (2000) Biosphere atmosphere interactions over West Africa. II: multiple climate equilibria. Q. J. R. Meteorol. Soc. 126, 1261–1280
- 10 Claussen, M. (1998) On multiple solutions of the atmospherevegetation system in present-day climate. *Glob. Change Biol.* 4, 549–559
- 11 Foley, J.A. et al. (2003) Regime shifts in the Sahara and Sahel: interactions between ecological and climatic systems in Northern Africa. Ecosystems 6, 524–539
- 12 Ainsworth, E.A. and Long, S.P. (2005) What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2 . New Phytol. 165, 351–372
- 13 Korner, C. (2003) Ecological impacts of atmospheric CO₂ enrichment on terrestrial ecosystems. *Phil. Trans. R. Soc. B* 361, 2023–2041
- 14 Korner, C. et al. (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO₂. Science 309, 1360–1362
- 15 Hungate, B.A. et al. (2003) Nitrogen and climate change. Science 302, 1512–1513
- 16 Hanson, P.J. *et al.* (2005) Importance of changing CO_2 , temperature, precipitation and ozone on carbon and water cycles of an upland-oak forest: incorporating experimental results into model simulations. *Glob. Change Biol.* 11, 1402–1423
- 17 Melillo, J.M. et al. (2002) Soil warming and carbon cycle feedbacks to the climate system. Science 298, 2173–2176
- 18 Sellers, P.J. et al. (1996) Comparison of radiative and physiological effects of doubled atmospheric CO₂ on climate. Science 271, 1402–1406

- 19 LaDeau, S. and Clark, J. (2001) Rising $\rm CO_2$ levels and the fecundity of forest trees. Science 292, 95–98
- 20 Oren, R. et al. (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO_2 enriched atmosphere. Nature 411, 469–472
- 21 Norby, R.J. et al. (2004) Fine-root production dominates response of a deciduous forest to atmospheric CO2 enrichment. Proc. Natl. Acad. Sci. U. S. A. 101, 9689–9693
- 22 Davidson, E.A. et al. (2000) Soil warming and organic carbon content. Nature 408, 789–790
- 23 Gu, L. et al. (2004) Fast labile carbon turnover obscures sensitivity of heterotrophic respiration from soil to temperature: a model analysis. Glob. Biogeochem. Cycles 18, 1022–1032
- 24 Eliasson, P.E. et al. (2005) The response of heterotrophic CO_2 flux to soil warming. Glob. Change Biol. 11, 167–181
- 25 Giardina, C.P. and Ryan, M.G. (2000) Evidence that decomposition rates of organic carbon in mineral soil does not vary with temperature. *Nature* 404, 858–861
- 26 Knorr, W. et al. (2005) Long-term sensitivity of soil carbon turnover to warming. Nature 433, 298–301
- 27 Fang, C. et al. (2005) Similar response of labile and resistant soil organic matter pools to changes in temperature. Nature 433, 57–59
- 28 Fung, I. et al. (2005) Evolution of carbon sinks in a changing climate. Proc. Natl. Acad. Sci. U. S. A. 102, 11201–11206
- 29 Wardle, D.A. (2002) Communities and Ecosystems: Linking the Aboveground and Belowground Components, Princeton University Press
- 30 Fontaine, S. and Barot, S. (2005) Size and functional diversity of microbe populations control plant persistence and long-term soil carbon accumulation. *Ecol. Lett.* 8, 1075–1087
- 31 VEMAP Members Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO2 doubling. *Glob. Biogeochem. Cycles* **9**, 407–437
- 32 Cramer, W. et al. (2001) Global response of terrestrial ecosystem structure and function to CO2 and climate change: results from six dynamic global vegetation models. *Glob. Change Biol.* 7, 357–373
- 33 Dufresne, J.L. (2002) On the magnitude of positive feedback between future climate change and the carbon cycle. *Geophys. Res. Lett.* 29, 43-1-43-4
- 34 Williamson, D.L. (1995) Skill scores from the AMIP Simulations. In Proceedings of the AMIP Scientific Conference (Gates, W.L., ed.), pp. 253–258, World Climate Research Program
- 35 Sperber, K.R. and Participating, A.M.I.P. (1999) Modelling Groups Are revised models better models? A skill score assessment of regional interannual variability. *Geophys. Res. Lett.* 26, 1267–1270
- 36 Milly, P.D. et al. (2005) Global pattern of trends in streamflow and water availability in a changing climate. Nature 348, 347–350
- 37 Clark, J.S. et al. (2001) Ecological forecasts: an emerging imperative. Science 293, 657–660
- 38 Baldocchi, D. et al. (2001) FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. Bull. Am. Meteorol. Soc. 82, 2415–2434
- 39 Kerr, J.T. and Ostrovsky, M. (2003) From space to species: ecological applications for remote sensing. *Trends Ecol. Evol.* 18, 299–305
- 40 Bakwin, P.S. et al. (2004) Regional carbon dioxide fluxes from mixing ratio data. Tellus 56, 301
- 41 Foley, J.A. et al. (1996) An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. Glob. Biogeochem. Cycles 10, 603–628
- 42 Caspersen, J.P. et al. (2000) Contributions of land-use history to carbon accumulation in U.S. forests. Science 290, 1148–1151
- 43 Prentice, I.C. and Webb, T., III. (1998) Biome 6000: reconstructing global mid-Holocene vegetation patterns from paleoecological records. J. Biogeogr. 25, 997–1005
- 44 Moorcroft, P.R. (2003) Recent advances in ecosystem-atmosphere interactions: an ecological perspective. Proc. R. Soc. B 270, 1215–1227
- 45 Betts, A.K. et al. (1993) Comparison between the land surface response of the ECMWF model and the FIFE 1987 data. Q. J. R. Meteorol. Soc. 119, 975–1001
- 46 Xue, Y. et al. (1996) Impact of vegetation properties on U.S. summer weather prediction. J. Geophys. Res. 101, 7419–7430
- 47 Levin, S.A. et al. (1997) Mathematical and computational challenges in population biology and ecosystems science. Science 275, 334–343

- 48 Gause, G.F. (1934) The Struggle for Existence, Williams & Wilkins
- 49 Tilman, D. et al. (1997) The influence of functional diversity and composition on ecosystem processes. Science 277, 1300–1302
- 50 Moore, P.D. (2005) Roots of stability. Nature 437, 959–961
- 51 Loreau, M. et al. (2002) Biodiversity and Ecosystem Functioning, Oxford University Press
- 52 Vertenstein, M. et al. (2004) Community Land Model Version 3.0 (CLM3.0) User's Guide, National Center for Atmospheric Research, Boulder, USA
- 53 Moorcroft, P.R. *et al.* (2001) A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecol. Monogr.* 74, 557–586
- 54 Hurtt, G.C. et al. (2002) Projecting the future of the US carbon sink. Proc. Natl. Acad. Sci. U. S. A. 99, 1389–1394
- 55 Pacala, S.W. et al. (2001) Carbon storage in the US caused by land-use change. In Present & Future Modeling of Global Environmental Change (Matsumo, T., ed.), pp. 145–172, Terra Publications
- 56 von Foerster, H. (1959) Some remarks on changing populations. In *The Kinematics of Cellular Proliferation* (Stohlman, F., Jr., ed.), pp. 382–407, Grune and Stratton
- 57 Clark, J.S. (1993) Shifting mosaic population dynamics. In *Patch Dynamics* (Levin, S. *et al.*, eds), pp. 224–246, Springer Verlag
- 58 Clark, J.S. and Ji, Y. (1995) Fecundity and dispersal in plant populations: implications for structure and diversity. Am. Nat. 146, 72-111
- 59 Botkin, et al. (1972) Some ecological consequences of a computer model of plant growth. Ecology 60, 849–873
- 60 Shugart, H.H. and West, D.C. (1977) Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. J. Env. Manage. 5, 161–179
- 61 Shugart, H.H. (1990) Using ecosystem models to assess potential consequences of global climatic change. Trends Ecol. Evol. 5, 303–307
- 62 Pacala, S.W. et al. (1996) Forest models defined by field measurements: estimation error analysis and dynamics. Ecol. Monogr. 66, 1–43
- 63 Bugmann, H.K.M. (1996) A simplified forest model to study species composition along climate gradients. *Ecology* 77, 2055–2074
- 64 Friend, A.D. and White, A. (2000) Evaluation and analysis of a dynamic terrestrial ecosystem model under preindustrial conditions at the global scale. *Glob. Biogeochem. Cycles* 14, 1173–1190

- 65 Foley, J.A. et al. (1998) Coupling dynamic models of climate and vegetation. Glob. Change Biol. 4, 561–579
- 66 Bonan, G.B. *et al.* (2003) A dynamic global vegetation model for use with climate models: concepts and description of simulated vegetation dynamics. *Glob. Change Biol.* 9, 1543–1566
- 67 Reich, P.B. et al. (1997) From tropics to tundra: global convergence in plant functioning. Proc. Natl. Acad. Sci. U. S. A. 94, 13730–13734
- 68 Wright, I.J. et al. (2004) The worldwide leaf economics spectrum. Nature 428, 821–827
- 69 Muller-Landau, H.C. (2004) Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* 36, 20–32
- 70 Malhi, Y. et al. (2004) The above-ground coarse wood productivity of 104 neotropical forest plots. Glob. Change Biol. 10, 563–591
- 71 Sugden, A.M. (1992) Using biotic interactions to forecast the consequences of global climate change. *Trends Ecol. Evol.* 7, 35–36
- 72 King, D.A. et al. (2006) The role of wood density an dstem support costs in the growth and mortality of tropical trees. J. Ecol. 94, 670–680
- 73 Baidya-Roy, S. and Avissar R. (2002) Impact of land use/land cover change of regional hydrometeorology in Amazonia. J. Geophys. Res. 107, LBA 4-1 – LBA 4–12
- 74 Farquhar, G.D. and Sharkey, T.D. (1982) Stomatal conductance and photosynthesis. Annu. Rev. Plant Physiol. 33, 317–345
- 75 Ball, J.T. et al. (1986) A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In Progress in Photosynthesis Research (Biggins, J., ed.), pp. 221–225, Nijhoff
- 76 Collatz, G.J. et al. (1991) Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. Agri. For. Meteorol. 54, 107–136
- 77 Collatz, G.J. et al. (1992) Coupled photosynthesis stomatal conductance model for leaves of C4 plants. Aust. J. Plant Physiol. 19, 519–538
- 78 Woodward, F.I. (1990) From ecosystems to genes: the importance of shade tolerance. *Trends Ecol. Evol.* 5, 111–115
- 79 Haxeltine, A. and Prentice, I.C. (1996) BIOME3: An equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. *Glob. Biogeochem. Cycles* 10, 693–709

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