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Feedbacks of Terrestrial Ecosystems to Climate Change*

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Abstract

Most modeling studies on terrestrial feedbacks to warming over the twenty-first century imply that the net feedbacks are negative—that changes in ecosystems, on the whole, resist warming, largely through ecosystem carbon storage. Although it is clear that potentially important mechanisms can lead to carbon storage, a number of less well-understood mechanisms, several of which are rarely or incompletely modeled, tend to diminish the negative feedbacks or lead to positive feedbacks. At high latitudes, negative feedbacks from forest expansion are likely to be largely or completely compensated by positive feedbacks from decreased albedo, increased carbon emissions from thawed permafrost, and increased wildfire. At low latitudes, negative feedbacks to warming will be decreased or eliminated, largely through direct human impacts. With modest warming, net feedbacks of terrestrial ecosystems to warming are likely to be negative in the tropics and positive at high latitudes. Larger amounts of warming will generally push the feedbacks toward the positive.

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1. INTRODUCTION

The responses of terrestrial ecosystems to a changing climate have many dimensions. They also have many implications for sustainability, biodiversity, and the provision of ecosystem goods and services to people. All of these are potentially diverse, far reaching, consequential, and persistent. There are strong motivations for investments in understanding the full range of climate change impacts. The motivation is especially strong, however, for the ecosystem impacts that feed back to climate change, either amplifying or suppressing the initial forcing. Throughout the history of climate change science, ecosystem feedbacks have played a major role in scientific and public debates, with some arguments that responses of terrestrial ecosystems largely eliminate the risk of dangerous climate change (1) and others that ecosystem responses increase that risk (2). Both kinds of

argument are supported by reasonable conceptual frameworks. A very large body of observational, experimental, and theoretical work increasingly allows these arguments to be replaced with detailed analysis. But there are still important gaps in our understanding. Several of the potentially key mechanisms have not been studied in detail and are either absent from or sketchily represented in models. Here, we summarize the available information and make a preliminary assessment of the potential impacts of poorly known mechanisms.

Climate change responses of terrestrial ecosystems can feed back to climate through two broad mechanisms (**Figure 1**). One is modulating the concentration of atmospheric greenhouse gases (GHGs) (3), especially carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O). The other is modulating the absorption or distribution of solar energy in the atmosphere or at the land surface (4). As with most of the processes in Earth's system, ecosystem feedbacks are complicated by four important factors. First, they rarely occur in isolation, and their implications are typically amplified or suppressed by a wide range of other mechanisms. Second, they occur over a wide range of temporal and spatial scales, with very different implications on different scales. Third, they potentially influence diverse aspects of climate, ranging from global-scale temperature to local precipitation intensity. And fourth, they are intimately involved with human actions, both as drivers and responders.

Over the past three decades, most of the research on feedbacks of terrestrial ecosystems to climate change has focused on their potential role as carbon sources or sinks. The conclusion that atmospheric CO₂ was growing more slowly than expected, on the basis of estimated emissions and ocean uptake, led to the idea of a "missing sink" (5) and to the hypothesis that increased plant photosynthesis in response to elevated atmospheric CO₂ might provide the explanation. After many years of study, the mystery of the missing sink

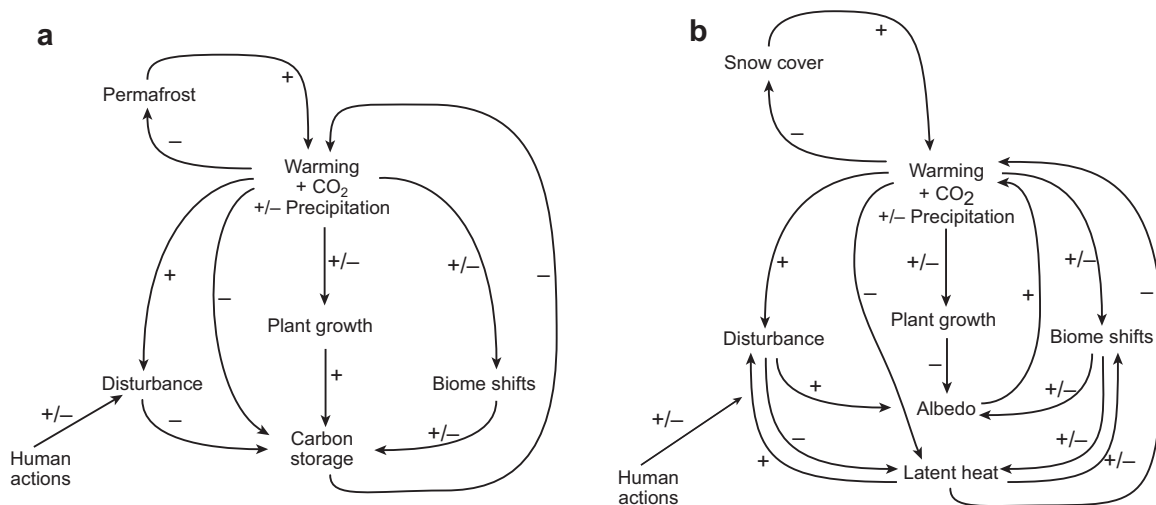


Figure 1

Schematic diagram of major processes involved in the control of CO₂ feedbacks (panel *a*) and physical feedbacks (panel *b*) in the climate system. A plus (+) symbol indicates that an increase in one process leads to an increase in the next, and a minus (-) symbol indicates that an increase in one process leads to a decrease in the next. Note that the set of driving processes (plant growth, biome shifts, and disturbance) is mostly the same for the CO₂ and physical feedbacks.

is still incompletely resolved. It is clear, however, that several mechanisms, and not just CO₂ fertilization, play a role (6). Early models tended to treat ecosystem responses to climate change with a single equation or a small set of equations describing the CO₂ sensitivity of photosynthesis and the temperature dependence of plant and microbial respiration (7). Although these were a reasonable starting point, they ignored a wide range of potentially critical processes, including changes in the distribution and dominance of different species and life forms, constraints from soils or nutrient availability (8–10), changes in the action of disturbance mechanisms like wildfire and disease, and direct modification of ecosystems by humans. Recent progress in understanding and modeling these processes is opening new perspectives on carbon cycle feedbacks.

The potential for global change responses of ecosystems to modify climate through processes other than GHG concentrations also has a long history of research (Figure 1). But because the climate effects of these kinds of

feedbacks tend to be local, their prominence in discussions of ecosystem feedbacks has been muted. Much of the research has focused on albedo (i.e., the fraction of incident radiation not absorbed by the surface) effects of northward expansion of high-latitude forests (11), but the domain of potentially important climate feedbacks is much richer than this. Especially when the discussion is broadened to include potential effects on aerosols (12), optical properties of clouds, precipitation (13), the distribution of energy between sensible and latent heat (14), and the implications of wind-blown dust for the ocean carbon cycle (15), ecosystem feedbacks from non-GHG mechanisms acquire a global sweep.

In the past, few studies (e.g., 16) have explicitly included human actions in assessments of ecosystem feedbacks. In fact, the large majority of studies on ecosystem responses and feedbacks to climate change treat the system as if actors completely external to the system were performing a single-factor experiment by releasing CO₂ into the atmosphere. A small but growing number of studies acknowledge

that the pattern and scale of deforestation, the style and intensity of agriculture, or the spread of invasive species have elements that are integral components of ecosystem responses to climate change and that have important implications for ecosystem feedbacks to climate.

In the following sections, we first review ecosystem feedbacks that operate via changes in GHGs, followed by a discussion of feedbacks that affect climate directly through physical changes in the land surface. Section 4 then discusses the potentially important but seldom modeled interaction of human activity with these ecosystems feedbacks. Section 5 conceptually integrates the effects of all major mechanisms and estimates the net expected impact of ecosystem feedbacks on climate.

2. GREENHOUSE GAS FEEDBACKS

Ecosystem processes potentially exert a major influence on atmospheric concentrations of four important GHGs that have increased dramatically during the industrial era—CO₂, CH₄, N₂O, and tropospheric ozone (O₃). Ecosystem effects on a fourth GHG, water vapor, can also be important. Carbon dioxide has increased by 37% since 1750 (17), exerting 1.66 W m⁻² of new GHG forcing. Methane, N₂O, and tropospheric O₃ have increased 152%, 18%, and 36%, respectively, accounting for 0.6, 0.16, and 0.35 W m⁻² of new GHG forcing (18). The high global warming potential (GWP) of CH₄ [GWP = 23 for the 100-year horizon (19)] and N₂O [GWP = 296 for the 100-year horizon (19)] relative to CO₂ (GWP = 1) amplifies the effect of these gases on climate.

The mechanisms through which ecosystems influence CO₂, CH₄, N₂O, and tropospheric O₃ concentrations are very different. CO₂ is removed from the atmosphere in the process of photosynthesis in green plants, and it is returned in respiration by plants, animals, and microbes, or by combustion (**Figure 1**). CH₄ is a waste product released by microorganisms that

grow in low-oxygen environments, especially wet soils and the guts of some insects (especially termites) and ruminants (e.g., cattle, giraffes). CH₄ is consumed by microorganisms of oxygen-rich soils and water bodies that use it as an energy source. N₂O is produced by soil microorganisms that make a living oxidizing ammonium (nitrifiers) as well as by those that use nitrate as an energy source (denitrifiers). Ecosystems influence the atmospheric lifetimes of CH₄ and N₂O both directly, through their role as sources or sinks, and indirectly, through effects on the oxidizing potential of the atmosphere, effects mediated largely through emissions of hydrocarbons, which consume hydroxyl ions (the atmosphere's primary cleaning agent) (20). Ecosystem effects on tropospheric O₃ are largely through the indirect mechanism.

Ecosystems are a net sink for carbon, removing CO₂ from the atmosphere, when plant photosynthesis exceeds the sum of respiration and combustion, and they are a source when respiration and combustion exceed photosynthesis. The sum of photosynthesis and respiration (or net ecosystem production) provides one window on ecosystem influences on atmospheric CO₂, and the sum of photosynthesis, respiration, combustion, harvesting, and other forms of offsite transport (net biome production) provides another (21).

Climate changes can produce CO₂ sources and sinks through a wide range of mechanisms (22). Possible routes to sinks include (*a*) stimulation of photosynthesis by elevated atmospheric CO₂ or improved growing conditions (warmer temperatures, more favorable moisture balance, improved nutrient availability, or decreased pollutants such as tropospheric O₃), (*b*) decreased plant or microbial respiration as a result of altered chemical or physical composition of the plants and soil organic matter, (*c*) altered ecological conditions, leading to the replacement of lower biomass by higher biomass ecosystems, or (*d*) decreased disturbance from natural or anthropogenic processes. The converse processes can make ecosystems act as carbon sources. Because the

mechanisms are diverse, operate on different temporal and spatial scales, and are non-independent, it is very difficult to formulate simple rules or patterns that apply across diverse ecosystems and timescales. A wide range of models address increasingly comprehensive subsets of these mechanisms. In general, mechanistic understanding decreases in moving from effects on photosynthesis to effects on growth, decomposition, ecological interactions, and disturbance.

Climate change effects on CH₄, N₂O, and tropospheric O₃ feedbacks are equally diverse. Ecosystem sources of CH₄ are likely to increase when (a) wetland areas increase, (b) CH₄ consumption in nonflooded soils decreases, (c) ecological changes allow CH₄ to be transported more efficiently from areas of production to the atmosphere, or (d) ecological changes or altered management leads to increases in either the abundance of the animals that harbor methanogens in their guts or the fraction of the carbon these organisms release as CH₄, with further effects from the (ecosystem-mediated) oxidizing potential of the atmosphere. Sources of N₂O will tend to increase with (a) increased cycling of biologically available nitrogen (N) or (b) an increased fraction of the soil in the moisture regime favorable to N₂O production, with both processes potentially sensitive to a number of ecological influences and to further feedbacks from the oxidizing potential of the atmosphere.

Ecosystems underlain by permafrost have the potential for climate change responses that influence the atmosphere through yet another mechanism. Cold ecosystems can operate as carbon sinks over extended periods, gradually incorporating organic matter into the continuously frozen zone that is effectively removed from the active parts of the carbon cycle (23). Thawing of permafrost or the rearrangement of ice-rich soils through thermokarst returns this organic matter to the active carbon cycle, potentially leading to sources of CO₂ (24, 25) or CH₄ (26) through decomposition (**Figure 1**), CO₂ sinks from in-

creased growth in response to increased nutrient availability, or decreased CH₄ emissions as a result of drying. The large pool of carbon in frozen soils, coupled with the potential for large amounts of thawing over the current century (27), gives these mechanisms unusual leverage as climate feedbacks.

Some aspects of this diverse suite of feedback mechanisms are well known, but others are not. A wide range of models synthesizes current understanding of many of the mechanisms, including both direct and indirect feedbacks. A recent generation of models that actively couples aspects of the carbon cycle with a global or regional climate models (28) provides an unusually comprehensive approach to large-scale feedbacks. It is important to remember, however, that even the most comprehensive currently available models address only a subset of the mechanisms discussed here. Although it is clear that some mechanisms predominate on the smaller spatial and temporal scales where relatively good information is available, it is far from clear that any of the potential mechanisms is likely to be unimportant over decades and large spatial scales.

2.1. Plant Growth and Organic Matter Decomposition

Effects of climate change on photosynthesis, growth, respiration, and decomposition, plus feedbacks of these processes to GHG forcing of climate change (**Figure 1**), are probably the best understood responses and feedbacks discussed in this review. They are described in recent reviews by Reich et al. (9) and Luo (29). In general, exposure to elevated CO₂ leads to initial increases in photosynthesis and growth in plants with the C₃ photosynthesis pathway. These initial increases may persist indefinitely, but they frequently degrade as a consequence of downregulated biochemical capacity for photosynthesis (9). In young plantation forests, effects of elevated CO₂ on photosynthesis are accurately predicted by the photosynthesis model of Farquhar et al. (30),

and responses of net primary production are well predicted by changes in photosynthesis (31). Although the initial stimulation of photosynthesis does not occur in plants with the C₄ photosynthesis pathway, these plants often realize increased carbon gain as a result of improved water balance (32). The tendency for elevated CO₂ to increase photosynthesis is typically greatest at hot temperatures, a consequence of the temperature sensitivity of rubisco, the primary carboxylating enzyme in C₃ plants, and of its ability to distinguish CO₂ from O₂ (33).

Responses of photosynthesis and growth to warming are typically hump shaped, with increases at lower temperatures and decreases at warmer temperatures (34). The temperature response of plants from contrasting habitats is usually tuned to local conditions such that local warming increases photosynthesis under conditions that are cool by local standards and decreases it under conditions that are hot by local standards (35). Extreme events, including both cold and hot events, can have profound, persistent effects on photosynthesis and growth, ranging from suppression over hours or days to death of the plant. In empirical studies to date, warming can lead to either increased or decreased plant growth (29).

The tendency of warming to increase levels of tropospheric O₃ (36) can decrease both growth and photosynthesis. In a meta-analysis of 53 studies involving plants exposed to 70 ppb O₃, shoot biomass was decreased by an average of 34%, and seed yield was decreased an average of 24% (37).

The responses of plant and soil respiration to global change are tightly coupled to the responses of plant growth. A large-scale experiment with litter from many sites confirms the important role of litter's initial N concentration in controlling the rate of decomposition (38). Although the short-term response of decomposition to warming is usually a strong increase, in large-scale geographic patterns, ecosystem responses to experimental warming are typically weaker (29). In a meta-

analysis of warming experiments at 32 sites, soil respiration increased by 20% (39).

Indirect effects can dominate the direct effects of climate change on photosynthesis, growth, and decomposition. Potentially important indirect effects include changes in the availability of soil moisture and mineral nutrients, plus changes in the relative abundance of plant and microbial species that differ in sensitivity to CO₂, temperature, and other environmental conditions. In some ecosystems, especially those with sufficient phosphorus (40), growth of plants under elevated CO₂ increases the competitiveness of plants with N-fixing symbioses, leading to increased N fixation and N availability (41, 42), but it can also lead to decreased N fixation (43). Changes in the efficiency of nutrient recovery from senescent tissues could alter nutrient availability, but the changes are small in experiments to date (44). Changes in the species composition of the decomposer community can substantially influence rates of decomposition. In Florida shrubland exposed to elevated atmospheric CO₂, an increase in the abundance of fungi relative to bacteria led to an increase in decomposition and a loss of soil carbon (45).

A very large number of empirical studies address changes in ecosystem carbon as a consequence of altered growth and decomposition in response to elevated atmospheric CO₂ (9), altered climate (29), altered air pollution (46), or some combination of these three aspects of climate change. Relatively few, however, combine all three components into a realistic simulation of future conditions. As a result, the vast majority of results from empirical studies need to be understood as exploring ecosystem responses to selected aspects of climate change. The rapidly growing suite of experiments that combine warming with an altered atmosphere (e.g., 47–49) typically ignore changes in air pollution, plant species dynamics, disturbance, and direct human impacts.

In many modeling studies, changes in photosynthesis, growth, and decomposition have been considered the only mechanisms

through which ecosystem responses to climate change feed back to climate. We consider this a highly simplified and potentially misleading view. Still, these responses, including indirect components, lay an important foundation on which other processes operate. For the models that treat only photosynthesis, plant growth, and decomposition in the terrestrial carbon cycle, the general result is that increasing atmospheric CO₂ leads to a current carbon sink that persists through the century (50). Estimates of the size of the current CO₂-driven component of the sink range from 1 to 3 Pg (1 Pg = 10¹⁵ g = 1 billion metric tons) C y⁻¹, increasing to 3 to 7 Pg C y⁻¹ by the end of the century. When the same models are given a future that includes both elevated CO₂ and climate change, current carbon sinks are little changed, but 2100 sinks decrease by about 50%.

Estimates of terrestrial sources and sinks that are based on inverse analysis of atmospheric observations provide some of the strongest evidence for stimulation of large-scale carbon sinks by elevated atmospheric CO₂. In the tropics, evidence for a terrestrial sink that is comparable in magnitude to the deforestation source (51) supports the hypothesis that CO₂ fertilization contributes to recent carbon sinks, as it is unlikely that other mechanisms are active in those regions.

A number of recently developed models link climate models with ocean and ecosystem carbon models (52). The leaders of these modeling groups have been collaborating in a model intercomparison project called C⁴MIP (Coupled Climate-Carbon Cycle Model Intercomparison Project). About half of the models in the C⁴MIP analysis of coupled carbon-climate models treat terrestrial ecosystems as including no processes beyond plant growth and decomposition (i.e., models without a dynamic vegetation model) (28). Results from these models are qualitatively similar to those from uncoupled models, with carbon storage for a climate scenario with high emissions continuing through the twenty-first century (54, A2 scenario). The

storage is always smaller when the model is run in a coupled rather than in an uncoupled mode because coupling creates a positive feedback in which decreased carbon sinks lead to increased temperatures, which further decrease carbon sinks (28). For the models with growth and decomposition only, the magnitudes of the simulated cumulative sinks are large, ranging from 400 to 500 Pg C over the twenty-first century.

Over the past several years, an increasing fraction of terrestrial biogeochemistry models have broadened beyond the plant growth/decomposition focus to include dynamic vegetation models (55), allowing the possibility of biome shifts and disturbances (especially fire) (28). Both biome shifts and disturbances (**Figure 1**) have the potential to amplify, suppress, or even reverse the carbon cycle responses from changes in growth and decomposition.

2.2. Species Dynamics and Biome Redistributions

Several global correlations link vegetation change with GHG feedbacks to climate. The distribution of Earth's biomes correlates with climate. This correlation forms the basis of the "climate envelope" approach to understanding and predicting biome distribution. Aligning with this pattern, there are differences in net primary production, rooting depth, and the depth distribution of soil organic carbon across biomes or principle life forms (56–58). These relationships support the expectation that significant changes in climate will lead to shifts in vegetation and that vegetation change will feed back to the climate via ecosystem changes in carbon balance and other mechanisms.

For biome distributions to shift, organisms must migrate, or minor species within ecosystems must become vegetation dominants. Comprehensive reviews have assembled strong evidence causally linking climate change and the shift of many species to higher latitudes and/or altitudes, as well as changes

in seasonal activities (59–61). Not all species, however, will successfully adjust. When migration constraints are incorporated in coupled climate models, biomes that are shifting under a doubled- CO_2 climate lose on average a tenth of their endemic biota, and some biomes may lose up to two fifths (62). If these losses are not offset by functional redundancy among species, the expected linkages among climate, biome characteristics, and carbon feedbacks may break down. Even if functional integrity remains, changes in climate and vegetation may occur on different timescales, especially when migration is required (63).

Expansion and contraction of woody vegetation. Carbon feedbacks are likely to change the most when an ecosystem experiences a major change in the relative abundance of major growth forms. Significant carbon feedbacks are likely with shifts that involve large gains or losses of woody plants, such as tree-line advance, forest expansion or retreat, and conversions between grassland and savanna. However, these vegetation changes also result in albedo feedbacks that are likely to oppose and, in some cases, exceed carbon feedbacks (Section 3.1).

In Arctic tundra, experimental studies provide clear evidence that climate warming is sufficient to account for expansion of shrubs and graminoids at the expense of lichens and mosses (64). Other major changes in Arctic vegetation, such as changes in tree line and conversion of boreal forest from evergreen to deciduous species, involve not only direct climatic drivers, but also natural disturbances such as fire and insects, as well as human activities, all of which interact (23).

A major transition to woodiness is occurring at lower latitudes in mesic to arid environments across all vegetated continents. In grasslands ranging from temperate tall-grass prairie to subtropical savanna and desert grassland, woody species have colonized or increased in abundance (65). Woody encroachment has been attributed to many factors, es-

pecially overgrazing and fire suppression, although some field experiments demonstrate a potential role of increased moisture, acting directly and/or via conserved moisture under elevated CO_2 (65, 66). Conversion from grasslands to savannas, and from savannas to shrublands, has been viewed as a potentially large terrestrial sink for atmospheric CO_2 because primary production by invading shrubs often outweighs any decline by grasses (67).

The potential carbon sink owing to woody encroachment is partially offset, however, by “woody elimination,” or the conversion of desert scrub, arid shrublands, and savannas to grassland and lower storage potential (68, 69). This conversion is occurring on several continents and is driven by burning, invasion by annual grasses that increase fire frequency, or harvesting of trees for firewood. In the western United States, roughly one fifth of the area most susceptible to woody encroachment is likely to instead be invaded by cheatgrass (*Bromus tectorum*) (68).

In forests of the tropics, determinations of standing forest biomass and rates of forest loss are critical to determining vegetation feedbacks to climate, but they are incomplete (70). Recent assessments on the basis of forest inventory and flux measurements have debated the current carbon balance of intact tropical forests, placing them somewhere between significant carbon sinks and small sources (71, 72).

Drought and seasonality. Satellite remote sensing indicates that climate warming has resulted in a longer growing season in the tundra, which results in increased net primary production (NPP) (73, 74). However, increased carbon gain by plants may be balanced or exceeded by loss of soil organic matter, at least in the short term. Both nutrients and hydrology have the potential to modulate the magnitude, and even the sign, of carbon balance with Arctic warming (23). Drought stress may reverse the effects of warming on growing season length (75, 76) or reduce decomposition rates in warmed soils

(77). Coupled climate-carbon cycle models point to the Arctic becoming a weak carbon sink with continued warming (78).

Predictions of the future carbon balance of tropical forests are very sensitive to assumptions about regional climate interactions and the relative effects on transpiration by stomata and leaf area index, which determine the magnitude of warming-induced drought (79, 80). Strong sensitivity to warming-induced drought is suggested by analyses of El Niño/Southern Oscillation droughts, which switch the Amazonian rainforest from being a carbon sink to being a source (81).

2.3. Disturbance

Fire, pest outbreaks, diseases, and extreme weather reshape ecosystems. Whether they consume fixed carbon directly or initiate processes that do, these disturbances result in rapid carbon loss and alter the future productive capacity of ecosystems (82). Disturbance regimes are also major interacting modulators of the climate-biome relationship (**Figure 1**). Ecosystems prone to burning cover two fifths of Earth's land surface and include roughly half the land area where forests would be expected on the basis of climate alone (83). Plant pathogens and insect defoliators are even more pervasive disturbance agents, impacting more than 40 times the acreage of U.S. forests damaged by fire (84). In Canada, insect damage has stand-replacing consequences over areas comparable to fire (85). These modulators affect both the climatic conditions where a vegetation type can exist and the feedbacks from vegetation to climate. Human activities, often interacting with climate change and its modulators, are a major factor affecting biome distribution and other aspects of carbon feedbacks (Section 4).

Fire. Wildfire is a significant factor in the global carbon budget, releasing to the atmosphere about 3.5 Pg C y^{-1} from 1997–2001, or more than a third of the carbon of fos-

sil fuel emissions (86). Interactions between fire and climate warming are complex, as fire substantially alters carbon feedbacks to climate over multiple timescales (12). In Alaskan forests, fire frequency interacts with warming to define a trifurcated outcome in forest structure—black spruce, deciduous trees, or invasion and dominance by lodgepole pine (87). Lodgepole pine's flammable structure and serotinous cones tend to reinforce its dominance via fire, consistent with the idea that flammability has evolved as a competitive mechanism (88). Plant adaptations to fire also interact with other trophic levels. In savannas, grazers disproportionately reduce grass fuel loads around woody stands, improving the postfire recovery of the woody plants. The lower decomposability of grass litter relative to shrub makes invasive grasses a key element of fire cycles, especially in high-rainfall years that stimulate grass production (89, 90).

The drying effects of a warmer climate suggest that the overriding tendency in the future will be increased fire frequency in many areas. In the western United States, recent increases in fire season length and fire duration may be partly a consequence of decades of fire suppression, but recent work points to warming-intensified drought as a cause (91). In tropical rainforests, climate warming increases wildfire risk (92, 93). In addition, fragmented forests have reduced humidity and rainfall (94) and increased fire risk (95). Fire can also decrease rainfall through effects on cloud properties (13).

Because the hydrologic cycle is intensified with climate warming (96), precipitation will increase in some regions rather than decrease. Despite this, the frequency and impact of fires are likely to increase globally because altered precipitation affects several biomes asymmetrically. In environments that are not water limited and rarely burn, such as intact rainforest, increased moisture will have little effect, but decreased precipitation will make them more fire prone (92, 93). In arid environments, fire frequency is likely to increase with increased precipitation (97), which facilitates

the invasion and growth of invasive grasses that decompose relatively slowly and constitute a high fuel load. Reduced precipitation in arid regions may increase tissue flammability, but this will be balanced by a reduced fuel load. These asymmetries in the effects of altered precipitation may be important in driving a global trend of increased wildfire frequency and impact. This trend is likely to be compounded by the geographical distribution of precipitation changes and human activities. For example, the southern and eastern Amazon basin is likely to become drier, not wetter (18), and to experience greater forest clearing.

Insects and pathogens. The consumption of fixed carbon by herbivorous insects is similar to fire in some respects: Both involve temperature dependence, either directly or indirectly through relative humidity, and both can propagate from a point of origin. But a wide array of factors makes the climate responses and feedbacks of insects and pathogens far more complex, including host specificity, interactions between direct effects of climate and effects mediated by host plants, evolutionary adjustments, and interactions with higher trophic levels. Nonetheless, increases in pest outbreaks are expected for an expanding number of insect species in temperate regions (98). In tropical rainforests as well, more frequent insect outbreaks are expected because warmer and drier conditions are likely to favor insects relative to their predators and parasitoids (99).

Independent of changes in insect populations or the frequency of outbreaks, there are robust indicators that rates of food plant consumption by herbivorous insects will increase in a warmer, higher CO₂ future. This results from both the direct effects on herbivorous insects and effects mediated by plants. A meta-analysis of experiments on plant-herbivore interactions under factorial warming and elevated CO₂ indicates that these factors reinforce one another in their effects on leaf N concentration and C:N ratio (both factors decrease leaf N and increase leaf C:N),

whereas their effects on other determinants of feeding rate tend to offset or even cancel one another (100). The implication of this finding is that for insect herbivores to acquire a given amount of N in a warmer, higher CO₂ future, they will have to consume more leaf material, ultimately releasing more carbon. A trend toward higher leaf C:N ratio under a warmer climate is also supported by global surveys of leaf N, which have observed decreases in leaf N with increases in mean annual temperature and with decreases in latitude (101).

2.4. Permafrost

High-latitude warming has the potential to produce carbon sources from the decomposition of carbon released in the melting of permafrost, or carbon sinks from the northward expansion of high-biomass shrublands and forests (**Figure 1**) (23). The release of carbon from permafrost is a special kind of carbon cycle feedback because it returns to the active carbon cycle material that has been locked away from the active carbon cycle, in some cases for many millennia.

Frozen soils contain vast quantities of carbon, concentrated in two ecosystem types. One is wetland soils, which are often peat and characterized by very high organic matter contents. The other is loess soils, windblown sediments that accumulated in nonglaciated areas during past ice ages. Total carbon is not well known, but is estimated at 455 Pg in arctic wetlands (102) and 400 Pg in loess regions (103). Some of this is in areas without permafrost or in the current active (annually thawed) layer, but much of this carbon is permanently frozen.

Permafrost melting can occur along two major pathways. With a gradual deepening of the active layer, the pool of carbon in the active cycle grows slowly. The collapse of ice-rich regions, or thermokarst, often forms lakes, but it can also cause landslides, rapidly exposing the carbon in a large pool of previously frozen soil. Although thermokarst is widely recognized to be a critical process in permafrost

dynamics, it is not represented in the current generation of models. Using a global climate model and the SRES A2 (strong warming) scenario (54), Lawrence & Slater (27) concluded that twenty-first century warming could lead to the loss of permafrost from as much as 80% of its current distribution. Important limitations of the global climate models make it likely that estimate is too high, but we lack global estimates from more detailed, permafrost-specific models. Strong warming at high latitudes will accelerate loss of permafrost.

The decomposability of organic matter released in the melting of permafrost is not well known, but it is often quite high. When thawing leads to drainage, wetland soils become strong carbon sources with decomposition increasing fourfold in response to drying (104). Much of the organic matter in melting loess soils is more like frozen roots than soil organic matter. It decomposes rapidly, with decomposition factors in the range of 3% per year, with little or no sensitivity to temperature after the first few months of decomposition (105).

Estimates of the total carbon potentially vulnerable to release from permafrost soils in the twenty-first century are very rough. Gruber et al. (106) used a risk assessment approach to estimate that as much as 100 Pg C could be released. Dutta et al. (105) calculated that thawing of 10% of Siberian permafrost could lead to the release of 40 Pg in 40 years.

High-latitude wetlands are an important source of CH₄. Drainage and drying of wetland soils could decrease CH₄ fluxes, but expansion of thermokarst lakes could increase them. Walter et al. (26) concluded that warming from 1980 to 2000 increased the area of thermokarst lakes in the northeast region of Siberia by 14.7%, increasing the area of the narrow band around the lakes' perimeters that is the source of CH₄ by 58%. The combination of decreased CH₄ fluxes from some regions but increased fluxes from others makes it difficult to project even the sign of the response at the global scale.

2.5. Other Greenhouse Gases

Climate change is likely to increase CH₄ emissions and consumption in some ecosystems but decrease them in others. Emissions will depend on climate change impacts on the distribution and status of wetlands, cattle production, termites, and wildfire. In a climate model experiment that included CH₄ emissions from wetlands, expanding tropical and high-latitude wetlands in a doubled CO₂ climate led to a 78% increase in wetland CH₄ emissions (107). Some of any increase could be consumed, however, if uptake rates in upland soils increase. Experimental rainfall exclusion in Brazilian evergreen forest increased CH₄ consumption more than fourfold (108).

Recent increases in the area of thermokarst lakes in loess regions of Siberia have led to substantial increases in CH₄ emissions (26), a pattern that is likely to continue over several decades. In peaty wetlands, CH₄ emissions increase strongly with warming (109–111) and drainage (104), suggesting increased future fluxes. Increased wildfires could also increase the CH₄ source (112).

Tropical reservoirs can also be substantial CH₄ sources, especially reservoirs with a seasonally varying water level (113). If future climate changes lead to increased construction of reservoirs in the tropics, this mechanism could be a globally important source.

Methane from agriculture—rice paddies and enteric fermentation in cattle—is an important part of the global budget, contributing about a third of the total emissions (114). Effects of climate change on yields from rice agriculture or on the viability of raising cattle could significantly alter the global CH₄ budget, especially if approaches for minimizing CH₄ emissions are not widely deployed.

Fluxes of N₂O from ecosystems to the atmosphere occur in both managed and unmanaged ecosystems. In managed ecosystems, the fluxes are often estimated as a fixed fraction of N applied in fertilizer, although the actual fraction is sensitive to the type and timing of fertilizer, type of soil, type of crop,

and management practices (115). N_2O fluxes through animal waste can dominate the N_2O balance of agriculture, placing a priority on sophisticated waste management. Some approaches to increasing C storage in agricultural soils also lead to increased N_2O emissions, either partially or completely offsetting the negative climate forcing from the CO_2 sequestration (116). In unmanaged ecosystems, N_2O fluxes tend to increase with N deposition from pollution (117).

In pasture ecosystems, elevated CO_2 can lead to increased N_2O fluxes under conditions when N availability is high (118). Decreased winter snow cover in temperate forest ecosystems can also lead to increased N_2O emissions (119). If warming is accompanied by drying, however, N_2O emissions can decrease (120).

Broad trends in N_2O emissions from unmanaged ecosystems will depend on future patterns of soil moisture and N deposition, with wetter soils and higher N deposition favoring increased N_2O emissions. Climate changes that push agriculture to increase N addition rates will tend to increase N_2O emissions, although these can be decreased with a range of management techniques, including timing and level of fertilization (121) and decreasing or eliminating tilling (122). The large GWP of N_2O makes it an attractive candidate for aggressive investments in control.

3. OTHER CLIMATE FEEDBACKS

In addition to affecting GHG cycles, ecosystems can provide feedbacks to climate change by modifying the land-atmosphere exchange of energy and water (**Figure 1**). These physical effects include changes in albedo, evapotranspiration, energy partitioning, and roughness length of the land surface, which in turn can affect both local and remote climate (123). In general, changes in water or energy balance tend to influence climate on smaller spatial scales than changes in carbon uptake because CO_2 is a well-mixed gas. Biophysical feedbacks are therefore relatively more important for regional than global climate, although

their cumulative effect at the global scale can be significant.

Comparison of physical feedbacks with GHG feedbacks is complicated by at least three factors. First, the spatial scale of influence can differ significantly, and therefore the relative importance of physical and GHG effects will be a function of the scale and climate variable of interest. Second, the relative importance of physical and GHG feedbacks will also change with time. For example, the climate effects of CO_2 losses from an ecosystem will diminish through time as the atmosphere equilibrates with the ocean and some of the CO_2 is absorbed by the ocean. In contrast, changes in surface albedo will cause a persistent change in net absorbed radiation at the surface that will equally affect current and future climates. Third, whereas changes in surface albedo can be expressed as a radiative forcing, changes in factors such as energy partitioning do not involve a net change in absorbed radiation and therefore cannot be evaluated within the traditional framework of radiative forcing used for GHGs (124).

Given these difficulties, Earth system models that simulate energy, water, and carbon exchanges between the land, ocean, and atmosphere are needed to fully evaluate and compare physical and GHG feedbacks (4). Such models are still in their infancy but have already yielded significant insights into ecosystem feedbacks.

3.1. Albedo

Warming and increased atmospheric CO_2 levels are likely to promote the expansion of shrubs and forests into new areas, particularly those that are too cold or arid in the current climate (**Figure 1**) (see Section 2.2). For example, an expansion of shrub cover has already been observed in the Alaskan Arctic (125, 126). There is less evidence for expansion into arid regions, although this is expected in the future because of greater water use efficiency under elevated CO_2 (127). Warming is also expected to lengthen the growing season in

high-latitude regions, thereby increasing the fraction of the year that tree canopies mask underlying snow.

From a climate perspective, snow and arid soils represent two of the most reflective surfaces in the world, so that increased vegetation cover in boreal or arid regions can substantially reduce albedo. The climate effects of these albedo changes in boreal ecosystems are substantial, as the presence of forests can warm local annual average temperatures by $\sim 5^{\circ}\text{C}$ and spring temperatures by more than 10°C (11, 128, 129). These large local changes propagate in the atmosphere and can even cause slight warming in tropical ecosystems (11).

Albedo changes provide a positive feedback to climate change that will be most important at high latitudes, where the local feedback can exceed the warming effects of GHGs (126). At the global scale, a key question is the extent of shrub and tree expansion that occurs as the result of climate change and increased CO_2 . Bala et al. (130) used a coupled climate-carbon model with dynamic vegetation to estimate the response of global ecosystems to elevated CO_2 alone (the radiation model used current CO_2 levels, thus ignoring the direct effects of GHGs on climate). They found a net global warming of 0.65°C by 2300 owing to a 13% increase in forest cover that resulted from higher CO_2 and caused reduced albedo. For comparison, the GHG effect of elevated CO_2 , estimated from the total carbon uptake and the model's climate sensitivity, was a cooling of 1.2°C . In a related study (131), projected global forest cover increases by 8% by 2100 and 19% by 2300 in response to the combined effect of climate change and CO_2 . These scenarios, although based on several tentative assumptions about vegetation dynamics, support the notion that albedo feedbacks will represent a significant positive feedback to climate change, with a magnitude that approaches the negative feedback of enhanced carbon uptake at the global scale.

Changes other than vegetation expansion, such as switching of ecosystem composition

between evergreen with deciduous species (132) or between short and tall grass species, may also affect surface albedo. Even though the quantitative importance of these feedbacks is not well known, it is likely smaller than the positive feedback from forest expansion in boreal and cool temperate regions.

Another possible mechanism of albedo feedback is increased fire frequency in high latitudes caused by a longer fire season, which leads to deposition of black carbon on snow and sea ice that can substantially reduce albedo. However, this effect appears short lived, with snow and ice albedo returning to initial values after one year (12). The main consequences of fire are therefore via the release of GHGs and the increase in surface albedo resulting from tree mortality, the effects of which tend to cancel out over the life of a fire cycle (12).

3.2. Energy Partitioning

One of the most rapid and well-understood responses of plants to elevated atmospheric CO_2 is a reduction in stomatal conductance (a measure of the width of leaf-surface pores that allow the exchange of CO_2 or H_2O between the atmosphere and internal leaf) (14). These adjustments lead to lower rates of water vapor loss by most plants as atmospheric CO_2 levels rise, which in turn causes an increase in sensible heat flux as less incident energy is used to evaporate water (**Figure 1**). Sellers et al. (14) showed that surface warming of as much as 1°C in the tropics can result from the increased sensible heat flux associated with doubled atmospheric CO_2 levels.

Over timescales of years to decades, however, most species also exhibit greater leaf area in response to elevated CO_2 , which increases the total surface area over which transpiration occurs. Betts et al. (133) demonstrated that the combined effect of increased leaf area and reduced conductance per leaf was a small net change in total canopy evapotranspiration. As a result, the total shift in energy partitioning

between latent and sensible heat fluxes is likely to provide a relatively small feedback to climate change, at least at the global scale. This conclusion is supported by Bala et al. (130), who simulated a small net change in evapotranspiration in response to elevated CO₂ that was dwarfed by albedo feedbacks from vegetation expansion.

3.3. Clouds and Aerosols

Cloud feedbacks are the single most important factor in explaining model differences for simulated climate sensitivity to GHG concentrations (134). Therefore, any changes in cloud amount or optical properties arising from ecosystem responses to climate change could represent a potentially important feedback to climate. Modeling studies have shown clearly that extreme reductions in vegetation transpiration, such as those caused by tropical deforestation, lead to a significant decrease in cloud cover that amplifies warming (135). Less understood is how changes in other factors, such as surface albedo, stomatal conductance, and fire frequency, will influence clouds.

4. INTERACTING CLIMATE AND HUMAN FACTORS

The uncertainties in climate change projections that arise from responses of natural ecosystems to climate change may be substantially modified by consideration of more direct interactions of humans with ecosystems. For example, more than 30% of Earth's land surface is currently cultivated for crops or grazed, with upward of 40% of global NPP appropriated by humans (136, 137). It is therefore reasonable to expect that ecosystem responses to climate change will depend significantly on human activities. To date, few models of ecosystem feedbacks have considered the interactive role of other human activities, and therefore the contribution of these interactions to climate change uncertainty is not well understood.

In some cases, human activity will likely increase the uncertainty associated with ecosystem feedbacks. For example, if climate change causes significant losses in crop yields, humans will likely respond by converting more forested land to agriculture. The degree to which this occurs represents an added source of uncertainty to climate projections. But human interactions may reduce other sources of uncertainty. As an extreme example, the response of forests in the Brazilian Amazon to climate change and elevated CO₂ would become irrelevant if the area is entirely deforested for reasons unrelated to climate change. Below, we focus on a few examples of human interactions that may be important for estimating ecosystem feedbacks and associated uncertainties.

4.1. Land Use

Projections of human land use over the next century depend on myriad demographic, economic, and environmental factors that are often more complex than the climate system itself. Therefore, it is difficult to say with great precision how forest areas will grow or shrink as a direct result of human land-use decisions. Scenarios of land use that correspond to the Intergovernmental Panel on Climate Change SRES narratives have been produced by the IMAGE group (138, 139). Global cropland area in these simulations for 2100 range from 27% in an A2 scenario to 10.8% in a B1 scenario, compared to a baseline value of 14.5% in 1990. Thus, projections range from a slight net afforestation on a global scale to massive deforestation that nearly doubles current cropland area. All scenarios are characterized by large geographic variation, with deforestation tending to occur mainly in tropical latitudes where food demand growth and arable land potential are greatest. Afforestation tends to occur at higher latitudes (**Figure 2**).

Deforestation will generally play two important roles in modulating ecosystem feedbacks to climate. First, the total amount of deforestation itself may change in response to

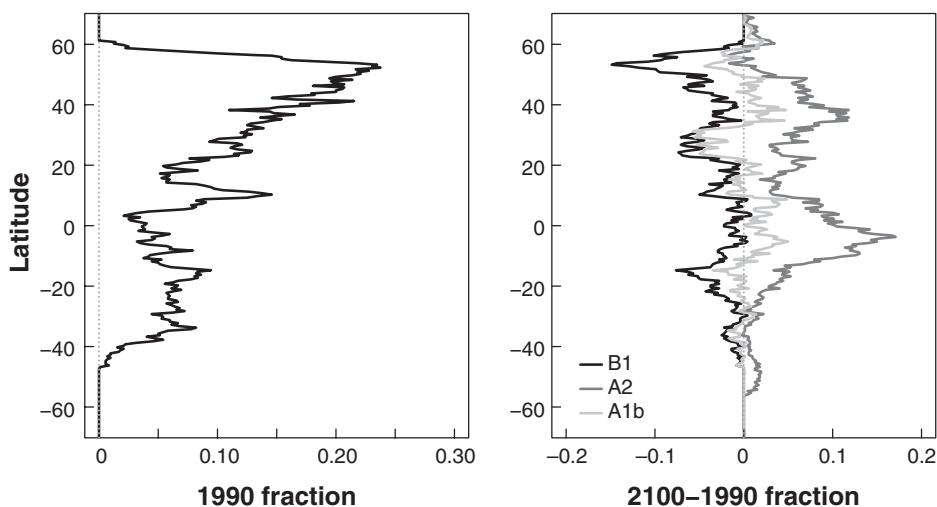


Figure 2

The fraction of Earth's surface used as cropland in 1990 for different latitudes (*left*) and change in fraction by 2100 (*right*) for three different projections of the IMAGE model. Future deforestation and afforestation is more likely to occur at low and high latitudes, respectively (138, 139).

climate change. One plausible scenario is that lower crop yields caused by climate change will lead to higher food prices and thereby promote faster deforestation. A measure of the potential for this feedback is provided by a sensitivity study with the IMAGE model by Leemans et al. (139), where the CO₂ fertilization effect was turned off. The resulting drop in simulated crop productivity led to 440 Mha of deforestation compared to the baseline A1B scenario, and changed the net global deforestation from -8.5% (net afforestation) to 1.1%.

The impact of climate change on crop productivity can therefore be considered a major source of uncertainty for predicting future deforestation. As seen in **Figure 2**, the majority of deforestation will likely occur in tropical latitudes. In these regions, forests generally have a net cooling effect because of large effects on evapotranspiration and carbon balance that outweigh reductions in albedo (140–142). Faster rates of deforestation in response to climate change would therefore provide a positive feedback to warming. Limited deforestation may also occur at high latitudes in response to warming, where it would likely provide a net negative feedback associated with albedo changes. For example, Fischer et al. (143) project that the area of land too cold for cul-

tivating crops shrinks from 13.2% in present day to 5.2% by the end of the twenty-first century in a high-emission scenario (A1FI), potentially stimulating a small increase in high-latitude croplands (e.g., in Canada and Russia).

A second important role for deforestation is that it will modify the extent and functioning of natural ecosystems, thereby preventing some feedbacks or promoting others. For example, the carbon sink [or source, e.g., (144)] provided by forests in response to elevated CO₂ would be greatly reduced if the forests were replaced by annually harvested croplands or pasture for livestock grazing. Similarly, the ability of rangelands to sequester carbon will likely be affected by extensive livestock grazing, which may increase in response to growing demand for meat. Range-fed grazing of livestock is the single most dominant land use worldwide, currently occupying 27% of global land area (65).

Deforestation may also cause ecosystems to be more sensitive to climate change. For example, deforestation-induced fragmentation can greatly increase the susceptibility of tropical ecosystems to fire in dry years (95). These fires would then provide a positive feedback to climate change by releasing substantial amounts of stored carbon and reducing evapotranspiration.

Few climate models have considered interactions between climate change and land use. As a consequence, the regional and global effects of these interactions are not well quantified. Overall, it appears that land-use changes will be greatest in tropical regions where they will likely act to reduce negative feedbacks and/or enhance positive feedbacks. In higher latitudes, where the responses of natural ecosystems are more likely to provide positive feedbacks (**Figures 1 and 2**), land use will play a much more limited role, or areas formerly used for agriculture or forestry may be reforested. It therefore appears that inclusion of land use in simulations of climate change would almost certainly reduce negative feedbacks or increase positive feedbacks and thereby increase the projected warming.

4.2. Nitrogen Deposition

The potential of ecosystems to take up carbon is constrained in many regions by the availability of nutrients required for plant production, particularly N (145). Human alteration of the global N cycle, through combustion of fossil fuels and synthetic fertilizer production, is greatly increasing the rate and magnitude of N deposition such that global anthropogenic N fixation now exceeds that of all natural sources (146). Increased N deposition may therefore alter the feedbacks provided by ecosystems to climate.

Without supplemental N additions or decreases in N losses, the availability of mineral N declines with time in ecosystems exposed to elevated atmospheric CO₂ in comparison with N availability at low CO₂ levels (i.e., progressive N limitation) (147). Simulation models linking nutrient cycling to plant production and C sequestration consistently predict less terrestrial CO₂ uptake and storage than models that do not incorporate N regulation of carbon-related processes (40). Furthermore, a recent meta-analysis of 80 observations from 41 published and unpublished studies concluded that the response of soil carbon se-

questration to elevated atmospheric CO₂ is constrained directly by N availability and indirectly by nutrients required to support N₂ fixation, including phosphorus, molybdenum, and potassium (148). Even in the case where worldwide per capita N deposition increases to the level now prevalent in the northeastern United States, this amount of N may still be inadequate to meet the demand for C sequestration in response to gradually rising atmospheric CO₂ concentration (8). Thus, N fixation holds considerable weight in determining whether ecosystems will sequester substantial anthropogenic CO₂ emissions in the coming decades (9).

The ability of additional N deposition to stimulate additional carbon sequestration may be limited. Although some plant communities exhibit increased productivity in response to low levels of N deposition, others experience little or no response of plant growth. Many ecosystems, particularly those in the low latitudes, are P limited (149). NPP does not increase in response to increased N additions in these environments. Moreover, high levels of N deposition may lead to N saturation of forests, a set of feedbacks in which N deposition exceeds the ability of plant communities to retain it, leading to decreased plant productivity and cation (calcium, magnesium, potassium) deficiencies (150). This effect may be exacerbated when N deposition occurs in the form of acid rain, which can reduce stress tolerance in some temperate forest tree species, leading to dieback of forest canopies, as well as greater tree susceptibility to herbivore infestations, disease, and drought (151). Furthermore, enhanced decomposition rates for material accumulated under higher atmospheric N may result in higher CO₂ emissions from terrestrial ecosystems and increased release of dissolved organic matter (152).

4.3. Biofuels

Recent increases in the production and consumption of biofuels have been driven in part by concerns about global climate change,

recent price volatility in global petroleum markets, and concern about energy independence. To the extent that biofuel expansion is a response to the perceived threat of climate change, this trend can be viewed as a feedback of human activity to climate that involves the active management of ecosystems. From the perspective of ecosystem feedbacks (and independent of any fossil fuel use offset by the use of biofuels), increasing biofuel production will have effects related to the contrast in the carbon content, albedo, surface roughness, and energy partitioning of the ecosystems it replaces. When at least some potential biofuel crops are grown on degraded land, soil carbon can increase, providing both carbon sequestration and carbon for energy (153). By contrast, the replacement of high-biomass forest with oil palms or other biofuel crops, which is occurring in some areas (154), likely results in carbon releases that dwarf the annual energy recovery in biofuels.

Global demand for food and transportation fuels may double in the next 50 years (155, 156). Parallel increases in the demand for food and biofuels may create large pressures for bringing additional land into cultivation, foreclosing on ecosystem responses that would otherwise occur. These pressures would likely be increased by climate changes that decrease the productive potential for food or biofuels.

5. INTEGRATION

The fundamental challenge of assessing climate feedbacks from ecosystem responses to climate change is finding a useful way to integrate factors and processes characterized by very different levels of understanding. Many kinds of ecosystem responses to climate change have been studied in controlled experiments and/or are represented in detailed mechanistic models. Others are known only qualitatively, often using historical observations or space for time substitutions. Still others are based on known or strongly suspected mechanisms but have not been observed or

simulated. Interactions among processes of all these types, plus feedbacks of these processes to influence the amount of climate change, have the potential to further complicate the situation.

Past approaches have addressed the knowledge heterogeneity problem in two main ways. Most mechanistic models have focused on the best-known mechanisms, avoiding poorly understood processes and feedbacks. In contrast, vulnerability studies (157) tend to use simple formulations that do not attempt to explicitly represent the full range of processes and feedbacks but that attempt to capture their effects through varying key model parameters over appropriate ranges. Some probabilistic models combine elements of both approaches. For example, Matthews & Keith (2) use a probabilistic coupled climate-carbon model to conclude that ecosystem feedbacks increase the risk of extreme warming. The weakness of the mechanistic modeling approach is it misses the potentially large effects of processes not represented in the models. The main weakness of the vulnerability studies is that they provide limited guidance on pathways for improving understanding.

We believe a hybrid approach can add value, enhancing capacity for assessing possible impacts of poorly known processes and, as a consequence, enhancing capacity for understanding both integrated ecosystem responses and their feedbacks to climate change. The basic idea of the hybrid approach is extending formal simulation results with a conceptual framework for integrating poorly known but potentially important mechanisms. In many cases, there may be sufficient information to estimate the forcing at which a poorly known mechanism activates and to estimate its impact when forcing is high, medium, or low. In some cases, a conceptual synthesis of the literature may be a sufficient foundation for this kind of assessment (106). In others, expert elicitation (158) or a formal meta-analysis (159) may be more useful. Here, we emphasize the first approach, building on the studies

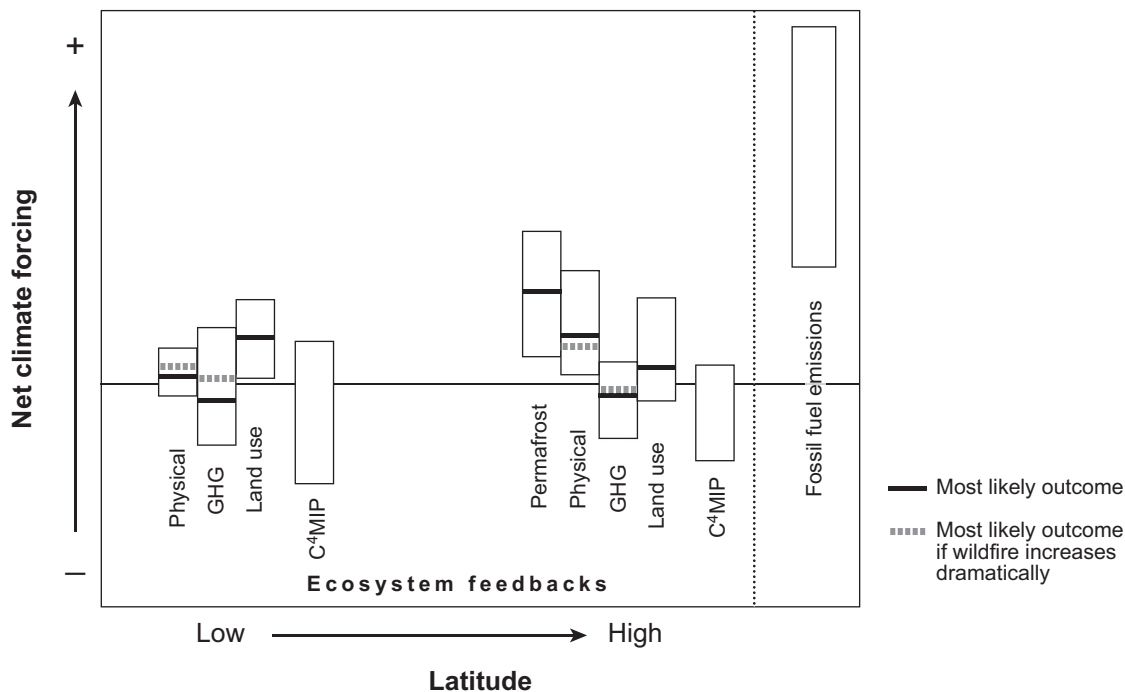


Figure 3

Estimated quantitative range for net climate forcings from a range of ecosystem feedbacks at high and low latitudes [a plus sign (+) is net warming, and a minus symbol (–) is net cooling]. Black horizontal bars represent most likely outcomes, based on our conceptual model. Gray dashed lines represent most likely outcomes if wildfire increases dramatically. Note that the net effect of all of the poorly modeled processes is likely to be positive net forcing, but also note that all of the ecosystem forcings are small in relation to the net forcing from fossil emissions. Abbreviations: GHG, greenhouse gas; C⁴MIP, Coupled Climate-Carbon Cycle Model Intercomparison Project.

summarized in previous sections. The underlying formal simulations are the C⁴MIP results of Friedlingstein et al. (28). The conceptual extensions for this analysis include (a) albedo and other biophysical feedbacks, (b) permafrost melting, (c) non-CO₂ GHGs, (d) wildfires, (e) tropical deforestation, and (f) nutrient limitation. On the basis of current understanding and recent trends, we consider these the most important mechanisms largely omitted from most or all of the current generation of models.

Over the twenty-first century, we expect each of these five mechanisms to produce, at the global scale, a net positive forcing of warming (Figure 3). Each of the individual mechanisms has the potential to account for net forcing equivalent to tens or even hun-

dreds of petagrams (billion tons) of carbon emissions. Acting together, the cumulative effect could be sufficient to convert the net effect of the land surface from a large net negative forcing of warming (28) to neutral or positive.

At high latitudes, trends in the northward expansion of forests will tend to be correlated with decreases in albedo, increases in carbon loss from melting permafrost, and increased emission of CH₄ from expanding Arctic lakes or draining wetlands (Figure 4). Because every study to date indicates that, at high latitudes, positive forcing by decreased albedo is larger than negative forcing by carbon uptake (Section 3.1), it is very likely that the net forcing at high latitudes will be positive. Conversion of 100% of tundra area to boreal

forest could store up to 21 Pg C, on the basis of current aboveground carbon in each (160). But the positive forcing of climate by an albedo effect of 25.9 W m^{-2} (126) over this same area would be equivalent to an extra 32 Pg C in the atmosphere (converting between W m^{-2} and Pg C in the atmosphere on the basis of anthropogenic radiative forcing and atmospheric CO_2 in 2005 from Reference 18). This net effect of high-latitude forest expansion would be augmented by up to 100 Pg C forcing from permafrost melting (106) and CH_4 equivalent to an additional 2 to 10 Pg C (26). The likely larger magnitude of positive albedo effects over negative carbon storage effects will mean that any increase in wildfires or loss of forested area to insects could lead to a small negative net forcing, and continuation of the trend toward an increase in forested area could lead to a small positive net forcing of warming at high latitudes.

At low latitudes, where carbon storage in the C^4MIP models tends to be largest, increased forest biomass tends to produce a negative forcing for warming through both carbon and biophysical effects (Figure 4). In these regions, the question for the future is whether trends in deforestation or wildfire allow the projected storage to occur. A crude estimate can be based on continuing the current rate of deforestation, which annually releases an amount of carbon equal to about 0.4% of the aboveground stock in tropical forests (161). Over the century, continued deforestation could not only release carbon but also prevent C storage on approximately 40% of the total tropical forest area. On the basis of a conservative estimate that 30% of future sinks is in the tropics, elimination of 40% of tropical forest as a potential sink decreases the estimated sinks by 10% to 15% or 40–70 Pg C over the century. Increasing the rate of forest loss by 50% to allow for increased wildfires (Section 2.3) could release another 40–70 Pg C to the atmosphere directly and prevent the emergence of sinks that could store an additional 20–30 Pg C. Together these effects could either release or prevent the storage of

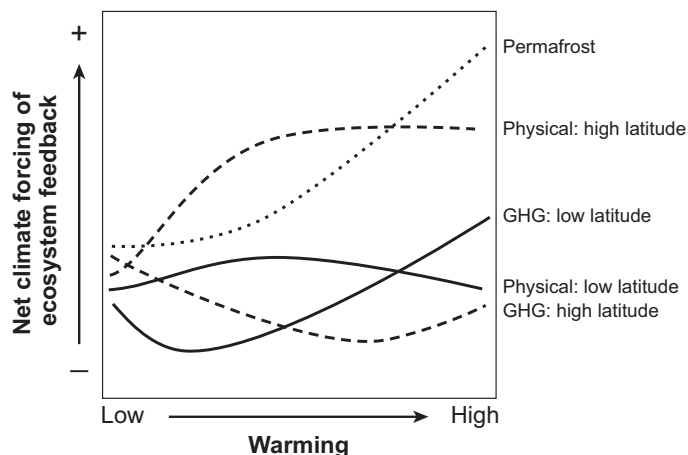


Figure 4

General form of the relationship between net temperature forcing and the amount of warming for climate feedbacks from permafrost melting, greenhouse gas (GHG) effects other than permafrost melting, and physical effects. Greater warming is expected to amplify positive feedbacks and/or reduce negative feedbacks. The location of 0 on the Y axis depends on the starting point, prior to the forcing of ecosystem properties by climate change. The GHG feedbacks turn toward the positive as warming leads to the loss of biomass and/or soil carbon stocks. The physical forcing at low latitudes turns toward the negative as tropical forests are replaced by savannas or grasslands.

over 150 Pg C. If the average biophysical forcing from loss of rainforest is 5 W m^2 locally, then the loss of 60% of global tropical forest area by 2100 would produce additional warming comparable to an extra 12 Pg C in the atmosphere.

In the middle latitudes, where carbon sinks have been most active recently, the net climate effect of increases in forest area and/or biomass is likely to be close to neutral, as a consequence of albedo and carbon storage effects that are comparable in magnitude but opposite in sign. Greater CO_2 fertilization will increase carbon sinks but also increase positive forcing of warming by albedo. Greater than expected nutrient limitation or increases in wildfire will have the opposite effect, but with a net climate forcing that is still close to neutral.

In sum, our analysis suggests that extra forcing of warming from high latitudes and tropical regions could have effects comparable

to the effects of an additional C release, over the century, of 300 Pg or more, decreasing the net negative forcing of warming by land ecosystems by more than half.

SUMMARY POINTS

1. Over the high and middle latitudes, climate feedbacks from carbon and albedo work in opposite directions. Ecosystems with increased carbon storage tend to have lower albedo (**Figure 1**). The effect of these opposing climate forcings is that climate is not as sensitive to ecosystem structure in these latitudes as it would appear from a focus on only one mode of climate forcing. In general, albedo effects tend to dominate carbon storage effects at high latitudes with dominance switching gradually to carbon effects in the tropics. This increasing importance of carbon at low latitudes reflects the combined effects of a lower albedo contrast and a higher carbon and evapotranspiration contrast between low- and high-carbon ecosystems in the tropics. In general, the albedo effect of replacing herbaceous with woody vegetation probably saturates at relatively low levels of canopy biomass, whereas the carbon effect continues to increase.
2. Processes that result in increased ecosystem carbon all tend to be slow, with carbon accumulating over decades or centuries. Processes that result in carbon loss can be slow or fast. The fast processes, including deforestation, fire, and other disturbances, will likely have a tendency to increase over a wide range of warming, and the processes that lead to uptake will have a range of responses, including long-term increase, saturation, and transition from increase to decrease. Saturation and transition from increase to decrease are most likely in ecosystems that are hot already. The combination of the faster dynamics and of the larger range over which the effect is an increase argues that the processes leading to rapid loss of carbon will become increasingly important in hot ecosystems, as anthropogenic warming increases. This also implies that ecosystem feedbacks are especially important for estimating the probability of extremely warm climate change scenarios.
3. Humans now have the capacity to disrupt or augment ecosystem feedbacks to climate on a massive scale. Deforestation already creates carbon fluxes that are comparable in magnitude to natural sinks at the global scale. This capacity is likely to increase in the future. It could be expressed in increased or decreased harvesting and deforestation, increased or decreased fire suppression, and increased investments in forest fertilization, genetic improvement, or pest or disease control. As a consequence, the direction of the human impacts on many of the world's ecosystems will depend on whether they are managed primarily for climate or for other purposes. In the tropics, continued or increased deforestation will preclude a range of natural ecosystem feedbacks, with rates of deforestation potentially sensitive to climate change-induced losses in crop productivity, or increased demand for biofuel crops.
4. Although there are many uncertainties in the feedbacks of ecosystem responses to a changing climate, the uncertainties should not impede the development of global change policy tools. The net effect of terrestrial ecosystems in forcing warming over the twenty-first century is likely to be small in relation to the net forcing from human actions. In addition, the risk that the net effect of ecosystem feedbacks changes from net cooling to net heating increases as the amount of warming increases.

FUTURE ISSUES

1. This review has focused on net forcing of warming from changes in the characteristics of terrestrial ecosystems, but it has not addressed a broad range of other potentially important ecosystem–climate feedbacks. These include forcing from altered precipitation or extreme events and forcing mediated through nutrients transported from the land to the oceans.
2. We have concentrated on the net forcing of climate at the global scale. However, biophysical feedbacks can have small-scale effects that are much more important locally than globally. Implications of the local-scale effects, both for people and for ecosystems, need to be addressed in detail.
3. Feedbacks to climate change from human actions could take a wide range of forms. We have discussed only land-use change related to agriculture and biofuels. Other potentially important feedbacks could involve climate change–induced human migrations, consequences of warfare, or changes in the impacts of major diseases.
4. Feedbacks to climate change from human actions could also include geoengineering, such as deliberate efforts to offset warming by decreasing the amount of solar radiation that reaches Earth’s surface. The feasibility and consequences of this kind of feedback are very poorly known.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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