EVOLUTION AND FUNCTION OF EARTH'S BIOMES: TEMPERATE FORESTS

Willis K.J.
University of Oxford, Mansfield Road, Oxford, UK

Keywords: Evolution, temperate forest, deciduous trees, early Tertiary evolution, full-glacial refugia, interglacial succession, migration, extinction, climate change, disease, human impact, ancient woodland

Contents

Summary

Covering over 20% of the available landmass in mid- and high latitudes, the temperate forest biome is a highly productive and dynamic ecosystem that continuously changes in response to climate, disease, and human activities. This article examines the temperate forest biome from the evolution of the first temperate trees, approximately 90 million years ago (90 Ma; late Cretaceous) through to the almost total demise of "ancient" temperate woodland over the past 100 years. In particular, it focuses on the earliest global distribution of the temperate forests, the impact of the Quaternary glacials on both the composition and size of the biome, and temperate forest dynamics during interglacials. Human impact on the temperate forest biome is discussed in terms of the activities of the earliest farmers, the differences between timing of impact in the Northern and Southern Hemispheres, and the scale of impact in recent years.

1. Introduction

In terms of net primary production (t ha^{-1} yr^{-1}) the temperate forest biome is one of the most productive on the globe and in terms of human occupation, it is one of the most heavily populated. In geological terms, however, the temperate forest biome is one of the most recently established. Most of the trees found presently within this biome evolved from approximately 90 Ma to 70 Ma (the late Cretaceous), and a composition of trees similar to what is presently classified as "temperate forest biome" became established only approximately 60 Ma (during the Tertiary). This article presents the location of the present-day temperate forest biome within a geological and historical framework, and examines the influence of long-term human activity in determining its current dynamics, composition, and distribution.

Following a description of the current location of temperate forests and the dominant tree types in this biome, the geological evidence for the first temperate trees is presented. Climatic conditions at the time of initial evolution and growth of the first temperate trees are described and then compared briefly to present-day physiological requirements of temperate trees.

From the first established temperate forest onwards, there is evidence to suggest that this biome has remained one of the most dynamic in terms of both its composition and global distribution. The spatial coverage of the temperate forest biome through time is presented through examination of the first global occurrence, changes that occurred in response to the glacial–interglacial cycles of the Quaternary, and changes that have occurred during the present interglacial (the Holocene).

Arguably, the most dramatic influence upon the temperate forest biome during the Holocene has been human impact. The final section of this article therefore concentrates on the effect of 7000 y of human activity upon the temperate forest biome. Evidence for early human impact on the temperate forest biome beginning with the small-scale activities of the first farmers in Europe approximately 8,000 BP is described and followed by a consideration of the impact of more recent human activities (i.e., those in the historic rather than prehistoric record). The article concludes by asking how much of the present-day "temperate forest biome" can be classified as ancient woodland.

2. Present-day Distribution of the Temperate Forest Biome and Conditions Determining Growth

Globally there are seven broad regions classified as temperate forest biome. In the Northern Hemisphere these are eastern North America, western and central Europe, and east Asia; in the Southern Hemisphere, the drier parts of Patagonia (South America), New Zealand, the south-eastern edge of Australia, and north and west Tasmania.

Trees in the temperate forest biome are predominantly deciduous in the Northern Hemisphere and include oak (*Quercus*), alder (*Alnus*), birch (*Betula*), beech (*Fagus*), elm (*Ulmus*), lime (*Tilia*), hornbeam (*Carpinus*), sycamore (*Acer*), walnut (*Pterocarya*), ash (*Fraxinus*), and chestnut (*Castanea*). By contrast, in the Southern Hemisphere, the most predominant tree is the southern beech (*Nothofagus*) which has both deciduous and evergreen species. Other trees in the Southern Hemisphere temperate forest biome include various species of eucalyptus (*Eucalyptus*), various species of acacia such as blackwood (*Acacia melanoxylon*), mimosa (*Acacia verticillata*), and silver wattle (*Acacia dealbata*), and a number of conifers (e.g., *Podocarpus, Dacrydium, Araucaria*). Conditions determining a temperate forest biome include a marked seasonality with warm moist summers and mild winters, and seasonal variation determined more by temperature than by precipitation. It is the response of the temperate forests to the marked climatic contrast between summer and winter that is one of the most distinctive features of the biome. During the winter months the temperate forest effectively "shuts down" or goes into dormancy. This process of dormancy involves three distinctive phases: a cessation of active growth; the loss of leaves from the trees (abscission); and a series of biochemical changes that protects the trees from drought, starvation, and frost damage. These biochemical changes include, for example, the accumulation of starches and sugars, reduction of water tissue content, the release of hardiness promoting hormones, and the triggering of certain enzyme reactions so that the plants can resist severe dehydration. Although all three phases are equally important for the winter survival of temperate trees, it is the abscission of leaves that is visually the most striking. This feature has also provided an important marker in the geological record for the onset of deciduousness and the global distribution of the first temperate forests.

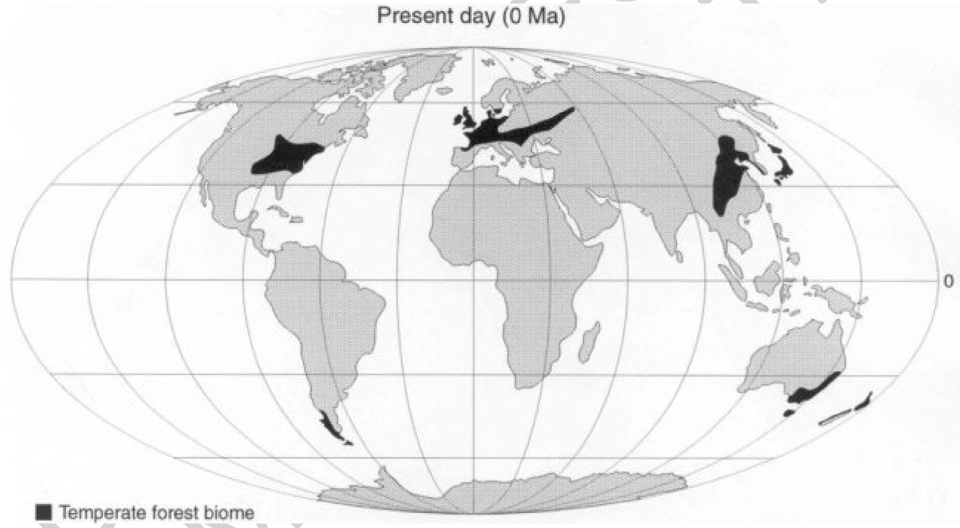

Figure 1. Present-day distribution of the temperate forest biome
After Archibold O.W. (1995). *Ecology of World Vegetation*, 510 pp. London: Chapman and Hall.

3. Geological Evidence for the First Temperate Trees

Trees currently classified as being in the temperate forest biome are predominantly flowering plants or angiosperms. In geological terms, they are one of the most recent groups to evolve. The first evidence for flowering plants in the fossil record (leaves, pollen, and fruits) is apparent approximately 140 Ma. To put this in context, the first green vascular plants were apparent in the geological record approximately 410 Ma (Devonian), the first spore-producing trees approximately 380 Ma (mid-Devonian/Carboniferous), and the first seed-producing trees (gymnosperms) approximately 360 Ma (Carboniferous).

Evidence from the geological record, in particular of the shape and size of the fossil leaves, suggests that the first angiosperms to evolve were small weedy plants similar to those found presently growing in streamside situations, in semi-aquatic habitats, or as an understory. By approximately 100 Ma, however, leaf shapes similar to extant species typical of late successional plants started to appear in the fossil record and evidence for angiosperm wood first appeared approximately 90 Ma (late Cretaceous). It is suggested therefore that the first angiosperms were probably early successional plants that were herbaceous and small, and that angiosperm trees only became part of the global flora approximately 90 Ma.

Some of the earliest angiosperm trees to evolve were members of the Ulmaceae, Fagaceae, Betulaceae, Myricales, and Juglandaceae families. All have a significant presence in the present-day temperate forest biome and include genera such as *Ulmus*, *Castanea* (chestnut), *Nothofagus*, *Alnus*, *Betula*, and *Juglans*. Even though these families now form an important part of the temperate forest biome, it is interesting to note that the first occurrence of these groups, with the possible exception of *Nothofagus*, was in tropical low-latitude environments between lat 20°N and 20°S. This "tropical fingerprint" is still apparent in many extant angiosperm groups. It has been estimated, for example, that despite the current global distribution of many angiosperm groups in higher latitudes (including those in the temperate forest biome), over three-quarters of all flowering plant families attain optimum development and diversity in a tropical environment.

The early Cretaceous was a period of significant global environmental change. It is often suggested that angiosperm evolution was closely linked to this. Between 120 Ma and 70 Ma (Cretaceous) dramatic changes occurred in the continental configurations. It was a period of rapid plate spreading resulting in the formation of the continents of Africa and South America, and the distinguishing of India, Australia, and Antarctica as attached plates.

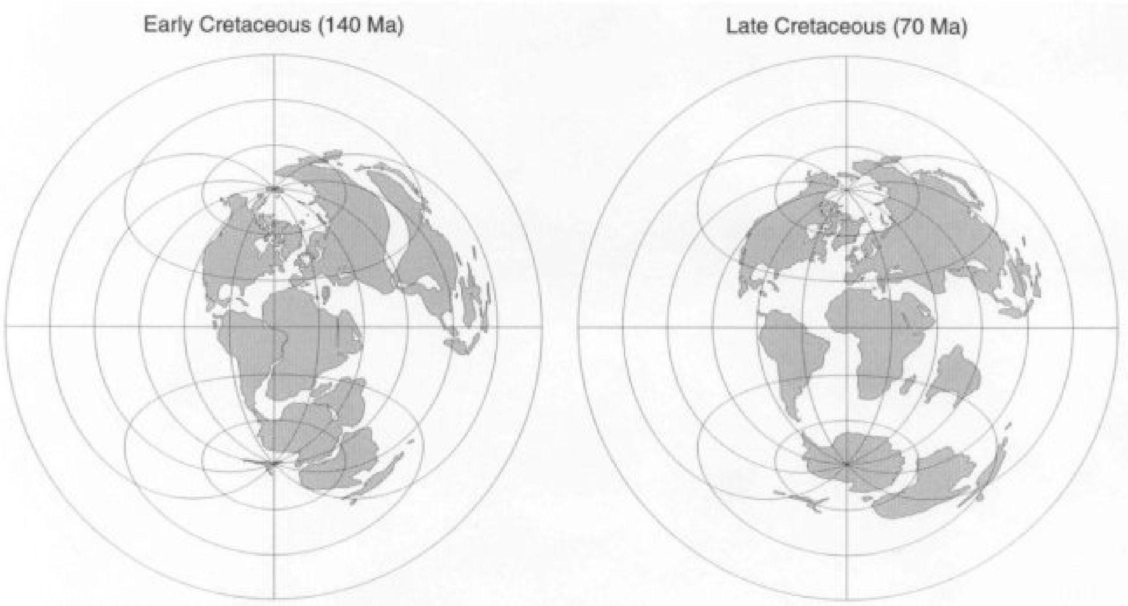

Figure 2: Continental configurations in the early and late Cretaceous
After Smith A.G., Smith D.G., and Funnell M. (1994). *Atlas of Mesozoic and Cenozoic Coastlines*, 99 pp. Cambridge: Cambridge University Press.

During this time, large-scale changes were also occurring in global sea levels and atmospheric concentrations. A rise in sea level during the Cretaceous is thought to have been in direct response to the divergence of tectonic plates in the ocean, which would have displaced water from the oceanic basins to form epicontinental seas. Extensive seas, for example, were established in the interiors of North America, southern Europe, Australia, Africa, and South America. In addition, the increased volcanism associated with the plate movements would have pumped CO_2 into the atmosphere. Geological evidence suggests, for example, that there was the eruption of a mantle superplume approximately 120 Ma and that this significantly increased global temperatures through the greenhouse effect.

Modeling of these various changing environmental scenarios has led to the suggestion that during the Cretaceous, global temperatures increased to an average of from 5 °C to 8 °C higher than present-day temperatures. Other lines of evidence to support the suggestion of a warm Cretaceous climate include geological evidence for no ice at the poles and evidence for coral reefs, which require warm water, ranging as much as 1500 km closer to the poles. But why would increased warmth promote angiosperm evolution? There are various features in certain groups of extant angiosperms that make them resistant to drought. These include tough leaves that are commonly reduced in size, a tough resistant seed coat that protects the young embryos from drying out, vessel members providing efficient water conducting cells, and perhaps most importantly, a deciduous habitat. The latter would have been crucial during periods of drought. Although some of these features were present in earlier groups, for example certain early gymnosperms such as the Glossopteridales, it is suggested that the predominance of such features in the early angiosperms gave them a competitive advantage in an increasingly dry climate.

3.1. Global Distribution of the First Temperate Forests

Although it was during the late Cretaceous (from 100 Ma to 70 Ma) that temperate trees became part of the global flora, in terms of their biogeographic distribution they were mixed in with other plant groups and did not form a recognizable temperate forest biome until approximately 60 Ma. From 60 Ma (early Tertiary) a polar broad-leaved deciduous forest became established at approximately lat 70°N and 70°S and above in both the Northern and Southern Hemispheres. The nearest living equivalent to this polar broad-leaved deciduous forest in terms of composition is the temperate forest biome. However, the land area covered by this first temperate forest biome is presently either polar desert or under polar ice.

In the Northern Hemisphere, this polar broad-leaved deciduous forest included trees characteristic of the present temperate forest biome such as *Alnus, Betula, Quercus, Juglans, Populus,* and *Acer*. However, it also contained deciduous conifers such as *Ginkgo, Larix, Metasequoia, Pseudolarix,* and *Taxodium* that do not form part of the present-day temperate forest biome. In the Southern Hemisphere the fossil record suggests that the predominant trees were the southern beech, *Nothofagus*, plus the conifers, *Araucaria*, *Podocarpus*, and *Dacrydium*.

Approximately 50 Ma, global climates started to cool significantly. This was due to a number of environmental factors including further changes to the configuration of the continents, both in the relative positions of the land and sea, and in the topography of the continents through mountain building activity. In the Southern Hemisphere, for example, Australia and New Guinea moved northwards to their present position and Antarctica separated from Australia and the South American archipelago. This separation resulted in the development of a seaway between Australia, Antarctica, and South America that prevented warm equatorial currents from penetrating into the southern polar regions and the development of a transglobal current around Antarctica (called Drake's Passage). It has been proposed that the development of this transglobal current was the main factor responsible for cooling at the South Pole and the initiation of the Antarctic ice sheet.

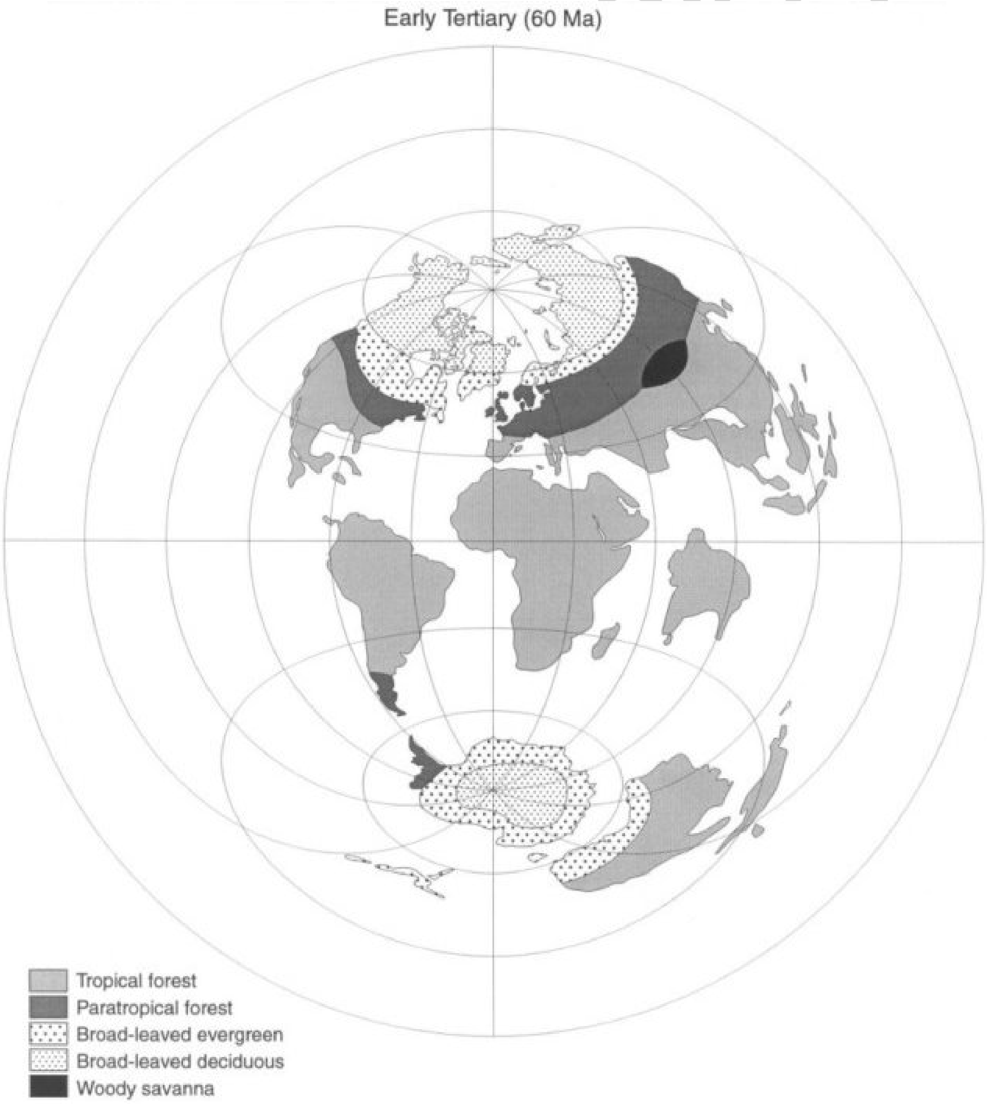

Figure 3. Biogeographic distribution of global vegetation during the early Tertiary
After Briggs J.C. (1995). *Global Biogeography*, 600 pp. Amsterdam: Elsevier Science.

By approximately 38 Ma (Oligocene), the impact of this global cooling had started to have a significant effect upon the global distribution of vegetation.

Tropical and paratropical vegetation became restricted into a decreasingly small equatorial band and polar deciduous forest disappeared from the high latitude locations to be replaced by a mixed coniferous–deciduous forest. In the Northern Hemisphere, this was composed of *Metasequoia* and *Alnus*, and in the Southern Hemisphere, *Nothofagus* and *Podocarpus.* The broad-leaved deciduous woodland that formerly extended to the poles became located in a more southerly band in the central part of the Eurasian and North American continents and the uppermost part of the African continent. This forest contained so-called "cold–temperate" hardwoods such as *Alnus*, *Betula*, *Corylus*, *Nyssa*, and *Salix Quercus*, and "warm–temperate" hardwoods such as *Carya*, *Liquidambar*, *Cercidiphyllum*, *Glyptostrobus*, and *Sequoia*. Presently the species in this "warm–temperate" group form an important deciduous component of the subtropical forest biome.

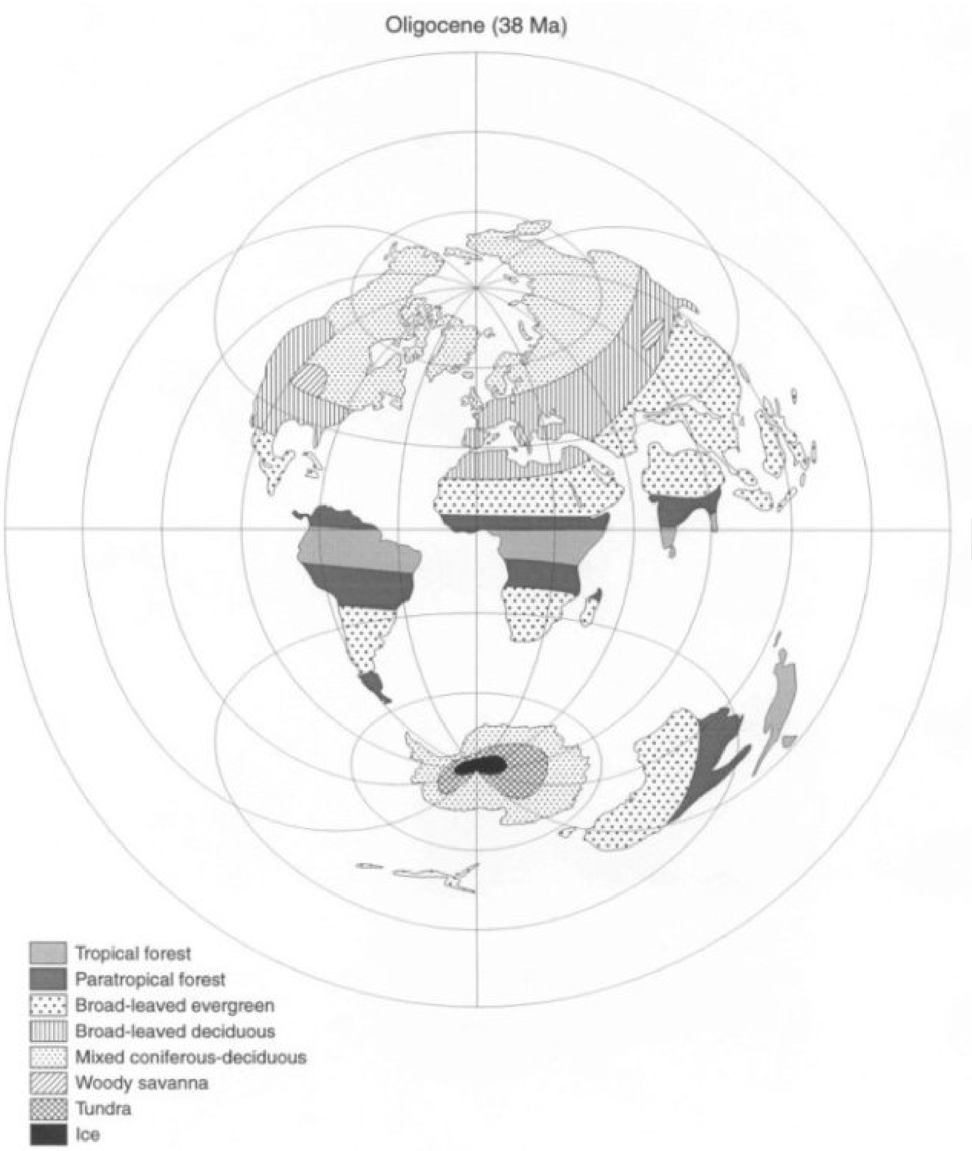

Figure 4. Biogeographic distribution of global vegetation during the Oligocene
After Briggs J.C. (1995). *Global Biogeography*, 600 pp. Amsterdam: Elsevier Science.

In the final stages of the Tertiary (approximately from 10 Ma to 2 Ma), there was a steady decline in global temperatures and a continuation of the drying trend in the high latitudes of both the Northern and Southern Hemispheres, which contrasted strongly with increasing temperatures in the equatorial regions. Major ice caps covered much of Antarctica, and the initiation of ice rafting and buildup of ice sheets was occurring in the northern polar regions. Ice at the poles effectively landlocked a large amount of the global water supply, resulting in falling sea levels and decreased moisture availability. In consequence, continental interiors became increasingly arid, and large areas of the shoreline were exposed. In the European continent, for example, sea levels were so low that the Mediterranean Sea dried out and a land bridge between North Africa and southern Europe was created.

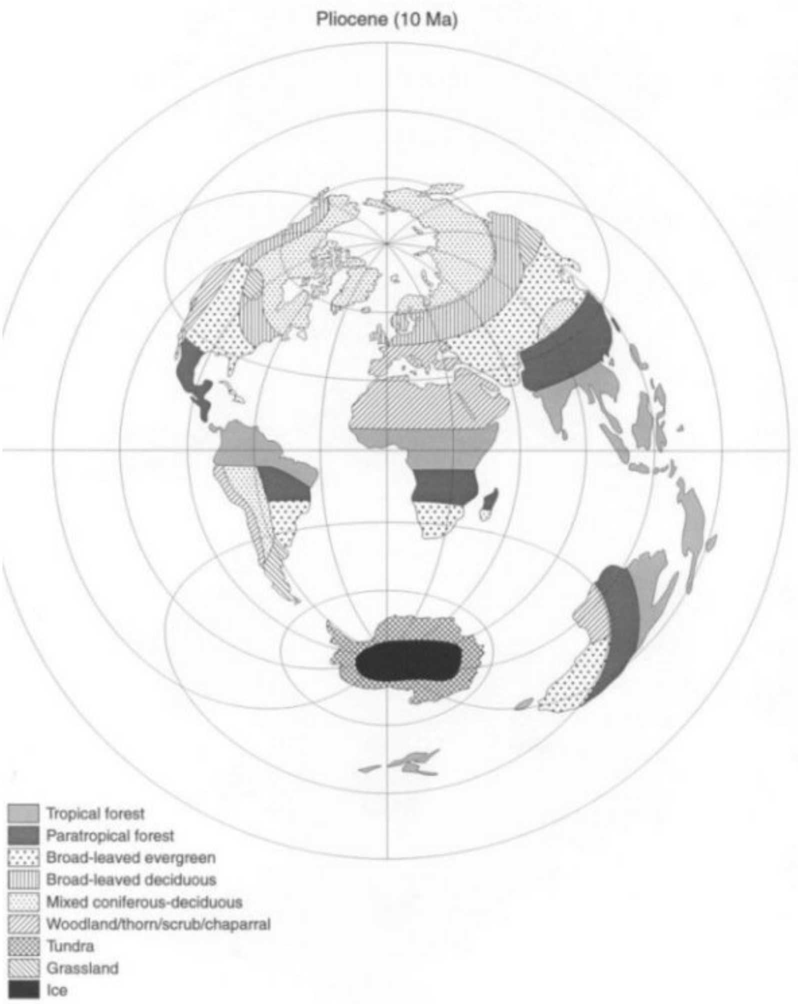

Figure 5. Biogeographic distribution of global vegetation during the late Tertiary (Pliocene). After Briggs J.C. (1995). *Global Biogeography*, 600 pp. Amsterdam: Elsevier Science.

In terms of the global biogeographic distribution of vegetation, the Pliocene is the time when most of the present-day biomes became established in their current locations. The temperate forest biome, for example, formed a broad band extending from mid- to high latitudes in the Northern Hemisphere and a few specific regions in the Southern Hemisphere.

-
-
-

Bibliography

Archibold O.W. (1995). *Ecology of World Vegetation*, 510 pp. London: Chapman and Hall. [This is one of the most recent descriptions of the biogeographic distribution of the world's vegetation into global biomes.]

Bennett K.D. (1997). *Evolution and Ecology: the Pace of Life*, 241 pp. Cambridge: Cambridge University Press. [This book presents a clear and highly detailed account of the importance of the Quaternary ice ages in shaping present-day global biodiversity.]

Bennett K.D. (1998). The power of movement in plants. *Trends in Ecology and Evolution* **13**, 339–340. [This paper reviews recent research demonstrating that ecological processes observable now cannot account fully for the distribution of present-day organisms.]

Bennett K.D., Boreham S., Sharp M.J., and Switsur R. (1992). Holocene history of environment, vegetation and human settlement on Catta Ness, Lunnasting, Shetland. *Journal of Ecology* **80**, 241–273. [This paper presents a well-dated pollen sequence detailing vegetation change in the UK during the Holocene.]

Bennett K.D., Tzedakis P.C., and Willis K.J. (1991). Quaternary refugia of north European trees. *Journal of Biogeography* **18**, 103–115. [This paper presents a discussion of the possible location of European temperate tree refugia during the last full glacial and its implications for the distribution of present-day populations.]

Bennett K.D., Haberle S.G., and Lumley S.H. (2000). The last glacial–interglacial transition in southern Chile. *Science* **290**, 325–328. [This paper presents a well-dated pollen sequence detailing vegetation change in the UK during the Holocene.]

Briggs J.C. (1995). *Global Biogeography*, 600 pp. Amsterdam: Elsevier Science. [This book contains a fascinating account of the global distribution of organisms during approximately the past 600 Ma.]

Cheddadi R., Yu G., Guiot J., Harrison S.P., and Prentice I.C. (1997). The climate of Europe 6000 years ago. *Climate Dynamics* **13**, 1–9. [This paper presents computer simulated modeling of the European climate 6,000 BP to support the suggestion that the changing composition of the European forests were due to climate change.]

Delcourt H.R. and Delcourt P.A. (1991) *Quaternary Ecology—a Paleoecological Perspective*, XXX pp. London: Chapman and Hall. [This book presents an account of ecological change during approximately the past 1.8 Ma.]

Diamond J. (1997). *Guns, Germs and Steel: A Short History of Everybody for the Last 13,000 Years*, XXX pp. London: Jonathan Cape. [This book presents is a fascinating theory as to why the Northern Hemisphere became industrialized so much earlier than the Southern Hemisphere.]

Edwards M.E. (1986). Disturbance histories of four Snowdonian woodlands and their relation to Atlantic bryophyte distributions. *Biological Conservation* **37**, 301–320. [This paper presents results from a paleoecological study that directly challenges the use of certain bryophytes to assess the location of ancient woodlands.]

Follieri M., Magri D., and Sadori L. (1988). 250,000-year pollen record from Valle di Castiglione (Roma). *Pollen et Spores* **30**, 329–356. [This paper presents one of the longest continuous Quaternary paleoecological sequences from Europe.]

Fuller J.L. (1997). Holocene forest dynamics in southern Ontario, Canada: fine-resolution pollen data. *Canadian Journal of Botany* 7**5**, 1714–1727. [This paper presents a well-dated paleoecological sequence detailing North American vegetation dynamics during the Holocene.]

Fuller J.L. (1998). Ecological impact of the mid-Holocene hemlock decline in southern Ontario, Canada. *Ecology* **79**, 2337–2351. [This paper presents clear paleoecological evidence for the North American hemlock decline.]

Fuller J.L., Foster D.R., McLachlan J.S., and Drake N. (1998). Impact of human activity on regional forest composition and dynamics in central New England. *Ecosystems* **1**, 76–95. [This paper presents the results of a fascinating paleoecological study that examines the impact of human activity on the long-term composition of the North American temperate forests.]

Hughes N.F. (1994). *The Enigma of Angiosperm Origins*, XXX pp. Cambridge: Cambridge University Press. [This book presents a clear and detailed account on the origins of flowering plants.]

Imbrie J. and Imbrie K.P. (1979). *Ice Ages: Solving the Mystery*, XXX pp. London: Macmillan. [This book was one of the first to link the timing and duration of the Quaternary ice ages to the cyclical changes in incoming solar radiation termed Milankovitch cycles.]

Janis C.M. (1993). Tertiary mammal evolution in the context of changing climates, vegetation and tectonic events. *Annual Review of Ecology and Systematics* **24**, 467–500. [This paper presents a broad synthesis of the changing global distribution of plants and animals over the past 65 Ma.]

Lumley S.H. and Switsur R. (1993). Late Quaternary chronology of the Taitao Peninsula, southern Chile. *Journal of Quaternary Science* **8**, 161–165. [This paper presents a well-dated paleoecological sequence detailing South American vegetation dynamics during the Holocene.]

MacDonald G.M. (1993). Fossil pollen analysis and the reconstruction of plant invasions. *Advances in Ecological Research* **24**, 67–109. [This paper presents calculation of the rate of postglacial increase of tree populations in North America from paleoecological sequences.]

Magri D. (1995). Some questions on the late-Holocene vegetation of Europe. *The Holocene* **5**, 354–360. [This paper questions the theory that the large-scale transition from woodland to grassland apparent in much of Europe beginning approximately 4,000 BP is due to human impact.]

Newnham R.M., Lowe D.J., and Green J.D. (1989). Palynology, vegetation and climate of the Waikato lowlands, North Island, New Zealand, since c. 18,000 years ago. *Journal of the Royal Society of New Zealand* **19**, 127–150. [This paper presents a well-dated paleoecological sequence detailing New Zealand vegetation dynamics during the Holocene.]

Newnham R.M., Lowe D.J., and Williams P.W. (1999). Quaternary environmental change in New Zealand: a review. *Progress in Physical Geography* **23**, 567–610. [This paper presents a detailed review of the paleoecological sequences detailing environmental change in New Zealand during the Quaternary.]

Peglar S.M. and Birks H.J.B. (1993). The mid-Holocene *Ulmus* fall at Diss Mere, South-East England—disease and human impact. *Archaeobotany* **2**, 61–68. [This paper presents a well-dated paleoecological sequence detailing the mid-Holocene elm decline in the UK.]

Roberts N. (1998). *The Holocene*, second edition, XXX pp. Oxford: Blackwell. [This book provides a concise account of changes that have occurred in the distribution of global fauna and flora during the past 12,000 y.]

Smith A.G., Smith D.G., and Funnell M. (1994). *Atlas of Mesozoic and Cenozoic Coastlines*, 99 pp. Cambridge: Cambridge University Press. [An atlas indicating inferred positions of global paleoshorelines over the past 240 Ma.]

Tallis J.H. (1991). *Plant Community History: Long-term Changes in Plant Distribution and Diversity*, First Edition, XXX pp. London: Chapman and Hall. [This book provides a long-term perspective (covering approximately the past 65 Ma) on the changes in distribution and diversity of global vegetation.]

Willis K.J. (1993). How old is ancient woodland? *Trends in Ecology and Evolution* **12**, 427–429. [This paper reviews paleoecological research that demonstrates that much of present-day European and North American temperate woodland that is classified as "ancient" has very little claim to antiquity and is no more than 100 y old.]

Willis K.J. (1995). Where did all the flowers go? The fate of temperate European flora during glacial periods. *Endeavour* **20**, 110–114. [This paper presents the paleoecological and genetic evidence for the location of temperate tree refugia in Europe during the last full glacial.]

Willis K.J. and Bennett K.D. (1994). The Neolithic transition—fact or fiction? Paleoecological evidence from the Balkans. *The Holocene* **4**, 326–330. [This paper uses the paleoecological record to question the scale of impact of the first farmers on the European landscape.]

Willis K.J., Braun M., Sümegi P., and Tóth, A. (1997). Does soil change cause vegetation change or vice versa? A temporal perspective from Hungary. *Ecology* **78**, 740–750. [This paper presents a model to explain the postglacial transition from podsol to brown earth soils and its relationship to postglacial vegetation change.]

Willis K.J., Sümegi P., Braun M., Bennett K.D., and Tóth A. (1998). Prehistoric land degradation in Hungary: who, how and why? *Antiquity* **72**, 101–113. [This paper uses paleoecological evidence in conjunction with archeological evidence to examine the impact of different Prehistoric populations on the northeastern Hungarian landscape.]

Willis K.J. and Whittaker R.J. (2000). The refugial debate. *Science* **287**, 1406–1407. [This paper examines recent research for and against discrete areas of refugia of temperate and tropical trees during the last full glacial.]

Biographical Sketch

Katherine J. Willis is a University Lecturer in Physical Geography and Fellow of St. Hugh's College, University of Oxford. Her first degree was in Geography and Environmental Science at the University of Southampton followed by a Ph.D. in the Godwin Institute for Quaternary Research, Department of Plant Sciences, University of Cambridge. Her research focuses on the long-term relationship between vegetation dynamics and global environmental change. Projects have centered on the use of paleoecological techniques to provide a detailed temporal perspective to ecological, archeological, and geological models, and have focused on topics from rates of postglacial soil development to processes responsible for the initiation of the Northern Hemisphere glaciation. Research sites have included lakes, bogs, and volcanic maars in central and southeastern Europe. Before taking up her University Lectureship she held a Trevelyan Research Fellowship, a NERC Postdoctoral Fellowship and then a Royal Society University Research Fellowship in the University of Cambridge. Publications to date have included a number of primary research articles, review articles, and book chapters. Her first book, *Plant Evolution: from the First Cell to the Flower in 2 Billion Years*, is to be published shortly by Oxford University Press. Current editorial positions include associate editor for the journal *The Holocene* and editorial advisory board member of *Global Ecology and Biogeography*, *The Norwegian Journal of Geography*, and *Porocilo Slovenski.*