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Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests

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The world's forests influence climate through physical, chemical, and biological processes that affect planetary energetics, the hydrologic cycle, and atmospheric composition. These complex and nonlinear forest-atmosphere interactions can dampen or amplify anthropogenic climate change. Tropical, temperate, and boreal reforestation and afforestation attenuate global warming through carbon sequestration. Biogeophysical feedbacks can enhance or diminish this negative climate forcing. Tropical forests mitigate warming through evaporative cooling, but the low albedo of boreal forests is a positive climate forcing. The evaporative effect of temperate forests is unclear. The net climate forcing from these and other processes is not known. Forests are under tremendous pressure from global change. Interdisciplinary science that integrates knowledge of the many interacting climate services of forests with the impacts of global change is necessary to identify and understand as yet unexplored feedbacks in the Earth system and the potential of forests to mitigate climate change.

Forests cover ~42 million km² in tropical, temperate, and boreal lands, ~30% of the land surface (Fig. 1A). These forests provide ecological, economic, social, and aesthetic services to natural systems and humankind (1), including refuges for biodiversity, provision of food, medicinal, and forest products, regulation of the hydrologic cycle, protection of soil resources, recreational uses, spiritual needs, and aesthetic values. Additionally, forests influence climate through exchanges of energy, water, carbon dioxide, and other chemical species with the atmosphere.

Forests store ~45% of terrestrial carbon (Fig. 1B), contribute ~50% of terrestrial net primary production (2), and can sequester large amounts of carbon annually (Fig. 1C). Carbon uptake by forests contributed to a "residual" 2.6 Pg C year⁻¹ terrestrial carbon sink in the 1990s, ~33% of anthropogenic carbon emission from fossil fuel and land-use change (3). Forests have low surface albedo and can mask the high albedo of snow (Fig. 1D), which contributes to planetary warming through increased solar heating of land. Forests sustain the hydrologic cycle through evapotranspiration, which cools climate through feedbacks with clouds and precipitation. The ratio of evapotranspiration to available energy is generally low in forest compared with some crops and lower in conifer forest than in deciduous broadleaf forest (Fig. 1E).

That forests influence climate has long been postulated. From the onset of European settlement of North America, it was believed that clearing of forests for cultivation, wood products, and settlement altered climate (4). Today, scientists have a diverse array of methodologies, including

eddy covariance flux towers, free-air CO₂ enrichment systems, satellite sensors, and mathematical models to investigate the coupling between forests and the atmosphere. It is now understood that forests and human uses of forests provide important climate forcings and feedbacks (3), that climate change may adversely affect ecosystem functions (5), and that forests can be managed to mitigate climate change (6). What is lacking, however, is science that integrates the many interacting climate services of forests with the impacts of global change to inform climate change mitigation policy.

Accordingly, this article reviews biosphere-atmosphere interactions in tropical, temperate, and boreal forests. Emphasis is placed on biogeophysical processes (albedo and evapotranspiration) (7), their comparison with biogeochemical processes (carbon cycle) (8), and alteration of forest-atmosphere coupling through biogeographical processes (land use and vegetation dynamics) (9).

The Ecology of Climate Models

The influence of forests on large-scale climate is difficult to establish directly through observations. Careful examination of climatic data can sometimes reveal an ecological influence, such as the effect of leaf emergence on spring-time evapotranspiration and air temperature. Eddy covariance flux towers and field experiments provide local-scale insight to forest-atmosphere interactions, and advances in remote sensing science can aid extrapolation of this knowledge to larger spatial scales. More often, however, our understanding of how forests affect climate comes from atmospheric models and their numerical parameterizations of Earth's land surface (10). Paired climate simulations, one

serving as a control to compare against another simulation with altered vegetation, demonstrate an ecological influence on climate.

Atmospheric models require fluxes of energy, moisture, and momentum at the land surface as boundary conditions to solve numerical equations of atmospheric physics and dynamics. The first generation of land surface parameterizations developed in the late 1960s and 1970s used bulk aerodynamic formulations of energy exchange without explicitly representing vegetation [supporting online material (SOM)]. Soil water availability regulates latent heat flux, and the hydrologic cycle, when included, was simplified to a "bucket" model of soil water. In this approach, precipitation fills the soil column up to a specified water-holding capacity, beyond which rainfall runs off.

By the mid-1980s, the second generation of land surface parameterizations, included the hydrologic cycle and the effects of vegetation on energy and water fluxes. These models explicitly represent plant canopies, including radiative transfer, turbulent processes above and within the canopy, and the physical and biological controls of evapotranspiration (Fig. 2A). Snow cover, the soil water profile, and vegetation influences on the hydrologic cycle are also included (Fig. 2B). In the mid-1990s, plant physiological theory further advanced the incorporation of biological control of evapotranspiration in the third generation of models. Models now routinely link the biochemistry of photosynthesis with the biophysics of stomatal conductance. Leaf photosynthesis and conductance are scaled to the plant canopy based on the optimal allocation of nitrogen and photosynthetic capacity in relation to light availability. Simulations with these models have routinely demonstrated biogeophysical regulation of climate by vegetation through albedo, turbulent fluxes, and the hydrologic cycle (10).

The current generation of models has capability beyond hydrometeorology and incorporates ecological advances in biogeochemical and biogeographical modeling (10). Many models simulate the carbon cycle (Fig. 2C) and vegetation dynamics (Fig. 2D). In these models, the biosphere and atmosphere form a coupled system whereby climate influences ecosystem functions and biogeography, which feed back to affect climate. Much of the natural vegetation of the world has been cleared for agriculture (Fig. 3D), and some models also include land-use change.

Tropical Forests

Climate model simulations show that tropical forests maintain high rates of evapotranspiration, decrease surface air temperature, and increase precipitation compared with pastureland (SOM). The most studied region is Amazonia, where large-scale conversion of forest to pasture creates a warmer, drier climate. Surface warming arising from the low albedo of forests is offset by strong evapo-

rative cooling. Similar results are seen in tropical Africa and Asia, and the climatic influence of tropical forests may extend to the extratropics through atmospheric teleconnections. However, forest-atmosphere interactions are complex, and small-scale, heterogeneous deforestation may produce mesoscale circulations that enhance clouds and precipitation.

Flux tower measurements in the Brazilian Amazon confirm that forests have lower albedo compared with pasture, greater net radiation, and greater evapotranspiration, particularly during the dry season (11, 12), producing a shallow, cool, and moist boundary layer. Observations show that forest transpiration is sustained during the dry season (11); this is seen also in CO₂ fluxes (12) and satellite monitoring of vegetation (13, 14), to a greater extent than represented in many models.

Tropical forests contain ~25% of the carbon in the terrestrial biosphere (Fig. 1B), account for ~33% of terrestrial net primary production (NPP) (2), and can sequester large amounts of carbon annually (Fig. 1C). Deforestation released 1.6 Pg C year⁻¹ during the 1990s, chiefly in the tropics (3). Atmospheric analyses suggest that tropical forests are carbon neutral or carbon sinks, which implies offsetting of carbon uptake by undisturbed tropical ecosystems (3, 15).

The net balance among these processes is likely a positive benefit that mitigates global warming through evaporative cooling and carbon sequestration (8). Yet a more complete analysis of forest-atmosphere interactions is required. The biogeochemistry of tropical forests and biomass burning affects atmospheric chemistry and aerosols, which can alter clouds and rainfall (16). Interannual climate variability modulates forest-atmosphere coupling. There is net release of carbon from the biosphere to the atmosphere during warm, dry El Niño years, seen in high atmospheric CO₂ growth rates (3), especially in the tropics (17). Drought makes tropical forests more susceptible to burning during land clearing (18). However, tropical forest productivity may be more resilient to drought than expected (14).

The future of tropical forests is at risk in a warmer, more populous 21st-century world. Tropical forests are vulnerable to a warmer, drier climate (19), which may exacerbate global warming through a positive feedback that decreases evaporative cooling, releases CO₂, and initiates forest dieback (20). Loss of natural forests worldwide in the tropics during the 1990s was as high as 152,000 km² year⁻¹ (1), and Amazonian forests were cleared at a rate of ~25,000 km² year⁻¹ (19). Such land-use pressures are expected to continue in the future and may shift the Amazonian region to a permanently drier climate once a critical threshold of clearing is reached.

Boreal Forests

Climate model simulations show that the low surface albedo during the snow season, evident in local flux measurements (21) and satellite-derived surface albedo (Fig. 1D), warms climate compared to when there is an absence of trees (SOM). Consequently, the boreal forest has the greatest biogeophysical effect of all biomes on annual mean global temperature (7). Loss of boreal forest provides a positive feedback for glaciation (22), whereas forest expansion during the mid-Holocene 6000 years ago amplified warming (23).

Boreal forests differ in their partitioning of net radiation into sensible and latent heat fluxes. Conifer forests have low summertime evaporative fraction (defined as the ratio of latent heat flux to available energy) compared with deciduous broadleaf forests, producing high rates of sensible heat exchange and deep atmospheric boundary layers (21). Flux tower measurements illustrate the potential for changes in species composition, arising from change in the fire regime, to affect climate (24). Along an 80-year fire chronosequence in Alaska, annual net radiation declined by 31% at a 3-year-old postburn

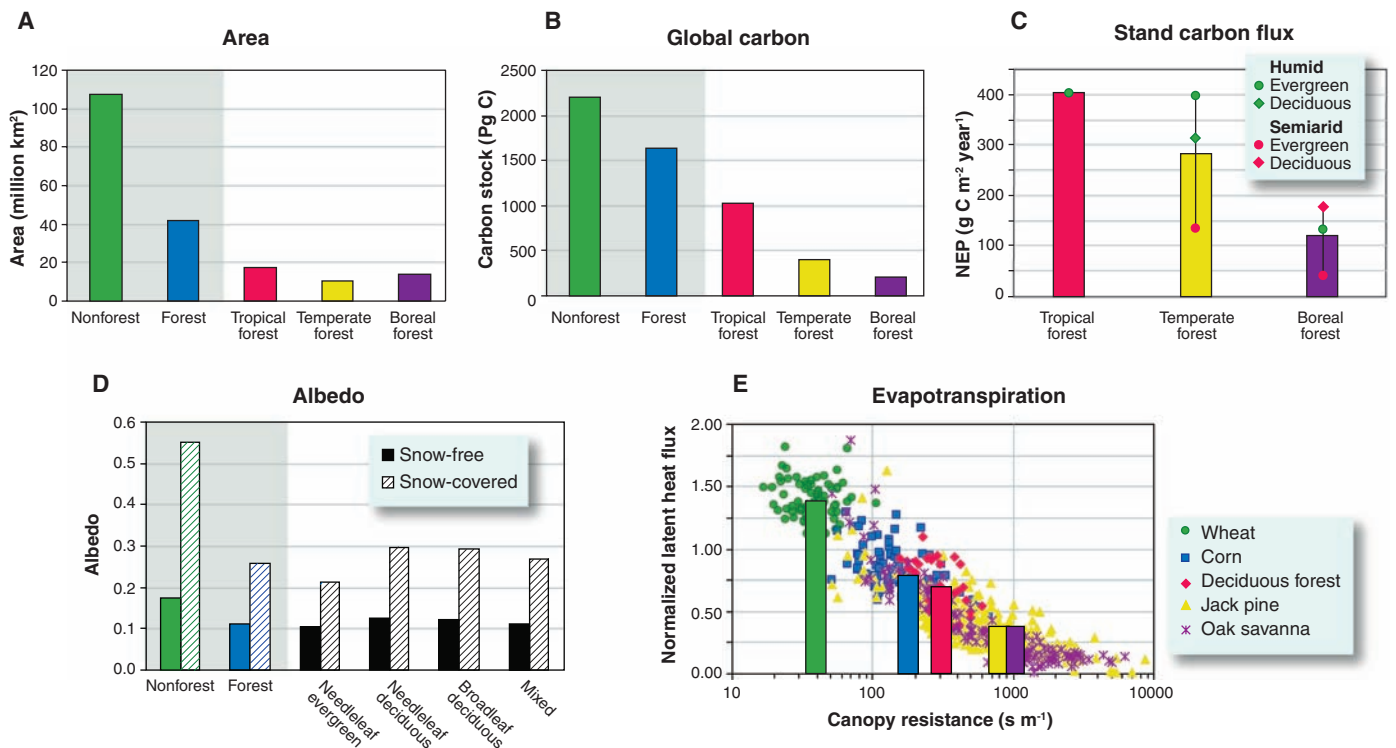


Fig. 1. Biogeochemical (carbon) and biogeophysical (albedo and evapotranspiration) processes by which terrestrial ecosystems affect climate (SOM). (A and B) Geographic extent and total (plant and soil) carbon stock of nonforest (green) and forest (blue) biomes (2). Individual forest biomes are also shown and sum to the forest total. (C) Net ecosystem production (NEP) for tropical, temperate, and boreal forest (47). Individual symbols shown mean NEP for humid evergreen tropical forest, three types of temperate forest, and

three types of boreal forest. Vertical bars show NEP averaged across forest types. (D) Satellite-derived direct-beam albedo for snow-covered and snow-free nonforest (green) and forest (blue) biomes (48). Also shown are individual forest biomes. (E) Evapotranspiration normalized by its equilibrium rate in relation to canopy resistance for wheat, corn, temperate deciduous forest, boreal jack pine conifer forest, and oak savanna (49, 50). Shown are individual data points and the mean for each vegetation type.

Forests in Flux

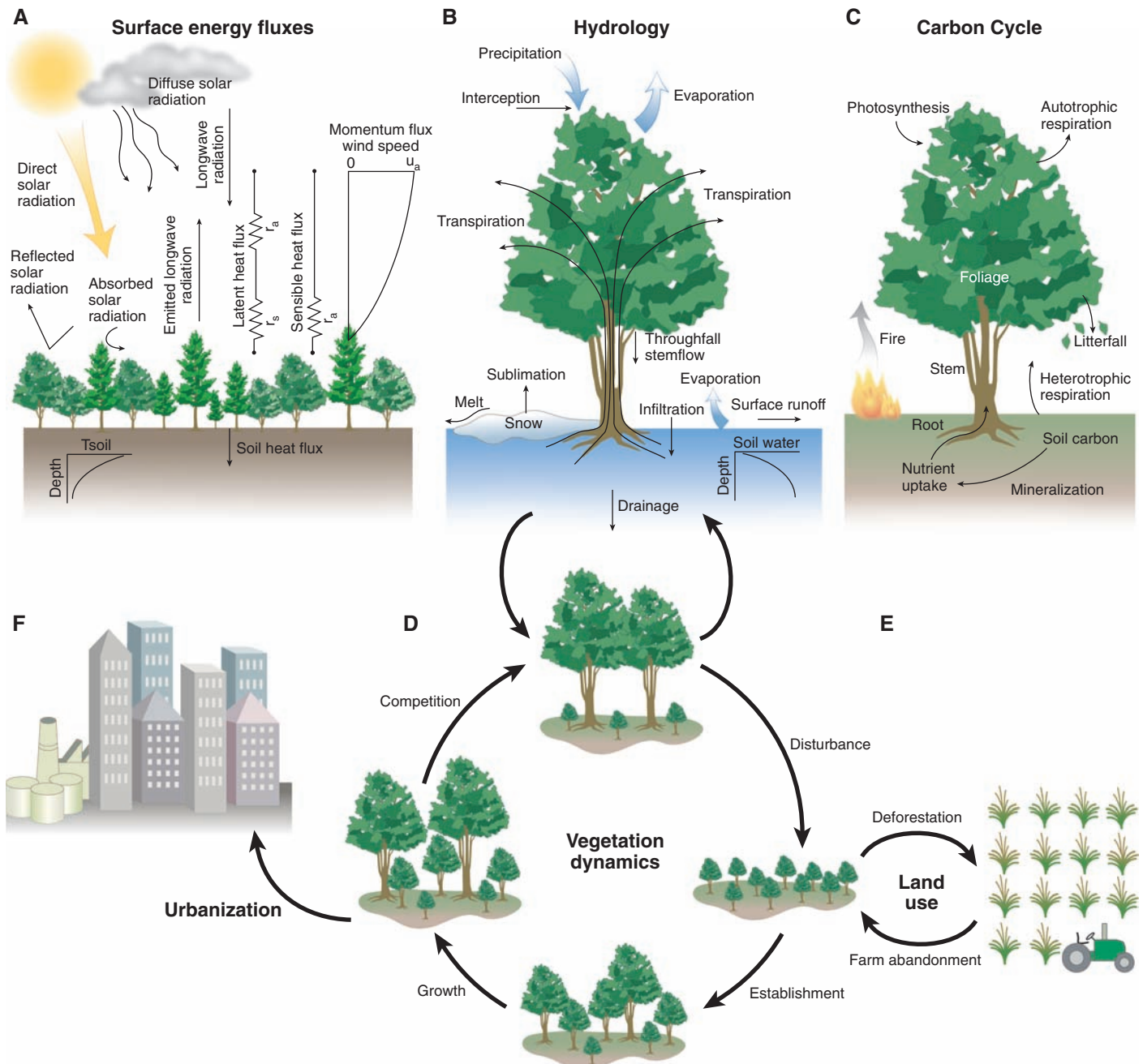


Fig. 2. The current generation of climate models treats the biosphere and atmosphere as a coupled system. Land surface parameterizations represent the biogeophysics, biogeochemistry, and biogeography of terrestrial ecosystems. **(A)** Surface energy fluxes and **(B)** the hydrologic cycle. These are the core biogeophysical processes. Many models also include **(C)** the carbon cycle and **(D)** vegetation dynamics so that plant ecosystems respond to climate change. Some models also include **(E)** land use and **(F)** urbanization to represent human alteration of the biosphere.

site dominated by grasses and a 15-year-old aspen (*Populus tremuloides*) forest compared with an 80-year-old black spruce (*Picea mariana*) forest, primarily in spring and summer. Annual sensible heat flux decreased by more than 50% compared with the 80-year site, mostly in spring and summer. During summer, the aspen forest had the highest latent heat flux, lowest sensible heat flux, and lowest midday Bowen ratio (defined as the ratio of sensible heat flux to latent heat flux).

Boreal ecosystems store a large amount of carbon in soil, permafrost, and wetland (2) and contribute to the Northern Hemisphere terrestrial carbon sink (3), although mature forests have low annual carbon gain (Fig. 1C). The climate forcing from increased albedo may offset the forcing from carbon emission so that boreal deforestation cools climate (8). Similar conclusions are drawn from comprehensive analysis of the climate forcing of boreal fires (25). The long-term forcing is a balance between postfire increase in surface

albedo and the radiative forcing from greenhouse gases emitted during combustion. Averaged over an 80-year fire cycle, the negative forcing from surface albedo exceeds the smaller positive biogeochemical forcing. Yet in the first year after fire, positive annual biogeochemical forcing from greenhouse gas emission, ozone, black carbon deposited on snow and ice, and aerosols exceeds the negative albedo forcing.

Boreal forests are vulnerable to global warming (5). Trees may expand into tundra, but die back

along southern prairie ecotones. In the main boreal forest, there may be loss of evergreen trees and a shift toward deciduous trees. Siberian forests may collapse in some areas and become more evergreen in the north. Increased disturbance from fire or insect outbreaks will shift the forest to a younger age class. Climate forcing arising from younger stand age may be comparable to that arising from biome shifts (24).

Temperate Forests

Much of the temperate forests of the eastern United States, Europe, and eastern China have been cleared for agriculture (Fig. 3D). Croplands have a higher albedo than forests (Fig. 1D), and many climate model simulations find that trees warm surface air temperature relative to crops (SOM). Masking of snow albedo by trees is important in cool temperate climates with snow. Studies of eastern United States forests find that trees also maintain a warmer summer climate compared with crops because of their lower albedo, augmented by evaporative cooling from crops and feedbacks with the atmosphere that affect clouds and precipitation (26). The influence of crops on evapotranspiration is seen in flux tower measurements. Growing season evaporative cooling is greater over watered crops compared with forests, and these plants exert less evaporative resistance (Fig. 1E).

Although global climate models find that temperate forests in the eastern United States warm summer temperature (26), mesoscale model simulations of the July climate of the United States find that trees increase evapotranspiration and decrease surface air temperature compared with crops (27, 28). Atmospheric feedbacks that alter cloudiness affect the magnitude of the temperature response in these simulations. Flux tower analyses show that conifer and deciduous broadleaf forests in North Carolina have lower surface radiative temperature than grass fields because of greater aerodynamic conductance and evaporative cooling of trees compared with grasses (29), but the same may not pertain to cropland (Fig. 1E).

Interannual climate variability affects biosphere-atmosphere coupling. In western Europe, forest and agricultural land have comparable surface radiative temperature when soil is moist but respond differently to drought (30). Forest maintains green vegetation, as indicated by the normalized difference vegetation index, although surface temperature and sensible heat flux increase with drought. Vegetation greenness in cropland declines by ~50%, the surface warms 13°C more than in forest, and the drought enhancement in sensible heat flux is greater than for forest. The different response to drought arises from the deep roots of trees and their access to deeper reservoirs of soil water.

Temperate forests hold ~20% of the world's plant biomass and ~10% of terrestrial carbon (Fig. 1B). Carbon sequestration rates of mature forests are high (Fig. 1C), but temperate forests in the United States historically have been carbon sources because of deforestation (31). Socioeco-

nomic trends in reforestation and fire suppression have shifted these forests to a carbon sink. Similar trends are seen in Europe (3).

The net climate forcing of temperate forests is highly uncertain. Competing biogeophysical forcings from low albedo during winter and evapotranspiration during summer influence annual mean temperature (7). Higher albedo with loss of forest cover could offset carbon emission so that the net climatic effect of temperate deforestation is negligible (8), or reduced evapotranspiration with loss of trees could amplify biogeochemical warming.

The future of temperate forests and their climate services is highly uncertain. The present carbon sink in eastern United States forests is likely to decline as recovering forests mature (31), and these forests face uncertain pressure from climate change, atmospheric CO₂ increase, and anthropogenic nitrogen deposition (5). Change in the balance between deciduous and evergreen trees is likely in the future. Temperate forests are particularly vulnerable to human land use. The trend over the past several decades has been toward farm abandonment, reforestation, and woody encroachment from fire suppression, but meeting the needs of a growing global population could place greater pressures on these forests.

Carbon Cycle Feedbacks

The carbon cycle has long been recognized as important for understanding climate change. Climate models that include the terrestrial and oceanic carbon cycle simulate a positive feedback between the carbon cycle and climate warming that increases the airborne fraction of anthropogenic CO₂ emission and amplifies warming (3, 32). In a comparison of 11 models of varying degrees of complexity, carbon cycle-climate feedbacks increase atmospheric CO₂ at the end of the 21st century by 4 to 44% (multimodel mean, 18%), equivalent to an additional 20 to 224 (parts per million) (ppm) (multimodel mean, 87 ppm) (3). Analyses of observed atmospheric CO₂ concentrations indicate that such a decline in the efficiency of the carbon cycle to store anthropogenic CO₂ in ocean and land is occurring, and to a greater extent than estimated by models (33).

Much of the model uncertainty arises from the terrestrial biosphere (3, 32). Plants respond to rising atmospheric CO₂ through photosynthetic enhancement, and this "CO₂ fertilization" is a negative feedback to higher atmospheric CO₂ concentration. In the multimodel comparison, land carbon storage increases with higher atmospheric CO₂ in all models, driven by a 12 to 76% increase in NPP with CO₂ doubling (multimodel mean, 48%), offset slightly by enhanced heterotrophic respiration (3). Free-air CO₂ enrichment studies in forests find that a ~50% increase in atmospheric CO₂ concentration sustained over several years enhances NPP by 23% (34), but the long-term outcome is unclear, especially when interactions with nitrogen availability are considered (5).

Climate change reduces carbon storage from CO₂ fertilization. Terrestrial carbon storage declines

with warming in the 11 models (multimodel mean, -79 Pg C °C⁻¹), but this varies greatly among models (3). Soil carbon turnover rate increases by 2 to 10% °C⁻¹ in all models in a positive climate feedback (multimodel mean, 6% °C⁻¹). Terrestrial NPP decreases by up to -6% °C⁻¹ in seven models (multimodel mean, -3% °C⁻¹) and increases by 1 to 2% °C⁻¹ in four models. Climate change can enhance NPP (negative feedback) in boreal forests where temperature increases and decrease NPP (positive feedback) in tropical forests where greater evaporative demand dries soil (35).

Ecological responses to climate change alter the biogeophysical functioning of forests and also provide climate feedback. These "indirect" carbon cycle feedbacks include changes in stomatal conductance, leaf area index, and species composition. Decreased stomatal conductance with higher atmospheric CO₂ concentration reduces evapotranspiration and reinforces warming (SOM). More extensive tree cover may enhance warming in boreal forests by decreasing surface albedo. Reduced evapotranspiration in a drier climate may initiate a positive climate feedback leading to loss of tropical forest (20).

Land-Use Forcing

Although carbon emission from forest clearing has long been studied, only recently has the biogeophysical forcing of climate from land use been recognized. Vast tracts of forestland have been converted to agriculture (Fig. 3D), and climate warming over the industrial era may be smaller than that expected from rising atmospheric CO₂ alone, primarily from increased spring albedo with loss of extratropical forests (36).

Carbon emission from land use dampens biogeophysical cooling. The dominant competing signals from historical deforestation are an increase in surface albedo countered by carbon emission to the atmosphere. Biogeophysical cooling may outweigh biogeochemical warming at the global scale (37) or may only partially offset warming (38). The net effect of these competing processes is small globally but is large in temperate and high northern latitudes where the cooling due to an increase in surface albedo outweighs the warming due to land-use CO₂ emission.

Climate trends over the 21st century, too, should be driven by interactions among CO₂ emission, land use, and forest-atmosphere feedbacks. The biogeophysical land-use forcing of climate may in some regions be of similar magnitude to greenhouse gas climate change. The Intergovernmental Panel on Climate Change (IPCC) Special Report on Emission Scenarios (SRES) A2 narrative storyline has high CO₂ emission (SOM), and climate model simulations of Feddema *et al.* (39) produce 2°C warming of planetary temperature over the 21st century in the absence of land cover change. The A2 storyline describes widespread agricultural expansion with most land suitable for agriculture used for farming by 2100 to support a large global population (fig. S1). Forest loss leads to additional warming in Ama-

Forests in Flux

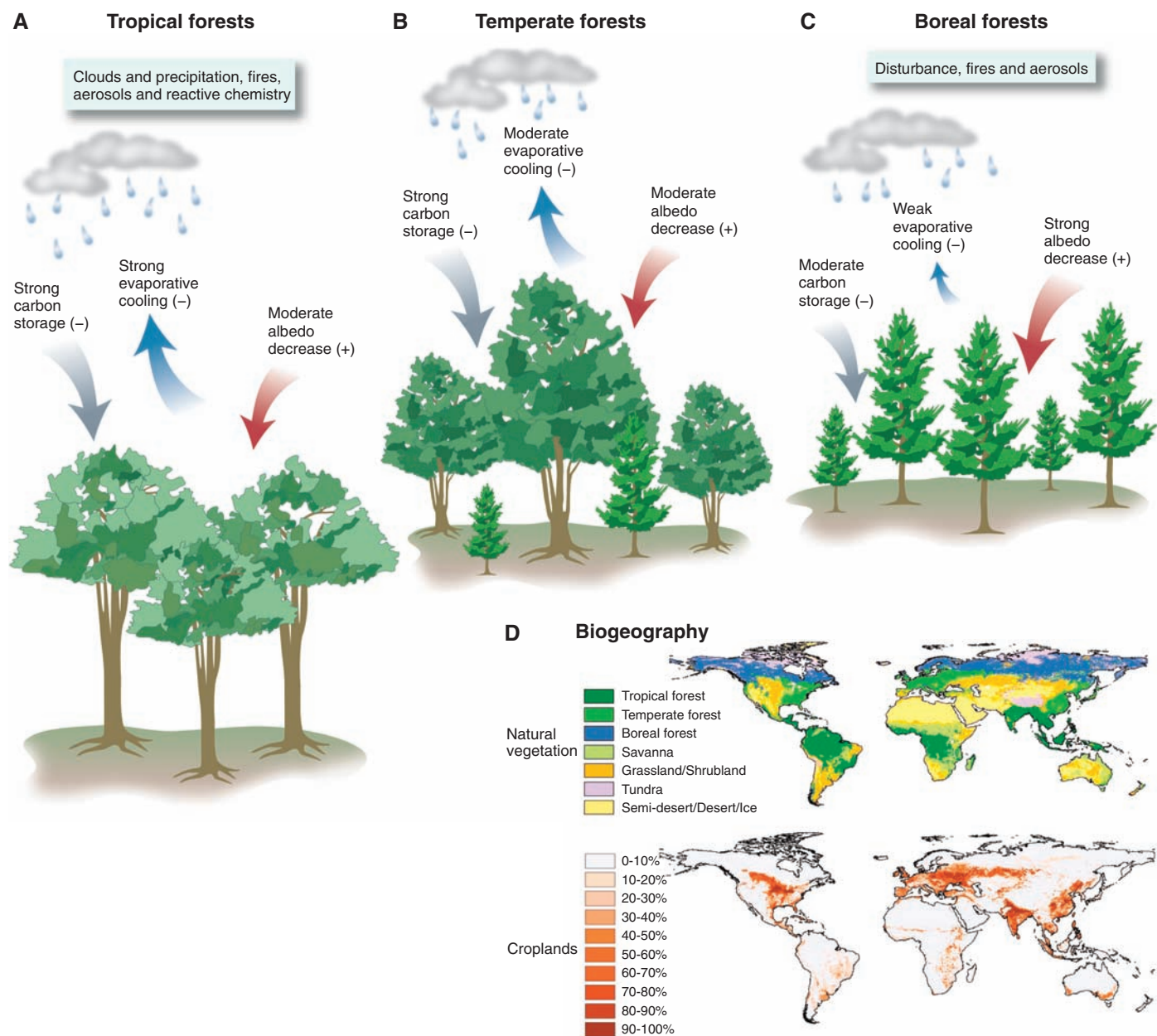


Fig. 3. Climate services in (A) tropical, (B) temperate, and (C) boreal forests. Text boxes indicate key processes with uncertain climate services. (D) Natural vegetation biogeography in the absence of human uses of land and cropland (percent cover) during the 1990s. Vegetation maps are from (51).

zonia, but cooling that mitigates warming in mid-latitudes (39). The B1 narrative storyline is a low greenhouse gas emission scenario. Farm abandonment and reforestation yield loss of farmland by 2100 because of assumed increases in agricultural efficiency and declining population (fig. S1). The model simulates 1°C warming in the absence of land cover change and weaker land-use forcing.

When the carbon cycle is included, the different SRES storylines of fossil fuel emission and land use may yield similar 21st-century climates despite vastly different socioeconomic trajectories (9). Widespread expansion of agriculture in A2 leads to biogeophysical cooling. Biogeophysical processes lead to warming in B1, primarily because

of temperate forest regrowth. In the A2 and B1 storylines, net carbon loss from deforestation causes biogeochemical warming, greatest in A2 because of extensive deforestation and weaker in B1 because of temperate reforestation and less tropical deforestation. Biogeochemical warming offsets biogeophysical cooling in A2 to provide net global warming. The B1 net warming is similar to A2 because moderate biogeophysical warming from temperate reforestation augments weak biogeochemical warming from tropical deforestation.

Research Needs

Through albedo, evapotranspiration, the carbon cycle, and other processes, forests can amplify or damp-

en climate change arising from anthropogenic greenhouse gas emission. Negative climate forcing in tropical forests from high rates of carbon accumulation augments strong evaporative cooling (Fig. 3A). The combined carbon cycle and biogeophysical effect of tropical forests may cool global climate, but their resilience to drought, their status as carbon sinks, interactions of fires, aerosols, and reactive gases with climate, and the effects of small-scale deforestation on clouds and precipitation are key unknowns. The climate forcing of boreal forests is less certain (Fig. 3C). Low surface albedo may outweigh carbon sequestration so that boreal forests warm global climate, but the net forcing from fire must also be considered, as well as effects of dis-

