

The influence of terrestrial ecosystems on climate

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Terrestrial ecosystems influence climate by affecting how much solar energy is absorbed by the land surface and by exchanging climatically important gases with the atmosphere. Recent model analyses show widespread qualitative agreement that terrestrial ecological processes will have a net positive feedback effect on 21st-century global warming, and, therefore, cannot be ignored in climate-change projections. However, the quantitative uncertainty in the net feedback is large. The uncertainty in 21st-century carbon dioxide emissions resulting from terrestrial carbon cycle–climate feedbacks is second in magnitude only to the uncertainty in anthropogenic emissions. We estimate that this translates into an uncertainty in global warming owing to the land surface of 1.5°C by 2100. We also emphasise the need to improve our understanding of terrestrial ecological processes that influence land–atmosphere interactions at relatively long timescales (decadal–century) as well as at shorter intervals (e.g. hourly).

Introduction

What is the relationship between terrestrial ecosystems and climate? In 1936, Köppen [1] suggested that undisturbed natural vegetation ‘mirrored’ the local climate so perfectly that it represented the long-term average weather conditions far better than they could ever be measured. This concept of the influence of climate on a passive land surface has driven many subsequent studies of plants and soils, their distribution and functioning (e.g. [2–4]). However, the idea that terrestrial ecosystems and climate influence each other is much newer, but it is now recognised as being crucial to our understanding of Earth system processes, including climate change [5,6].

Charney [7] was the first to suggest that the land surface influences climate. He reasoned that, because the sparsely vegetated land surface in the Sahara reflects radiation strongly, it acts to reinforce the aridity of its own climate by suppressing rainfall through reduced heating near the land surface. Subsequent global climate models have included increasingly complex representations of such land–atmosphere interactions. During the past decade, climate models combining atmospheric and oceanic processes [ocean–atmosphere general circulation

models (OAGCMs)] have begun to be coupled to a new generation of terrestrial ecosystem models, dynamic global vegetation models (DGVMs). DGVMs represent the terrestrial ecology component of the Earth system and model vegetation and soil processes. They are used to calculate the fluxes of energy and gases between the land surface and the atmosphere. DGVMs also incorporate processes such as mortality and competition among functionally discrete plants, the influence of which on land–atmosphere fluxes varies according to the relative dominance and functional characteristics of the different plant types (e.g. [8,9]). When a DGVM is fully coupled to a climate model, the resulting biosphere–atmosphere–ocean model is sometimes referred to as an ‘Earth system’ model.

Fully coupled Earth system model studies are still rare, but early studies have underlined the importance of using an integrated modelling framework. For example, dynamically coupling the terrestrial carbon cycle (represented in the DGVM) with an OAGCM resulted in increased carbon dioxide (CO₂) emissions from the soil and net losses in forest cover, including a marked loss of forest in tropical South America [10]. The result nearly doubled the previously estimated amount of CO₂ that might be released to the atmosphere during the 21st century. Climate warming was hence strongly accelerated in this study compared with that found for the same OAGCM in the absence of the terrestrial carbon cycle. However, other studies using different OAGCM and DGVM formulations have indicated smaller positive feedbacks between 21st-century climate warming and the terrestrial carbon cycle [11,12]. The differences among these results, although significant, are dominated by uncertainties in the response of terrestrial ecosystems to changes in climate and the atmospheric CO₂ concentration. Improving how we represent terrestrial ecology in Earth system models will thus have a significant impact on our ability to predict future changes in climate [13] and also to understand the impacts of land-use change on the global carbon cycle [14–16].

The potential range of land–atmosphere interactions that is likely to impact local and regional climate is large and includes biophysical and biogeochemical feedbacks. Here, we review the principal climatic feedback processes influenced by vegetation and soil; quantify the current uncertainty in 21st-century climate scenarios associated with Earth system analyses; and, selecting one scale-based

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problem of spatial representation in DGVMs and two contrasting processes in the canopy and soil, illustrate how the limits to our understanding of different processes contribute to the uncertainty in quantifying dynamic interactions between the land surface and the climate.

The influence of vegetation and soil on climatic feedback processes

Ecosystems exchange variable amounts of energy and mass with the atmosphere because of differences in their biophysical surface properties and in their influence on biogeochemical transformations, such as photosynthesis, respiration and mineralisation.

Biophysical processes

The fraction of solar radiation that is reflected by the land surface (its albedo) can strongly influence the temperature by affecting how much energy the land absorbs. For example, the high albedo of snow tends to result in localised cooling because it reflects so much radiation. Forests are usually darker and absorb more radiation than does non-forested land. This effect is accentuated in boreal or cool-temperate zones after snowfall, as tree canopies tend to shed their snow readily and thus remain darker than the surrounding fields, where snow accumulates. The result is enhanced warming of forested boreal areas during the winter and early spring relative to nearby land that is covered by little or low-stature vegetation [17]. The effect is so significant that artificially increasing forest cover in the boreal zone through planting might enhance global warming despite the increased capture of CO₂ from the atmosphere by the additional forested area [18,19].

Energy that is absorbed by the land surface either causes heating directly or drives the evaporation of water, creating a cooling effect. The balance between these two processes controls changes in the surface temperature. The presence of vegetation can further increase the evaporative (cooling) flux component in at least two further ways: (i) using their roots, plants can extract additional water from the soil that would otherwise not evaporate easily because it resides at depth; and (ii) vegetation, particularly forest, makes the surface rougher than the land would be without it and this increases wind turbulence near the surface, also enhancing evaporation. Vegetation can therefore enhance cooling if the radiation that it absorbs leads to a significant increase in the total amount of evaporation. These opposing biophysical effects of vegetation, warming through increased energy absorption (i.e. relatively low albedo) and cooling through increased evaporation, each tend to dominate at different latitudes. Thus, whereas forest cover in the boreal zone has a net warming effect relative to nearby fields, strong year-round evaporative cooling tends to be the dominant process for tropical rain forests, leading to lower maximum temperatures relative to grassland or savannah.

Incorporation of these effects into DGVMs or simpler, non-dynamic soil–vegetation–atmosphere transfer models has a profound impact on climate simulations, strongly influencing, for example, the modelled effects of large-scale tropical deforestation through reductions in

evaporation and precipitation. In the Amazon, total forest loss could lead to strong regional warming of 1–2°C [20] and drying (early studies suggesting reductions in rainfall of up to 30%, [21]), with the additional possibility of climatic consequences at remote locations, such as rainfall shortages in the Mid-West, USA [22]. Simulations of the influence of albedo on past and future climate have produced equally marked results: the increase in absorbed radiation resulting from the advance of (low albedo) forest into tundra probably doubled the rate of Holocene warming 6000–9000 years ago [23]. The same positive feedback could accelerate global warming: Levis *et al.* [24] predicted an enhancement of 21st-century global warming (estimated at 3.3°C) by a further 1.1–1.6°C as a consequence of a modelled northward expansion of boreal forest under climatic warming.

Biogeochemical processes

Ecological and physiological processes in soil and vegetation strongly influence the exchange of a wide range of climatically important gases, such as methane [25,26], nitrous oxide [27] and isoprene [28], as well as water vapour and CO₂. DGVMs represent some of these processes, but a principal modelling focus falls on the balance of photosynthesis and respiration. DGVMs translate leaf-level variation in processes such as photosynthesis into ecosystem-scale fluxes, and represent global diversity with only a few (usually 5–13) different ‘plant functional types’. The divisions between these groups are crude (e.g. grasses, shrubs, evergreen or deciduous trees), but form the basis for differences in competitive ability among plants that fix and store different amounts of carbon under different environmental conditions. Those groups that acquire more carbon are competitively successful and, depending on their rates of mortality and reproduction, become dominant or decline under different combinations of climatic change and soil type.

An understanding of short- and longer term processes in vegetation and soil is therefore needed to simulate land–atmosphere interactions, which range from instantaneous energy and carbon exchange to changes in vegetation type and soil properties. For example, photosynthesis varies with atmospheric CO₂ concentration and is intimately linked with the control of transpiration [29]. Higher atmospheric CO₂ concentrations enhance the rate of photosynthesis by increasing the rate of diffusion of CO₂ through stomata to the sites of carboxylation in leaves. Pot- and plot-scale studies (e.g. [30]) have shown that this enables plants to increase drought resistance at higher atmospheric CO₂ concentrations by reducing their stomatal apertures, thus reducing water loss without a reduction in photosynthesis. When modelled at large scales, inclusion of this short-term effect in scenarios where the atmospheric CO₂ concentration is doubled has reduced transpiration and thus caused an additional ‘physiologically forced’ global warming of 12%, or 0.4–1.0°C [31,32]. The suppression of transpiration through CO₂-induced stomatal closure might also significantly enhance river runoff, potentially helping to mitigate against shortages of freshwater in the 21st century [8].

However, the longer term responses to increasing atmospheric CO₂ concentrations are uncertain and might be significant: the extent of the positive photosynthetic response in leaves to increased CO₂ varies among species, declines in all species beyond a threshold concentration of CO₂, and might be constrained by insufficient nitrogen supply from the soil because of the high nitrogen requirement of photosynthetic enzymes (e.g. [33–35]). Photosynthetic saturation at high atmospheric CO₂ concentrations contributes to many DGVM results that predict changes in vegetation and/or, a declining terrestrial carbon sink during the second half of the 21st century, although there is significant variation among model predictions [8].

Thus, model representations of even the best-studied terrestrial biogeochemical processes such as photosynthesis can lead to uncertainty in their climatic impact, especially when longer (decadal or greater) timescales are considered [36]. Here, we examine the overall role of land–atmosphere interactions in contributing to uncertainty in simulations of 21st-century climatic change, and then consider selected problems in modelling land surface processes for which improved representation could significantly influence that contribution.

Land–atmosphere interactions and 21st-century climate scenarios

Until recently, traditional climate modelling tended to neglect the dynamic interactions between the terrestrial carbon cycle and the atmosphere by prescribing changes in the atmospheric CO₂ concentration without full reference to the effects of climate change on the terrestrial and oceanic sinks. In reality, the atmosphere–land and atmosphere–ocean fluxes of CO₂ are sensitive to (and affect) climate. For example, the growth-rate of the atmospheric CO₂ concentration varies with the interannual climate variability associated with El Niño Southern Oscillation events [37], and was also affected by the climate perturbation following the Mount Pinatubo volcanic eruption [38].

The first OAGCM climate projections to include an interactive carbon cycle using a DGVM showed a positive climate carbon cycle feedback, owing mainly to the negative impacts of climatic change on terrestrial carbon storage [10,11]. These two and eight other modelling groups have recently completed climate–carbon cycle projections, as part of the Coupled Climate–Carbon Cycle Model Intercomparison Project, C⁴MIP [12]. Using a standard anthropogenic emissions scenario (Box 1), all ten C⁴MIP model outcomes were qualitatively consistent with the two preceding analyses [10,11], and resulted in increased CO₂ accumulation in the atmosphere during the 21st century. The magnitude of this positive feedback between climatic warming and terrestrial CO₂ emissions varied among models by an order of magnitude, introducing an uncertainty of ~200 ppmv in the estimated atmospheric CO₂ concentration by 2100. Thus, the contribution from the land to overall uncertainty in CO₂ emissions during the 21st century is larger than from all other system components except for that from anthropogenic sources (Box 1, Figure 1a), and translates into an estimated uncertainty in climatic warming owing to the

Box 1. Terrestrial carbon cycle feedbacks: a key uncertainty in climate projections

Ten climate modelling groups recently completed climate–carbon cycle projections as part of the Coupled Climate–Carbon Cycle Model Intercomparison Project, C⁴MIP [12]. Each group carried out simulations using the ‘SRES A2’ anthropogenic CO₂ emissions scenario (<http://www.grida.no/climate/ipcc/>), which is intended to reflect the effects of economic growth occurring with a regional emphasis and at an intermediate rate [5]. All models predicted a positive feedback with global warming, but the size of this feedback varied from a 20 ppm to a 200 ppm increase in the atmospheric CO₂ concentration by 2100. Figure 1a summarises the key uncertainties in terms of the predicted CO₂ concentration by the end of the 21st century based on the range of sensitivity parameters diagnosed from the C⁴MIP models [12]. The largest uncertainty is associated with future CO₂ emissions from human activities. However, uncertainties in the response of the terrestrial carbon cycle to increases in atmospheric CO₂ and the associated climatic change are also significant.

Based on the range of results produced by the C⁴MIP models, we estimate that uncertainties in the responses of vegetation and soil to climatic change and atmospheric CO₂ increase contribute ~1.5°C to the uncertainty in the predicted global temperature increase over the 21st century (Figure 1b). This is of a similar magnitude to uncertainties associated with the modelled transient climate sensitivity to CO₂ (~2.5°C) and to future anthropogenic emissions (~2°C).

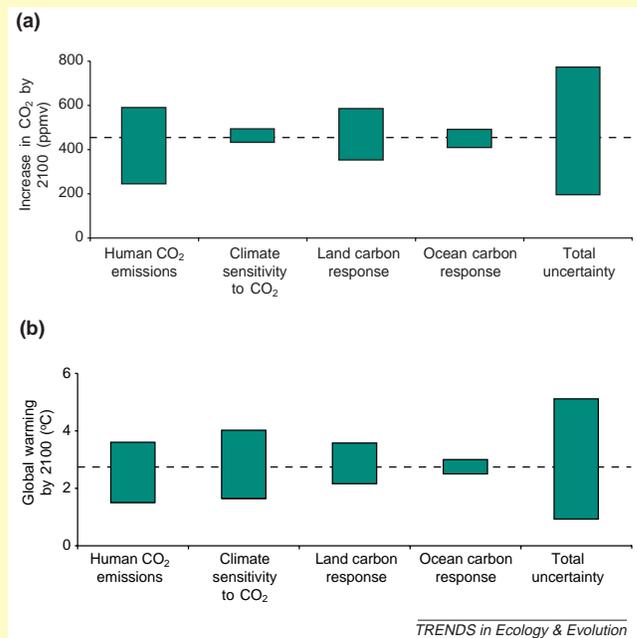


Figure 1. Uncertainties in projections of atmospheric CO₂ concentration and temperature for the 21st century. (a) Contributions from anthropogenic and Earth system components to uncertainties in the increase in atmospheric CO₂ concentration by 2100. The values (maximum to minimum) are estimated using the sensitivity parameters diagnosed from the C⁴MIP models [12] and the upper and lower range for 21st century anthropogenic CO₂ emissions from the SRES scenarios. The dotted line represents the ‘central estimate’ based on the mean model sensitivity parameters and the SRES A2 emissions scenario. (b) Contributions to uncertainties in the predicted global mean temperature increase by 2100. Other details as for (a).

terrestrial carbon cycle alone of nearly 1.5°C by 2100 (Box 1, Figure 1b). Together with previous studies, these results highlight the crucial need to improve our understanding and representation of terrestrial ecological processes in analyses of 21st-century climatic change.

Box 2. Aerosols in the climate system

Aerosols are particles suspended in the atmosphere that vary in size from 0.002 to 200 μm . They are diverse in composition and origin, arising, for example, from sea spray, dust storms, volcanoes, biomass burning, fossil fuel burning and industrial processes. Aerosols affect climate by influencing incoming radiation and cloud properties, although their total climatic impact is still unknown [5]. Aerosols also affect photosynthesis because they cause a shift in the balance between direct and diffuse solar radiation. Direct (solar beam) radiation is not efficiently used by plants because chloroplasts on the sunlit surfaces experience light stress, whereas those on shaded surfaces are insufficiently illuminated. Thus, although the total solar radiation received at the surface is diminished when the air contains a large concentration of aerosols (and indeed the much-discussed 'global dimming' is attributed to aerosols [56,57]), the rate of photosynthesis can increase [58,59].

Measurements over Amazonian rain forests show aerosol 'haze' to comprise pollen, leaf fragments, fungi, algae and small particles containing organic acids and carbonaceous materials derived from biomass burning [45,46]. Many volatile organic compounds (VOCs) emitted by plants during photosynthesis might also have a role in particle formation [28,47]. In some forests, up to 2% of the carbon fixed in photosynthesis is emitted as the simple hydrocarbon isoprene, C_5H_8 , which, globally, could amount to 300–500 million t C yr^{-1} . Broadleaved species are often strong isoprene emitters, whereas

coniferous species usually emit substantial quantities of terpenes, which are derived from isoprene as $(\text{C}_5\text{H}_8)_n$.

Recently, Claeys *et al.* [28] demonstrated that aerosols over the Amazon contained previously unobserved polar compounds that have been formed from isoprene: 2-methylthritol and 2-methylerythritol. These polyols have a low vapour pressure and condense to form secondary organic aerosols with hygroscopic properties. These could increase in size to form cloud condensation nuclei, stimulating the formation of clouds, speeding up the hydrological cycle and reducing the incoming solar radiation over large areas. Such mechanisms are not restricted to rain forests. Measurements made at a Scots pine forest in southern Finland also show 'bursts' of small particles, especially in cloudless conditions during the spring, when cold arctic air arrives from the north [47]. As fluxes of aerosols from vegetation become better understood, climate modellers are likely to need to take account of this process [60].

A similar mechanism has been proposed for marine biota, linking the production of dimethyl sulphide by phytoplankton to the formation of aerosols and clouds over the ocean [61,62]; this has been suggested as an important negative feedback in the climate system [63]. Terrestrial vegetation might also be involved in a similar feedback loop (Figure 1), but the underlying processes are less well studied and the magnitude of the climatic feedback as yet unquantified.

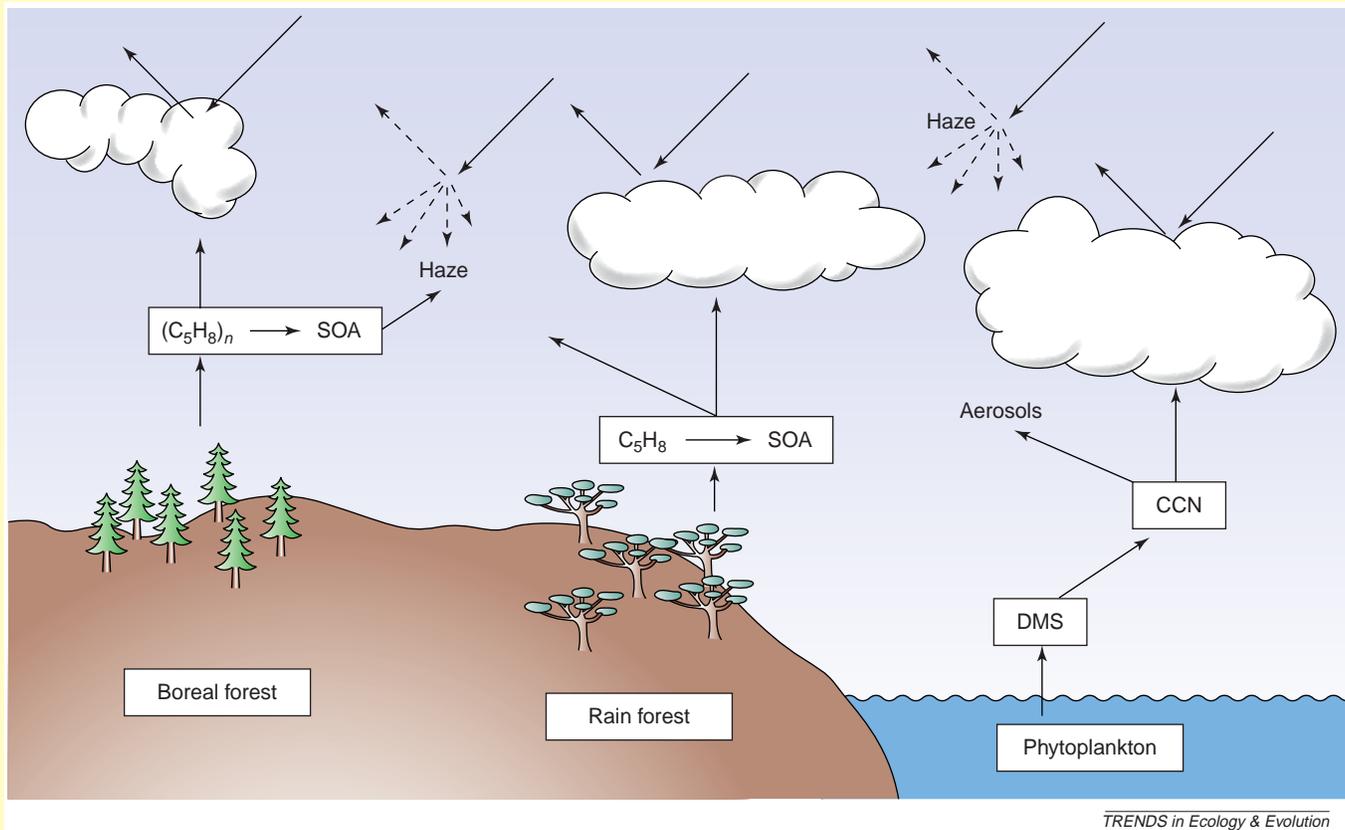


Figure 1. Vegetation, aerosol production and climate. Isoprene is emitted by vegetation and reacts with hydroxyl radicals in the atmosphere to form secondary organic aerosols (SOAs). These enhance cloud formation and form part of a wider system of feedbacks between biogenic aerosols and climate.

This wide range in model results is perhaps inevitable given the complexity of ecosystem responses to climate and the relatively simplistic nature of first-generation global vegetation models, including DGVMs [8]. Below, we discuss three issues relating to the current uncertainty in land surface modelling. We first consider the difficulty of representing individual organisms in models operating at large scales. Limitations in the understanding of key

biophysical and biogeochemical processes also hamper consistency among model outcomes, thus, we select two such processes to illustrate the range in scientific uncertainty (see also Boxes 2,3). We initially note how new discoveries revealing the influence of biogenic aerosols on climate have highlighted the potential need for much better parameterisation of the relevant ecological and atmospheric processes. Finally, although the

importance of the feedbacks between climate and soil CO₂ emissions is widely recognised, we explain how limits to understanding, especially in terms of changes over the longer term, have led to important differences in the representation of this process among models.

Uncertainty in land–atmosphere interactions

Modelling at large scales

One general problem that all DGVMs have is in representing ecologically important processes, such as mortality, fire and species effects, that occur at scales much smaller than the grid scale of current DGVM and OAGCM calculations (~100 km×100 km). Finer scale models that can incorporate such processes (e.g. [39]) have computational requirements that are too large for them to be fully coupled with OAGCMs. This problem remains unresolved, but one recently proposed approach [40] uses ecological techniques developed to account for the dynamics of heterogeneous populations (e.g. [41–43]) to represent sub-grid-scale biotic heterogeneity. Using a system of partial differential equations designed to track the fine-scale impacts of disturbance, Moorcroft *et al.* [40] have argued that it is possible to scale short-term (e.g. leaf-level) processes in a functionally diverse plant assemblage to the scale of an ecosystem, and over the long term, without needing to resort to computationally expensive simulations of individual plants. Although it is not yet clear how successful this approach will be, it could address the theoretical problems relating to the simplification of biodiversity in DGVMs and to the representation of fine-scale spatial heterogeneities, such as mortality and disturbance (e.g. [44]).

Biogenic aerosols

Aerosols are important in the climate system because they absorb, reflect and scatter incoming solar radiation, typically causing a cooling effect. Some of them grow to form cloud condensation nuclei, leading to more numerous and smaller droplets, and thus brighter and longer-lived clouds. Forests are an important source of aerosol particles [45–47] and recent work [28] has further suggested that the production of biogenic volatile organic compounds such as isoprene adds to aerosol concentrations, enhancing cloud formation and significantly changing the radiation received by the vegetation below (Box 2). The uncertainty surrounding aerosol effects on climate [5] underlines the need for an improved understanding of their biogenic sources, but gaps in our understanding of these processes have limited the incorporation of them into DGVMs.

Soil respiration

Multi-component linkages also determine the emission of CO₂ from soil to the atmosphere, the process known as ‘soil respiration’ (Box 3). In contrast to the uncertainty relating to the climatic effects of biogenic aerosols, the central importance of properly representing soil respiration has been known for some time [48,49]. The sensitivity of soil respiration to warming partially determines how quickly Earth system models simulate a 21st-century decline in

Box 3. Soils: climate warming effects on respiration and nutrient supply

Belowground processes could strongly affect terrestrial ecosystem–climate feedbacks. Two key uncertainties concern how soil CO₂ emissions might respond to climatic warming and to the increase in productivity that might occur as the atmospheric CO₂ concentration increases.

The biggest terrestrial source of respired CO₂ is the soil. The process causing this flux of CO₂ is called ‘soil respiration’, although in reality it is the microbes (heterotrophic respiration, R_h) and roots (autotrophic respiration, R_a) rather than the ‘soil’ that respire. This distinction is important because R_a is partly driven by plant growth [53], whereas R_h is partly driven by the supply of substrates suitable for microbial growth.

However, R_h and R_a are also influenced by soil moisture and temperature. Similar to any (bio)chemical reaction, soil respiration increases in rate with temperature. The consequences of this for climatic-change predictions are profound because of the possible positive feedback with climatic warming: warming leads to faster rates of respiration, increased net CO₂ release to the atmosphere and further warming through the greenhouse effect. This feedback is partly responsible for the modelled prediction that the global land surface could switch from being a net carbon sink to being a source of CO₂ by 2050, as respiration losses overtake photosynthetic gains under climatic warming [8]. The strength and permanence of the underlying temperature response of soil respiration has been a focus of much debate (e.g. [64]). However, the long-held view [65] that soil carbon resides in different ‘pools’, some of which can be broken down easily (‘labile’ carbon) and some of which have longer residence times (including ‘recalcitrant’ carbon that is resistant to decomposition), prevails. In this view, a positive feedback with climatic change is possible because the respiration rates of different carbon pools respond similarly to temperature [66]. However, if the carbon available for decomposition declines or is not replenished fast enough, then R_h might decline [67], dampening or removing any positive feedback.

The interaction of increased atmospheric CO₂ concentration and temperature on carbon processing in soils, particularly over the long term, is also a focus of debate. For example, whereas increased atmospheric CO₂ concentration can promote vegetation growth, this extra growth might be limited by nutrient supply [36,68]. Climatic warming can augment the nutrient supply (and hence growth) by increasing mineralisation through enhanced soil microbial activity [69], but the growth response to increasing CO₂ concentrations can also add to R_h through increased fine root litter and exudate production, potentially leading instead to a positive feedback with climatic change [70]. Some insight into the complexity of the links among belowground processes is revealed in a recent meta-analysis of the impact of CO₂ on mycorrhizal fungi [71], which shows that, when young trees are grown at high CO₂ concentrations, fungal growth is increased substantially.

the terrestrial carbon sink [8,38] and the use of a globally uniform temperature response function (e.g. [10]) has attracted significant debate [50,51]. In reality, the temperature sensitivity in soil respiration is strongly dependent on soil component properties and on the supply of carbon to the soil, which itself is influenced by the photosynthetic activity of the vegetation above it and the allocation of photosynthate below ground [52,53]. Therefore, in addition to the direct effects of soil type, we can also expect short- and long-term variations in soil respiration to be affected by changes in the growth rate and type of vegetation that might occur in response to climatic change (Box 3). There are many individual studies analysing the climatic, edaphic and biotic controls on soil respiration, but a new integrated framework is needed whereby the supply of substrate to the different

respiring components of soil can be modelled quantitatively as a function of all three drivers.

Conclusions

The terrestrial carbon cycle exerts a large and significant influence over the physical and chemical aspects of the Earth system, but our understanding of this influence is still limited. New measurements as well as new modelling studies are needed to address the underlying questions, and to assess fully the importance of terrestrial ecosystem–climate interactions for 21st-century climatic change. Better-constrained predictions of future changes in ecosystems and climate will also require improved links between data and models, perhaps through the application of formal data assimilation techniques such as those developed for numerical weather forecasting [54].

These approaches will enable us to refine key elements of process-level understanding and to begin to address the difficulty of accurately representing change over relatively long timescales among interacting system components. Rather ironically, the very conditions of rapid global change that give rise for current concern [5,55] also provide us with the unintended opportunity to observe and understand ecological and atmospheric processes more fully, and could ultimately enable us to predict future Earth system changes with more certainty.

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