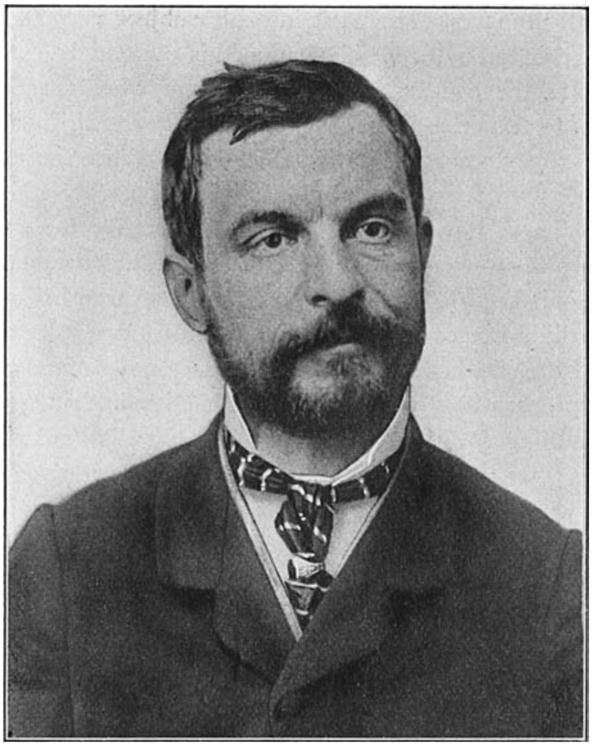

Figure B9.1(c) Wilhelm Hofmeister (1824–1877) uncovered the alternation of generations in plants and published a monograph on the topic in 1851 (from Goebel 1905).

published his ground-breaking monograph that documented the alternation of generations in plants. This appeared in 1851, eight years before Darwin published *The Origin of Species*. Not until 1863 (at the age of 39) was Hofmeister employed as a professor.

9.3 | $>10^4$ years: the Pleistocene glaciations

The Pleistocene is the second to last epoch in the Earth's history; it was a period of climatic instability that began about 2 million years ago during which extensive ice sheets and other glaciers formed repeatedly (e.g., Delcourt and Delcourt 1991, Levin 1994). For this reason, its popular name is the "Ice Age." The Pleistocene and the Holocene (the last 10 000 years) together comprise the Quaternary Period. Although there have been many ice advances and retreats in the Earth's history, much of its surface has been shaped by the last great period of glacial advance and retreat – a period which ended only about 10 000 years ago. No student of plant ecology can afford to be ignorant of the effects that the last ice advance had upon the landscape. The effects are often very local and their results may vary from heavily scoured landscapes lacking soil, to great terminal moraines, to wind-deposited soils, to large lakes. Thus the influences in any particular area should be examined in more detail than a text like this can provide. It is, however, essential that you learn about Quaternary Period events that shaped your particular region of the world; this will require you to seek out relevant monographs and papers. The comments here will serve only to place these specific details in a larger context.

Now a comment on names. The defining event of the Pleistocene has been the repeated advance of large sheets of ice. In general, the advances and retreats consisted of four major advances interspersed with three major warm periods. The names of the advances differed depending upon where the field-work had been done. In North America they were named, from youngest to oldest, Wisconsinan, Illinoian, Kansan, and Nebraskan; in Great Britain, Devensian, Wolstonian, Anglian, and then a further series of at least four other advances. In Europe they were Weichselian, Saalian, Elsterian, and then a different set of at least three advances. It has proven difficult to put these together in one large picture, particularly as the numbers of advances and retreats have expanded with our knowledge of glacial geology. In fact, marine isotope records suggest that a much more complicated series of advances and retreats occurred (Section 1.10), although ice core records indeed show four glacial periods (Figure1.17(b)).

9.3.1 Erosion and deposition by glacial ice

During the last glacial advance and retreat, substantial portions of the Earth were covered by ice as little as 25 000 years ago, and many temperate areas were uncovered only within the last 10 000 years. As the ice retreated, it left behind the present-day topography. Soil was scoured away and pushed south of the ice margin. (American farmers now grow corn using the soil that was once on my Canadian land.) The landscape was ground flatter in the north and then covered with a variety of glacial deposits from moraines and eskers to clay and sand plains (Figure 9.10). You should obtain a physiographic map of your own home landscape in order to develop an appreciation of the local impacts of events near the end of the Pleistocene Epoch. As one example of the influence of glacial history, consider the quite remarkable changes in the shape and drainage of the Great Lakes during this period (Figure 9.11). The distribution of many vegetation types in this area can still be best explained by past events. For example, the distribution of the nationally rare plant, *Rhexia virginica*, is still associated with areas once covered by glacial Lake Algonquin. The southernmost location of the arctic species *Saxifraga aizoon* is in a canyon that formed when once the Great Lakes drained through Algonquin Park. The extensive pine forests of the upper Ottawa Valley occur on an old delta where a glacial river drained into the Champlain Sea.

9.3.2 Loess

Wind moved large volumes of soil exposed during glacial events. Deposits of wind-blown soil, called loess, cover large areas of

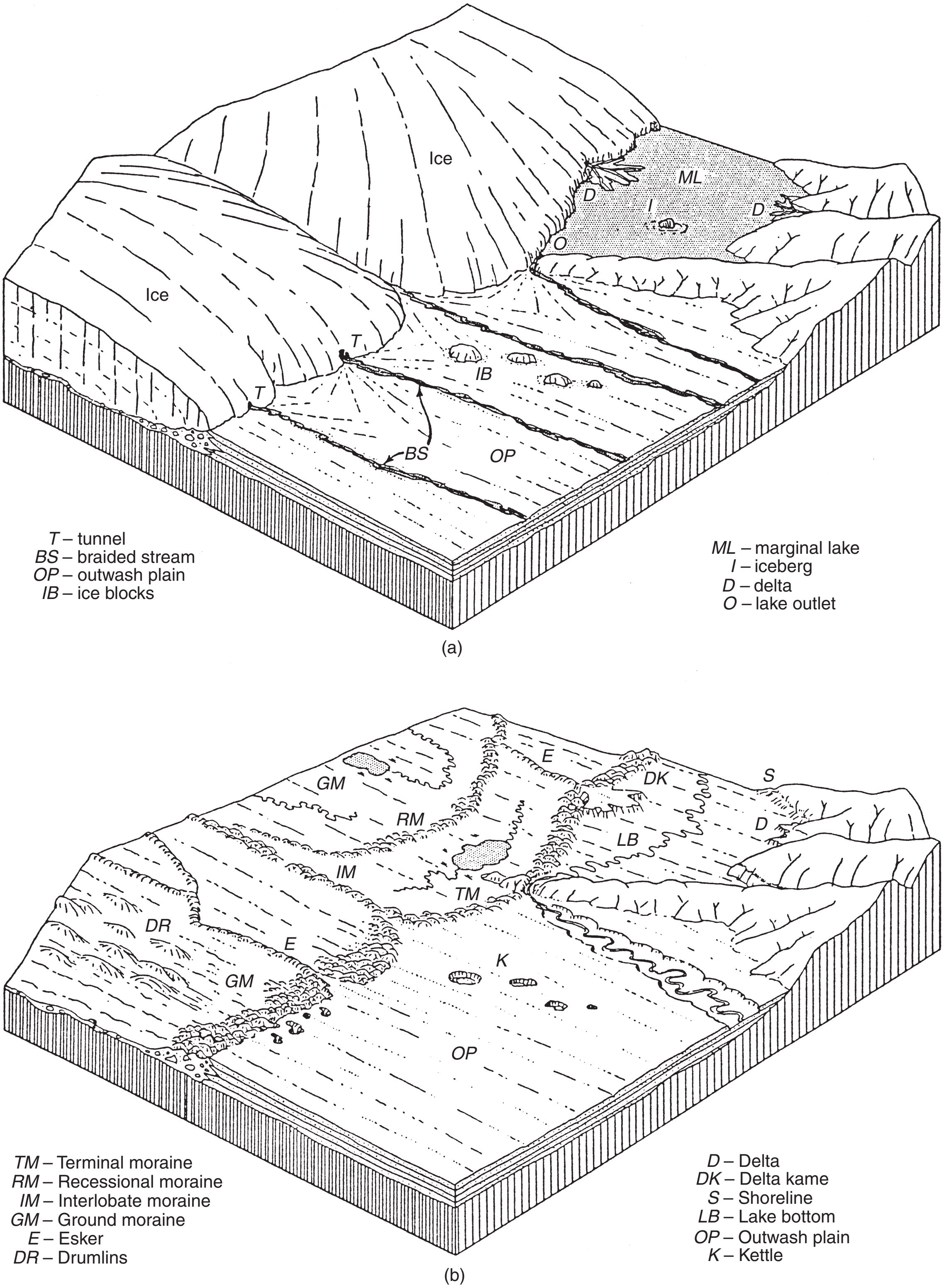

Figure 9.10 Landforms produced near the margin of an ice sheet. (a) Ice margin in almost stagnant condition. (b) Ice entirely gone, revealing subglacial forms (from Strahler 1971).

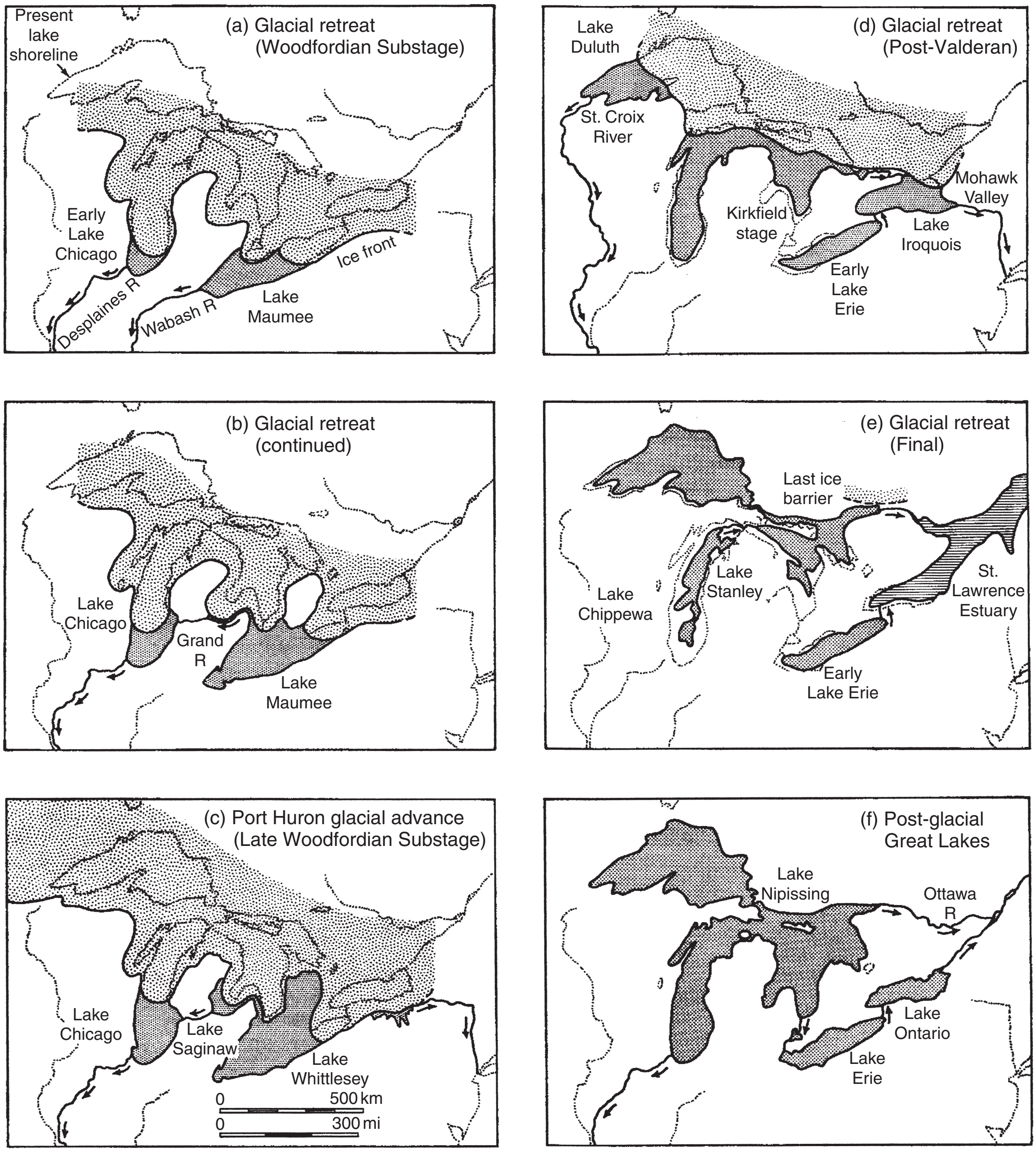

Figure 9.11 Sequence of stages in the development of the Great Lakes (from Strahler 1971).

the Northern Hemisphere: the central and northwestern United States, Alaska, the east European plain (Figure 9.12), and southern Europe. It is thought that loess was derived from the floodplains of braided rivers draining away from the glaciers as well as from glacial debris. The deep deposits of loess in China appear to have been swept in from the Gobi Desert; in places they are 100 meters thick.

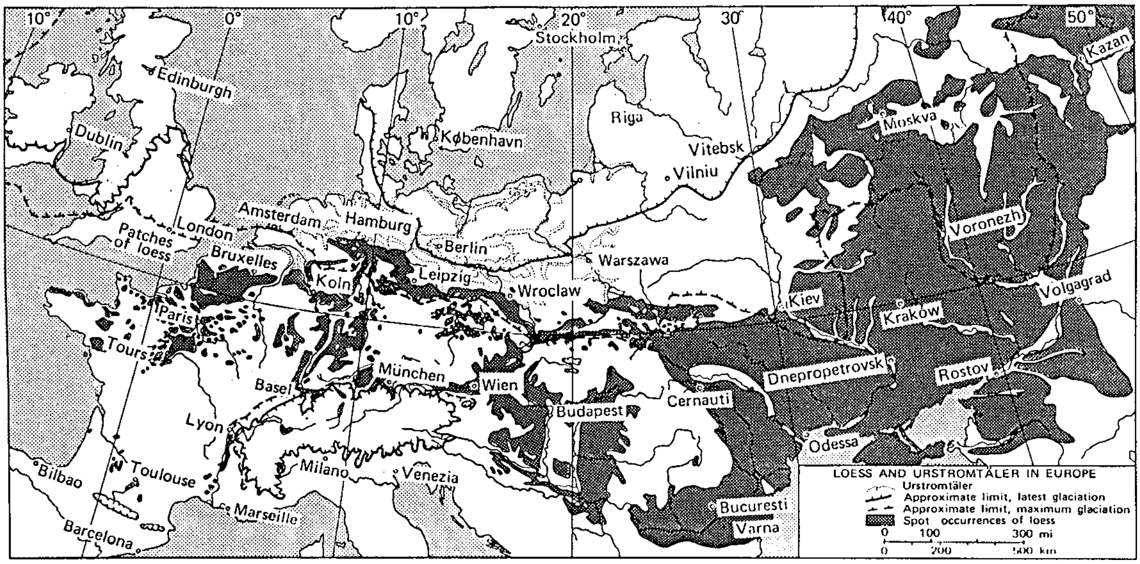

Figure 9.12 Loess and loess-like deposits in Europe (from Flint 1971).

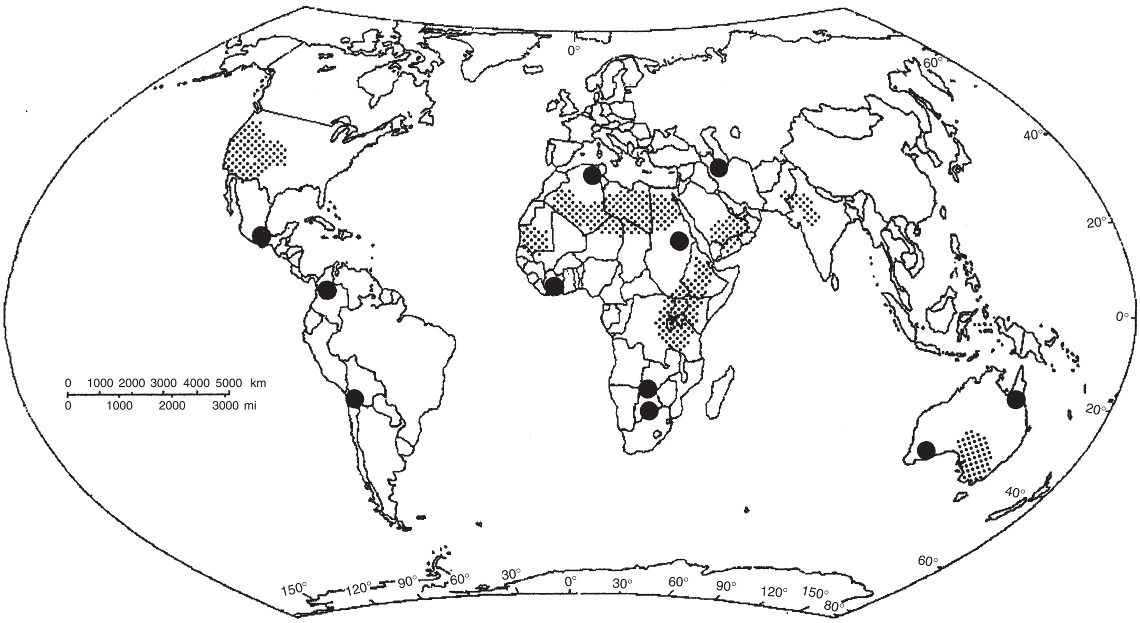

Figure 9.13 Over the last 30 000 years pluvial lakes have formed in and then disappeared from the shaded regions of the Earth. Dots show isolated lakes (after Street and Grove 1979).

9.3.3 Pluvial lakes

Changes in water balance south of ice sheets caused the accumulation of water in previously arid areas (Flint 1971). Large lakes formed in areas such as the southwestern United States, central Australia, and Africa (Figure 9.13). Many of these lakes are now entirely dry or greatly reduced in size.

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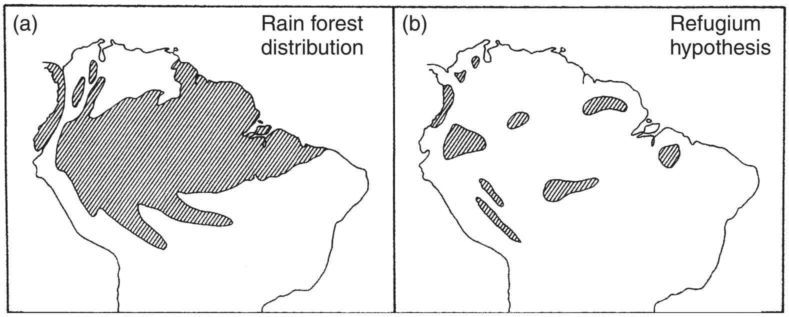

Figure 9.14 (a) Rain forest currently covers the Amazon basin in northern South America. Current evidence indicates that this region remained forested during the last glacial period. (b) The falsified hypothesis. It has been suggested that the rain forest may have shrunk to small refugia during ice advances, but current data provide no evidence to support this hypothesis (Colinvaux et al. 1996, 2000, 2001) (after Pielou 1979).

9.3.4 Drought and tropical forests

Just as some areas became wetter during glacial advances (Figure 9.13), other areas may have become dryer. Tropical forests currently cover the Amazon basin (Figure 9.14(a)). How, if at all, did these forests change during colder, glacial periods? Perhaps changes in these rain forests were minimal, since this area is near the equator and far from advancing ice sheets. Alternatively, perhaps drier periods allowed savanna to invade substantial areas of the Amazon, and perhaps the rain forests contracted to isolated refugia (Figure 9.14(b)). The hypothesis of isolated refugia (e.g., Haffer 1969) has seemed attractive to many, since each ice advance would have fragmented the forests, allowing periods of isolation and speciation. If this had happened, the cycle of glacial periods (Figure 1.17(b)) might have acted as diversity pump, conveniently explaining both the high diversity of the Amazonian forests, the higher numbers of species in certain regions, and the distributions of some species. (This model may also appeal to another audience for another reason, since it implies that rain forests may be relatively insensitive to disturbance, and that large areas may be lost with few consequences for diversity.) Of course, one might equally argue that it was the very absence of recurring disturbance that allowed so many species to evolve and survive in the Amazon, and that some regions have species (if they do) as a consequence of other factors like more kinds of habitats (Chapter 11).

Contrasting hypotheses are a part of science, and knowledge increases only when data are collected to test among them. Given the enormous area of Amazonia, and the many concerns about the loss of primary (frontier) rain forests (Chapter 12), these contrasting hypotheses need to be tested, and the incorrect one(s) discarded.

Here is a challenge: how does one test whether savanna invaded the Amazon during drier periods tens of thousands of years ago? There are at least three sources of biological data available. The first is the Amazon delta. If the rain forests periodically receded, this should be mirrored in changes in the characteristics of sediments in the delta. Samples of Amazon River detritus taken from coastal sediment indicate that the Amazon basin remained continually forested, at least up to 70 000 years ago (Kastner and Goñi 2003).

A second source of evidence could come from sediment cores taken from lakes. Periods of savanna should be marked by layers having pollen grains from grasses and other savanna plants. Finding good pollen records is much more difficult in the Amazon than at higher latitudes (Colinvaux et al. 2001). The Amazon basin has few old lakes with long sediment records, and further, many rain forest trees produce little pollen that could drift into lakes, since the pollen is dispersed by animals. These problems have been slowly overcome, and a number of cores taken for study (including a 40 000 year pollen record from Lake Pata on a 500–600 m tall inselberg, a rock outcrop that emerges above the rain forest (Colinvaux et al. 1996). This core, and others like it, show no evidence of periods of savanna expanding into the rain forest (Colinvaux et al. 2000, 2001). A third source of evidence comes from fossil plants. Fossil plant assemblages that predate the Quaternary glaciations show that high plant diversity occurred long before such hypothetical refugia might have formed (Wilf et al. 2003). Hence, this evidence indicates that the map of refugia in Figure 9.14(b) is wrong, and that the Amazonian rain forests were relatively unaffected by changing climate during the ice ages. Moreover, the hypothesis is not needed to explain tree diversity, since this diversity predated the Quaternary. In the words of Colinvaux et al. (2001): "All geological data from Amazonian landforms imply continuous humid weathering throughout late Tertiary and Quaternary times . . .. All available Amazonian pollen data, without exception and including new data, imply biome stability . . .. The 'aridity with refuges paradigm' now impedes Amazonian research and should be discarded."

Although the evidence is now clear that savannas did not recently intrude into Amazonia, savannas are widespread elsewhere in South and Central America, and in the world, and their distribution is very sensitive to drought and fire. In drier climates, or drier locations, savanna can replace forests. Recurring fire is a natural part of this process (Figure 9.15), and the type of savanna that forms will depend up fire frequency (Myers et al. 2006). In tropical landscapes with high fire frequencies, most species of trees survive only in narrow strips of forest along water courses (termed riparian forest or gallery forest). During wetter periods with lower fire frequency, the forest may expand into upland areas, while during drier periods with higher fire frequency, the forest may shrink to the margins of rivers. In order to investigate the potential importance of riparian forests as refugia for forest plants, Meave and Kelmman (1994) explored an area of Belize that was mostly savanna, and enumerated the tropical tree species they encountered in riparian forests. A total of 292 species was found in a cumulative sample of only 1.6 ha. Some tracts of riparian forest had as many tree species as continuous forests elsewhere in Central America. Moreover, small changes in flood frequency and soil fertility can produce different types of riparian forest (Veneklaas et al. 2005), which may further increase the number of species of trees that can survive in landscapes that are largely

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Figure 9.15 In drier climates, and in drier locations, tropical broadleaf forests can be replaced by open savanna. Recurring fire is a natural part of this process. In fire-dominated landscapes, narrow strips of forest along watercourses may be the only remnants of broadleaf forest in the landscape. (Caribbean pinelands of the Rio Platano Biosphere Reserve in Honduras, courtesy Ronald Myers).

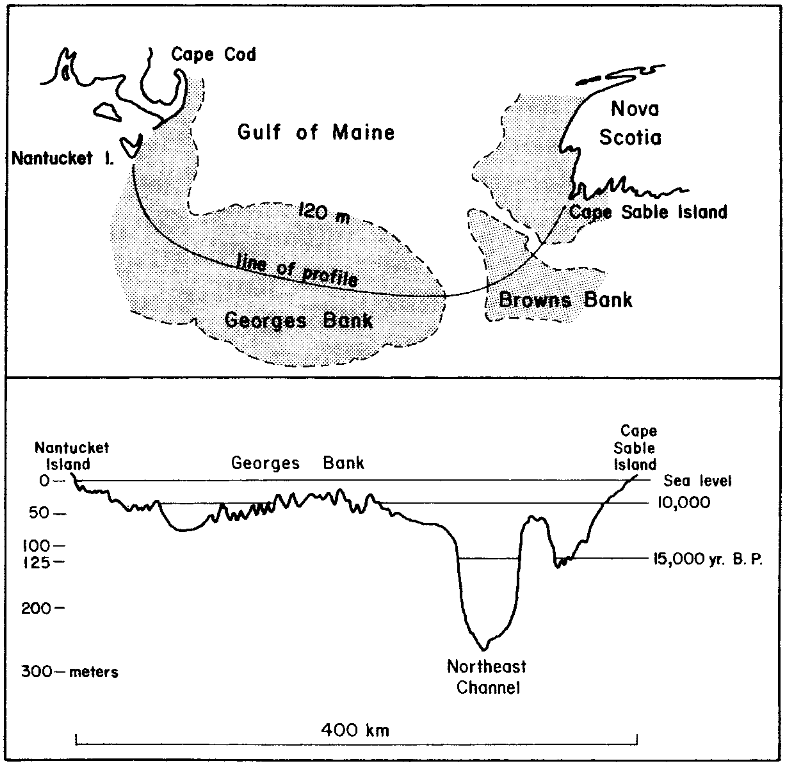
savanna. Hence, all the evidence suggests that the refugium hypothesis mapped in Figure 9.14(b) is incorrect.

In summary, we know that drought and fire can shift the relative distribution of forest and savanna in a landscape. The hypothesis that drought reduced Amazonian rain forests to small refugia during the last ice age (Figure 9.14(b)) is not supported by current evidence. However, there is good evidence that in drier climates elsewhere, where drought and fire do allow savanna to expand, water courses are an important refuge for trees to escape recurring fire.

9.3.5 Sea level decrease

The enormous amounts of water locked into glacial ice lowered sea levels by as much as 100 m. This would have opened up new areas of habitat along previously submerged coastal plains, as well as created land bridges between some continents. The continental margins of eastern North America, for example, appear to have had a rich wetland flora appropriately called the Atlantic Coastal Plain flora; peat

Figure 9.16 Changes to sea level in relation to a profile from Nantucket Island, Massachusetts, to Cape Sable Island, Nova Scotia (from Keddy and Wisheu 1989).



balls recovered from offshore illustrate how well developed the peatlands in these areas were. When the sea level rose, most of this habitat was submerged, which left widely spaced fragments of this distinctive wetland habitat along the eastern coast of North America. The distribution of *Sabatia kennedyana* in the Carolinas, Cape Cod, and southwestern Nova Scotia suggests that at one time these areas were connected by land, but when the sea level rose the areas of *S. kennedyana*'s distribution were no longer contiguous (Figure 9.16).

Similarly, Beringia would have been exposed enough to allow an exchange in fauna and flora between Eurasia and northern North America. During the peak of the ice age, this connection between the two continents was covered by xeric tundra, which provided food for large grazing mammals and allowed them to survive as they migrated across the land bridge. Snow sheep, musk-oxen, moose, lynx, and black bear arrived from Siberia (Hopkins 1967, Pielou 1979). Another species that is thought to have migrated eastward across this land bridge was a hominid known as *Homo sapiens*.

9.3.6 Migration

Changes in sea levels, pluvial lake levels, and ice cover would have forced major changes in the distributions of plant and animal species. Picture the world's vegetation types at the maximum of the last ice advance; Figure 9.17 shows that the vegetation of eastern North

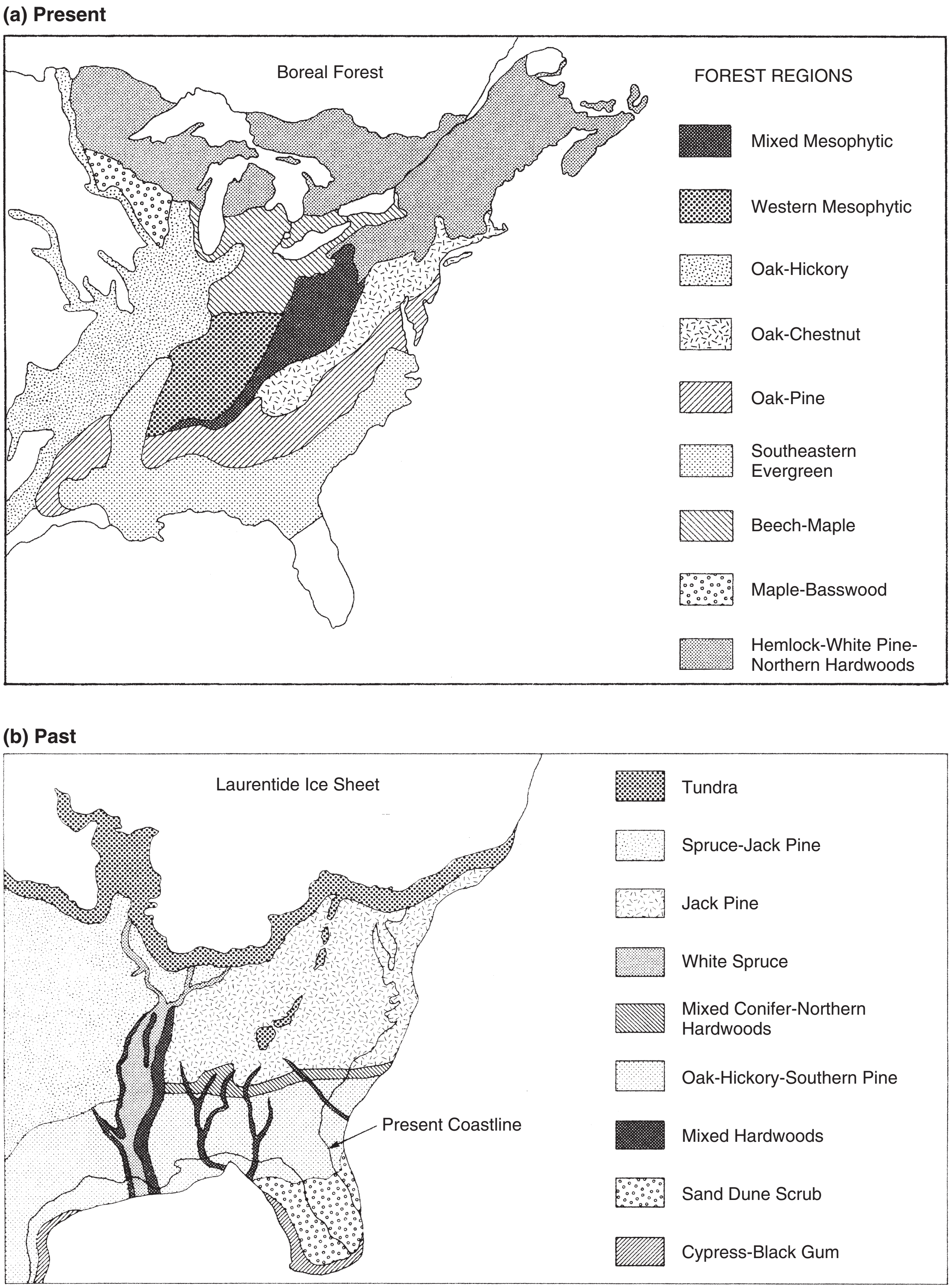


Figure 9.17 (a) Major associations within the deciduous forests of eastern North America, and (b) reconstruction of the vegetation of eastern North America during the Wisconsin glacial maximum about 18 000 years BP (from Archibold 1995).

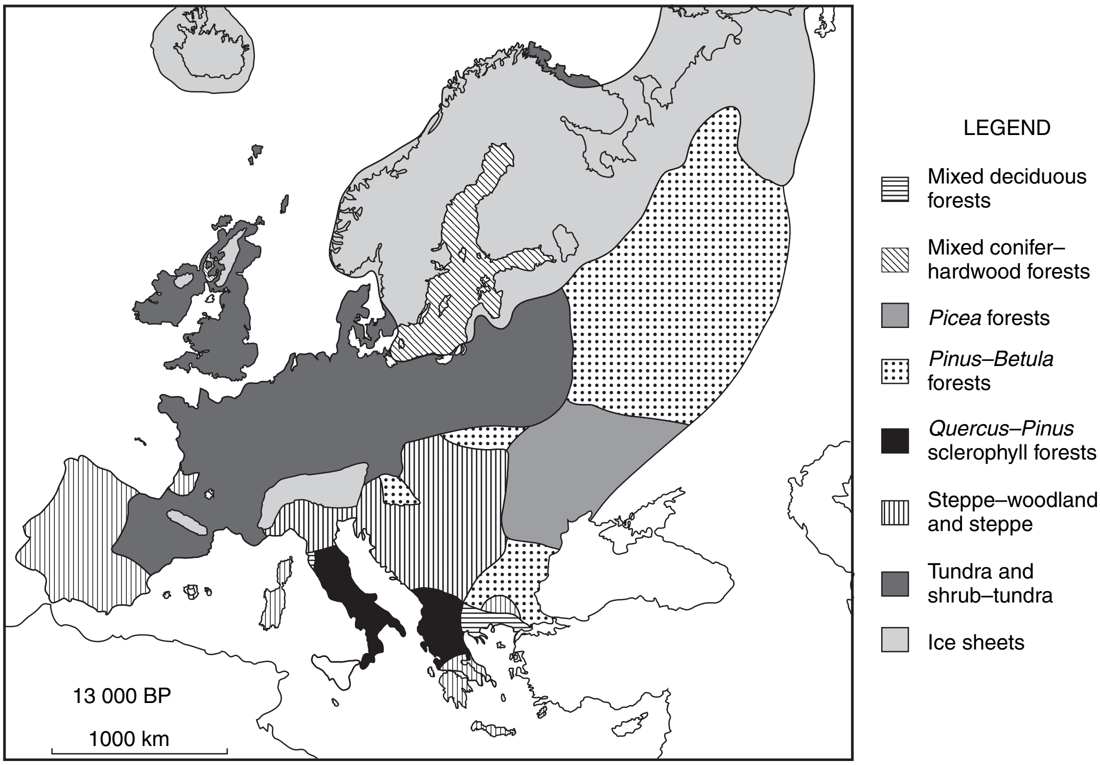


Figure 9.18 Simplified paleo-vegetation map of Europe for 13 000 BP based upon palynological data (from Huntley 1990).

America was vastly different from that today. In Europe, temperate zone trees such as *Carya*, *Liquidambar*, *Robinia*, and *Tsuga* became extinct around this time, perhaps because the Alps prevented southward migration as the ice advanced (Daubenmire 1978). Figure 9.18 shows the vegetation of Europe at 13 000 BP. Note the restriction of deciduous forests to two small regions, one on the west coast of Italy and the other north of the Adriatic Sea.

While species distributions today are obviously different from distributions in the past, knowledge of how plant species responded to the various dramatic changes that occurred is still incomplete. This has led to debates about whether the world's vegetation zones are, in fact, in equilibrium with today's climate or whether they represent delays in migration following the retreat of the ice. Palynological research carried out over the last half of the twentieth century tends to confirm that there was rapid recolonization northward as the ice retreated (Figure 9.19). The need for accurate reconstructions of past events has now been given an added impetus by fears that we are altering Earth's climate (Section 1.10). Establishing a connection between climate and vegetation in the past provides a vital tool for forecasting changes in vegetation.

9.3.7 Hominids

Modern humans (*Homo sapiens*) appear during the last Pleistocene interglacial, about 100 000 years ago. At this time Neanderthals

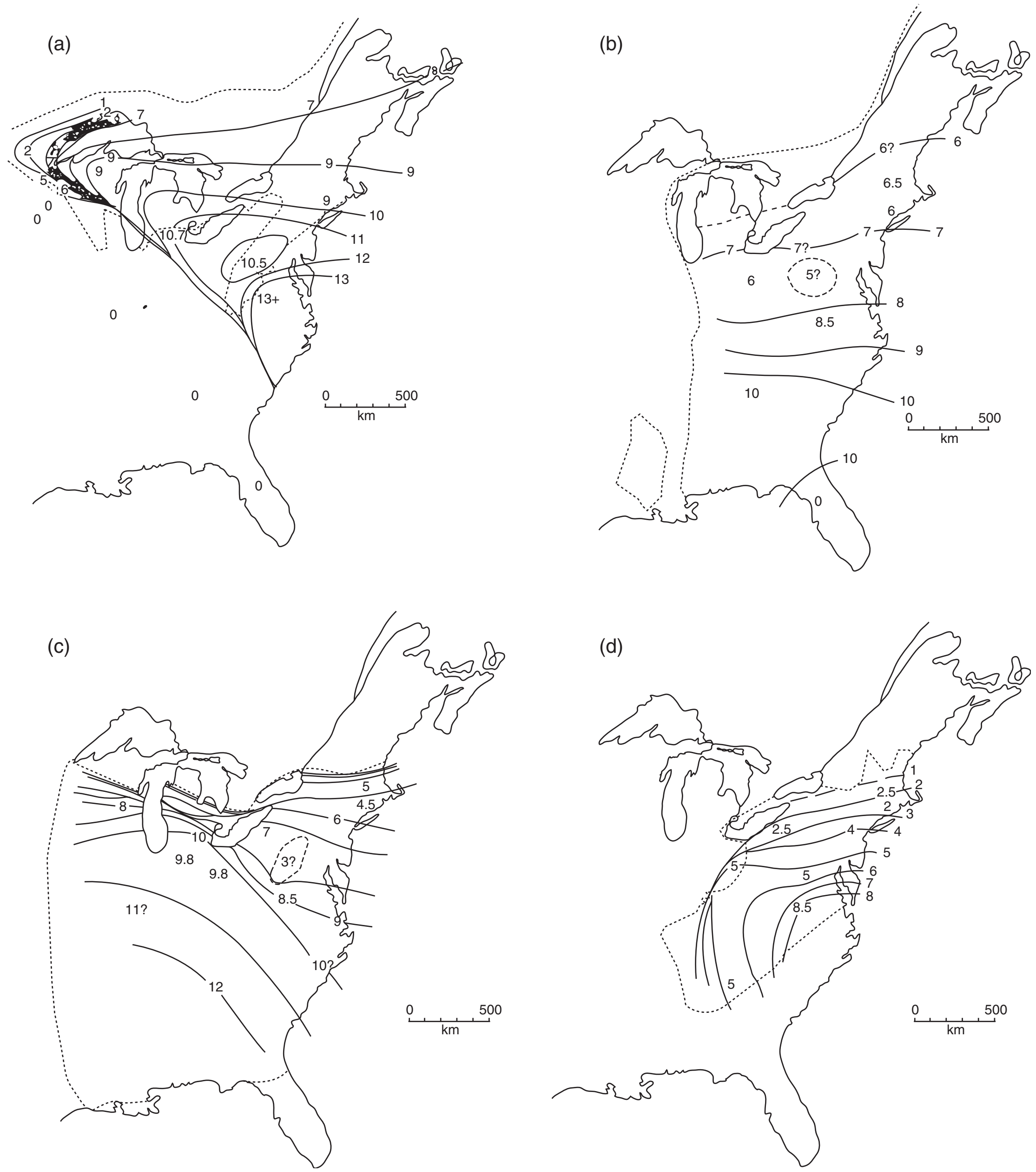


Figure 9.19 The northward migration of trees as the continental glaciers receded. (a) white pine, (b) chestnut, (c) hickory, (d) beech. Note that each species apparently re-invaded from slightly different refugia, some of which may have been on the now-flooded continental shelf. Solid lines mark the advancing frontiers at 1000-year intervals and dotted lines surround the modern ranges of the species (from Davis 1976).

(*H. neanderthalensis*) were in Europe and parts of Asia. It is thought that *H. sapiens* arrived in North America only some 10 000 years ago by crossing the Bering land bridge, although archaeologists are still struggling to date the exact time of arrival (Pringle 1996). As *H. sapiens* spread across North America, there was a massive die off of large mammals, and paleo-ecologists still argue about whether climate change or over-hunting was responsible for this wave of extinction. The fact that similar waves of extinction are associated with the arrival of humans in other areas including Australia and Easter Island (Section 12.3.2) suggests that even our

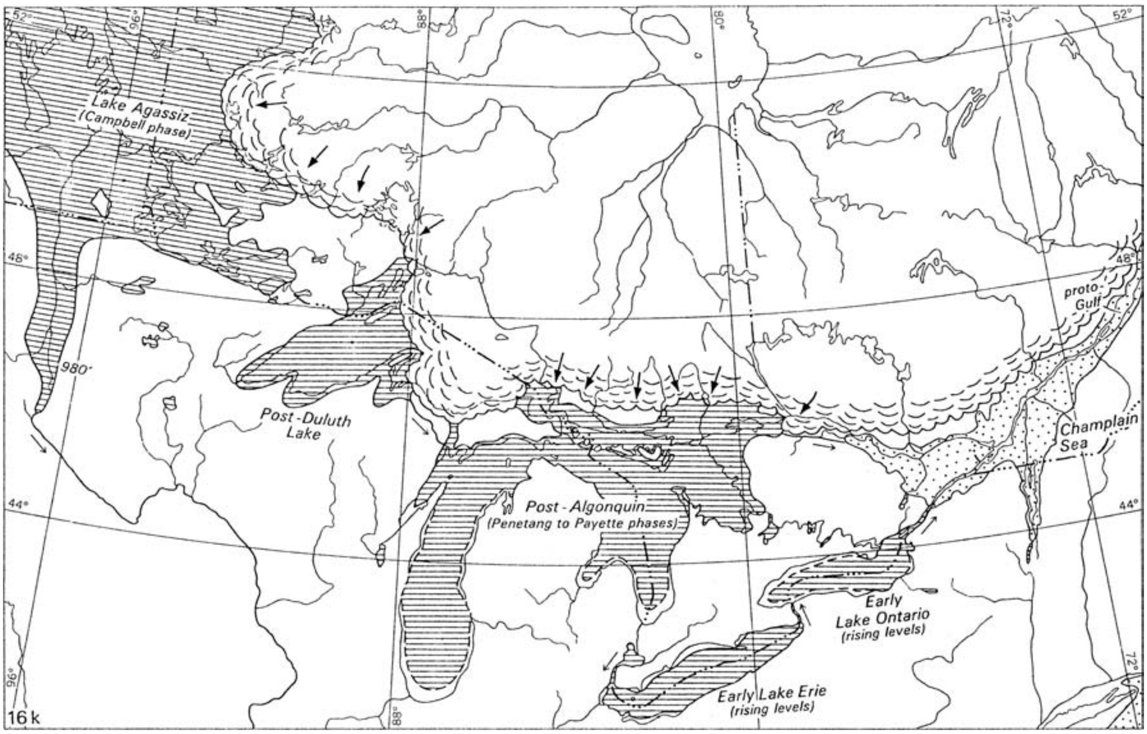


Figure 9.20 As the continental ice sheet retreated, the Great Lakes began to take their modern form. The Atlantic Ocean flooded southern Quebec, eastern Ontario, and northern New England, forming the shallow Champlain Sea. During one short period about 11 200 BP, the receding ice allowed melt water to flow from glacial Lake Algonquin directly along the margins of the ice sheet and into the Champlain Sea. Relict plants such as *Saxifraga aizoon* still dot the ancient route of this glacial outlet (from Douglas 1972).

ancestors were busily destroying the new lands they encountered. In the period since the last major glaciation, our species has spread around the world and multiplied until its numbers (in mid-2006) exceed six and a half billion.

9.3.8 Flooding

At the time the glaciers finally began to retreat, the weight of glacial ice had depressed northern areas so much that sea water flooded far inland. The Champlain Sea formed in eastern North America (Figure 9.20), the Hudson Bay lowlands were inundated (Glooschenko 1980, Abraham and Keddy 2005), and much of northern Russia and Scandinavia were submerged. As these regions still continue to rebound from the weight of the ice, they emerge from beneath the sea with lines of raised beaches (Stevenson et al. 1986, Bégin et al. 1989). Similarly, in South America the entire Amazon valley appears to have been drowned about 15 000 BP. During this period, a large freshwater lake 1500 km long and up to 100 km wide may have extended inland from the mouth of the Amazon (Irion et al. 1995, Müller et al. 1995). Sediments deposited in this lake would have produced deltas in the middle Amazon.

In summary, the effects of ice advances and retreats, and the associated changes in climate and sea level, caused major changes in the biota of the Earth. Such major changes provide the physiographic and ecological template upon which more recent processes are laid.