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Ecosystems and Climate

1.1 Chapter Summary

When viewed from space, Earth is seen as a blue marble. The dominant features of the planet are the blue of the oceans and the white of the clouds traversing the atmosphere. It is an image of fluids – water and air – in motion. Indeed, the study of Earth's climate is dominated by the geophysical principles of fluid dynamics. With closer inspection, however, one can discern land masses – the continents – and the plants that grow on the land. The blue of the oceans gives way to the emerald green of vegetation. Weather, climate, and atmospheric composition have long been known to determine the floristic composition of these plants, their arrangement into communities, and their functioning as ecosystems. Earth system scientists now recognize that the patterns and processes of plant communities and ecosystems not only respond to weather, climate, and atmospheric composition, but also feedback through a variety of physical, chemical, and biological processes to influence the atmosphere. The geoscientific understanding of planet Earth has given way to a new paradigm of biogeosciences. Ecological climatology is an interdisciplinary framework to study the functioning of terrestrial ecosystems in the Earth system through their cycling of energy, water, chemical elements, and trace gases. Changes in terrestrial ecosystems through natural vegetation dynamics and through human uses of land are a key determinate of Earth's climate.

1.2 Common Science

Ecology is the study of interactions of organisms among themselves and with their environment. It seeks to understand patterns in nature (e.g., the spatial and temporal distribution of organisms) and the processes governing those patterns. Climatology is the study of the physical state of the atmosphere – its instantaneous state, or weather; its seasonal-to-interannual variability; its long-term average condition, or climate; and how climate changes over time. These two fields of scientific study are distinctly different. Ecology is a discipline within the biological sciences and has as its core the principle of natural selection. Climatology is a discipline within the geophysical sciences based on applied physics and fluid dynamics. Both, however, share a common history.

The origin of these sciences is attributed to the Greek scholars Aristotle (ca. 350 BCE) and Theophrastus (ca. 300 BCE) and their books *Meteorologica* and *Enquiry into Plants*, respectively, but their modern beginnings trace back to natural history and plant geography. Naturalists and geographers of the seventeenth, eighteenth, and nineteenth centuries saw changes in vegetation as they explored new regions and laid the foundation for the development of ecology

Table 1.1 Relationship between de Candolle's plant types and Köppen's climate types

de Candolle plant type	Köppen climate type	Dominant vegetation
Megatherms	Humid tropical	Tropical rainforest
		Tropical savanna
Xerophiles	Dry	Desert
		Grassland
Mesotherms	Moist subtropical mid-latitude	Warm temperate deciduous forest
		Warm temperate coniferous forest
		Mediterranean
Microtherms	Moist continental	Cool temperate deciduous forest
		Cool temperate coniferous forest
		Boreal forest
Hekistotherms	Polar	Tundra

Source: Adapted from Colinvaux (1986, p. 326) and Oliver (1996).

and climatology as they sought explanations for these geographic patterns. Alexander von Humboldt, in the early 1800s, observed that widely separated regions have structurally and functionally similar vegetation if their climates are similar. Alphonse de Candolle hypothesized that temperature creates latitudinal zones of tropical, temperate, and arctic vegetation and in 1874 proposed formal vegetation zones with associated temperature limits. This provided an objective basis to map climatic regions, and in 1884 Wladimir Köppen used maps of vegetation geography to produce climate maps. His five primary climate zones shared similar temperature delimitations as de Candolle's vegetation (Table 1.1). The close correspondence between climate and vegetation is readily apparent, and many secondary climate zones such as tropical savanna, tropical rainforest, and tundra are named after vegetation. Although vegetation is no longer used to map the present climate, it is a primary means to reconstruct past climate from relationships of temperature and precipitation with tree-ring width, pollen abundance, and leaf form.

Despite shared origins, twentieth-century advancement of ecology and climatology proceeded not as an integrated and unified science, but rather in the typical disciplinary framework of science into specialized fields of study that favored reductionism. Plant ecology splintered into topical studies of physiology, populations, communities, ecosystems, landscapes, and biogeochemistry. The study of the atmosphere became organized around spatial scales of micrometeorology, mesoscale meteorology, and global climate and topical fields such as boundary layer meteorology, hydrometeorology, radiative transfer, atmospheric dynamics, and atmospheric chemistry.

With lack of communication across disciplines, ecologists and climatologists can draw different insights from the same observations. Pieter Bruegel the Elder's painting "Hunters in the Snow" exemplifies this (Figure 1.1). The painting has been used in climatology textbooks to illustrate climate change (Lamb 1977, pp. 275–276; Lamb 1995, pp. 233–235). Bruegel painted this scene in the winter of 1565 and it depicts, from a climatologist's perspective, Bruegel's impression of the severe winters of that era. It was the beginning of prolonged artistic interest in Dutch winter landscapes that coincided with an extended period of colder than usual European winters. Ecologists have similarly used this painting to illustrate the ecological concept of a landscape (Forman and Godron 1986, pp. 5–6). Instead of a visual record of an unusually cold climate, the ecological perspective perceives an expression of the core tenets of landscape ecology. From an ecological point of view, the painting depicts heterogeneity of

Fig. 1.1 "Hunters in the Snow" (Pieter Bruegel the Elder). Reproduced with permission of the Kunsthistorisches Museum (Vienna).

landscape elements, spatial scale, and movement across the landscape.

Earth, too, has long been viewed differently by ecologists and climatologists. Ecologists have historically seen weather, climate, and atmospheric composition as external forcings that shape plant communities and ecosystem functions. The manner in which ecosystems influence weather, climate, and atmospheric composition was not examined in classic ecology textbooks. Similarly, climatology textbooks emphasized the physics and fluid dynamics of the atmosphere, not the vegetation at the lowest boundary of the atmosphere.

The advent of global models of Earth's climate in the 1970s and 1980s altered the disciplinary study of ecology and climatology. These models require a mathematical representation of the exchanges of energy, water, and momentum between land and atmosphere. These processes are regulated in part by plants, which with their leaves, stomata, and diversity of life do not conform to the mathematics of fluid dynamics. Atmospheric scientists developing climate models had to expand their geophysical framework to a biogeophysical framework (Deardorff 1978; Dickinson et al. 1986; Sellers et al. 1986). The ongoing evolution of climate models to models of the Earth system is marked by recognition of the central role of terrestrial ecosystems in regulating Earth's climate through physical, chemical, and biological processes and the critical influence that human appropriation of ecosystem functions has on climate (Pitman 2003; Bonan 2008; Arneth et al. 2010, 2014; Levis 2010; Seneviratne et al. 2010; Mahowald et al. 2011). Models of Earth's land surface, including its terrestrial ecosystems, for climate simulation have expanded beyond their hydrometeorological heritage (with emphasis on surface energy fluxes and the hydrologic cycle) to include carbon, reactive nitrogen, aerosols, anthropogenic land use, and vegetation dynamics. These models are important research tools to study land–atmosphere interactions and climate feedback from ecological processes.

1.3 Deforestation and Climate – Some Early Views

The notion that vegetation affects climate is not new. Over two thousand years ago, Theophrastus

Fig. 1.2 Sketches of land clearing in western New York (clockwise from top left). In the first panel, the initial forest clearing is small, only to fell trees for the small log house and to raise a few livestock. The second panel shows the settler has cleared a few acres of land. Ten years have passed in the third panel. Thirty to forty acres of land have been cleared, and neighbors have cleared their land. The final panel depicts 45 years following the initial clearing. From Turner (1849, pp. 562–566).

wrote that draining marshes removed the moderating effect of water and created a colder climate, while deforestation exposed the ground to the Sun and warmed climate (Glacken 1967, p. 130; Neumann 1985). The concept that forests increase rainfall can be traced back to the Roman natural philosopher Pliny the Elder and his *Natural History*, written in the first century AD (Andréassian 2004). European naturalists in the seventeenth and eighteen centuries, too, believed that the wide-ranging clearing of forests and cultivation of land in Europe had moderated the climate since antiquity (Fleming 1998). Settlers of the New World carried with them a similar sentiment, and a vigorous debate arose about whether the extensive land clearing (Figure 1.2) was indeed changing the climate of America (Thompson 1980; Fleming 1998). Like debates arose in Australia, where much of the native forest and woodland was cleared following British settlement, and similarly with British colonization of India.

One question concerned whether deforestation and cultivation of land created milder winters. A popular view, espoused by the Scottish philosopher David Hume, was that deforestation opened the land to heating by the Sun during winter. In an essay (ca. 1750) he explained that warmer winters occurred because "the land is at present much better cultivated, and that the woods are cleared, which formerly threw a shade upon the earth, and kept the rays of the sun from penetrating to it" (Hume and Miller 1987, p. 451). Because of this, Hume declared that "our northern colonies in America become more temperate, in proportion as the woods are felled." Similar views are seen in the writings of the New England Puritan minister Cotton Mather, who observed that "our cold is much moderated since the opening and clearing of our woods" (Mather 1721, p. 74). Benjamin Franklin, too, believed that climate was warming because "when a country is clear'd of woods, the sun acts more strongly on the face of the earth" (Franklin and Labaree 1966). Franklin's contemporary Hugh Williamson, a physician, scholar, and politician, predicted that with continued clearing of interior lands "we shall seldom be visited by frosts or snows, but may enjoy such a temperature in the midst of winter, as shall hardly destroy the most tender plants" (Williamson 1771). Thomas Jefferson agreed that "a change in our climate … is taking place very sensibly" (Jefferson 1788, p. 88) and urged climate surveys "to show the effect of clearing and culture towards changes of climate" (Jefferson and Bergh 1905). Samuel Williams, a Congregational minister, professor at Harvard, and founder of the University of Vermont, believed that as trees were cut down and settlements increased "the cold decreases, the earth and air become more warm; and the whole temperature of the climate, becomes more equal, uniform and moderate" (Williams 1794, p. 57). This climate change "is so rapid and constant, that it is the subject of common observation and experience."

Not all agreed with this sentiment. In addition to being a lexicographer, Noah Webster of Connecticut was a political writer. He strongly refuted the notion of such changes in climate in an essay published in 1799. Direct observations of climate change were lacking, he noted, and evidence of a warmer climate relied on anecdotes and personal memories. Yet, he, too, admitted to differences between forests and cleared land that altered local climate (Webster 1843, pp. 145). "While a country is covered with trees," he wrote, "the face of the earth is never swept by violent winds; the temperature of the air is more uniform, than in an open country; the earth is never frozen in winter, nor scorched with heat in summer."

The writings of Europeans attested to the prominence of the forest–climate debate, and also to the difference in opinions. Constantin-François Volney published a book in 1803 based on his travels in eastern North America. He observed that "for some years it has been a general remark in the United States, that very perceptible partial changes in the climate took place, which displayed themselves in proportion as the land was cleared" (Volney 1804, p. 266). Alexander von Humboldt responded in 1807 that "the statements so frequently advanced, although unsupported by measurements, that since the first European settlements in New England, Pennsylvania, and Virginia, the destruction of many forests … has rendered the climate more equable, – making the winters milder and the summers cooler, – are now generally discredited" (Humboldt et al. 1850, p. 103). The *Edinburgh Encyclopaedia* asserted that the theory of land-use climate change "is, we fear, to be regarded rather as the birth of a lively fancy, than the offspring of accurate science" (Brewster 1830, pp. 613–614).

Another belief was that forests contributed to the plentiful rainfall in America and that deforestation decreased rainfall. Christopher Columbus developed such a view from his travels to the New World. His son wrote in a biography that he attributed the rainstorms of Jamaica to "the great forests of that land; he knew from experience that formerly this also occurred in the Canary, Madeira, and Azore Islands, but since the removal of forests that once covered those islands, they do not have so much mist and rain as before" (Colón and Keen 1959, pp. 142–143).

Natural scientists developed similar views. John Evelyn declared in 1664 that forests "render those countries and places more subject to rain and mists" (Evelyn 1801, pp. 29–32). John Clayton, an English naturalist and clergyman, attributed the violent thunderstorms of coastal Virginia to the dense forests (Clayton 1693; Berkeley and Berkeley 1965, pp. 48–49). His compatriot John Woodward described how the "great moisture in the air, was a mighty inconvenience and annoyance to those who first settled in America," but that after clearing the forests "the air mended and cleared up apace: changing into a temper much more dry and serene than before" (Woodward 1699). Samuel Williams accounted for the plentiful rainfall because "the immense forests … supply a larger quantity of water for the formation of clouds, than the more cultivated countries of Europe" (Williams 1794, p. 50). Hugh Williamson described a feedback by which forest evaporation enhances rainfall and cools climate (Williamson 1811, pp. 23–25): "The vapours that arise from forests, are soon converted into rain, and that rain becomes the subject of future evaporation, by which the earth is further cooled." In the Caribbean islands, which had undergone widespread forest clearing to grow sugar cane, forest preserves were created to promote rainfall (Anthes 1984).

Settlement of the Great Plains in the 1870s and 1880s shifted the debate from deforestation to afforestation, with the premise that tree planting would increase rainfall (Emmons 1971; Kutzleb 1971; Thompson 1980; Williams 1989). An official in the United States Department of Interior claimed that "the planting of ten or fifteen acres of forest trees on each quarter section [160 acres] will have a most important effect on the climate, equalizing and increasing the moisture" (United States General Land Office 1867, p. 135). That some official believed that "if one-third the surface of the great plains were covered with forest there is every reason to believe the climate would be greatly improved" (United States General Land Office 1868, p. 197). Congress agreed and enacted the Timber Culture Act of 1873 to promote afforestation. Popular science gazettes, too, advocated tree planting to increase rainfall (Oswald 1877; Anonymous 1879). Samuel Aughey, of the University of Nebraska, promoted the notion that plowing the prairie sod was the cause of an increase in rainfall observed at that time. Cultivation allowed the soil to retain more rainfall, which evaporated and rained back onto the land, he theorized (Aughey 1880, pp. 44–45). Charles Wilber popularized this notion with the phrase "rain follows the plow" (Wilber 1881, p. 68). He described how an "army of frontier farmers … could, acting in concert, turn over the prairie sod, and … present a new surface of green, growing crops instead of the dry, hard-baked earth covered with sparse buffalo grass. No one can question or doubt the inevitable effect of this cool condensing surface upon the moisture in the atmosphere."

A sharply divided debate on forest–climate influences continued in the latter half of the nineteenth century and into the twentieth century. Conservationists, botanists, and foresters argued for such influences. George Perkins Marsh devoted a large portion of his treatise *Man and Nature* to forest–climate influences (Marsh 1864). The botanist Richard Upton Piper agreed that "forests trees should be preserved for their beneficial influence upon the climate" (Piper 1855, p. 51). The fledgling forestry division of the United States Department of Agriculture issued reports supportive of the burgeoning field of forest meteorology and forest–rainfall influences (Hough 1878; Fernow 1902; Zon 1927).

Climatologists of the day, however, dismissed the study of forests and climate. A publication on the climate of the United States asserted that "the great differences of surface character which belong to the deserts, woodlands, and other more striking features, are believed to have their *origin* in climate, and not to be agents of causation themselves" (Blodget 1857, p. 482). The geographer Henry Gannett suggested that faulty reasoning was behind the belief that forests increase rainfall. His analysis of precipitation records found no change in rainfall in regions that had undergone increases and decreases in tree cover, and he complained that "a satisfactory explanation of this supposed phenomenon has never … been offered" (Gannett 1888). He further explained that "it may be that in this case an effect has been mistaken for a cause, or rather, since it is universally recognized that rainfall produces forests, the converse has been incorrectly assumed to be also true" (Anonymous 1888). The eminent meteorologist William Ferrel argued in favor of large-scale control of precipitation by atmospheric circulation, not by surface conditions (Ferrel 1889). His colleague Cleveland Abbe wrote that "rational climatology gives no basis for the much-talked-of influence upon the climate of a country produced by the growth or destruction of forests … and the cultivation of crops over a wide extent of prairie" (Abbe 1889). Abbe believed that "the idea that forests either increase or diminish the quantity of rain that falls from the clouds is not worthy to be entertained by rational, intelligent men" (Moore 1910, p. 7).

Foresters and climatologists in the United States Department of Agriculture were sharply divided over forest influences on rainfall. While the foresters issued reports in support of the science (Hough 1878; Fernow 1902; Zon 1927), their colleagues in the department's Weather Bureau (the predecessor of the present-day National Weather Service) resoundingly dismissed these ideas. Mark Harrington, chief of the Weather Bureau, rejected his forestry colleagues' belief that forests affected climate in any manner (Fernow 1902). Willis Moore, Harrington's successor, also rebuffed studies relating forests and climate with the retort that "while much has been written on this subject, but little of it has emanated from meteorologists" (Moore 1910, p. 3). "Precipitation," he explained, "controls forestation, but forestation has little or no effect upon precipitation" (Moore 1910, p. 37). The caustic rhetoric confused a writer in the journal *Nature*, who reported that "the literature on the subject is somewhat bewildering" (Anonymous 1912).

The views about ongoing climate change in colonial America ultimately proved to be false. Climate was not changing; winters were not becoming milder with land clearing; rainfall was not decreasing because of deforestation or increasing because of tree planting and soil cultivation. However, meteorologists of that era, too, were ultimately proved wrong. As they sought physical explanations for geographic variations in climate, they were too quick to dismiss the precept that forests, grasslands, croplands, and other ecosystems do indeed influence climate. Interest in the climatic effects of deforestation, cultivation, and overgrazing reemerged in the 1970s, with recognition that human activities do indeed change climate and that land use is one such mechanism for climate change (Landsberg 1970; Otterman 1974, 1977; Schneider and Dickinson 1974; Sagan et al. 1979). One hundred years after a writer to *Nature* found the debate to be "belwidering," the journal published another paper that found that tropical forests do indeed increase rainfall (Spracklen et al. 2012).

1.4 Ecological Climatology

Scholars of the eighteenth and nineteenth centuries lacked the scientific tools to properly ascertain forest influences on climate, but scientists in the latter part of the twentieth century had a new tool – global climate models – with which to study how plants and ecosystems affect climate. Scientific interest over the past few decades in the coupling between climate and life has paralleled the trend by atmospheric scientists to recognize the planet as a system of interacting spheres.

Today, scientists identify four main components of the Earth system: atmosphere, air; hydrosphere, water; biosphere, living things; and geosphere, solid portion of Earth. The geosphere can be subdivided into other spheres. The lithosphere is the solid outer layer of Earth including the crust and upper mantle. Its outermost layer is called the pedosphere, or soil. Some scientists separately identify the cryosphere, or frozen portion of Earth. The influence of humans is so prevalent, especially after the Industrial Revolution, that a new sphere, the anthroposphere, has been proposed to describe that part of Earth modified by people for human activities or habitats. Earth's climate must be understood in terms of a system of interacting spheres (atmosphere, hydrosphere, biosphere, geosphere, and anthroposphere); the energy, water, and biogeochemical cycles that link these spheres; and the interactions with human systems that alter these cycles. This parallels a progression in atmospheric sciences from (Figure 1.3): atmospheric general circulation models, which considered atmospheric physics and dynamics; to atmosphere–ocean general circulation models, which included the coupling of the atmosphere with models of ocean and sea-ice physics and dynamics; to global climate models, which additionally accounted for hydrometeorological coupling with land; and now to Earth system models, which also include atmospheric chemistry, terrestrial and marine ecology, and biogeochemistry.

At the intersection of these spheres is an interdisciplinary field of study called biogeoscience that bridges the earth and life sciences (Figure 1.4). Biogeoscience is the study of the interactions between life and Earth's atmosphere, hydrosphere, and geosphere. It has long been synonymous with the study of

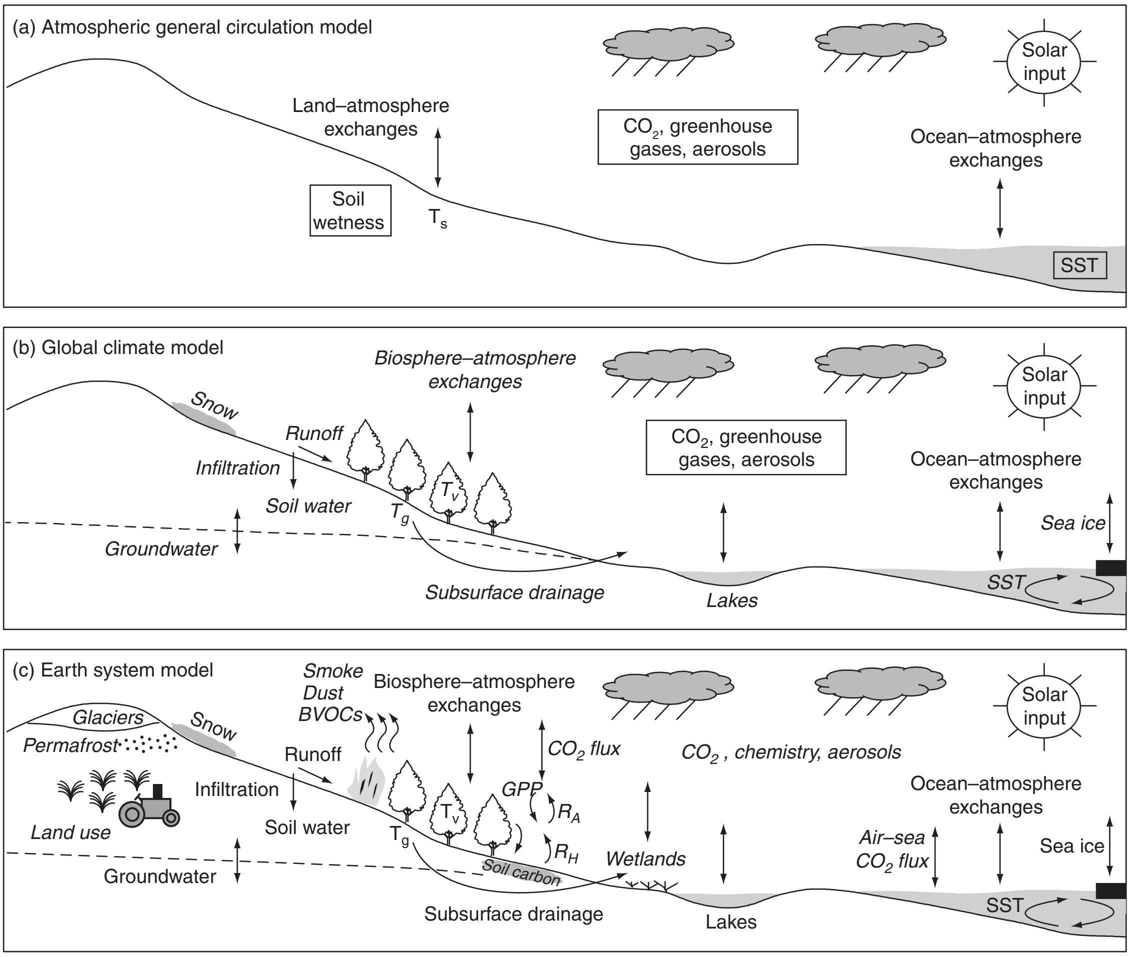

Fig. 1.3 Components of the Earth system, their processes, and interactions as represented in global models. New processes added to each model are highlighted in italics. The distinction among models is not precise, and the transition among models is in fact blurred. (a) Atmospheric general circulation models circa 1970s. These models used prescribed inputs of atmospheric CO_2, other greenhouse gases, and aerosols. They calculated land and ocean physical flux exchanges using prescribed soil wetness and sea surface temperature. (b) Global climate models circa 1990s. These models added the hydrologic cycle on land and plant canopies. They included ocean general circulation models to calculate sea surface temperature, sea ice, and ocean dynamics. (c) Earth system models circa 2010s. These models added the carbon cycle and other biogeochemical processes, anthropogenic land use, wetlands, glaciers and cryospheric processes, atmospheric chemistry, and aerosols.

biogeochemistry, but is broader and includes the interactions between living organisms and the physical environment and the manner in which organisms modify physical systems.

This book examines one element of that science – the commonality between ecological and atmospheric sciences that affect weather, climate, and atmospheric composition. The study of plants and terrestrial ecosystems, and human appropriation of ecosystem functions, is as essential to the study of Earth's climate as is the study of atmospheric physics and dynamics. This book merges the relevant areas of ecology and climatology, broadly defined to include weather, climate, and atmospheric composition, into an overlapping study of ecological climatology. Ecological climatology is an interdisciplinary framework to understand the functioning of plants and terrestrial ecosystems in the Earth

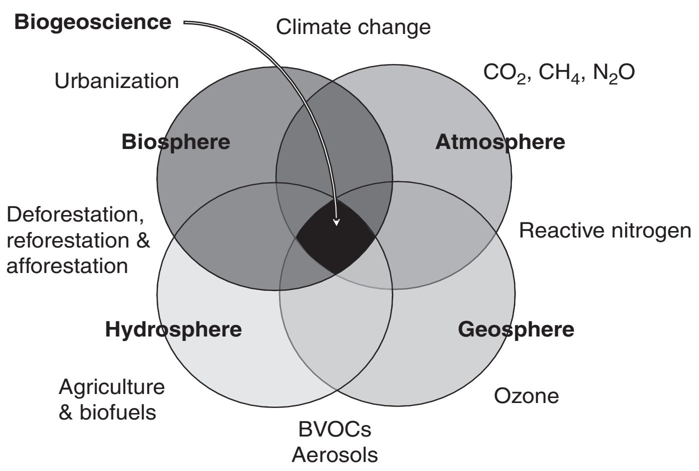

Fig. 1.4 Biogeoscience as the intersection of the atmosphere, hydrosphere, biosphere, and geosphere. Human influences are shown in the text outside the spheres.

system and the physical, chemical, and biological processes by which the biosphere affects atmospheric processes. A central theme of the book is that plants and terrestrial ecosystems, through their cycling of energy, water, chemical elements, and trace gases, are a critical determinate of climate. Changes in terrestrial ecosystems through natural vegetation dynamics, through human land uses, and through climate change itself significantly affect the trajectory of climate change.

Figure 1.5 illustrates five core areas: the *biogeophysical* and *biogeochemical* processes that regulate the exchanges of energy, water, momentum, and chemical materials with the atmosphere over periods of minutes to hours; *watersheds* and *ecosystems* and the hydrological and ecological processes that regulate these exchanges over periods of days to months; and *landscape dynamics* and the ecological and anthropogenic processes controlling the arrangement of plants into communities, the functioning of ecosystems, and temporal changes in response to disturbance over periods of years to centuries.

Biogeophysics is the study of physical interactions of the biosphere and geosphere with the atmosphere. It considers the transfers of heat, moisture, and momentum between land and atmosphere and the meteorological, hydrological, and ecological processes regulating these exchanges. Momentum is transferred when plants and other rough elements of the land surface interfere with the flow of air. Heat and moisture are exchanged when net radiation at the surface (R_n) is returned to the atmosphere as sensible heat (H), latent heat (λE), or stored in the ground (G). Biogeophysical feedbacks are understood through the surface energy balance:

$$R_n = (S\downarrow - S\uparrow) + (L\downarrow - L\uparrow) = H + \lambda E + G \qquad (1.1)$$

where $S\downarrow$ and $L\downarrow$ are downwelling solar radiation and longwave radiation onto the surface, respectively, and $S\uparrow$ and $L\uparrow$ are the upward radiative fluxes from the surface. Collectively, these four radiative fluxes comprise net radiation. The typical unit of measurement is the flux of energy per unit area (J s^{-1} m^{-2}, or W m^{-2}).

The surface energy balance highlights several important land–atmosphere interactions. One relates to surface albedo (Figure 1.6a). An increase in surface albedo, which can occur with loss of vegetation cover, increases reflected solar radiation, reduces the absorption of solar radiation at the surface, and cools the surface climate. Less energy returns to the atmosphere as sensible and latent heat, which promotes subsidence of air aloft and may reduce precipitation. Such albedo influence on rainfall is particularly important in semiarid climates. In cold, snowy climates, tall trees protrude above the snowpack and reduce surface albedo. Vegetation masking of the high albedo of snow creates a warmer climate than in the absence of trees.

Another important aspect of land–atmosphere coupling is surface roughness (Figure 1.6b).

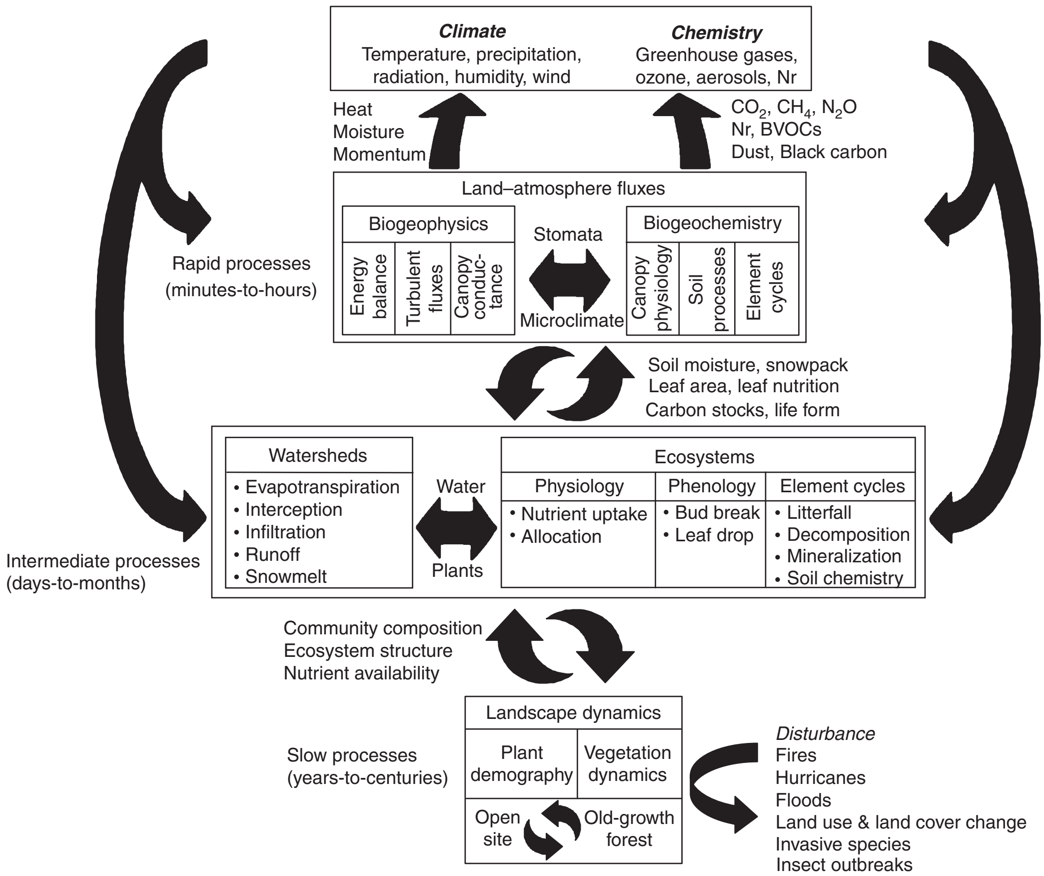

Fig. 1.5 A generalized scope of ecological climatology showing the biogeophysical and biogeochemical processes by which terrestrial ecosystems affect weather, climate, and atmospheric composition, the watershed and ecosystem processes that govern biosphere–atmosphere coupling, and the role of landscape dynamics in initiating change.

Rough surfaces such as forests generate more turbulence and have higher sensible and latent heat fluxes than smoother surfaces such as grasslands, all other factors being equal. A decrease in roughness length, by decreasing turbulence and aerodynamic conductance, can lead to a warmer, drier atmospheric boundary layer.

Biogeochemistry is the study of element cycling among the biosphere, geosphere, and atmosphere. Carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) are greenhouse gases regulated in part by terrestrial ecosystems. The net storage of carbon in the biosphere in the absence of fire and other losses, known as net ecosystem production (*NEP*), is the balance of carbon uptake during gross primary production (*GPP*), carbon loss during plant respiration (R_A), and carbon loss during decomposition (R_H):

$$NEP = GPP - R_E = (GPP - R_A) - R_H = NPP - R_H \tag{1.2}$$

The typical unit of measurement is the mass of carbon exchanged per unit area over some period of time (e.g., g C m^{-2} yr^{-1}). The net carbon uptake by plants ($GPP - R_A$) is known as net primary production (*NPP*), and the total ecosystem respiration is $R_E = R_A + R_H$. The signature of terrestrial ecosystems is seen in the annual cycle of atmospheric CO_2, which has low concentration during the growing season when plants absorb CO_2 and high concentration during the dormant season. It is also evident in the uptake