


REVIEW ARTICLE

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Special Collection:
Quantifying Nature-based
Climate Solutions

Key Points:

- Nature-based climate solutions have been advocated for centuries, but have been distorted by academic bias and colonialist prejudice
- Earth system science, while recognizing the climate services of the biosphere, has a geophysical bias in interdisciplinary collaboration
- To realize the potential for planetary stewardship, Earth system models must embrace the living world equally with the fluid world

Supporting Information:

Supporting Information may be found in the online version of this article.

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Reimagining Earth in the Earth System

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Abstract Terrestrial, aquatic, and marine ecosystems regulate climate at local to global scales through exchanges of energy and matter with the atmosphere and assist with climate change mitigation through nature-based climate solutions. Climate science is no longer a study of the physics of the atmosphere and oceans, but also the ecology of the biosphere. This is the promise of Earth system science: to transcend academic disciplines to enable study of the interacting physics, chemistry, and biology of the planet. However, long-standing tension in protecting, restoring, and managing forest ecosystems to purposely improve climate evidences the difficulties of interdisciplinary science. For four centuries, forest management for climate betterment was argued, legislated, and ultimately dismissed, when nineteenth century atmospheric scientists narrowly defined climate science to the exclusion of ecology. Today's Earth system science, with its roots in global models of climate, unfolds in similar ways to the past. With Earth system models, geoscientists are again defining the ecology of the Earth system. Here we reframe Earth system science so that the biosphere and its ecology are equally integrated with the fluid Earth to enable Earth system prediction for planetary stewardship. Central to this is the need to overcome an intellectual heritage to the models that elevates geoscience and marginalizes ecology and local land knowledge. The call for kilometer-scale atmospheric and ocean models, without concomitant scientific and computational investment in the land and biosphere, perpetuates the geophysical view of Earth and will not fully provide the comprehensive actionable information needed for a changing climate.

Plain Language Summary Terrestrial ecosystems provide a natural solution to planetary warming by storing carbon, dissipating surface heating through evapotranspiration, and other processes. That forests, in particular, influence climate is a centuries-old premise, but its potential for planetary stewardship has not been realized. In an acrimonious controversy spanning several centuries, managing forests to purposely change climate was advocated, legislated, and resoundingly dismissed as unscientific. Similar intellectual bias is evident in today's Earth system science and the associated Earth system models, which are the state-of-the-art models used to inform climate policy. The popular characterization of Earth system science lauds its interdisciplinary melding of physics, chemistry, and biology, but the models emphasize the physics and fluid dynamics of the atmosphere and oceans and present a limited perspective of terrestrial ecosystems in the Earth system. Ecologists studying the living world increasingly have a voice in Earth system science as we move beyond the physical basis for climate change to Earth system prediction for planetary stewardship. As we once again look to forests to solve a climate problem, we must surmount the disciplinary narrowness that failed to answer the forest-climate question in the past and that continues to limit the interdisciplinary potential of Earth system science.

1. Introduction

Earth system science is described as providing the interdisciplinary knowledge to manage the planet for a growing human population (Steffen et al., 2020). A key tool is Earth system models, which are the most complex in a progression from atmospheric general circulation to the physical climate system to treating Earth as an interacting

physical, chemical, and biological system driven by human actions. Although Earth system models are defined to include biology (G. M. Flato, 2011; Jones, 2020; NRC, 1986; Steffen et al., 2020), the integration of the biosphere into the models has not been straightforward. One telling example is the model source code itself. The models include terrestrial and marine ecosystems and many ecological processes that influence climate, but model code (i.e., the number of lines of code) is dominated by the physics of atmosphere and ocean circulation (Alexander & Easterbrook, 2015).

Earth system models originated with models of atmosphere and ocean, and attempts to incorporate biological processes have subordinated ecology to the physical geosciences. As described in the sixth assessment report of the Intergovernmental Panel on Climate Change (IPCC), Earth system models “build on the fundamental laws of physics (e.g., Navier-Stokes or Clausius-Clapeyron equations)” (D. Chen et al., 2021, p. 215). Neglected in this definition is that life is a planetary force that shapes climate and other Earth processes (Beerling, 2007; Budyko, 1974, 1986; Lenton et al., 2004; Lovelock, 1979; Schneider & Londer, 1984). On land, where the influence of plants, microbes, and other organisms on climate and atmospheric composition is profound, biosphere-atmosphere coupling is driven not just by physical laws and constraints but also by biological and ecological processes. Missing from the IPCC description of Earth system models is the physiology of leaves and plants, the organization of plants into populations and communities, the pattern of communities across landscapes resulting from disturbance and successional dynamics, and the biology and chemistry of soils. These aspects of the biosphere are not described by the laws of thermodynamics and fluid dynamics. Similar arguments can be made for the importance of marine ecology as well (Bonan & Doney, 2018).

The origin story of Earth system science itself fails to adequately represent its interdisciplinarity. The conceptualization of the biosphere in the Earth system is commonly traced to Vernadsky's *The Biosphere*, which framed the biosphere in terms of biogeochemistry (Steffen et al., 2020; Vernadsky et al., 1998). In fact, forests have long been known to influence temperature, precipitation, humidity, and wind, and forests have been purposely managed to improve climate. From the 1500s and into the 1900s, in what has been called the “forest-climate question,” the effect of deforestation on climate and whether reforestation was required to prevent desiccation of the land were the subject of scientific, public, and political debate (Bonan, 2023; Coen, 2018; Davis, 2016; Ford, 2016; Fressoz & Locher, 2020; Grove, 1995; Moon, 2013; Zilberstein, 2016). Forest clearing in British and French America during the 1600s and 1700s was thought to warm the harsh winter climate, as indeed the climate of Europe was thought to have warmed from centuries of deforestation. Subsequent deforestation of tropical islands, India, Australia, and elsewhere led to concern for a decline in rainfall and calls throughout the 1800s for reforestation and forest protection. An interdisciplinary science of forest meteorology arose before prominent meteorologists at the close of the nineteenth century, seeking a geophysical understanding found in large-scale atmospheric dynamics, wrongly rejected forest influences on the macroclimate. Today, the biosphere is known to influence climate at multiple spatial and temporal scales through many physical and chemical processes, but a common science across disciplines is lacking.

The forest-climate question presents a complex storyline, and history holds a cautionary lesson. The climate benefits of forests have long been used to defend the illegal seizure of lands from their Indigenous stewards (Davis, 2007, 2016; Rajan, 2006). Moving forward, research on interactions between land use and climate change should be carried out with due respect for the rights of Indigenous and marginalized communities and, ideally, in partnership with them and integrating Indigenous knowledge into land management (Mistry et al., 2016; Orlove et al., 2022). Additionally, the forest-climate controversy incorrectly shaped our perception of climate. In dismissing forest influences, the premise that human actions can alter climate was also rejected (Bonneuil & Fressoz, 2016; Fressoz & Locher, 2020). Moreover, a central tenet of Earth system science—the interconnectedness of the biosphere and atmosphere—was denied (Bonan, 2023).

If Earth system science is to meaningfully inform future socioeconomic pathways, participation must include academic disciplines, knowledge sources, and peoples not commonly involved in the modeling (Coen & Jonsen, 2022; NASEM, 2022). The exclusion of social sciences from Earth system science has been recognized (NASEM, 2022; Steffen et al., 2020). Using the example of managing climate with forests, we examine intellectual biases in climate science and ecology that have shaped the conceptualization of Earth as a system, hindered the implementation of ecology in Earth system models, and limited the potency of nature-based climate solutions. We focus on forest ecosystems because of the multi-century interest in managing climate with forests and the relevance of the historical controversy to present-day nature-based climate solutions, although similar arguments

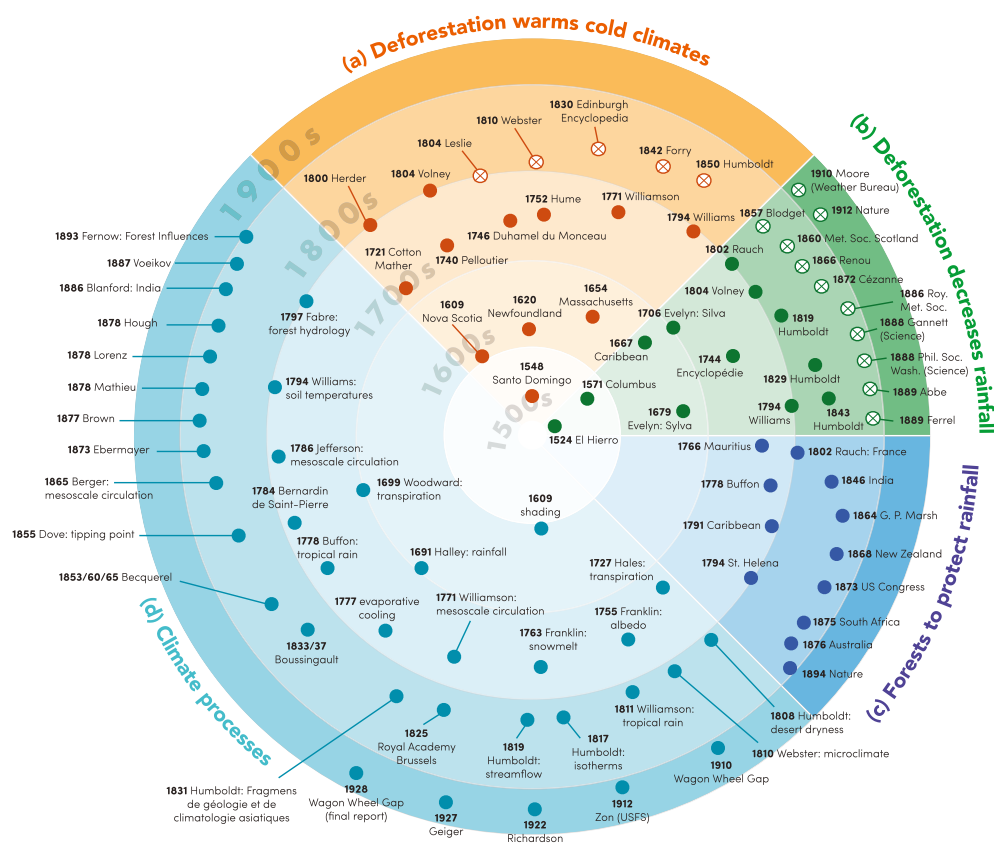


Figure 1. Timeline of the forest-climate question in Western scientific thought. Shown is the progression from the 1500s to the early 1900s of the idea that forests influence climate and that deforestation changes climate. Each dot represents a key moment. Beginning in the 1500s, thinking radiated outward in four main themes of (a) deforestation warms cold climates, (b) deforestation decreases rainfall, (c) planting and conserving forests to protect rainfall, and (d) scientific discovery of ecologically-based climate processes. The forest-climate question peaked in the late 1800s, when concern over a drying of the land and calls for reforestation to ensure rainfall faced backlash from meteorologists. Open circles are studies that dismissed the influence of forests on climate. See Text S1 in Supporting Information S1 for a description of each entry and the corresponding reference.

could be made for other terrestrial ecosystems. As we show, Earth system science must be reframed to elevate the land, its vegetation, and soils—the earth in the Earth system.

We begin by reassessing the forest-climate question. Many of the concepts in today's science of ecosystem-climate coupling date to the 1700s and 1800s, but the discord prevented acceptance of an interdisciplinary science. We then show that divergent understanding of the biosphere in the Earth system is still evident in today's nature-based climate solutions, which, as in the past, aim to manage forests for climate protection. Next, we reexamine the modern origin of Earth system science to show that climate scientists have narrowly constrained ecology to energy and chemical fluxes. In Earth system models, climate scientists today are again defining the ecology of the Earth system. Then we consider what aspects of terrestrial ecology need to be included in Earth system models, not just for climate prediction but also for Earth's future. Terrestrial ecosystems are, after all, more than sources and sinks of energy and chemicals.

2. The Forest-Climate Question: Past Controversies

Though people have been managing forests to protect their environment for millennia, the forest-climate question gained prominence in Western scientific thought with European settlement of the Americas, first with confident belief that deforestation was improving climate, followed by worldwide concern for desiccation and then calls for reforestation to increase rainfall. The debate ultimately collapsed in a controversy of overheated claims for and against the science. Figure 1 provides a timeline of key thought in the West since the 1500s.

The different climate of the Americas compared with Europe was attributed to its vast forests, and colonial settlers in Canada and New England attempted to “improve” the climate by cutting down forests, draining swamps, and creating fields to lessen the winter cold, though the effectiveness was questioned even at the time (Figure 1a; see Text S1 in Supporting Information S1). Settlers of French Canada and British America in the 1600s believed that clearing forests warmed the cold winters by exposing the ground to the heat of the sun. By the mid-1700s, there was a belief that deforestation had warmed Europe and was likewise warming the northern lands of America. The changing American climate was common knowledge, seen in the many writings of American and European intellectuals. The premise of climate change lacked direct observations, however, and by the early to mid-1800s the idea of deforesting the land to moderate the cold winters was largely rejected when meteorological observations showed no evidence for a changing climate.

Another element to the forest-climate question was that forests cause the wet, humid climate found in the Americas and that deforestation, consequently, decreases rainfall (Figure 1b; see Text S1 in Supporting Information S1). The idea arose with Spanish exploration in the 1500s, was reported by Christopher Columbus, and spread with the clearing of Caribbean settlements during the 1600s. The English forest conservationist John Evelyn sounded the warning of uninhabitable Caribbean islands, and the idea that deforestation desiccated the land became entrenched among European and American scholars in the 1700s and into the 1800s.

In the 1600s and 1700s, concern that deforestation of tropical islands—in the Caribbean, on Mauritius, and elsewhere—had caused drought prompted early reforestation efforts (Figure 1c; see Text S1 in Supporting Information S1). By the 1800s, fears that deforestation was desiccating the land were widespread, especially in colonial settings such as British India and French North Africa (Davis, 2007; Rajan, 2006). In Europe, the forest-climate question was widely debated in France (Ford, 2016) and the Austro-Hungarian Empire (Coen, 2018). George Perkins Marsh wrote of the need for forest conservation in *Man and nature* (1864). The US Timber Culture Act (1873) legislated planting forests in the prairie to ensure rainfall, and the US foresters Franklin Hough and Bernhard Fernow, among others, stridently advocated the climate benefits of forests. As late as 1894, an article in *Nature* continued to advocate managing forests for climate protection.

Critical to the controversy was uncertainty over the extent to which forests really do affect climate. Many of the claims for the benefits of forests were overstated. Meteorologists in the mid-1800s, as their science advanced, forcibly denied an influence of forests on rainfall (Figure 1b; see Text S1 in Supporting Information S1). In the US, skeptics included Lorin Blodget, Henry Gannett (US Geological Survey), Cleveland Abbe (US Weather Bureau), William Ferrel, and Willis Moore (US Weather Bureau). Multiyear precipitation measurements had become available in many locations throughout the US. Finding no signal of forests in the observations, the meteorologists were confident in their claim, though the sparseness of the observational network limited the spatial coverage and statistical analysis of the time series was in its infancy. Gannett wrote of the “uselessness” of planting trees for their climate effects. To Abbe, the combination of measurements, statistical analysis, and theories of large-scale atmospheric dynamics, what he called “rational climatology,” proved that there was no influence of forests. Willis Moore, chief of the US Weather Bureau, dismissed forest influences on rainfall with the claim that “while much has been written on this subject, but little of it has emanated from meteorologists.” Many European meteorological societies and scientists agreed. A frustrated writer to *Nature* (1912) summed up the controversy with the comment that “the literature on the subject is somewhat bewildering.”

The historical forest-climate controversy can be viewed in many ways. One is as a lesson about the hubris of scientific expertise when confronted with Indigenous environmental knowledge. In many colonial contexts, especially in regions with unpredictable agricultural yields, planting trees on cleared or barren land appeared to colonial officials and scientists as a practical solution for regularizing rainfall and agriculture by returning to some preconceived ecological equilibrium (Davis, 2007, 2016; Grove, 1995; Rajan, 2006). This solution, though, was frequently predicated on a misguided colonial view of Indigenous land use as causing drought and ecological disequilibrium. This was especially the case in French colonial Africa.

From the mid-1800s onwards, colonial French foresters and settlers in the region encompassing Morocco, Algeria, and Tunisia had been wrongly convinced that land use practices by Indigenous peoples had steadily desiccated the region. To make the land more agriculturally productive, French foresters and settlers pushed for reforestation on lands seized from Indigenous peoples (Davis, 2007, 2016). Their theories were adopted and expanded upon by the English forester Edward Percy Stebbing, who blamed shifting cultivation, overgrazing, and fire for causing drought and the widespread encroachment of the Sahara into the Sahel. To counter this perceived

degradation, Stebbing proposed planting forest belts across the region (Stebbing, 1935). The French colonial administrator André Aubréville further contested that Indigenous land use practices were causing the whole of tropical Africa to become more arid and threatened by desertification (Aubréville, 1949). He proposed a continent-wide system of forest preserves, reforestation, and fire interdiction to re-equilibrate the African climate. Such natural solutions to halting desertification were reflected in the first United Nations Conference on Desertification in 1977, where part of the proposed plan of action was to plant trees, establish green belts, and protect existing vegetation from overgrazing, fuel collection, and degradation (UN, 1977, pp. 29–32). It is in this context that climate scientists have applied their models to study how land degradation in the Sahel contributes to drought (Charney et al., 1975; Xue & Shukla, 1993; Xue et al., 2004; Zeng et al., 1999).

Another dimension to the forest-climate question is that disciplinary divides hampered the study of Earth as an integrated system (Bonan, 2023). Meteorology became its own academic specialization, which, according to Abbe, “outranks all other branches of science in its universal importance and its difficulty” (Abbe, 1895, p. 712). The science of forest meteorology became equated with forest microclimates, not the large-scale macroclimate, seen, for example, in the work of Rudolf Geiger (Geiger, 1927). The US Forest Service originated from congressional concern in 1876 over the deterioration of climate caused by the destruction of forests, but US foresters turned away from the study of forests and climate, and the forest-climate controversy became seen as a stain on the forestry profession (Kittredge, 1948, p. 13; Kotok, 1940; Pinchot, 1905, p. 56). Ecology was emerging at that time as a science, but instead of viewing a coupled system, pioneering plant ecologists framed climate as an exogenous factor determining the vegetation in a region. Eugen Warming, in *Oecology*, acknowledged the air is cooler in forests, “and this may perhaps lead to an increase in the deposit of dew, in cloudiness, and in rainfall” (Warming, 1909, p. 76), but his book is a much more extensive treatise on climate as a determinant of growth form and plant communities. Frederic Clements likewise explained climax vegetation as an expression of climate (Clements, 1936).

However, several of the key ideas on biosphere-atmosphere coupling seen in today's science emerged during the forest-climate controversy. This knowledge would not be revisited until the modern tools of climate modeling, remote sensing, and eddy covariance flux measurements quantitatively demonstrated forest-climate interactions. The foundation for the new science, though, was established even as meteorologists rejected an influence of forests on the large-scale climate. Lewis Richardson, in his pioneering work on numerical weather prediction, needed to mathematically model stomatal conductance and transpiration to solve the equations of atmospheric state and motion (Richardson, 1922).

3. Ecosystem-Climate Interactions

From the forest-climate controversy grew an understanding of the processes through which the biosphere influences climate (Figure 1d; see Text S1 in Supporting Information S1). Transpiration was known to provide water vapor that condenses to rainwater in a recycling of precipitation. Georges-Louis Leclerc, Comte de Buffon, wrote in 1778 of a positive feedback whereby forest transpiration cools temperature and increases precipitation, further sustaining forest growth and lessening the tropical heat. Later, Alexander von Humboldt described how the absence of vegetation contributes to desert dryness. Others recognized the greater evaporative cooling of tropical forests compared with temperate forests. Modern science confirms that evapotranspiration is a primary mechanism by which vegetation cools the surface (Davin & de Noblet-Ducoudré, 2010; Shukla & Mintz, 1982). The cooling is greater in the tropics than in temperate forests (Alkama & Cescatti, 2016; Boysen et al., 2020; Davin & de Noblet-Ducoudré, 2010; X. Lee et al., 2011). The positive feedback described by Buffon and Humboldt is readily familiar to scientists studying tropical deforestation today (Gentine et al., 2019; Spracklen et al., 2018). Indeed, the Amazon is seen as a climate tipping point in which deforestation switches the region to a dry climate with savanna or dry seasonal forests (Lenton et al., 2008; Nobre & Borma, 2009; Oyama & Nobre, 2003; Steffen et al., 2018).

Another process that is now the mainstay of the science of biosphere-atmosphere coupling was also identified. Mid-eighteenth-century American scholars proposed that cleared land interspersed among forests generates atmospheric circulations because of the contrast in heating between the cool forests and warm fields (Figure 1d; see Text S1 in Supporting Information S1). Later scholars recognized that the climate response to small-scale deforestation differs from that of regional deforestation, and they advanced a theory by which precipitation increases when fields are interspersed among forests, but decreases with large-scale forest clearing. Today's science

confirms the existence of mesoscale atmospheric circulations created by landscape heterogeneity (Mahmood et al., 2014; Pielke et al., 2011; J. Wang et al., 2009). In the tropics, there may be a spatial threshold in which small-scale forest clearing increases rainfall but larger deforestation decreases rainfall (Khanna et al., 2017).

Experimental studies were devised to measure the effects of forests on climate (Figure 1d; see Text S1 in Supporting Information S1). Samuel Williams (1794) compared soil temperature in forests and fields. Antoine-César Becquerel in France (1860), Ernst Ebermayer in Germany (1873), and others established meteorological observatories to compare measurements in forests and fields. Later scientists used paired watershed experiments to study the effects of forest clearing. While establishing the influences of forests on local microclimates (e.g., air temperature), the meteorological observatories were inconclusive in demonstrating an effect on precipitation and became a target of criticism by meteorologists. Nonetheless, the observatories produced an interdisciplinary melding of meteorology, forest ecology, plant physiology, hydrology, and soil physics that is recognizable in today's science (Blyth et al., 2021; Bonan, 2016, 2019; R. A. Fisher & Koven, 2020). Notable in this respect are Becquerel and Ebermayer. Among their findings was that the deep roots of trees sustain evapotranspiration compared with grasses, thereby promoting surface cooling as confirmed in modern studies (Teuling et al., 2010; Zaitchik et al., 2006). The answer to the forest-climate question, these and other like-minded scientists were saying, could not be obtained from meteorology alone. Today's global network of several hundred eddy covariance flux towers in forest, grassland, cropland, and other biomes (Baldocchi et al., 2024; Pastorello et al., 2020) is the modern successor to the nineteenth century meteorological observatories and has identified forest-climate connections at the macroscale (Beer et al., 2010; Migliavacca et al., 2021) and temporally along post-disturbance successional trajectories (Goulden et al., 2011; Liu et al., 2005).

The meteorological observatories led to an understanding of what we recognize today as forest microclimates, but the investigators also examined scaling to larger regions. Becquerel discussed how foresting the Sahara would change atmospheric circulations, thereby altering the climate of Europe—an early example of an ecoclimatic teleconnection that connects distant locations. Modern science has identified several such teleconnections (Badger & Dirmeyer, 2016; Devaraju et al., 2015; Swann et al., 2018). Afforesting the mid-latitudes, for example, increases energy absorption in the Northern Hemisphere and causes the Hadley circulation to shift northwards to redistribute heat between the hemispheres (Laguë & Swann, 2016; Swann et al., 2012). The warmer, drier climate resulting from tropical deforestation can also alter the Hadley circulation, with consequences for extratropical precipitation and atmospheric transport from North Africa across the Atlantic to South America (Y. Li et al., 2021). As in the past, however, the science is challenged to reconcile the local influences of forests measured by flux towers (i.e., a spatial footprint less than a few km²) with the larger scale influences, though there is a recognition that the local influences directly within and above forests differ from the nonlocal, or remote, influences (Pongratz et al., 2021; Winckler et al., 2019).

Today, we have an understanding that forests affect climate at local, regional, and global scales through a myriad of processes (Figure 2). Forests warm the surface climate because of their low albedo compared with fields, especially when snow is on the ground such as in northern conifer and boreal forests. They cool the surface through evapotranspiration, and their tall canopies enhance turbulent mixing with the overlying air. Forests store large amounts of carbon in woody biomass and in the soil. Biogenic volatile organic compounds (BVOCs) emitted into the atmosphere and other biogenic particles (e.g., pollen, spores, bacteria) provide aerosols that scatter solar radiation, alter cloud radiative properties, and favor cloud droplet formation.

Several lines of evidence including satellite land surface temperature, air temperature observations, and climate model experiments reveal the influence of forests on temperature. Satellite measurements of land surface temperature show that forests are generally cooler than open land during the day and warmer at night, but the temperature signal varies with location and time of year (Alkama & Cescatti, 2016; Bright et al., 2017; Duveiller et al., 2018). Air temperature measurements above forests show similar local influences (X. Lee et al., 2011; M. Zhang et al., 2014). Climate model experiments that contrast a forested and deforested world show the large-scale impacts of deforestation (Boysen et al., 2020; Davin & de Noblet-Ducoudré, 2010). In general, multiple analyses find that tropical forests locally cool surface temperature in the annual mean, with lesser cooling in temperate forests and warming in some regions of the boreal forest (Figures 3a–3c).

A consensus is that tropical forests cool the surface climate, enhance rainfall, and contribute to the land carbon sink that removes anthropogenic CO₂ emissions from the atmosphere (D. Lawrence & Vandecar, 2015; Spracklen et al., 2018). The boreal forest, on the other hand, has conflicting biogeophysical and biogeochemical outcomes.

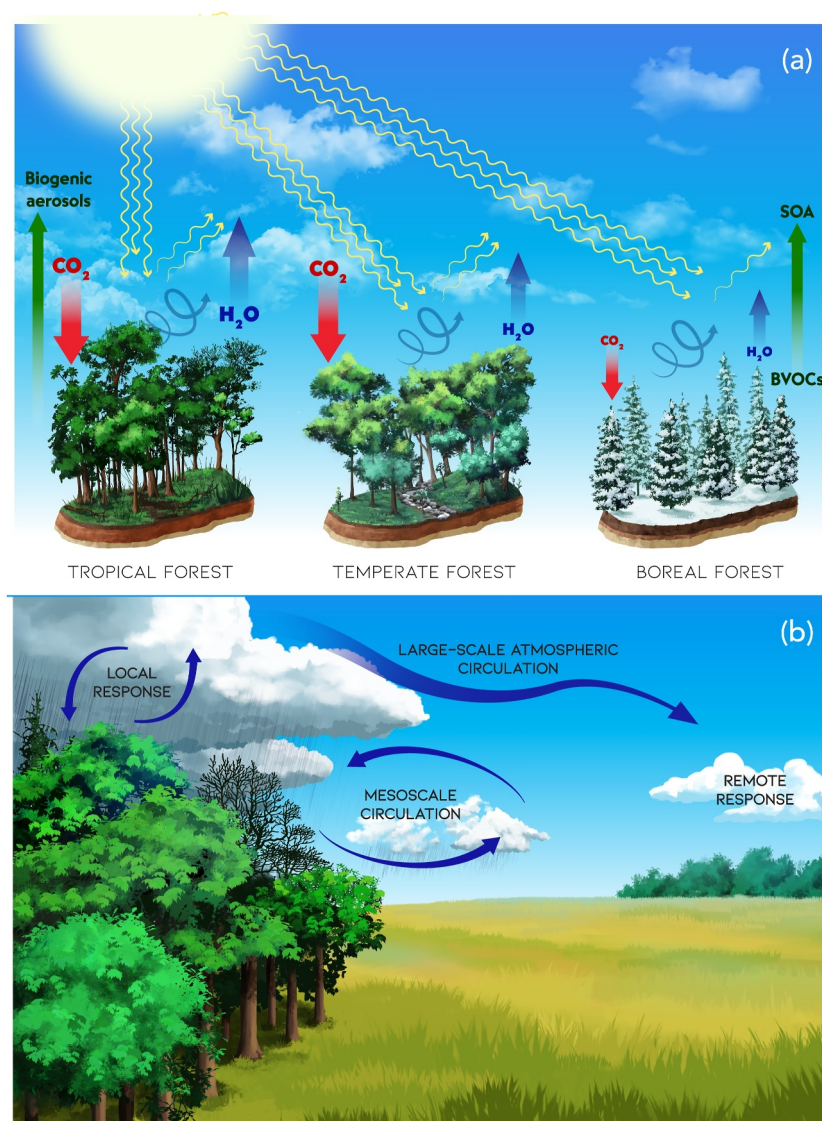


Figure 2. Climate services of forests. Updated from Bonan (2008) to distinguish local and nonlocal influences. (a) Shown are local influences of tropical, temperate, and boreal forests compared with cleared land. Reflection of solar radiation (albedo; yellow upward arrows), evapotranspiration (blue upward arrows), and turbulent mixing (spiral arrows) are three key biogeophysical processes. Biogeochemical processes include CO₂ storage in plant biomass and soils (red downward arrows) and biogenic aerosols (green upward arrows). Significant aerosol influences on climate have been identified in tropical and boreal forests. Tropical forests emit biogenic volatile organic compounds (BVOCs) and other biogenic aerosols. Boreal conifers emit BVOCs that produce secondary organic aerosols (SOA). These processes shape the atmospheric boundary layer above the canopy. The relative size of the arrows denotes differences in magnitude across forest biomes. (b) Nonlocal influences arise when large-scale forest clearing or planting alters atmospheric circulations. Mesoscale circulations can result from the different heating of forested and open land. Shifts in large-scale atmospheric circulation can change the climate in locations far from the altered forest cover.

Albedo, evapotranspiration, surface roughness, and carbon storage are all dependent on forest properties and functioning, and they interact in different ways to determine climate outcomes. The net balance among these processes, which operate across a range of spatial scales, remains uncertain in boreal forests, but the climate cooling is less than that of tropical forests (Windisch et al., 2021). Additional complexity arises because secondary organic aerosols (SOA) produced in the emission of BVOCs from boreal conifers cool temperatures by brightening clouds (Lihavainen et al., 2015; Scott et al., 2018; Yli-Juuti et al., 2021). Climate cooling from the biogenic aerosols produced by boreal conifer forests, in conjunction with carbon accumulation in wood and soil, may offset the warming from the low forest albedo (Kallioikoski et al., 2020; Kulmala et al., 2020). Fires, logging,

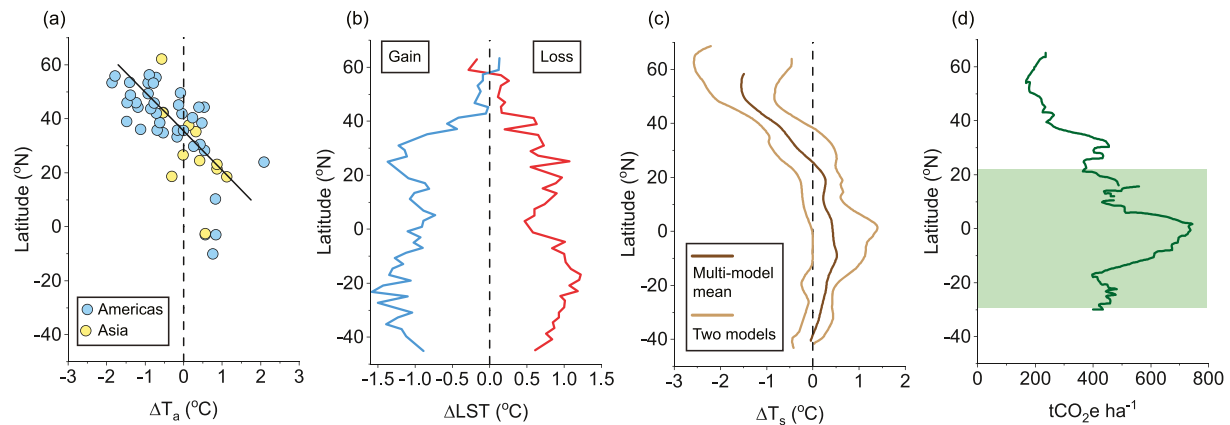


Figure 3. Forest influences on temperature in relation to latitude. (a) Annual mean difference in surface air temperature (ΔT_a) of open land compared with forest. Measurements were obtained for paired sites in North and South America and Asia. The black solid line shows the linear regression for all sites north of 10°N . Redrawn from M. Zhang et al. (2014). (b) Change in annual mean land surface temperature (ΔLST) with forest gain and loss. Land surface temperature was obtained from satellite measurements. Redrawn from Su et al. (2023). (c) Change in annual mean surface temperature (ΔT_s) after deforestation simulated by eight Earth system models. The central line is the multi-model mean and the outer lines are two individual models. Redrawn from Boysen et al. (2020). (d) Mitigation potential of forests at the end of the century as measured in terms of CO_2 equivalent biogeochemical and biogeophysical effects. The metric combines the CO_2 uptake of forests and the CO_2 equivalent of the local biogeophysical effect on temperature. Shown is the annual response in terms of metric tons of CO_2 equivalent ($\text{tCO}_2\text{e ha}^{-1}$) per hectare. The shaded region is where synergy between carbon and biogeophysical influences enhances the mitigation potential. Redrawn from Windisch et al. (2021).

and other disturbances that shift the landscape to younger forests alter the balance of these processes. Temperate forests can, in general, be considered transitional between tropical and boreal forests in their climate influences (Boysen et al., 2020; X. Lee et al., 2011). Analysis of eddy covariance flux measurements in temperate forests of the US show that forests are cooler than grasslands throughout the year, especially during the summer growing season (Burakowski et al., 2018; Juang et al., 2007; Q. Zhang et al., 2020), but studies of European forests show differing climate effects depending on drought (Teuling et al., 2010) and forest composition (Luyssaert et al., 2018; Naudts et al., 2016). Some studies find a role of temperate forests in increasing cloud cover (Cerasoli et al., 2021; Duveiller et al., 2021; Teuling et al., 2017).

4. Nature-Based Climate Solutions

Today's advocacy of forests as nature-based, or natural, climate solutions has its roots in the forest-climate question and prior calls to reforest the world to prevent desiccation of the land. Like that era of long ago, there is a complex storyline to forests as natural climate solutions that reflects a tenuous intersection between the disparate study of climate and ecology. Forests are again seen as essential to solving the climate problem, but there is no agreement on what climate processes should be included in nature-based solutions. Many natural climate solutions focus on carbon storage (e.g., Buma et al., 2024; Fargione et al., 2018; Griscom et al., 2017; Novick et al., 2022). The closely aligned climate-smart forestry, which aims to enhance forest adaptation to and mitigation of climate change, also focuses on carbon (Bowditch et al., 2020; Santopuoli et al., 2021; Yousefpour et al., 2018).

However, other processes can augment or offset the carbon benefits of forests (Figure 2a). Biogeophysical cooling adds to the benefits of carbon storage in tropical forests, but biogeophysical processes can conflict with carbon benefits in temperate and boreal forests depending on geographic location and time of year (Figure 3d; Windisch et al., 2021). In Europe, differences in albedo, evapotranspiration, and carbon storage between broadleaf deciduous and conifer forests can necessitate different forest composition and management depending on whether enhanced carbon mitigation or reduced surface air temperature is the desired outcome (Luyssaert et al., 2018). Planting broadleaf trees across Europe may mitigate climate warming because of their higher albedo and evaporative cooling compared with conifers (Schwaab et al., 2020). In boreal regions, surface warming from the low albedo of forests, especially when snow is on the ground, counters the climate benefits of carbon sequestration (Betts, 2000; Windisch et al., 2021). Forest management that favors carbon storage in older forests conflicts with the higher albedo of younger forests. The optimal management of northern temperate and boreal forests for climate services may be to decrease forest age so as to increase the albedo of the land (Lintunen

et al., 2022; Lutz et al., 2016). Additional complexity arises from BVOC emissions and secondary organic aerosol formation in boreal conifer forests. Older forests and conifer-dominated forests become more advantageous when the cooling of biogenic SOA is included as climate benefits (Kalliokoski et al., 2020).

Biogeochemical and biogeophysical processes differ in the temporal and spatial scales at which they influence climate. Carbon sequestration occurs over several decades as a forest grows, whereas changes in albedo and evapotranspiration occur much more rapidly. Consequently, the net benefit of a growing forest will vary with forest age (Randerson et al., 2006). In addition, CO₂ is well-mixed in the atmosphere so that its influence is felt globally. The biogeophysical effects of forests are more local and scale with the spatial extent of forest change (Laguë & Swann, 2016).

A more nuanced and integrated understanding of forests as natural climate solutions is required than has been evident to date. Calls to sequester carbon by planting trees and through forest conservation must also consider the biogeophysical influences of forests, but the means to combine the various processes into an integrated metric is not straightforward. Land surface temperature integrates the biogeophysical processes, but surface temperature is not the same as air temperature (Novick & Katul, 2020). Further complication arises in that temperature must be converted to a measure of equivalent CO₂ for comparison with carbon storage (Figure 3d). An integrated assessment of forests also requires consideration of biodiversity goals, which can be compatible with climate mitigation (Pörtner et al., 2021; P. Smith et al., 2022; Strassburg et al., 2020; Watson et al., 2018). The sustainability of climate services must be evaluated in light of a warmer climate with wildfire, insect outbreaks, and permafrost thaw (Anderegg et al., 2020; Roebroek et al., 2024). Restoring forests to store carbon is less useful in a warmer, drier world with more wildfires. Forest masking of snow albedo is less prominent in a warmer world with less snow cover. Evaporative cooling is less beneficial in a drier world without sufficient soil water. In addition, the land rights of local populations must be respected. One of the issues coursing through the forest-climate question in France, Austria-Hungary, and North Africa was a tendency for claims for the large-scale benefits of forests to undercut the traditional forest rights of local and Indigenous populations (Coen, 2018; Davis, 2016; Ford, 2016). As Earth's climate shifts, the climate services of forests are changing, as are the needs of human populations who depend on forests for their traditional livelihoods and sacred spaces. Moving forward, decisions about forest conservation should be made with close attention to these dynamic circumstances.

Spatial scale presents a challenge for nature-based climate solutions because there is not a clear framework to integrate the observations obtained at eddy covariance flux towers with a spatial footprint of less than a few square kilometers and the large-scale models with a spatial resolution on the order of 100 km (Figure 2b). There is a conceptualization of local versus nonlocal influences of forest cover change (Pongratz et al., 2021; Winckler et al., 2019) and ecological teleconnections (Badger & Dirmeyer, 2016; Devaraju et al., 2015; Y. Li et al., 2021; Swann et al., 2012, 2018), but the disparity in spatial scale remains a barrier to informing local solutions. For example, trees and other greenspace lessen the urban heat island (Schwaab et al., 2021; Wong et al., 2021; Ziter et al., 2019) and forests provide microclimatic refugia for wildlife conservation in a warming world (De Frenne et al., 2019), but Earth system models do not model these microclimates. Conversely, local forest conservation projects cannot consider remote climate consequences, which albeit negligible for a small project become non-negligible when aggregated over many local projects.

5. The Earth System: A Geophysical Perspective

The forest-climate question, both in the past and in today's nature-based climate solutions, reveals a missing interdisciplinary framework to study the biosphere and climate. The modern understanding of ecosystem-climate interactions is closely tied to the development of global models of Earth's climate, but climate scientists are conforming the biosphere to their viewpoint of Earth as a system of mass and energy flows rather than envisioning the biosphere as the habitat for life.

A report prepared by the US National Aeronautics and Space Administration (NASA) committee for Earth system sciences in 1986 formally outlined the scope of Earth system science (NRC, 1986). A diagram produced by the committee, the so-called “Bretherton diagram” named for Francis Bretherton, the committee chair, has been hailed for its multidisciplinary vision of Earth system science (NASSEM, 2022; Steffen et al., 2020). The committee conceived of a fluid Earth and a biological Earth represented by the “physical climate system” and “biogeochemical cycles,” respectively (Figure 4). Their conceptual diagram outlined the components seen in

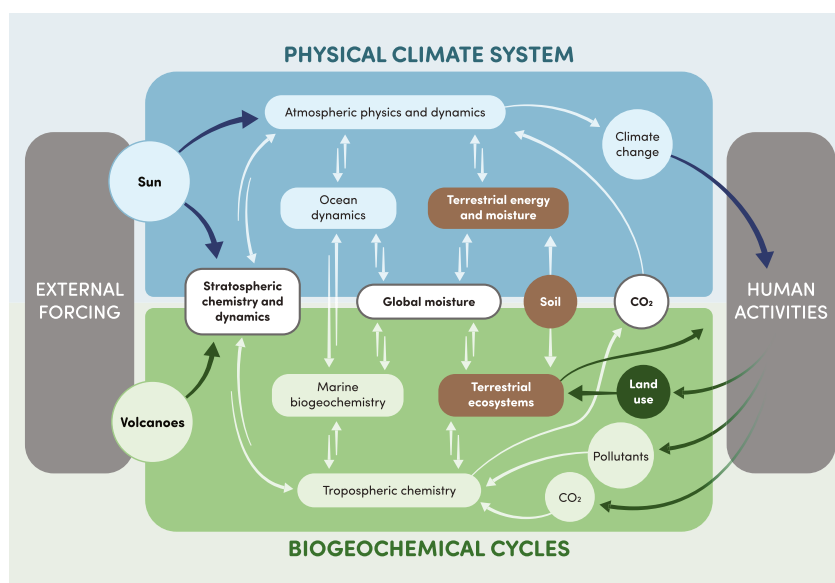


Figure 4. Representation of the Earth system as the physical climate system and biogeochemical cycles in the Bretherton diagram of Earth system science. Redrawn from NRC (1986). In the redrawing, the “physical climate system” and “biogeochemical cycles” parts of the Earth system have been colored to distinguish them. The subcomponents of “terrestrial energy and moisture,” “terrestrial ecosystems,” “soil,” and “land use” have been colored to highlight their placement in the diagram.

today's Earth system models, including atmospheric chemistry and terrestrial and marine biogeochemistry in addition to the atmosphere and oceans, as well as the role of humans to shape the Earth system.

Despite its interdisciplinary vision, the Bretherton diagram provides a limited depiction of terrestrial ecosystems in the Earth system. It associates terrestrial ecosystems with biogeochemical cycles (Figure 4, “terrestrial ecosystems”), separate from the biogeophysical processes controlling terrestrial energy and moisture (Figure 4, “terrestrial energy and moisture”) in the physical climate system. The diagram additionally separates terrestrial ecosystems from soils, which are placed at the intersection of biogeochemical cycles and the physical climate system (Figure 4, “soil”). Missing from this conceptual framing is that the biogeophysics and biogeochemistry of terrestrial ecosystems are regulated through interdependent processes (Bonan, 2016, 2019). Over vegetated land, the exchanges of energy, moisture, CO_2 , and other chemicals with the atmosphere are regulated by the amount of foliage, the type of leaves (e.g., broadleaf, needleleaf, deciduous, evergreen), the openness of stomata, the photosynthetic pathway (e.g., C3 or C4), the height of the canopy, the depth of roots, and soils among other processes. Further to this, the diagram places land use in the domain of biogeochemistry (Figure 4, “land use”), separating the carbon emissions of land use from the biogeophysical effects of land use mediated through changes in albedo, evapotranspiration, and surface roughness.

The piecemeal representation of the biosphere evidenced in the Bretherton diagram has been carried forth in the IPCC assessment reports. The first assessment report placed the physical processes of land albedo and surface fluxes (heat, moisture, momentum) in the domain of the atmosphere (Cubasch & Cess, 1990). The hydrologic cycle and soil moisture were separate from this, and the biosphere was conceived as an additional component controlling CO_2 and other greenhouse gas fluxes. The sixth assessment report still presents a fragmented view of land processes rather than a comprehensive assessment of an integrated science (IPCC, 2021). The climate consequences of land use and land-cover change are assessed in terms of the radiative forcing caused by changes in surface albedo, but changes mediated by evapotranspiration, sensible heat, and momentum fluxes do not conform to the radiative forcing framework (Davin et al., 2007; NRC, 2005). Carbon cycle feedbacks are examined independent of concomitant changes in stomatal conductance, leaf area, and canopy height that affect climate through altered evapotranspiration, albedo, and surface roughness. Across the full report, the processes by which changes on land affect climate (e.g., surface albedo, soil moisture, CO_2 emissions; IPCC, 2021) are treated separately from the impacts of climate change on terrestrial ecosystems (e.g., tree mortality, wildfire, drought; IPCC, 2022a) and land management for mitigation (IPCC, 2022b). An update to the Bretherton diagram

highlights integration with human systems and the social sciences as a critical frontier of Earth system science (Steffen et al., 2020). That is certainly needed, but so, too, is a more comprehensive knowledge of the terrestrial biosphere in the Earth system.

6. Terrestrial Ecology in the Earth System

The more than 30 years of climate modeling has greatly expanded the ecological scope of the models, but there is still much ecology that is missing. Others have reviewed the development of the land component models (Blyth et al., 2021; Bonan, 2019; R. A. Fisher & Koven, 2020), and R. A. Fisher and Koven (2020) provide a graphical timeline (their Figure 1). Figure 5 provides an alternative visualization for Earth system model development, framed around the IPCC assessment reports and highlighting the added ecological complexity with which the terrestrial biosphere has been represented.

The models used for the first IPCC assessment report (1990) subsumed the land into atmospheric general circulation models (Figure 5a; Cubasch & Cess, 1990). Land fluxes of energy, moisture, and momentum were seen as boundary conditions to the atmosphere and accordingly had simplistic bulk formulations without explicit parameterizations of plant canopies and without soil moisture (Kasahara & Washington, 1967, 1971; Manabe et al., 1965). The hydrologic cycle on land, if it was included, was encapsulated by analogy with a bucket that fills from precipitation, dries out from evaporation, and overflows as runoff when filled to capacity (Manabe, 1969).

The second assessment report (1995) saw more realistic models of processes that coupled vegetation control of surface fluxes, the cycling of water on land, and the atmosphere (Figure 5b; Dickinson et al., 1996). Vegetation was conceived as a “big leaf,” without vertical structure (Dickinson et al., 1986; Sellers et al., 1986). Radiative transfer by the canopy was explicitly modeled, and the turbulent fluxes of sensible and latent heat for the canopy and soil were represented by analogy with a network of resistances. Canopy greenness varied seasonally using data sets of leaf area index and vegetated fraction, but the models did not include long-term vegetation changes at timescales of decades to centuries. This generation of models initiated study of the effects on climate of tropical (Dickinson & Henderson-Sellers, 1988), boreal (Bonan et al., 1992), and temperate (Bonan, 1997) deforestation and regional land cover heterogeneity (Marshall et al., 2004; Pielke et al., 1997, 1999).

The climate models of the third assessment report (2001) still emphasized the biogeophysical fluxes of energy, moisture, and momentum, but with greater ecological detail of plant canopies (Figure 5c; Stocker et al., 2001). Some models incorporated advanced physiological principles, seen in the coupling of leaf photosynthesis (Farquhar et al., 1980) and stomatal conductance (Collatz et al., 1991) and scaling from leaf to canopy (Sellers et al., 1996). By including photosynthesis, the models began to simulate gross primary production and land-atmosphere CO₂ fluxes (Bonan, 1995; Cox et al., 1999, 2000; Denning et al., 1996).

The fourth assessment report (2007) brought substantial capabilities to model the biosphere as an interactive component of the climate system (Le Treut et al., 2007; Randall et al., 2007). Two classes of dynamic biosphere models were coupled to climate models (Prentice et al., 2000, 2007). Biogeochemical models represent ecosystems as discrete pools of vegetation carbon (e.g., foliage, woody stem, roots) and soil carbon (litter and soil organic matter in various stages of decay) (Figure 5d). They, along with ocean biogeochemical models, fulfilled the biogeochemical component of Earth system science with the goal to prognostically calculate atmospheric CO₂ concentration (e.g., Fung et al., 2005). In contrast, dynamic global vegetation models (DGVMs) include bioclimatic rules and simplified equations for competition to simulate temporal change in taxa in addition to the carbon cycle (Figure 5e). Their heritage extends to equilibrium bioclimatic models of plant geography, but they simulate vegetation change at more realistic timescales (Bonan et al., 2003; Cox et al., 2000; Foley et al., 1998; Sitch et al., 2003). The advent of DGVMs initiated study of how changes in vegetation structure and floristic composition affect ice age (Levis et al., 1999) and mid-Holocene (Levis et al., 2004) paleoclimates and anthropogenic climate warming (Alo & Wang, 2010; Cox et al., 2000; Levis et al., 2000).

By the fifth assessment report (2013), carbon cycle feedback with climate change was included in many models (Ciais et al., 2013; Cubasch et al., 2013; G. Flato et al., 2013). Most models in the sixth assessment report (2021) have expanded terrestrial biogeochemistry, including the nitrogen cycle, and land use and land-cover change (Figure 5f; Canadell et al., 2021; D. Chen et al., 2021). One model also included phosphorus (Law et al., 2017).

Today, cutting edge land models include carbon and nitrogen, other chemical exchanges (e.g., BVOCs, O₃, CH₄), mineral dust and biomass burning emissions, and land use and land-cover change (Blyth et al., 2021;

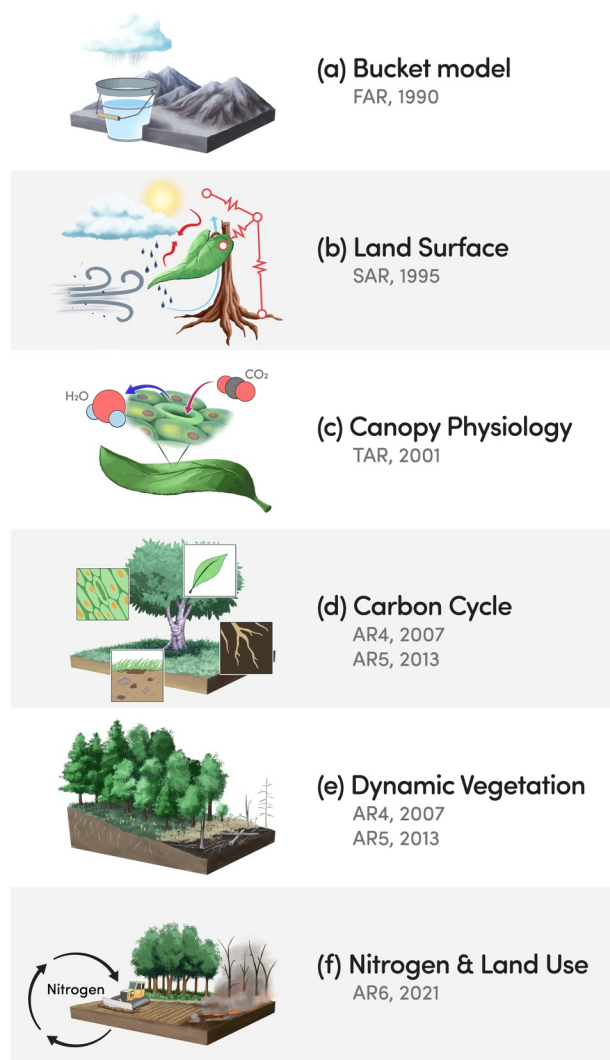


Figure 5. Visual representation of the development of the land component of Earth system models over the past 30 years as described in the Intergovernmental Panel on Climate Change first (FAR, 1990), second (SAR, 1995), third (TAR, 2001), fourth (AR4, 2007), fifth (AR5, 2013), and sixth (AR6, 2021) assessment reports. (a) Bucket model of land hydrology without plant canopies. (b) Big-leaf canopy model of land surface processes including radiative transfer, turbulent fluxes represented by a network of resistances, interception and throughfall, evapotranspiration, and soil and snow physics. (c) Coupled photosynthesis-stomatal conductance models. (d) Biogeochemical carbon cycle models. (e) Dynamic vegetation models with changes in plant taxa in addition to biogeochemistry. (f) Nitrogen and land use/land cover change.

Bonan, 2019; R. A. Fisher & Koven, 2020). However, the precise way to model these processes and their influence on climate are uncertain. There is large disagreement among models in the carbon cycle (Arora et al., 2020), nitrogen cycle (Davies-Barnard et al., 2020; Kou-Giesbrecht et al., 2023), wildfires (Hantson et al., 2020; F. Li et al., 2019), and land cover change (Boysen et al., 2020). Chemistry-climate interactions remain a modeling frontier (Scott et al., 2018; Unger, 2014; Weber et al., 2022, 2024). Permafrost processes are being incorporated into land models (Chadburn et al., 2015; Ekici et al., 2014; Koven et al., 2011, 2015; D. M. Lawrence et al., 2008, 2015), but only two Earth system models used in the sixth assessment report included permafrost carbon and further model development is required to better represent permafrost (Schädel et al., 2024).

Current modeling frontiers continue to advance these lines of development. The physiology of leaf gas exchange now incorporates principles of water-use efficiency optimization and plant hydraulics to model stomatal conductance (Kennedy et al., 2019; Lin et al., 2015; Prentice et al., 2014). Optimality theory is an emerging paradigm to parameterize ecophysiological processes (Dong et al., 2022; Harrison et al., 2021; N. G. Smith et al., 2019). The phosphorus cycle is being added (Law et al., 2017; Nakhavali et al., 2022; Yang et al., 2019). Soil biogeochemical models include vertically-resolved profiles of soil carbon (Burke et al., 2017; Koven et al., 2013) and explicit microbial populations (Kyker-Snowman et al., 2020; Sulman et al., 2019).

Missing from the current generation of models are concepts of plant succession and community organization, which were central to the development of ecology as a science (Golley, 1993; McIntosh, 1985). Key ecological processes that are lacking include: the population biology that determines the number and size of plants (Harper, 1977); principles of community ecology such as competition for resources, niche theory, competitive exclusion, and community assembly (Falster et al., 2021; Shugart, 1998); and competition for light in vertically structured plant canopies and the spatial mosaic of patches across the landscape resulting from gap dynamics (Shugart, 1984, 1998; Watt, 1947). These processes are needed to simulate ecological resilience to climate change (Levine et al., 2016).

In part, the simplicity, generalization, and computational efficiency required of global models determines the limited breadth of ecology that can be included in Earth system models. However, the narrowness of scope arises also from how terrestrial ecosystems were initially conceived in the Earth system. Ecosystem ecology is closely associated with biogeochemistry and the cycling of chemical elements. This is the conceptualization of the biosphere proposed by Vernadsky in 1926 (Vernadsky et al., 1998). It is seen in the seminal work of Howard and Eugene Odum and their study of energy (carbon) flows and the trophic structure of ecosystems (E. P. Odum, 1969; H. T. Odum, 1957, 1960). The Bretherton diagram of Earth system science conceives of terrestrial ecosystems in terms of biogeochemical cycles

(Figure 4), and for this, Vernadsky and the Odums have been credited with enabling the ecosystem ecology of Earth system science (Steffen et al., 2020).

The biogeochemical conceptualization of an ecosystem lends itself to a system of linear differential equations to describe transfers among various compartments, and this type of model, also known as a box model, gained credence during the 1960s and 1970s in the International Biological Program (IBP) (Patten, 1975). The IBP models, however, were criticized as too large and mathematically complex yet too biologically simple and are largely seen by ecologists and science historians today as failures (Aronova et al., 2010; Golley, 1993; Kwa, 1993, 2005; McIntosh, 1985). Nevertheless, biogeochemical box models provide a mathematically tractable way to

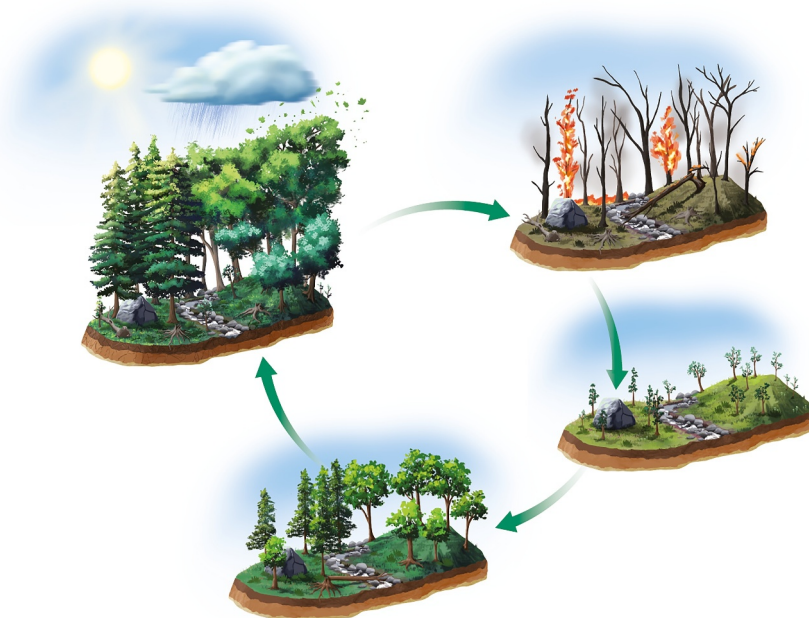


Figure 6. Shown is the cycle of forest regeneration and growth following disturbance that drives forest dynamics at the scale of a small patch. The panels show changes in population density, tree size, and floristic composition as the forest regrows from a cleared patch exposed to high sunlight to a mature forest with a closed canopy. The detailed panel for the mature forest illustrates interactions with the atmosphere.

model carbon and other elements in ecosystems (Luo et al., 2017), and they have become the predominant way to model the biosphere in Earth system models (Bonan, 2019). However, the current biogeochemical models, like the IBP era systems ecology, can be inordinately complex. For example, from an initial representation of 3 vegetation and 9 soil carbon pools (Fung et al., 2005), the biogeochemistry in the Community Land Model, the terrestrial component of the Community Earth System Model, has grown to 18 vegetation pools and 140 soil carbon pools (7 pools in each of 20 soil layers) (Lu et al., 2020).

The biogeochemical representation is only one tradition within the history of ecology. If we look back to ecology's origins in the early twentieth century, we find a focus on the nature of plant communities, with two competing visions. One school of thought is found in Clements' notion of a plant climax community as a “superorganism” with emergent properties (Clements, 1916, 1928). Today's ecosystem ecology similarly takes a top-down view that characterizes ecosystems through emergent properties such as biogeochemical cycles. Gleason (1917, 1926, 1939) offered an alternative plant-centric view, in which plant communities are not emergent units of ecological organization but rather contain competing individuals with similar environmental preferences that may, by mere coincidence, co-occur in space and time. Ecosystems, likewise, can be conceptualized using a bottom-up framework in terms of individual plants that happen to compete with one another to occupy physical space and acquire the resources needed for growth and survival. A.S. Watt sought to reconcile these two seemingly dichotomous viewpoints, writing, “As they stand, the two views are apparently mutually exclusive. But there is truth in each” (Watt, 1964). Rather than the individual plant, Watt proposed that the fundamental scale of ecological study is the patch of land in which plants compete for light and other resources after a disturbance that opens the canopy (Watt, 1947). A forest community and landscape is then the aggregation of many patches, each in a different stage of development. Carbon stores and element cycles thus arise from regeneration, growth, and mortality within those patches—plant demography—rather than ecosystem state per se.

So-called individual tree forest gap models utilize Watt's patch concept to simulate the population density of trees, their diameter and height, and community assemblage in a dynamic cycle of canopy gap formation, regeneration, canopy closure, and thinning (Figure 6; see also Botkin et al., 1972; Shugart, 1984; Shugart & West, 1977; Shugart et al., 2018, 2020). Many such patches are simulated to represent the forest community and landscape. Competition for light along with taxa-specific growth rate, environmental tolerances, size at maturity, longevity,

regeneration requirements, and stochastic mortality determine community assembly, forest structure, and temporal dynamics. Whereas biogeochemical models represent an ecosystem as a system of carbon balance equations (and additionally nitrogen and phosphorus), the governing equations of gap models simulate the diameter growth of individual trees, the associated increase in height, and the demographic processes that control mortality and regeneration in a small patch. The gap model framework readily incorporates biogeochemical pools and fluxes (Bonan, 1990; Pastor & Post, 1986). Gap models, with their focus on the drivers of change (e.g., disturbance), process response to the drivers (e.g., mortality), and resulting patterns (e.g., community composition, biomass), embody the concept of an ecosystem as originally proposed by Tansley (Shugart et al., 2020; Tansley, 1935).

Gap models have been implemented in numerous forest biomes worldwide at the stand scale (Shugart et al., 2018, 2020) and also spatially distributed across large regions including the Amazon basin (Rödig et al., 2017), Russia (Shuman et al., 2017), and interior Alaska (Foster et al., 2019). However, the principles of gap dynamics are not routinely found in the current generation of biosphere models used with Earth system models, most of which do not represent mixed-species community assemblages and the vertical competition for light in plant canopies (R. A. Fisher & Koven, 2020; R. A. Fisher et al., 2018). Instead, the models characterize vegetation as distinct subgrid tiles of homogenous plant functional types represented with a big-leaf canopy. Biogeochemical models simulate the carbon balance and other chemical elements within the tile. DGVMs take advantage of the subgrid tiling to update the carbon balance of the tile and additionally the area of the tile.

Newer vegetation demographic models provide a size- and age-structured representation of patch dynamics including competition for light in vertically-structured canopies; size-dependent growth, allocation, and mortality; competitive exclusion; and recruitment and regeneration following disturbance (R. A. Fisher et al., 2018). One class of these models, building upon the ecosystem demography computational framework (Longo et al., 2019; Ma et al., 2022; Moorcroft et al., 2001), allows for computationally efficient implementation in Earth system models, simulating plant size (represented by cohorts of plants of the same size and functional type) and age since disturbance (represented by patches with one or more cohorts). Prototype models are being developed for Earth system modeling at many modeling centers (R. A. Fisher et al., 2015; Koven et al., 2020; Martínez Cano et al., 2020; Weng et al., 2022). For example, a cohort in the Functionally Assembled Terrestrial Ecosystem Simulator (FATES) is modeled by a representative individual plant (size, height, and canopy position) and the population density (R. A. Fisher et al., 2015; Koven et al., 2020). Different functional types are defined by traits related to plant physiology, response to disturbance, and other life history characteristics. New cohorts are created as a result of recruitment, and existing cohort population density decreases as a result of mortality. Mortality, fire, or other disturbances create new patches from existing patches. A similar framework can be applied to model grasslands (Wilcox et al., 2023). Other approaches to represent cohorts and patches in Earth system models are possible (Argles et al., 2020; Döschner et al., 2022; Haverd et al., 2018). Vegetation models such as FATES link the aboveground plant demography with the decomposition of belowground litter and soil carbon pools and can be extended to include the biogeochemical cycling of nitrogen and phosphorus (Knox et al., 2024), as can other vegetation demography models (Dantas de Paula et al., 2021; Kou-Giesbrecht et al., 2021; Medvigy et al., 2019; B. Smith et al., 2014).

Vegetation demographic models continue a tradition of trait-based modeling of the biosphere-atmosphere system. Trait-based models aim to predict ecosystem patterns and processes as the outcome of fundamental physiological, biogeophysical, biogeochemical, and demographic processes rather than from empirical relationships. Early generation land models characterized vegetation in terms of biomes with associated parameters that captured key ecological traits. The Biosphere-Atmosphere-Transfer Scheme (BATS), for example, included lifeform, height, rooting depth, and maximum stomatal conductance (Dickinson et al., 1986). With the inclusion of photosynthesis, physiological parameters such as the maximum rate of carboxylation, light-use efficiency, and an empirical constant relating stomatal conductance to photosynthesis were needed (Bonan, 1995; Cox et al., 1999; Sellers et al., 1996). The carbon and nitrogen cycles require additional traits related to leaf mass per area, foliar nitrogen content, carbon allocation, carbon-to-nitrogen stoichiometry, and much more (Thornton et al., 2007; Y. P. Wang et al., 2010; Zaehle & Friend, 2010).

Vegetation demographic models open a richness of ecological detail that is currently missing from Earth system science. A novel line of research, for example, examines the plant traits that affect competition and coexistence (Buotte et al., 2021; R. A. Fisher et al., 2015; Kovenock et al., 2021; L. Li et al., 2023). Vertically-structured canopies with overstory and understory, as well as successional stages, introduce a notion of habitats into

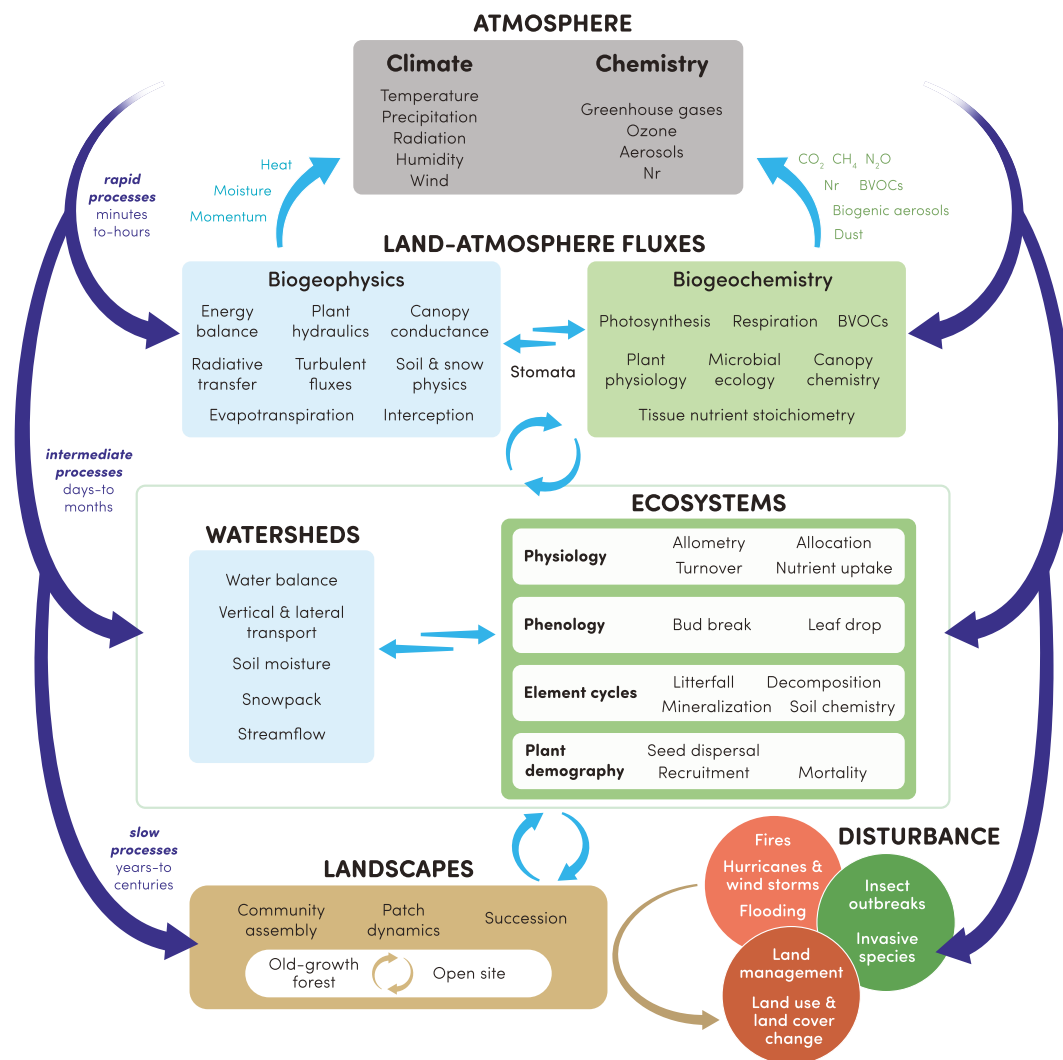


Figure 7. Schematic diagram of the ecosystem-atmosphere coupling at multiple timescales. The atmosphere is represented as physical climate and chemistry (gray box). Terrestrial ecosystems influence the atmosphere through exchanges of heat, moisture, momentum, and chemicals. Dark blue arrows denote atmospheric influences on components. Shown are rapid processes with timescales of minutes-to-hours related to biogeophysical and biogeochemical flux exchanges; intermediate processes at timescales of day-to-months related to watershed hydrology and ecosystems; and slow processes at timescales of years-to-centuries related to disturbances and landscape patterns. Text in the boxes and circles show component processes. Blue shaded boxes denote physical processes related to the surface energy balance and hydrologic cycle, which were the initial focus of land models. Green shaded boxes denote ecological processes added to the models to simulate biogeochemical cycles. Missing from the models are landscape processes that shape vegetation pattern and process following disturbance (brown shaded box). Wildfires and anthropogenic land use/land cover change are included in many models. Wind events, floods, insect outbreaks, and invasive species are additional forms of disturbance. Updated from Bonan (2016).

Earth system models. Vertically structured canopies also link successional development, the microclimate within canopies (i.e., temperature, humidity, and wind speed profiles; Bonan et al., 2021; Y. Chen et al., 2016; Naudts et al., 2015), and the atmospheric boundary layer and large-scale climate above canopies (Figure 6).

Figure 7 conceptualizes how various processes on land combine to influence climate and atmospheric composition. In contrast to the Bretherton diagram (Figure 4), Figure 7 presents an integrated interdisciplinary conceptualization of the biosphere-atmosphere system. Early in the development of land models, the tight coupling between fast timescale leaf energy fluxes (Figure 7, “biogeophysics”) and photosynthesis (Figure 7,

“biogeochemistry”) through stomatal conductance was recognized as essential (Collatz et al., 1991; Dickinson et al., 1981). Finnigan and Raupach (1987) emphasized the coupled system, in which “the physiological state of a plant community substantially influences the microclimate within it; in turn, the microclimate influences the physiological state, so that neither is independent of the other.” The hydrologic state of the land (e.g., soil moisture) sets constraints on the fast timescale biogeophysics and biogeochemistry, as does ecosystem structure and composition (e.g., leaf area index, height, lifeform, carbon and nitrogen pools). Anthropogenic land use and natural disturbances, both of which vary with climate, drive changes in the pattern of ecosystems across the landscape. The coupled system needs to be remembered as more ecology is added to the models.

7. Summary and Future Perspectives

The science of ecosystem-climate interactions has greatly advanced since the early days of atmospheric science and ecology. From the peremptory denial of forest influences on climate at the close of the nineteenth century, atmospheric scientists now perceive the biosphere as a necessary component of climate science. Ecologists recognize the climate influences of terrestrial ecosystems, albeit mostly in terms of biogeochemistry. Nature-based climate solutions are once again called for to solve a human-made climate problem. Nonetheless, there are still interdisciplinary challenges in an academically fragmented scientific culture. The interdisciplinary foundations of biosphere-atmosphere coupling, as in the past, are tenuous. Earth system science utilizes a geophysical perspective to model the planet, but other perspectives are both possible and needed to foster interdisciplinary collaboration (Coen & Jonsson, 2022; NASEM, 2022). This review focuses on one aspect of interdisciplinarity: the relationship between climate science and terrestrial ecology. Although there is much terrestrial ecology in Earth system models, the subordinate role of ecology in Earth system science is evident. There is a need to reframe Earth system science to more equitably encompass the living world along with the fluid world.

Others have voiced similar concern. Mitman (2018) described “the marginalization of ecology” in Earth system science as a result of the hubris of geoscientists reluctant to admit that humans are not the only life form with geophysical agency. Pielke et al. (2022) noted that climate and ecology are not yet considered studies of a common system. Vilà-Guerau de Arellano et al. (2023) called for integration across biology, chemistry, and atmospheric physics to advance understanding of the atmospheric boundary layer. Hampered exchange of knowledge between disciplines is the legacy of the forest-climate controversy, seen in the narrowness with which climate scientists view the Earth system and the limited way in which terrestrial ecosystems are represented in Earth system models.

The multifaceted nature of the biosphere precludes a simple description of terrestrial ecosystems in the Earth system, how to model them, and why to protect them. Terrestrial ecosystems are a source and sink of energy and materials exchanged with the atmosphere; a habitat for biodiversity; a provisioner of freshwater, food, fiber, and medicines; a place for recreation and contemplation; and the cultural heritage of humanity. The atmosphere component of the Earth system is aptly described as an atmosphere model, but the land, with its geology, geomorphology, watersheds, ecosystems, wildlife, and people, comprises multiple academic specialties in an interconnected system. Lack of clarity is evident in descriptors of the terrestrial component of an Earth system model: land surface model, soil-vegetation-atmosphere-transfer model, DGVM, terrestrial biosphere model, vegetation demography model (Bonan, 2019; J. B. Fisher et al., 2014) and more broadly based terms such as “land environment simulator” (Best et al., 2011) or “terrestrial system model” (Lombardozzi et al., 2023). None of these terms expressively captures the full breadth of the biosphere-atmosphere system.

A more inclusive intellectual framework is needed that integrates biogeophysical and biogeochemical fluxes, watershed hydrology, ecosystem processes, landscape ecology, and disturbance and their influences on climate and atmospheric composition (Figure 7). Earth system models present further barriers to non-modelers because of their software engineering and high-performance computing demands (Kyker-Snowman et al., 2022), but cyberinfrastructure tools can be created to lessen the burden and facilitate broader access to and participation with modeling (Keetz et al., 2023; Lombardozzi et al., 2023).

The division of climate science into the physical basis for climate change (IPCC, 2021); impacts, adaptations, and vulnerabilities to climate change (IPCC, 2022a); and mitigation of climate change (IPCC, 2022b) presents a key conceptual impediment to fully integrating the biosphere into Earth system science. Earth system models are seen as providing climate projections, and specialized ecological models are used for impact studies. However, many

of the impacts of climate change on terrestrial ecosystems, which form the basis for actionable Earth system science, feed back to affect the magnitude and trajectory of climate change (Bonan & Doney, 2018). Increased wildfire activity, for example, is a manifestation of climate change, but wildfire emissions also influence weather and climate (Fasullo et al., 2023; Makar et al., 2021). The physiological knowledge needed to understand the impact of drought on vegetation is the same knowledge that must be used to model transpiration in an Earth system model (Xu et al., 2023). An alternative framework, seen in the IPCC special report on climate change and land (IPCC, 2019), is to integrate the biogeophysical and biogeochemical effects of land use and land cover change, the impacts of climate change, and mitigation strategies related to agriculture, forestry and ecosystem management.

Physical climate bias is further evident in that Earth system prediction is portrayed by climate scientists as the seamless integration of weather and climate at timescales from subseasonal to decadal and the provisioning of actionable forecasts (Hazeleger et al., 2010; Meehl et al., 2021; Ruti et al., 2020). It largely considers the land in the narrow context of being a source of atmospheric predictability (NASEM, 2016). However, Earth system prediction is more than just predicting weather and climate and must include the biosphere and its resources (Bonan & Doney, 2018). For example, Earth system models can produce skillful forecasts of terrestrial carbon uptake at subseasonal to annual timescales (E. Lee et al., 2022; Lovenduski et al., 2019).

Today, the nations most vulnerable to climate change have the least access to information about their future climate. Their lack of meteorological infrastructure is an outgrowth of both colonial and neo-colonial policies; for instance, the International Geophysical Year of 1957–1958 gave control of new data centers to former imperial metropolises and Australia at the expense of data access for newly independent nations of the Global South (Aronova, 2017; Robinson et al., 2023). Recently, scientists have proposed that “digital twin Earth” models based on exascale computing and machine learning could alleviate the inequality between former colonizer and colonized nations when it comes to being able to predict local impacts of climate change.

The digital twin Earth, in which a 1-km resolution model simulates clouds and storm tracks that are nearly indistinguishable from observations, is a powerful call for predicting emerging weather and climate risks in the Earth system, but it assumes that higher resolution atmospheric and ocean models alone will provide the necessary information for a changing climate (Voosen, 2020). It perpetuates the hubris of the geophysical view of Earth, assuming that actionable information follows from “the laws of physics” alone (Bauer et al., 2021; X. Li et al., 2023). We should beware of such a narrow definition of the information needed to address climate change. Without adequate representation of the land and its ecosystems, how will a digital twin inform local climate-smart forestry and nature-based climate solutions, both of which are needed to adapt to and mitigate climate change? To do so, digital twins will need to incorporate highly detailed ecological models, bringing an understanding of complex, fine-scale ecological processes into Earth system models. The advent of vegetation demography models with patch dynamics, which we have highlighted in this review, is one such example. Permafrost researchers have identified a similar need and opportunity for bridging modeling communities and spatial scales (Schädel et al., 2024).

The broader challenge at the root of the past marginalization of ecology in Earth systems modeling is how to synthesize diverse ways of knowing nature without misrepresenting or overly reducing them. On this issue, the colonial history of the forest-climate question offers valuable lessons. Colonial scientists frequently miscast Indigenous land use in North Africa as automatically deleterious and, in doing so, dismissed Indigenous environmental knowledge out of hand (Davis, 2007; Fairhead & Leach, 1996). Confronting past hubris should guide current Earth systems scientists to adopt a more inclusive and respectful approach to integrating Indigenous knowledges. There can be no uniform prescription for recognizing Indigenous knowledge systems, given that they are inextricable from unique cosmologies, languages, and ways of life. Nonetheless, four principles have been recommended to guide the design and implementation of nature-based climate solutions (Orlove et al., 2022): full consultation with local and Indigenous communities from the project's inception; protection of intellectual property rights for Indigenous knowledge systems; data sovereignty for local and Indigenous communities participating in international research; and a commitment to promoting Indigenous languages, which are integral to Indigenous knowledge systems. Recent World Meteorological Organization (WMO) initiatives support open data and capacity building for the Global South, yet such programs should also make room for multiple ways of knowing climate change.

The successful design of nature-based solutions to climate change depends not only on knowledge of the ocean and atmosphere but on expertise about living landscapes. Ecologists studying the living world, the people managing the land for climate change mitigation, water resources, biodiversity, food, fiber, and other ecosystem services, the societies vulnerable to climate change, and Indigenous populations whose cultural heritage is tied to the land increasingly have a voice in Earth system science as we move beyond the geophysical perspective of climate to Earth system prediction for planetary stewardship. The earth in the Earth system must be reimagined if the promise of Earth system science is to be achieved.

Data Availability Statement

No data were used in this manuscript.

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