

# 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 CO<sub>2</sub> 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 led 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<sub>2</sub>, 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<sub>2</sub> 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<sub>2</sub>, 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 climatological 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.

**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<sub>2</sub> and water vapor exchange between terrestrial ecosystems and the atmosphere.

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### 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 CO<sub>2</sub> concentrations, soil hydrological conditions, and leaf physiological traits and phenology (Figure 1, 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 CO<sub>2</sub> 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 CO<sub>2</sub> accumulates in the atmosphere and, as a result, the rate of CO<sub>2</sub>-induced warming; and (ii) the enhancement of leaf photosynthetic rates would be accompanied by a CO<sub>2</sub>-induced decline in stomatal conductance, which could decrease the magnitude of the

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 1 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 CO<sub>2</sub>. 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 1, 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 1, green boxes). Initially developed as ‘offline’ models [41,79], coupled descendants 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 CO<sub>2</sub> feedback mechanisms by which decadal–centennial-scale changes in above- and belowground terrestrial carbon stocks influence atmospheric CO<sub>2</sub> concentrations (Figure 1, main text). These include the negative biogeochemical feedback that arises if CO<sub>2</sub>-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 CO<sub>2</sub> into the atmosphere (Figure 1, dashed arrow on right-hand side). There are also several more complex terms, whose sign and magnitude depend on how changes in climate and CO<sub>2</sub> 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.

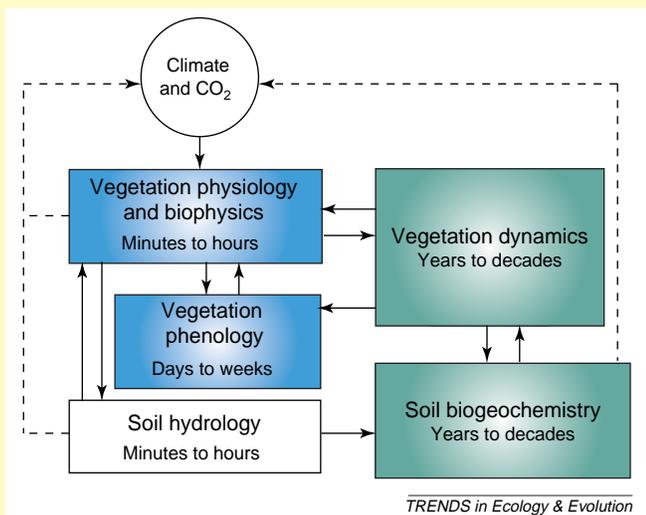


Figure 1.

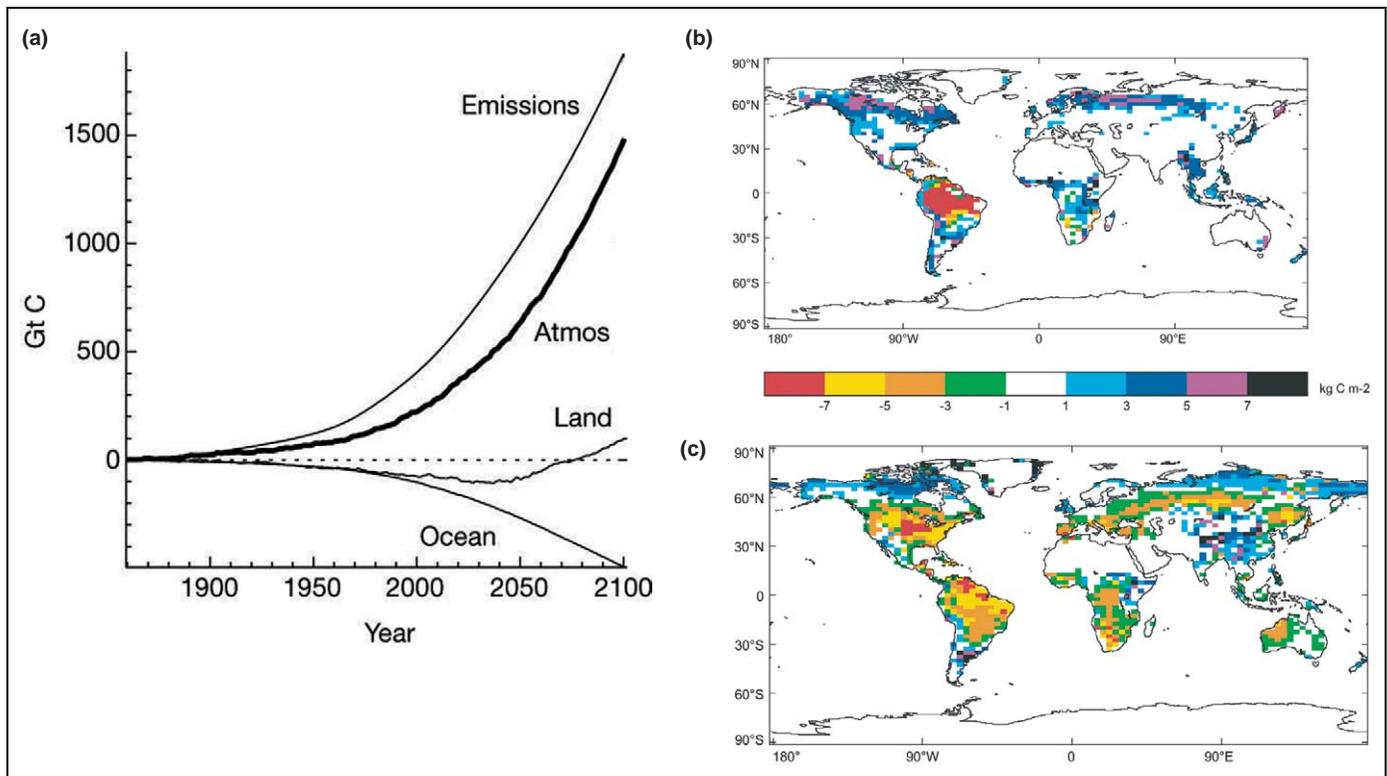
measure, and that make predictions at scales far larger than we are typically able to make measurements. As a result, the findings of terrestrial biosphere modeling studies are usually appropriately couched in terms of ‘potential feedback mechanisms’ [3–5]. Indeed, a harsh, but not entirely unwarranted, 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.

### 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<sub>2</sub> emissions [3,6]. Simulations for the period 1860–2100, in which the atmosphere is forced (driven) with a standard CO<sub>2</sub> 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<sub>2</sub> builds up in the atmosphere (Figure 1a). This occurs primarily as a result of a CO<sub>2</sub>-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<sub>2</sub> 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/>



**Figure 1.** Ecosystem–atmosphere feedbacks in the climatological response to continuing global anthropogenic CO<sub>2</sub> 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<sub>2</sub> concentrations; the thinner lines show the cumulative contributions of emissions, land fluxes and ocean fluxes to the pattern of atmospheric CO<sub>2</sub> build-up, with negative slopes implying CO<sub>2</sub> uptake. The terrestrial biosphere takes up CO<sub>2</sub> 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<sup>-2</sup>, 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<sub>2</sub>-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<sub>2</sub> build-up in the atmosphere. By 2100, CO<sub>2</sub> 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].

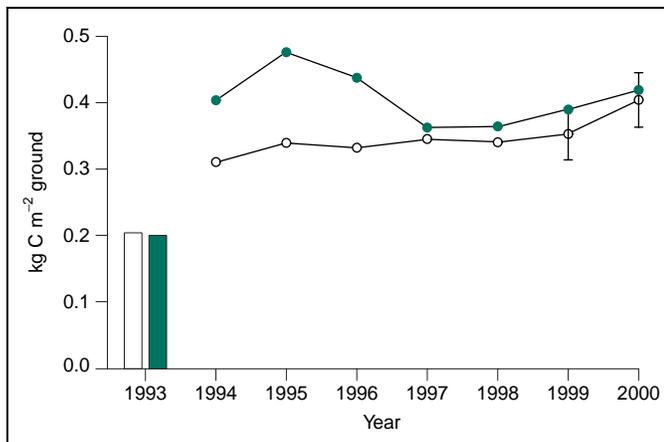
The existence of a regional-scale evapotranspiration feedback over Amazonia had been implied from early biosphere–atmosphere studies that explored the potential effects of deforestation on Amazonian climate by changing the lower boundary conditions for the atmosphere over continents within Atmospheric 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<sub>2</sub>-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<sub>2</sub> (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<sub>2</sub> 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<sub>2</sub> 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 CO<sub>2</sub> concentrations initiated in 1994 and ambient CO<sub>2</sub> concentrations, in the absence of nutrient addition. The figure shows a plot-level comparison between the free-air CO<sub>2</sub> enrichment prototype (FACEP; green dots) and a nearby untreated, ambient CO<sub>2</sub> 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 CO<sub>2</sub> treatment (open bar, ambient CO<sub>2</sub>; green bar, elevated CO<sub>2</sub>). Redrawn with permission from [20].

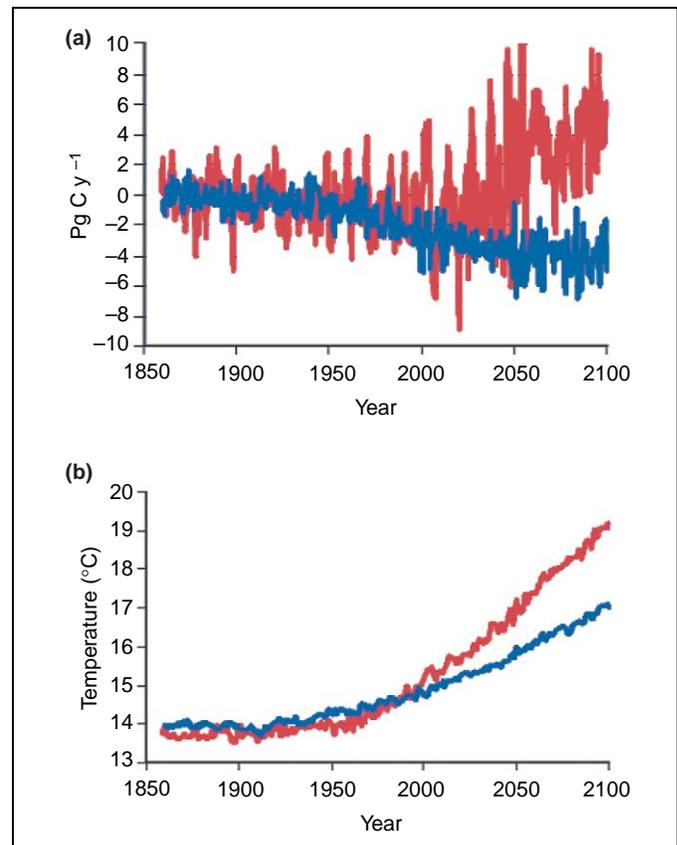
observations, which imply that terrestrial ecosystem responses to climate and CO<sub>2</sub> will be considerably different from current terrestrial biosphere model predictions.

#### 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<sub>2</sub> [12–14]. In particular, field-based CO<sub>2</sub> enrichment studies in temperate forests indicate that, although leaf-level photosynthetic rates appear to increase when CO<sub>2</sub> 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<sub>2</sub> [15–17]. If widespread acclimation occurs as suggested by the above observations, this will decrease the negative biogeochemical CO<sub>2</sub> 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<sub>2</sub> 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 down-regulation of photosynthesis as originally conceived in early modeling studies of the response of the terrestrial biosphere to increasing CO<sub>2</sub> [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 CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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 ‘black-box’ 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<sub>2</sub> 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<sub>2</sub> 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 CO<sub>2</sub> measurements at flask monitoring stations. However, as results from ‘off-line’ model intercomparisons and ‘on-line’ 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<sup>†</sup> provides site-level measurements of CO<sub>2</sub> 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 CO<sub>2</sub> flask monitoring network provide additional ‘top-down’ 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 10<sup>4</sup> and 10<sup>5</sup> km<sup>2</sup>) 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<sup>‡</sup>. However, the ‘big-

<sup>†</sup> <http://www.fluxnet.ornl.gov/fluxnet/index.cfm>

<sup>‡</sup> An important exception might be biosphere–atmosphere feedbacks in Amazonia. High-resolution atmospheric modeling studies suggest that sub-grid-scale land-surface 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<sub>2</sub> 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 CO<sub>2</sub> 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 CO<sub>2</sub> concentrations. The widespread evidence of whole-plant level acclimation responses to elevated CO<sub>2</sub> 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<sub>2</sub> increase is not occurring and, as a result, the rate of at which CO<sub>2</sub> 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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