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The Role that Diastrophism and Climatic Change Have Played in Determining Biodiversity in Continental North America

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1. Introduction

Diastrophism includes both tectonic movements and plate tectonics. Together with changes in climate, they largely explain the high number of endemic species and biodiversity of both plants and animals on the North American continent. Each continent has had a different climatic and geological history, which explains why each continent differs in its biota from the others, although there are considerable similarities in the evolution of the biota. Thus in Europe, there are relatively few endemic species of plants (Birks, 2008) in contrast to 70% endemic vascular plants in the North American Tundra and Boreal Forest of the western Cordillera of Canada (Harris, 2008), and close to 100% endemic species in some groups of insects. This chapter provides an outline of the evolution of the biota of North America from the time that it was part of the massive continent (Pangaea) occupying the area around the South Pole, until the present day.

2. Palaeozoic era

At the beginning of the Palaeozoic Era, Laurasia was near the equator on the periphery of Pangaea. The latter was a large land mass consisting of the progenitors of the existing continents that were located around the South Pole at that time. In the Cambrian Period (600-500 million years ago), North America was orientated so that the equator ran from western Mexico northwards to the Arctic Ocean along the Yukon-NWT border (Briden & Irving, 1964). During the Ordovician Period (500-425 million years ago), the continent rotated so that the equator lay in a line from just south of Baja California northeastwards to the east coast of Hudson Bay. The rotation of North America continued and by the Carboniferous Period (345-280 million years ago), it passed through San Diego east-north-

eastwards to Cape Breton. Thus the North American plate was rotating in a clock-wise direction as well as moving south relative to the Earth's magnetic poles, which are assumed to approximate the poles of rotation. Throughout this time, it lay in the Tropics.

It was during the Silurian Period (425-405 million years ago), that plants started to move from the sea on to the tropical parts of the land. Centipedes and spiders appeared amongst the vegetation. In the succeeding Devonian Period (405-345 million years ago), forests were spreading across the hot, humid land areas and the first amphibians appeared on land. By the Carboniferous Period (425-380 million years ago), the extensive coal beds in both Europe and North America indicate that parts of the area had a hot, continuously humid climate supporting a dense equatorial-type forest (Schwarzbach, 1961). Absence of evidence of glacial deposits but the presence of sand dune deposits suggests that there were also areas of hot deserts in the southwest of the United States. It is sometimes called the "Age of the Amphibians" since they were most numerous during the early part of this Period. Off-shore, extensive limestone deposits were being formed together with extensive coral reefs. By the end of this era, many of the genera of horsetails, conifers, reptiles and insects had already been evolved and were present on land. The tropical forests that produced the coal beds had a diverse fauna and flora, the remains of which are found entombed as fossils. The animals were of predominantly different species and genera than those present today, though the main groups of primitive plants were already well represented. The ancestral club-mosses (*Lycopodium*) that had first appeared in the Silurian Period in what is now Australia, grew to over 30m in height in these forests, as did the trees of the class *Cordiatales.* The first conifers subsequently evolved from these in the Permian Period. Giant horsetails (*Equisetum*) were also abundant. These plants were, of course, essential to support the terrestrial food chain, and the enormous production of coal indicates that there was a spectacular increase in release of oxygen and an enormous reduction in carbon dioxide in the atmosphere (Harris 2010), though some of the carbon dioxide was replaced by volcanic activity during the Permian Period. The swampy areas in the forests also supported a wide range of primitive animals including small amphibians, eel-like creatures and the first small reptiles. The latter were a reasonable match for the amphibians but were not capable of extirpating them. In the air, giant insects flitted about. However, these animals were adapted to a very specific microenvironment and when that ceased to exist due to erosion in the west and mountain building in the east, most were extirpated, e.g., the enormous flying insects. A few key species were able to adapt to the altered environment, and of these, some genera of mycchoriza fungi, *Lycopodium* and *Equisetum* are still to be found today.

By the Permian Period (280-230 million years ago), the equator lay in a line from the California-Oregon border to just north of Newfoundland. Much of the land area was now reduced to a low plain, although mountain chains were rising in the Appalachian region due to collisions of plates (the Appalachian Orogeny). Present-day North America continued to experience a tropical climate, but the mountain chains cut off the rain-bearing winds coming inland from the east coast. This dry environment was ideal for the evolution of a wide variety of dinosaurs from the survivors of the small Paleozoic reptiles, and extensive sand dunes occurred in the southwest of the United States. In the wet areas, the first true reptiles and the ancestors of the crocodiles, alligators and caimen appeared.

Amongst the new genera and species that evolved on this new landscape were the first Laurasian stoneflies (Plecoptera) and several other groups of insects (Illies, 1965; Zwick and Teslenko, 2000). The best record of these insects comes from the Baltic amber of Eocene age (38-54 million years ago) but by then, the fauna resembled the modern one (Hynes, 1988). The Mecoptera which consist of only about 500 species worldwide today (Penny & Byers, 1979) were particularly conspicuous across Laurasia in the Lower Permian sediments (Carpenter, 1930). In general, the genera and families present at that time are also found in the Mesozoic sediments, but died out during the Tertiary Era as the mean annual air temperatures decreased.

The jostling of the plates also resulted in tension, causing faulting in many parts of the continents, and this resulted in widespread out-pouring of basaltic magma. This released considerable quantities of carbon dioxide into the atmosphere which would provide sustenance for the tropical forests on the fans below the mountains. In these forests, the first Conifers became abundant, and those insects and amphibians that survived the environmental changes became more widespread. Laurasia began moving northwards away from Gondwanaland just before the end of this period. Since mammals were later to become important species on all the continents, it is probable that the first ancestors of the mammals evolved at this time, prior to the split, although the first known mammalian fossils are dated to about 200 million years ago in the early Jurassic Period.

3. Mesozoic era

The northward movement of the Laurasian plate during the Jurassic period (230-180 million years ago) began about 220 million years before present. The plate consisted of North America, northern Europe and northern Asia. Tropical forests grew in the wetter areas, while sand dunes existed in the drier regions. Laurasia had a varied topography with mountains, plains and shallow seas. The equator now lay across the continent from southern Baja California to New York, so that north-west Alaska was at 50°N (Briden & Irving, 1964, Figure 8). Since the land mass of North America was surrounded by warm oceans, the climate remained hot.

South of the land mass, the Tethys Sea was developing between Laurasia and Gondwanaland. It stretched from central and southern China westwards to the Atlantic Ocean and separated Laurasia from South America, Africa and India. The result was a circum-equatorial ocean. This had an enormous effect on the temperature of the Earth since water absorbs approximately five times as much solar radiation as soil. This ocean provided warm surface and thermohaline currents that carried heat northwards to the Arctic Ocean via the North Pacific, as well as hot tropical air masses (Harris, 2002a). The ice cap over Antarctica melted, leaving a series of large islands where a tropical forest evolved (Francis et al., 2008). A mega warm event had begun (Harris, 2012) that was to last from about 200 million years before present until 44 million years ago. Summer temperatures averaged 20°C during this global thermal maximum. The genera present in this Antarctic flora were the ancestors of the present-day tropical flora.

In the Northern Hemisphere, a tropical biota evolved that was adapted to much higher temperatures than the present-day tropical flora. This extended north to the polar areas, except perhaps on the highest mountains. A tremendous variety of dinosaurs evolved, some reaching gigantic proportions. The first mammals consisted of small rat-like creatures that managed to survive running around the feet of the large, dominant dinosaurs. The oldest known specimen of the Asilidae (robber flies) dates to about 110 million years ago (Grimaldi, 1990), though that author put the evolution of this group at about 144 million years before present. However, they could have originated before Laurasia parted from the southern continents (Yeates & Grimaldi, 1993, Yeates & Irwin, 1996). By Late-Cretaceous times, small primitive marsupials and insectivores similar to shrews and hedgehogs were fairly abundant, and would survive the Cretaceous/Tertiary die-off of the previously dominant Dinosaurs. Cycads and conifers were the main components of the forests, while crocodiles, turtles and lamellibranchs, e.g., oysters, were common in freshwater lakes and swamps. It was during this time that the first birds appeared, apparently evolving from certain groups of dinosaurs.

Eurasia was not a single land mass (Cox, 1974). Shallow epicontinental seas covered part of the plate, so that the Turgai Straits separated Scandinavia and Britain (which was part of North America at that time) from the main Asian land mass. Thus although Britain and Scandinavia were part of the same plate, movement of the terrestrial biota across the land areas to Asia was restricted in time and space.

About 150 Ma before present, North America and Eurasia started to separate at their southern margin, and the North Atlantic Ocean began to form. Initially, the biota of both continents remained the same and the opening proceeded slowly, but as the plates continued to move northwestwards, the biota that required very hot tropical conditions could no longer pass back and forth between Eurasia and North America. The first angiosperms appeared at 144 million years ago.

In early Cretaceous times (135-63 million years ago), an epicontinental sea (the Mid-Continental Seaway) encroached onto the land that is now along the Mackenzie valley, and gradually extended south until it reached the ocean in what is now the Gulf of Mexico. This divided the floras and faunas into eastern and western populations, but by Late Cretaceous times the sea had largely dried up. During this time, the two sides had developed different insect faunas since they could not cross the wide expanse of water, but these became homogenized when the sea no longer acted as a barrier. Combined with the Turgai Straits, the Mid-Continental Seaway also resulted in there being two distinct faunas of land animals including the dinosaurs (Cox, 1974, Noonan, 1988, Wolfe, 1975). One was called Asia-America (Asia plus western North America) with a connection between them at high latitude across present-day Alaska and Siberia, and the other, Euroamerica (eastern North America plus northwest Europe). These faunas remained distinct after the disappearance of the Mid-Continental Seaway. During the early phases of the opening of the North Atlantic in the Middle Cretaceous (90-95 million years ago), a rift is believed to have formed between Greenland and Labrador, resulting in Greenland, the Rockall Plateau and Europe being a single land mass separate from North America (Heirtzler, 1973).

About 80 million years before present, the Laurasian plate no longer had room to continue moving northwards. Eurasia became stationary, but North America started its western movement that continues until today. This gradually extended the Atlantic Ocean northwards as two separate plates were formed from the former Laurasian plate. It was also during the Mesozoic Era that South America, Africa and India separated from the land masses around the South Pole. Africa and India headed towards Eurasia, but South America moved northwestwards towards the eastern part of Asia-America.

4. Cenozoic era

At the beginning of the Cenozoic era (63 million years ago), the climate was still tropical, though North America was moving to much higher latitudes. The Pacific Plate was moving north-northwest, but about 43 million years before present, its direction changed to west-northwest, as indicated by the change in direction of the Emperor and Hawaiian sea-mount chains (Clague & Jarrard, 1973). At the same time, the Aleutian Trench and Chain started to form (Worrall, 1991). This altered the geometry of the Beringian Gateway for warm currents carrying heat to the Arctic Ocean. About 38 million years ago, the Turgai Strait Gateway to the Arctic Ocean closed (Marincovich et al., 1990, McKenna, 1975). At the end of the Paleocene (c. 60 million years ago) in the Southern Hemisphere, the tropical forests were gradually displaced by floras dominated by the *Araucaria* conifers and the southern beech *Notofagus* which could survive freezing winter temperatures. Australia and Antarctica were still joined, but Australia started moving north around 55 million years ago [Kamarovitch & Geoph, 2009]. Oxygen isotope data from the Atlantic seas of South America show that there was a marked cooling of the ocean where the planktonic foraminifera lived from about 19° C during the late Paleocene, resulting in sea temperatures of about 6° C by the early Oligocene (Shackleton & Kennett, 1995). A shallow water connection developed between the southern Indian and Pacific Oceans over the South Tasman Rise by about 39 million years ago, and at 38 million years before present, a large area of sea ice had developed over Antarctica. Bottom ocean temperatures plummeted and the thermohaline ocean circulation was initiated. The Drake Passage between Patagonia and Antarctica probably opened up about this time. Meanwhile in the Arctic Ocean, ice-rafted sediments were deposited on the sea floor from about 44 million years ago (Tripati et al., 2008). The mega cold event that we live in was beginning.

Soon after (before 29 million years ago), the Tethys Sea became fragmented into the Mediterranean Sea and an eastern portion including the Indian Ocean, as the Arabian plate collided with the almost stationary Eurasian plate. This resulted in the crumpling of the marine sediments in the former Tethys, which were uplifted into the mountains ranges of Iraq, Persia and Afghanistan (Nomura et al., 1997). Gone was a substantial part of the heat source for the Arctic, and the climate of the northern land areas was cooling (Harris, 2002a). The gradual closing of the gap between Asia and North America reduced the flow of warm ocean currents into the Arctic Basin by about 23.5 million years before present, though this was ultimately offset by currents flowing along the sea connection by the opening of the North Atlantic Ocean about 20 million years ago.

These events appear to have resulted in a dramatic drop in mean annual air temperatures around 35 million years ago (Frakes, 1979). This heralded the end for many of the tropical species of biota inhabiting the northern regions. They were replaced by species that could tolerate the cooler temperatures, and these changes in the biota have continued until today. The loss of the warm ocean currents entering the Arctic Basin would appear to be the most likely cause of the abrupt change in mean annual air temperature around the basin and the consequent extinction of so many species and genera that had survived for so long.

The Cenozoic was when the Mammals became the dominant land animals, aided by the presence of fur and by being warm-blooded. Within 10 million years, they had become greatly diversified and lived in almost all micro-environments. They included herbivores and carnivores, e.g., whales and bats. Those weighing more than about 45 kg are referred to as the Megafauna, and first appeared in Eocene times (55-30 million years ago). These became abundant in the early and middle Cenozoic, but largely died out in the Pliocene and Pleistocene. They included herbivores such as *Coryphodon*, *Uintatherium* and *Arsinoitherium*, together with carnivores such as *Andrewsarchus* and smaller wolf-like predators and sabre-toothed cats. About 40 million years ago, the first camels evolved (Harrington, 1978). At first, they were rabbit-sized with four toes, but they became much larger about 24 million years ago. By about 5 million years before present, some were substantially larger than the present-day camels of Africa and Asia (Harrison, 1985). They were common on the dry scrub grasslands of central North America from 600,000 years ago until about 10,000 years before today. A larger species of camel entered Alaska and crossed the Bering land bridge to Asia about 5 million years before present, and evolved into the species still surviving in Africa and Asia. About 20,000 years ago, they died out in North America. Among the other mammals that originated in North America are the horses, mastodons and mammoths. These also migrated across the Bering Strait, but subsequently died out in North America. Our ancestors are believed to have helped kill them off, though some mammoths survived in relatively inaccessible areas of Alaska (Haile et al., 2009) and Northern Siberia (Boeskorov, 2004, 2006, Vartanyan et al., 1993) well into the Holocene. The last wild horse carcass in Siberia dates from as late as 2,150 years ago, but horses were reintroduced into North America during the second invasion by the Spanish Conquistadors.

Stewart & Stark (2002, Figure 3.2) also conclude that a considerable number of genera of Plecoptera (stoneflies) moved across the Bering Land Bridge in both Miocene and early Pliocene times, since today part of their distribution extends south of Alaska to California. Before the closure of the North Atlantic Land Bridge, there was an exchange of at least 5 genera of stoneflies with Europe that now exhibit an Amphi-Atlantic pattern of distribution.

There was also a tremendous explosion of species in the other terrestrial groups including amphibians, birds, fish, insects and reptiles. Many are endemics, often with a very limited distribution. Weber (1965) discussed the plant geography of the southern Rocky Mountains, and determined that there were also a number of species now living in Colorado and California that are also found in sub-tropical Asia. He concluded that they must have crossed the Bering Land Bridge while the climate was still sub-tropical in late Cenozoic times.

As the Atlantic Ocean extended northwards, the remaining land connection was limited to higher and higher latitudes. The history of its extension is quite complex with several phases taking place (Hallam, 1981, 1994). In the latter part of the life of the land bridge, only warm temperate and subtropical biota could pass across from one continent to the other. Molecular studies suggest that some interchange in flora has continued until very recently, but the mechanism has yet to be determined. No similar evidence has been found for interchange of animals.

Northward movement of the Indian plate resulted in the uplift of the Himalayan mountain range about 21-17 million years before present, further reducing the size of the tropical seas. The northward movement of the African plate further reduced the remnants of the Tethys, producing the mountains of southern Europe including the Alps and Carpathians.

Cooling of the Northern Hemisphere continued, so that by 6 million years ago, an open Boreal mixed forest had become established in southern Alaska. By then, the species present had largely been replaced by the ancestors of the present-day biota that were adapted to the much colder environments. A land connection across the Bering Strait briefly allowed warm temperate species to be exchanged between Asia and North America. Subsequently, only Arctic and Subarctic biota could cross the Land Bridge due to the marked cooling. Matthews (1980) has argued that most of the modern genera and species of insects in most of North America date from about 5 million years ago and are endemic. Relatively few insects live in the Arctic, most being found further south in warmer climates.

5. Onset of major cold events in North America

About 3.5 million years ago, the first major cold event (extensive glaciations and development of permafrost) affected the Cordillera of western North America. Cold conditions also extended across northern Canada, and there must have been a substantial southward movement of the climatic zones. Another brief connection with Asia across the Bering Land Bridge occurred when the sea level dropped during this first major cold event. There were to be 5 subsequent occasions when the land bridge was open, the last one being during the late Wisconsin cold event about 15,000-20,000 years ago. Altogether there were about 13 major cold events (Harris, 1994; 2000; 2005) separated by shorter interglacials.

The biota that do not live in the Arctic or Subarctic could not move across the Bering Land Bridge during the few times it was open during the last 3.5 million years. These include the Hispine beetles (Staines, 2006). Only one species of Lasiopogon (*L. hinei*) is found on both sides of the Bering Strait (Cannings, 2002), but that species is exceptional in its wide range throughout Eurasia.

The second major cold event at 3 million years ago produced the most extensive glaciation in Alaska and the Yukon Territory. The moisture came primarily from the open Arctic Ocean, but by the time the third major cold event occurred (2.58 million years before today), the Arctic Ocean had frozen over and permafrost with tundra was present along the Arctic coast. This split the temperate humid vegetation into separate eastern and western

populations. These were forced to move south along the respective coasts as cooling continued, and any components of the biota that could not adjust to the changing environment were extirpated. Since the climate, topography and micro-environments were different on the two sides of North America, different Temperate and Subtropical species that lived in the more humid areas evolved on the two sides of the Continent. The eastern populations have significantly more species than the western populations. Likewise, the animal populations in the two areas show distinctive species adapted to the local environment. Only the Boreal Forest and Tundra biomes are distributed across the northern part of the continent. Further south, the dry central steppe (Prairies) separates the two populations of biota that are adapted to wetter climates. The Tropical conditions moved south into Central America, while Subtropical climates were limited to the extreme southern United States, even during the Interglacial periods.

Initially, the later glaciations only affected relatively small areas in the north, but subsequently, the ice caps have become far more extensive. Permafrost was particularly widespread across the northern parts of North America, and facilitated the spreading of the Tundra flora south along the western Cordillera (Harris, 2007a). Only in the last 100ka have the Milankovitch cycles become significantly correlated with the onset of glaciations (Harris, 2012, Imbrie & Imbrie, 1980). During the last cold event and probably during the earlier events of the last million years, permafrost extended down to the southern part of Arizona and New Mexico, so the biota of all the climatic zones had to migrate long distances to survive or else find local refugia. The ice sheets wiped out all the vegetation in their path as they advanced, and when they retreated, the biota had to rapidly migrate north again over distances in excess of 1500 km (Dynesius & Jansson, 2000; Harris, 2010a). The result was that only those species of plants and animals that could migrate, adapt or find a suitable refugium could survive.

Refugia were present throughout these climatic changes, providing suitable habitat for the biota, whether the changes involved mean annual air temperature, precipitation, or both. In the more northerly mountain valleys, a combination of cold air drainage, temperature inversions and steam fog provide a buffering of the mean annual air temperature, so that the effects of cooling events were greatly reduced (Harris, 2007b, 2010b). This undoubtedly helped the biota in the eastern part of Beringia survive during the major cold events of the last 3 million years.

It should be noted that there are multiple kinds of refugia. Until now, most of the literature only discusses the effects of variations in temperature (e.g., Willis and Whittaker, 2000; Stewart et al., 2010). As these authors point out, refugia exist for species during both warmer and colder conditions. However, the vegetation is actually controlled by a number of factors, of which the moisture regime is undoubtedly equally important. Since the vegetation cover is a critical part of the ecosystem, it is also a major factor in providing a suitable microenvironment for animals.

The colder climate of the Late Wisconsin event would have resulted in an expansion of the ranges of species adapted to the cold conditions southwards and also on to lands becoming

exposed by the eustatic drop in sea level along the Grand Banks area off Newfoundland, the Gulf coast of the southern United States and along the Beringian land bridge. Undoubtedly in the north, these provided expanded ranges for the arctic mammalian fauna, as well as the limited number of arctic insects such as butterflies (Layberry et al., 1998). Many Arctic mammalian species were destined to become extirpated by a combination of hunting and climate change, but 6 species of butterflies still live in both Alaska and the adjacent part of Siberia. The existence of closely related but different species of butterflies in eastern Beringia (Alaska and the Yukon Territory) and in western Beringia (East Siberia) is apparent evidence of Holocene speciation there.

In the southwest United States, the climatic changes were accompanied by widespread tectonic movements and volcanism (Wahrhaftig & Birman, 1965). This orogenic activity started in middle Miocene times and is continuing today. Pluvial lakes developed in the inland drainage basins (Morrison, 1965) and the sediments in these basins contain scattered vertebrate fossils, freshwater mollusks and diatoms, some dating back to 3.4 million years ago. Fossils in the marine terraces provide further evidence of the climatic changes and their effects on the local biota. The isolated volcanic mountains tend to have local endemic biotas that have evolved to cope with the local microenvironments. During pluvial events, animals such as voles are believed to have descended from the mountains and became widespread in the Great Basin and Mohave Deserts (Findley & Jones, 1962, Norris, 1958). Southward movement of sage voles and other animals resulted in their presence as fossils in the Isleta Caves of New Mexico (Harris & Findley, 1964). Around Lake Bonneville, speciation resulted in the appearance of a new species of *Oxyloma* (*O. missoula*, Succinidae) that is limited to that particular drainage area (Harris & Hubricht, 1982).

In the southeast United States, a narrow zone of subtropical and tropical vegetation may have persisted along the coast during the glaciations, but permafrost conditions were present along the higher and more northern parts of the Appalachian Mountains. Once again there is clear evidence of the southward migration of the biota during the glaciations. Remains of mammoths and other cold arctic fauna are well known from along the eastern seaboard of the United States, and have even been found in the sediments on the shallow sea floor that would have been exposed as dry land due to eustatic sea level changes during the glaciations. There was a gradual change in the mammalian fauna throughout the sequence of glaciations, indicating that speciation was fostered by the climatic changes (see Hibbard et al., 1965, for a summary). This contrasts with only slow speciation being reported in the insect world, since speciation in insects seems to have been slower than the speed of the major climatic changes (Matthews, 1980). Other animals, e.g., the Mollusca, tended to evolve in a similar way to the mammals in response to the environmental changes during the last 3.5 million years.

The aquatic biota also had to adjust their ranges. The north-south Mississippi River was very important, since it facilitated the migration south of fish and aquatic mollusks from the interior of the continental United States. The biota had to move into the warmer waters close to the Caribbean Sea which also diminished in size as sea levels dropped due to the accumulation of ice on land. During the last few glaciations, the Mississippi River acted as a spillway for the

melting ice to the north, so the biota would have had to find refugia in smaller tributary streams. During deglaciation, they would migrate upstream to reclaim their previous habitats, or find new ones. Migratory birds presumably altered their migration patterns as they do today, to dwell in suitable habitats. When a cold event ended, they would adjust their migrations to make use of the new environments as they became available.
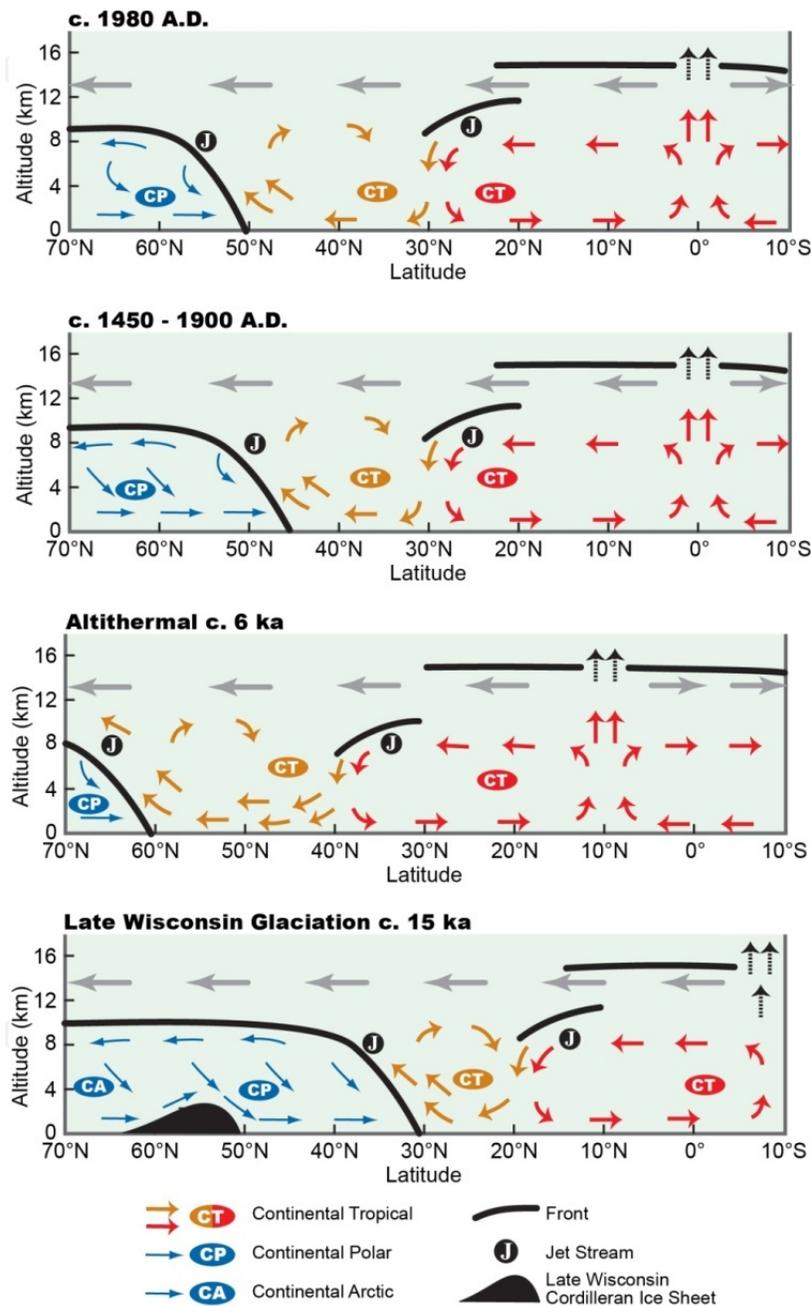
Figure 1. Changes in distribution of the main air masses during the main climatic extremes of the last 15,000 years along a north-south transect from the Arctic Ocean to Brazil along the Cordillera of the Americas (modified from Harris, 2010a). Note firstly that the zone of intertropical convergence moved south into northern Brazil during the Late Wisconsin cold event, and secondly, that the latitudinal range of the cold cA/cT air extended some 20° south of the ice sheets almost to the Mexican border along the Cordillera.

Origin	Common Name
North America	Rabbits
	Squirrel
	Field mice
	Cats
	Skunks and otters
	Foxes
	Bears
	Horses
	Camels and llamas
	Deer
South America	Opossums
	Armadillos
	Giant ground sloths
	Three-toed sloth
	Anteaters
	Monkeys
	Porcupines
	Guinea pigs

Table 1. Some mammal families that took part in the Great American Faunal Interchange (after Webb, 1997 and MacDonald, 2003).

6. Closing of the Panamanian Seaway

About 3.5 million years ago, the Panamanian Seaway between North and South America began a step-wise closure. The Isthmus of Panama was finally dry land by about 2.4 million years before today. South America had been moving northwestwards and had finally run into the southern margin of the North American plate. The northwards motion of the South America plate is still resulting in volcanism and the formation of the islands in the Caribbean Sea. Both plants and animals have taken part in exchanges between North and South America since then. During Interglacials, Tropical Rain Forest occurred along the Isthmus and permitted the exchange of that biota, but during major cold events, savannah conditions occurred there, allowing an exchange of the biota found in much drier areas (Harris, 2010a). As a result, many of the species of grasses and other vascular plants of

Guyana and northeast Brazil are the same as in Costa Rica, Honduras, sub-humid portions of Mexico and the south coast of the United States of America (FNA, 1993 - ?).

There was also a spectacular interchange of mammalian faunas between the two continents (Table 1, modified from Webb, 1997) that has been called "the Great American Interchange" (Marshall et al., 1982). The mammals from North America have tended to displace the marsupials of South America, whereas the marsupials could only move a limited distance north into the United States due to the cold winters and competition from the indigenous mammalian species. A small camel species crossed the Panamanian Land Bridge into South America and evolved into the present-day Llamas, Alpacas, Guanacos, and Vicunas. However only two genera (*Anacroneuria* and *Amphinemura*) of the Plecoptera which occur as a distinct Austral-American group in South America and two Nearctic groups in North America have managed to cross the Land Bridge (Stewart & Stark, 2002, p.16-17).

7. The Late Wisconsin Glaciation

This took place between about 25,000 years and 10,000 years ago in North America, although the timing of the glacial maximum is highly diachronous. Harris (2010) describes the evidence for the spectacular southward shift of the climatic belts along the western Cordillera during the main event (Figure 1). Permafrost extended down to Arizona and New Mexico, and the arid areas of Mexico moved south into Venezuela and the Guianas. The intertropical convergence zone moved at least 6 degrees to the south, so that sand dunes developed on the slopes just inland of the present-day coast of the Guianas (Harris, 2010a) and in northern Venezuela (Rabassa et al., 2005, Rabassa, 2008).

The ice sheets covered most of Canada (Figure 2), bull-dozing the landscape and destroying the vegetation in their paths. The cold events also allowed the migration of the biota adapted to the drier conditions occurring today in the area from the Mid-West down to Mexico to move south into South America across the Isthmus of Panama, since the climatic zones had moved south (Harris, 2010a). The rest of the biota had to adapt very quickly, or for those species living south of the ice sheets, migrate down the mountain sides and find a suitable refugium. Those that could not adapt perished. The Butterfly species, dependent on specific plants for survival, would have had to follow the changes in distribution of those plants. The species that migrate with seasonal changes would have needed to modify their migration patterns, probably shortening the distance of travel to adapt to the changing climatic zones.

Refugia around the ice sheets included Eastern Beringia (Harris, 2004), various islands along the northwest Pacific coast, the chief of which were the Queen Charlotte Islands (Calder & Taylor, 1968), unglaciated areas in southwest Alberta around Plateau Mountain (Harris, 2007a, 2008), the "Driftless Area" of southwest Wisconsin (Nekola & Coles, 2001, 2010), the Grand Banks east of New England, postulated areas in the far north of the Arctic Islands, and the area south of the ice sheets in the United States (Rogers et al., 1991). This was a time of rapid speciation of plants in the northern refugia (Harris, 2007a, 2008), the number of new species increasing with severity of the climatic change in the refugium. At least two species

of land snails (*Gastrocopta rogersensis* and *Vertigo meramecensis*) are regarded as having evolved in the Driftless Area (Nekola and Coles, 2001, 2010), while about 40 species of Arctic-Alpine vascular plants evolved in Eastern Beringia (Harris, 2007a; 2008). This represents far more speciation in a given sized population than during the same period in most environments south of the ice sheets.

8. Deglaciation

About 14,000 years ago, there was a marked change in the relative strengths of the air masses affecting North America (Figure 1). This resulted in the northward movement of the climatic zones and the zone of intratropical convergence. It was not a continuous process; the climate fluctuated with both warmer and colder periods, thus complicating the revegetation process. The exact timing of the fluctuations and their areal extent is still being examined. Localized readvances of glaciers provide evidence of these fluctuations, as do variations in pollen, diatom and finger clam distribution at the base of the oldest post-glacial sediments at the bottom of lakes in the formerly glaciated areas. During the early part of the deglaciation process, the Cordilleran ice sheet had rapid local readvances, but in general, it down-wasted in situ with widespread ice stagnation in the valleys in British Columbia and in the Prairies from south-central Alberta across to North Dakota (Alley, 1976, Harris, 1985, Prest et al., 1968). In the Cordillera, the mountain tops appeared first from under the ice and there were numerous lakes in the valleys, with ice blocking the centre of the valley. The former water levels are marked by gravel terraces and hanging deltas along the valley walls. In the main part of central and eastern Canada, the ice persisted as a single entity centered on Hudson Bay (Figure 2) until about 9,000 years ago (Prest et al., 1968). It then split into two parts, one centered on the highlands of northern Québec and the other on the highlands west of Hudson Bay. Complete deglaciation did not occur until 6-7ka in these centers and about 4ka on Baffin Island.

The warming first commenced in the south, and slowly and jerkily moved north (Wright, 1970). Thus the prairie vegetation at 20,000 years before present was limited to a narrow north-south zone extending from central Oklahoma to the east coast of Mexico (Ross, 1970). Lehmkuhl (1980) discusses the movement of insects into the evolving Prairies with their harsh temperature regime and unpredictable precipitation. In the case of the grasshoppers that are found today across the Prairies, Ross reports that only 3 out of 82 species are endemics, 31 species have moved in from the west, 34 from Mexico, 10 from the Caribbean coast, and 7 from the eastern part of the United States. In the case of aquatic Mollusca, Clarke (1973) estimates that only about 21 species out of a potential 103 species now populate the western interior of Canada, probably due to the vast distances, poor dispersal mechanisms, and harsh climate. In contrast, mammals and birds could migrate readily across the region.

The flora and fauna adapted to the cold permafrost land would have had to contract their ranges with some cold-adapted butterflies and rock crawlers (Gylloblattidae) still surviving in small areas on mountain summits along the Cordillera of western North America. The mountain sheep and goats survive in this way, whereas the larger herbivores such as Mammoths could not survive in the southern parts of their former ranges.
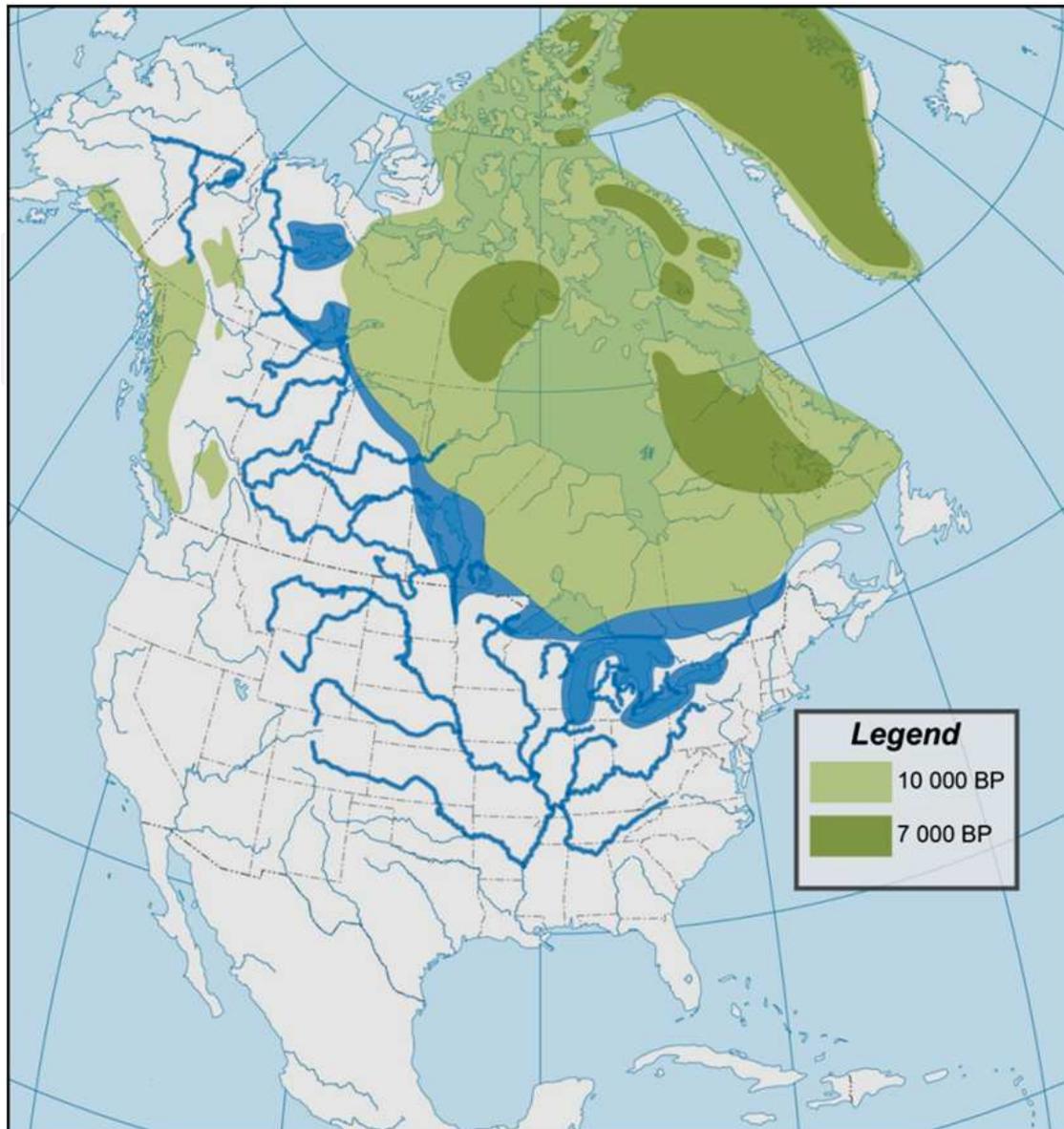
Figure 2. Position of the ice sheets in North America at 10,000 and 7,000 years before present (after Denton and Hughes, 1981). Also shown is the distribution of the proglacial drainage and the proglacial lakes that permitted the fishes and other aquatic biota to migrate northwards across present-day drainage divides. They were followed by many terrestrial snails that require moist microenvironments.

The flora and associated fauna of the more humid regions moved north through Mexico, divided into two coastal biotas by the semi-desert of the interior. The western group moved north into California and the Southern Rocky Mountain States, while the eastern biota moved east along the Gulf coast of the United States before moving further north. The results of this can be seen in the present distribution of the Monarch Butterfly (Urquhart, 1960). It feeds on various species of Milkweed that are found in southeast and southwest Canada, where it spends its summers (Figure 3). In winter, the two populations migrate south, the western population over-wintering on trees in the sheltered coastal canyons near Goleta, while the eastern populations over-winter in Florida or along the eastern coast of Mexico.
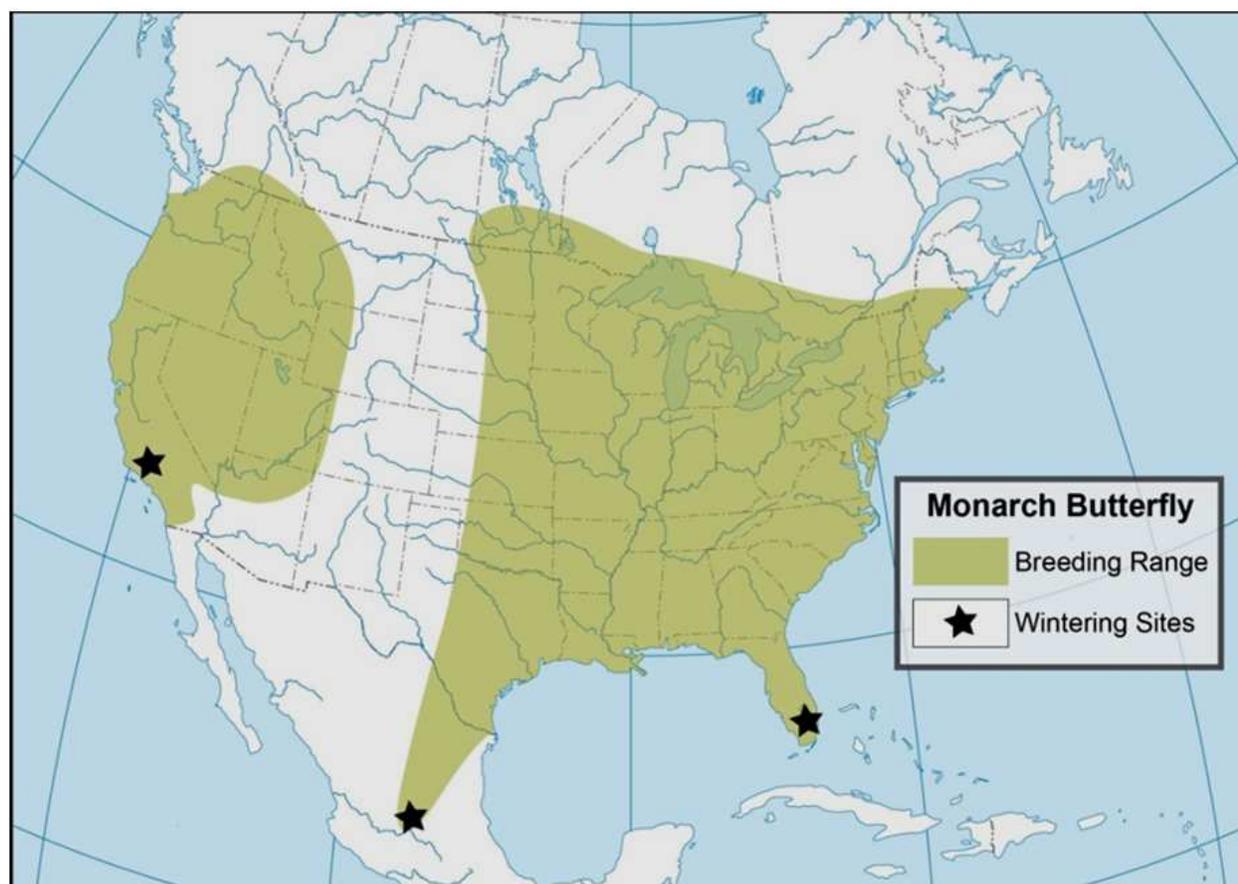
Figure 3. Present-day wintering sites and summer breeding range of the Monarch Butterfly (Partly after Urquhart, 1960). In winter, they migrate south, the western population forming giant clusters on groups of trees in California (Brower & Malcolm, 1991), e.g., in a gulley above the Pacific Ocean at Goleta, with the eastern population overwintering at several locations along the Caribbean coast of Mexico and near Mexico City (Wassenaar & Hobson, 1998). The Floridian group is believed to overwinter on the Yucatan Peninsula.

In the Western Cordillera of the United States, the basins dried up and the biota moved up the mountains, forming isolated ecosystems on the various mountain ranges. This accounts for the considerable endemism found in this region in the plants, reptiles and birds. In the case of the Kangaroo rats, the sharp boundaries between species distribution may be partly caused by competition (Brown & Lomolino, 1998). However in general, many species of birds and 80% of the butterflies rely on one or two families or even species of plants for food, so their distribution is limited by the distribution of the food plant. Additional tropical and subtropical species moved north, adding to the species richness of the region. Cacti, creosote bush and the associated biota moved into the semi-deserts from the south.

In the case of the trans-continental snake *Diadophis punctatus* (Figure 4), phylogeographic studies of the present–day populations in the United States indicate that there are 13 populations with distinctive DNA that are apparently adapted to specific environmental conditions (Fontanella et al., 2008). The nine southern populations have stable distribution boundaries and appear to represent a pre-glacial distribution that was relatively unaffected by the Late Wisconsin cold event (Figure 4). In the case of the 4 northern populations, they

are currently migrating northwards into the areas with suitable climates following deglaciation. The preglacial populations in these four areas would have been extirpated in the northern part of these ranges during the cold event. Since the snake has limited ability to migrate over long distances, the adjustment of its northern boundaries of distribution is still taking place as it expands northwards into suitable environments.
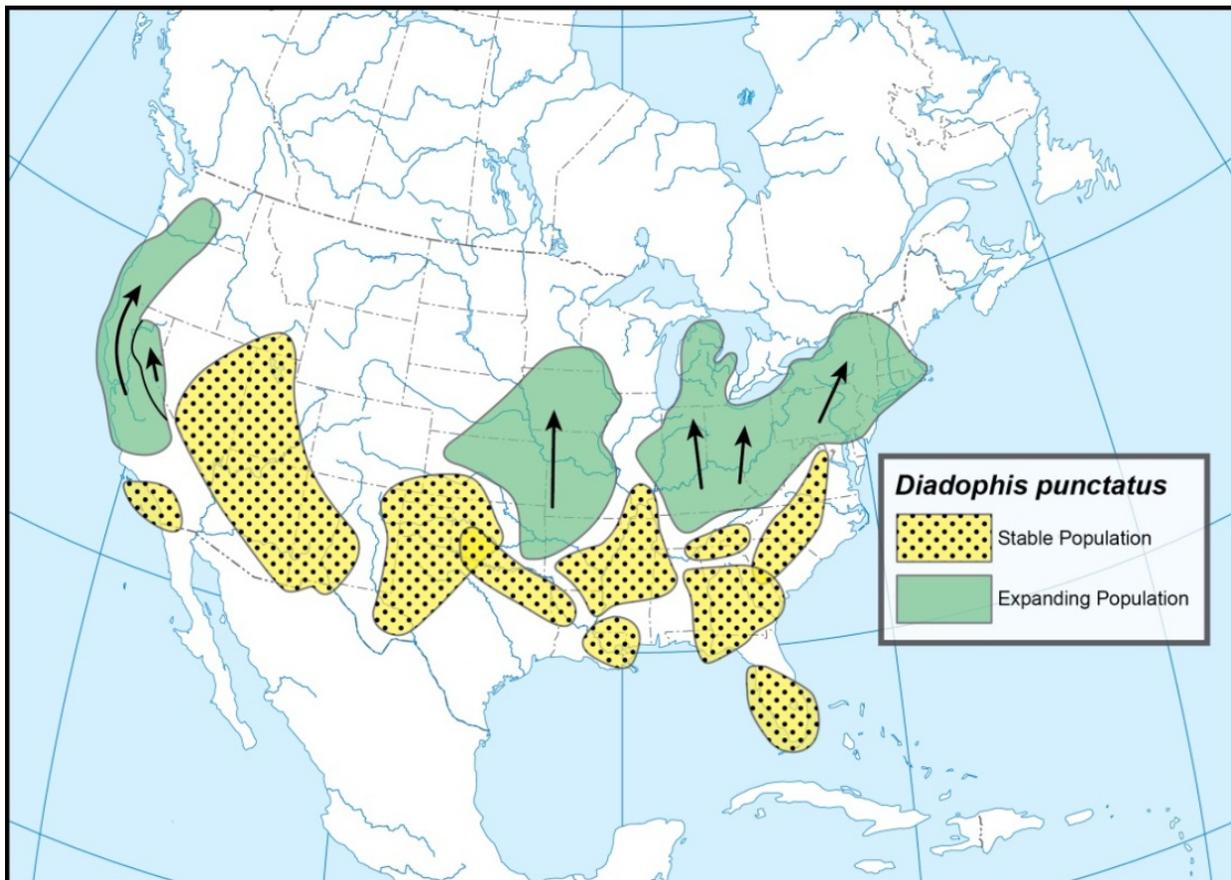
Figure 4. The distribution of the present-day distinct haplotypes (populations that have distinctive DNA) of the snake, *Diadophis punctatus* (after Fontanella et al., 2008). The distributions of the southern populations are stable, and may have lived in the same area since before the Late Wisconsin glaciations because of an acceptable microclimate. Also shown are the populations that are slowly expanding northwards to occupy areas that are now suitable for its existence, but were too cold for the snake during the Late Wisconsin Glaciation.

The formerly glaciated areas are another matter. The migration of species into the areas vacated by the glaciers was highly dependent on glacial history, distribution of refugia, the climate which limited the possible migrations, and the waterways in the case of aquatic and associated biota.

The downwasting of glaciers in western Canada and North Dakota slowed the recolonization process of trees (Figure 5), even though deglaciation commenced earlier at about 15,000 years ago. The Jack Pine, which survived the glaciations in the northeast United States, was able to move west along the Laurentide ice front, whereas the Lodgepole Pine that used the west coast as a refugium was largely blocked off from eastward

movement by the ice in the mountain valleys and the dry area on the Prairies (MacDonald & Cwynar, 1985). Western Red Cedar only penetrated the Coast Ranges into the Interior Plateau of British Columbia about 3,000 years ago.
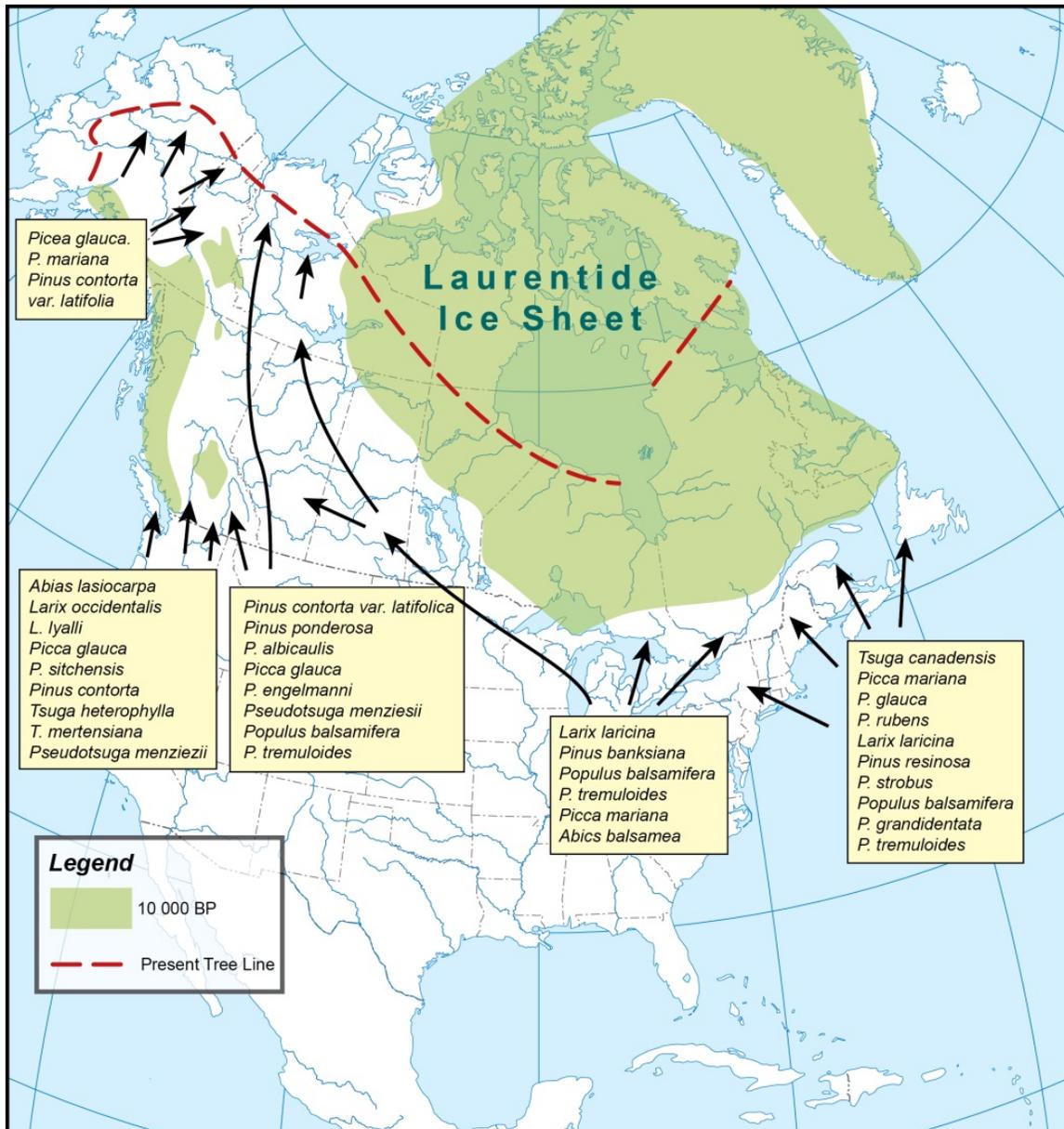
Figure 5. The influence of the residual ice masses on the migration of some of the common tree species into the deglaciated areas about 10,000 years ago.

In the case of the vascular plants of the present-day alpine tundra and boreal forest, revegetation in western Canada came primarily from Eastern Beringia (Figure 6), with only limited northward movement from the southern refugium (Harris, 2007a, 2008). The species in the SW Alberta refugium spread west across the limestone mountains, while those that survived the glaciation around the Queen Charlotte Islands moved north and south along the west side of the Coast Ranges. In the east, the vegetation gradually moved north following the retreating ice front in the period between 10,000 and 7,000 years ago.
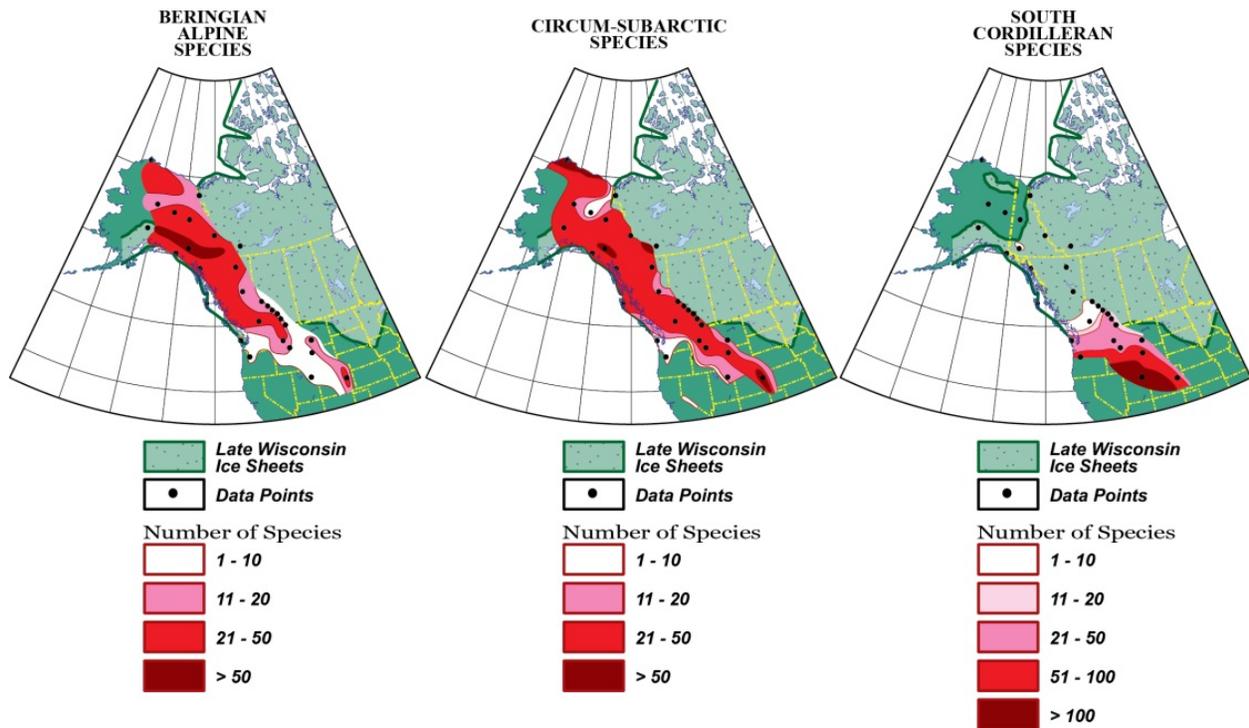
Figure 6. Migration of selected alpine tundra species from the Beringian refugium along the western Cordillera of North America contrasted with the limited northward migration from south of the maximum extent of the Cordilleran ice sheet (modified from Harris, 2007a). This migration had to occur in the short period when it was cold enough for their movement after the down-wasting of the ice sheet and before the mountain valleys became warm enough for invasion by the Montane Boreal Forest.

Various species of Succinidae (Mollusca) survived the glaciations in refugia (Figure 7), either in Beringia (e.g., *Succinea strigata*) or south of the ice sheets in the Rocky Mountains (*Oxyloma nuttalliana*), on the Central Plains (e.*g.*, *S. indiana*), south of the Great Lakes (*Catinella avara*, *O. retusum*, and *S. ovalis*), on the exposed Grand Banks (now inundated by the sea) or in the unglaciated parts of New England (e.g., *O. groenlandicum* and *O. verrilli*). A new species (*O. missoula*) evolved in the Lake Bonneville drainage, but it did not migrate elsewhere during the Holocene. Most of the species of the Succineids need to be close to water (c. 1-2 m) and the bodies of terrestrial snails consist of about 50% water. They must lay down a thin layer of mucus as they move, so they are particularly dependent on moisture for survival. As a result, they had difficulty moving on to the rocky and sandy substrates of the Laurentian Shield following deglaciation, except where the waters of Glacial Lake Agassiz drained northwards into Hudson Bay.

Climate certainly limited many northward migrations, e.g., many vascular plants and the freshwater bivalves. The latter only entered the previously glaciated Cordilleran areas in northern Washington, northern Montana and in Southern British Columbia. A few species were able to move further north in the Prairie Provinces, but many only just entered Southern Ontario and the Red River Valley in Manitoba. They only occur along the margins of the Shield on the calcareous rocks and sediments in southern Québec, though the late deglaciation and colder climate there undoubtedly inhibited the northward migration.

Figure 7. Migration routes of the various species of Succinedae that survived the Late Wisconsin glaciations south of the ice sheets, and moved north about 10,000 years ago following the proglacial drainage shown in Figure 2 (partly after Harris and Hubricht, 1975). Most of these species must live within one or two meters of water, and so they subsequently followed the water draining north from Lake Agassiz into the south end of Hudson Bay about 8700 years ago.

The biota that live all or part of their life in fresh water and could tolerate cold climates, e.g., fish and some insects (Lehmkuhl, 1980, Morgan & Morgan, 1980), moved along the main drainage-ways and proglacial lakes, e.g., Glacial Lake Agassiz, crossing into other watersheds using the temporary spillways. Many came from the unglaciated areas to the south, but others came from Beringia.

9. Altithermal/Hypsithermal event

The post-glacial warming culminated in a period of time when the mean annual air temperature was about 2 degrees warmer than at present in the Eastern Cordillera of Southern Alberta (Harris, 2002b). It reached its peak about 9,000 years ago in the southern United States, but the peak only affected the Prairie Provinces of Canada from about 6,500-4,500 years before today. It was the result of a weakening of the cP/cA air masses, resulting in the northward movement of the Arctic front (Figure 1). The vegetation zones migrated up the mountains, while those species that were at the mountain tops were extirpated. The Boreal Forest approached the Arctic Ocean about 5,000 years ago (Anderson et al., 1989, Ritchie and Hare, 1971) with White Spruce having been reported on the Tuktoyaktuk Peninsula at about the same time. It was at this time when the last remnants of the mammalian Megafauna disappeared in the isolated parts of Alaska and Siberia.

In the southern Canadian Cordillera, it began after 6,830 years ago. The westerly rain-bearing mP air mass as well as the cold cA/cP air mass weakened relative to the cT air mass, which was therefore able to move north into the southern Yukon Territory before turning east. This resulted in drought conditions across the Prairies with drying up of the ponds and lakes. The Prairie vegetation moved north of latitude 60° (Strong & Hills, 2003), and these authors concluded that it may have migrated westwards into the interior plateau of the Cordillera along the Liard River valley. Remnants of prairie-type vegetation may be found today around Carmacks and Kluane, Yukon Territory, e.g., *Krascheninnikovia lanata* (Douglas et al., 2001).

Harris & Pip (1973) demonstrated that there was considerable northward migration of land snails along the main river valleys. Tiny land snails that are currently limited to the east-central United States of America migrated along the major river flood plains to the Cordillera along the North Saskatchewan and Missouri rivers. Today remnants of these populations can be found surviving at sheltered places, but are slowly being extirpated (Figure 9). Thus *Gastrocopta armifera*, *G. similis* and *G. pentodon* were present in the vicinity of Lake Louise in 1880 but were extirpated when the CPR railroad was built. There are still some isolated occurrences of these species remaining at sheltered isolated sites along the river valleys.

10. Neoglacial events

A series of three cold Neoglacial events began about 4,500 years ago during which the MAAT was significantly cooler, and periodic localized increases in precipitation caused the glaciers to advance a short distance down-valley. The balance of the air masses north of about 48 degrees latitude changed (Figure 1), but this did not affect the area further south. There was also no change in the position of the zone of inter-tropical convergence. It was during the first event (3500 years ago) that the western red cedar (*Thuja plicata*) finally migrated up the Skeena River valley from the coast and colonized the wetter portions of the interior of southern British Columbia (MacDonald & Cwynar, 1975). The Prairies exhibited a large area of sand dunes during the last Neoglacial event (Wolfe et al., 2001; Wolfe & Hugenholtz, 2009). That is why the fur traders chose to paddle up the North Saskatchewan River rather than cross the sand dunes to reach the mountains. Similar sand seas existed in Nebraska. In the north, the Boreal Forest retreated 5 degrees to the south on the adjacent

Prairie by 4,000 years before today, while the Aspen Parkland moved about 1 degree south. These cooler events were separated by warmer intervals at least as warm as today, with that just before the last Neoglacial being even warmer. These changes favoured some species, but caused others to migrate latitudinally or altitudinally, or become extirpated. Similar changes took place throughout the continent.
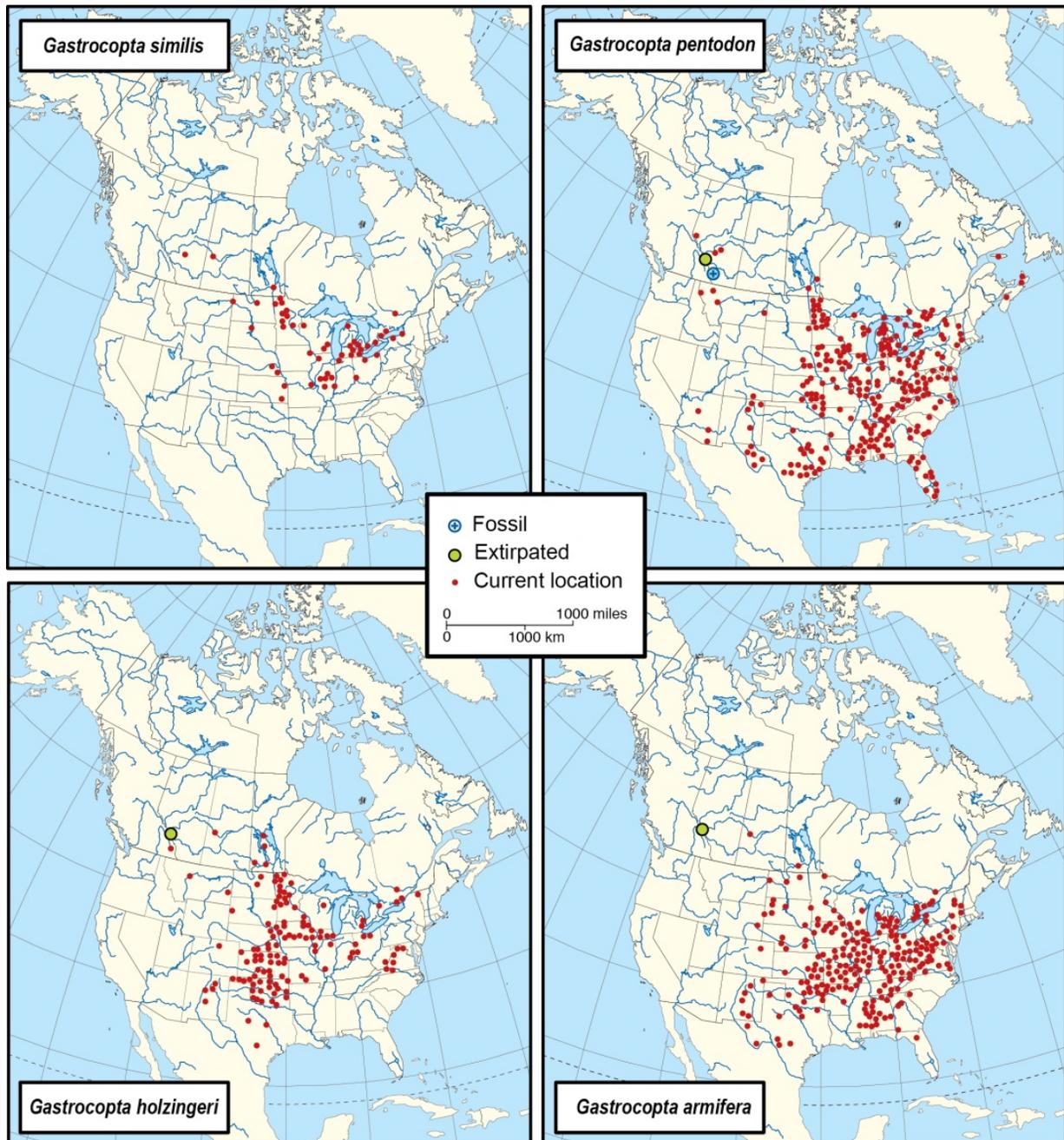
Figure 8. Distribution of 4 species of the genus *Gastropoda* that exhibit evidence of having extended their ranges westwards and northwards during the Altithermal/Hypsithermal warm event from their main area of present-day distribution. Today, remnants of the extended populations are found in favourable microenvironments along the river floodplains that they followed during the migration process. They are known to have been extirpated in the vicinity of Lake Louise, Alberta, since the late 1800s.

11. Post-Neoglacial changes

The last Neoglacial event ended about 110 years ago with the development of the present-day distribution of air masses (Figure 1), resulting in a minor change in temperature, but important changes in precipitation. There was a marked reduction in precipitation in the Eastern Cordillera, causing the vegetation that required more moisture to become limited to the high precipitation areas around Lake Louise (Harris, 2012). After 1943, the precipitation on the Canadian Prairies increased, and the sand dune field has largely become stabilized, though it is now used for irrigation farming. Grassland species such as the Prairie Swift Fox, the Sage Grouse and Black-Footed Ferret have almost been extirpated on the Canadian Prairies. In the last 500 years, the European settlers have gradually modified the landscape, starting in the east and south as well as at isolated coastal regions in the west. This has had an enormous effect on the biota, especially by destruction of habitat. An additional factor is the importation of species from other countries, especially Europe. Forty percent of the flora of Nova Scotia is from elsewhere (Zinck, 1998). Ships discharging water into North American waterways that is used as ballast are introducing fresh water fish and mollusks, e.g., the Zebra Mussel into the rivers and lakes. These then devastate the indigenous species.

12. Conclusion

Until the advent of European settlement, climatic changes and diastrophism essentially determined the biodiversity of the biota of North America. The species found today evolved in the last 6 million years in response to the marked cooling of the continent. There had been limited immigration of present-day species from Asia and South America, and little exchange with Europe. The alternating major warm and cold events caused repeated massive migrations latitudinally and altitudinally, unless a given species was fortunate enough to survive in a refugium. Species that could not adapt or migrate quickly enough were extirpated. The climatic changes also resulted in speciation in the vascular flora, though not in many of the insect groups. Speciation in most of the latter takes more time than the duration of most climatic major warm or cold events. This has resulted in a primarily endemic biota that is able to disperse into new environments rapidly. The exceptions are mainly found in the southwest United States on isolated mountain ranges currently surrounded by deserts. Of particular note is the split in the biota of the more humid regions at lower latitudes into eastern and western groups separated by the central semi-arid plains. This split is the result of the early glacial history of the continent. Clearly, the biota of North America has had a unique history that is significantly different to that of the other continents.

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Acknowledgement

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