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SECTION 1

Introduction



1

Integrating ecology and systematics in climate change research

T. R. HODKINSON

School of Natural Sciences, Trinity College Dublin

Abstract

Interactions between climate and biodiversity are complex and present a serious challenge to scientists who aim to reconstruct the ways in which climate change has shaped life in the past and will continue to do so in the future. This chapter introduces the contributions made to climate change research by the fields of ecology and systematics and outlines how their approaches and methods have, often through necessity, become increasingly integrated. It explores: (1) how climate change has influenced evolutionary and ecological processes such as adaptation, migration, speciation and extinction; (2) how these processes determine the diversity and biogeographic distribution of species and their populations; and (3) how ecological and systematic studies can be applied to conservation and policy planning in our rapidly changing world.

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1.1 Introduction to climate change, ecology and systematics

Not only does the marvellous structure of each organised being involve the whole past history of the earth, but such apparently unimportant facts as the presence of certain types of plants or animals in one island rather than in another, are now shown to be dependent on the long series of past geological changes, on those marvellous astronomical revolutions which cause a periodic variation of terrestrial climates, on the apparently fortuitous action of storms and currents in the conveyance of germs, and on the endlessly varied actions and reactions of organised beings on each other (Wallace, 1880).

Climate exerts a strong selective pressure on organisms and their ecosystems and has continuously presented new challenges to life since it began approximately 3.5 billion years ago (Knoll and Lipps, 1993; Fig 1.1). Species and their populations can respond to climate change by adaptive evolution or by migrating geographically to track their favoured climate. If they fail to do either of these, and if they lack sufficient phenotypic plasticity in terms of their climatic tolerances, they face extinction (Thomas et al., 2004, 2006; Pearson, 2006). Evolution has a tremendous capacity to offer solutions to changing selective pressures, but extinctions induced by climate change are inevitable.

Climate change is best seen as a driver for both creating diversity and reducing it. Climate change has left a record in the taxonomic and ecological patterns of the diversity that has existed on earth (a highly conservative four million species) and the evolutionary history of that diversity (Parmesan and Yohe, 2003; Root et al., 2003). It is important to study these fingerprints to understand the evolutionary and ecological potential of life to adapt to climate change and resist extinction (Woodward and Kelly, 2008). There is no evidence that life has ever gone totally extinct (Benton and Twitchett, 2003). This is a remarkable resilience given the global change it has endured throughout its history. The fossil record shows that there have been major periods of extinction, but life has never been totally eclipsed and forced to start again. Several megaextinctions are well known, but the role of climate change as a causal agent in these events is far from clear, even though it has been implicated in all of them (Raup and Sepkoski, 1982; Mayhew, Chapter 4).

Interactions between climate, evolution and ecosystems are complex, and their study has become a highly challenging and multidisciplinary research field (Lovejoy and Hannah, 2005; Rosenzweig et al., 2007). Ecological and systematic research is central to these efforts and essential for predicting the impacts of climate change. This chapter introduces the contributions made by these two key research fields and provides supporting information to make the book's content more accessible.

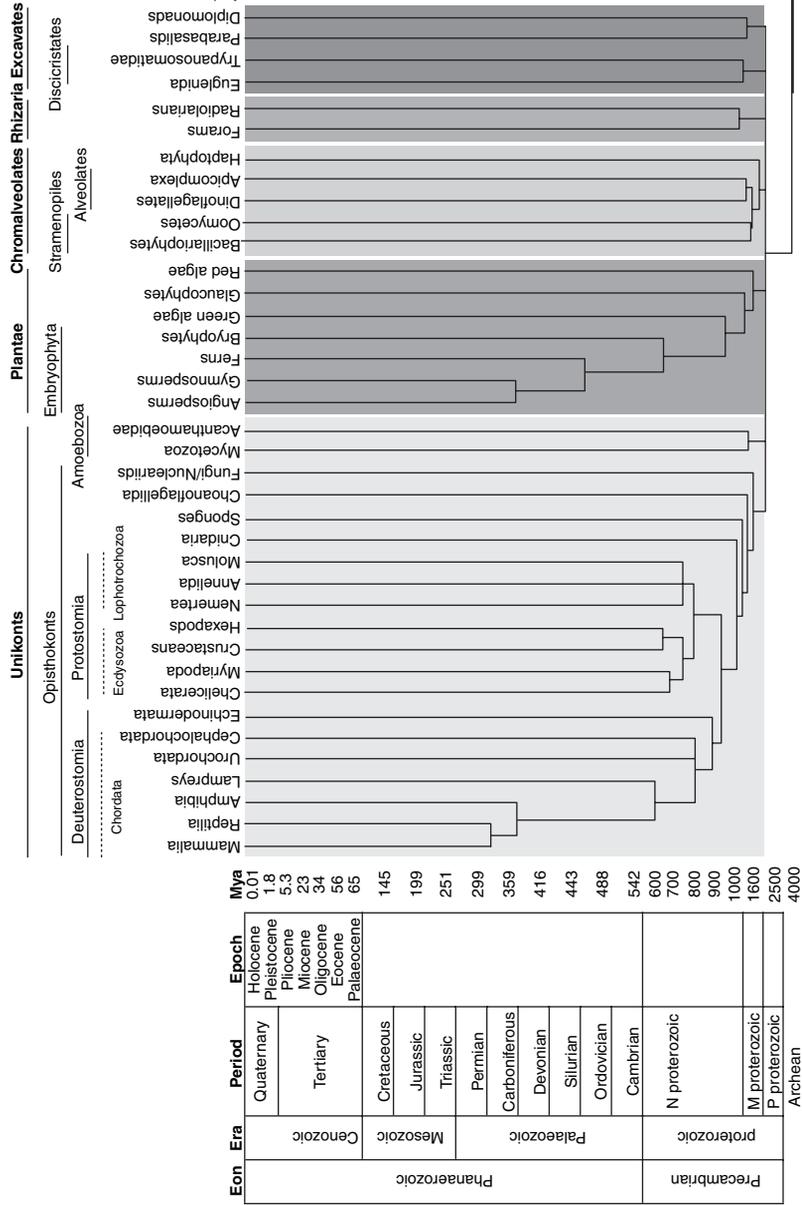


Figure 1.1 The geological timescale and evolution of life. Left, simplified geological timescale (modified from Ogg et al., 2008). Right, simplified phylogenetic tree of life. Node dates are predominantly taken from Hedges and Kumar (2009) but also from Palmer et al. (2004). Note that dates represent times when the taxa diverged from their common ancestor shown on the tree (root node) and do not represent dates for the age of the taxon listed (crown node). Supergroups of Eukaryotes are shown with thick black bars. Other major groups are shown with thin or dotted bars.

1.1.1 Climate and global change

According to the Intergovernmental Panel on Climate Change (IPCC, 2007a), climate change 'refers to a change in the state of the climate that can be identified (e.g. using statistical tests) by changes in the mean and/or the variability of its properties, and that persists for an extended period, typically decades or longer. It refers to any change in climate over time whether due to natural variability or as a result of human activity.' However, when evaluating the impacts of climate change on life it is necessary to consider atmosphere, geological factors, biogeochemical processes and several other aspects of global change. The term 'global change' is thus often used widely in the scientific community, and it can be defined as 'any consistent trend in the environment – past, present or projected – that affects a substantial part of the globe' (*Global Change Biology* journal homepage at www.wiley.com). The term includes climate change.

Evidence demonstrating the certainty of climate change comes from a range of sources including direct measurements, proxy data, ecological and evolutionary footprints, changes in sea level, and changes in the cryosphere. There is unequivocal evidence for recent global warming from such records (IPCC, 2007a; Trenberth et al., 2007). The cryosphere is shrinking, and we have witnessed widespread melting of snow, ice and glaciers and rising global sea level (IPCC, 2007a). At a global scale, we have direct thermometer readings of global air and ocean temperatures dating back about 200 years. The oldest humans alive today, have on average witnessed a global 0.7°C rise in temperature during their lifetime (100-year linear trend from 1906 to 2005 of 0.74°C – IPCC, 2007b). The linear warming trend over the 50 years from 1956 to 2005 is nearly twice that for the 100 years from 1906 to 2005 (0.13°C per decade – IPCC, 2007b). The temperature increase is greater at higher latitudes, where average Arctic temperatures have increased at almost twice the global average rate in the past century. Precipitation increases have been recorded in North and South America, northern Europe and northern central Asia, while precipitation declines have been recorded in the Sahel and Mediterranean, South Africa and parts of Asia. The frequency of extreme weather events, such as hot and cold days and heat waves, also appears to be variable. Climate change therefore shows regional and continental variation.

We must look to palaeoclimatic studies to infer prehistoric climates (Jukes et al., 2007). These studies make use of measurements of change derived from various sources including borehole temperatures, ocean sediment pore-water change and glacier extent changes, as well as proxy measurements involving the changes in chemical, physical and biological parameters that reflect past changes in the environment where the proxy grew or existed (Lowe and Walker, 1997; Stokstad, 2001; IPCC, 2007b). Some biological organisms alter their growth and/or population dynamics in response to changing climate. These climate-induced

changes are well recorded in the past growth of living and fossil specimens or assemblages of organisms such as corals or trees. Tree-ring width and tree-ring density chronologies are used to infer past temperature changes based on calibration with temporally overlapping instrumental data (IPCC, 2007a). Plant stomatal densities and size are also useful proxies of past carbon dioxide (CO₂) levels over recent (Woodward, 1987) and geological time (McElwain and Chaloner, 1995; Royer, 2001).

Palaeoclimatic studies have documented, amongst other things, contrasting periods of time that are known as 'icehouse' and 'hothouse' climatic periods (Caballero and Lynch, Chapter 2). Extreme icehouse conditions in the Neoproterozoic have been termed 'snowball earth' (Hoffman et al., 1998). Two periods of intense and long-lived icehouse glaciation periods can be defined in the Phanerozoic, the late Cenozoic (past 30 million years) and the Permian-Carboniferous (330–260 million years ago – mya), with a shorter glaciation in the late Ordovician (440 mya). The current global climate relative to these periods would be described as icehouse, and this has characterised the Quaternary (starting 1.8 mya), with the Last Glacial Maximum occurring *c.* 20 000 years ago (Lowe and Walker, 1997; Hewitt, 2000). Hothouse or warm periods in the earth's history can also be recognised (Huber et al., 2000; Huber and Sloan, 2001; Huber and Caballero, 2003; Caballero and Lynch, Chapter 2) and have, for example, occurred in the Eocene, Cretaceous and Jurassic (Eldrett et al., 2007; Zeebe et al., 2009). The Cretaceous probably witnessed the hottest temperatures of the Phanerozoic and represented the earth in an extreme greenhouse mode (140–65 mya), a period with substantial polar forests (Beerling and Woodward, 2001).

Evidence from palaeoclimatic studies therefore points to big swings in climate throughout geological time, including the Phanerozoic when 'complex' animals and plants diversified (McElwain and Punyasena, 2007; McElwain et al., Chapter 5). The 'Cambrian explosion', a period of rapid diversification of life at the beginning of the Palaeozoic, occurred during a period of markedly different climate and atmosphere than today (Royer et al., 2004). The remaining Palaeozoic was also an era of significant climate change (Caballero and Lynch, Chapter 2) during which the major radiation of land plants took place (Willis and McElwain, 2002; Palmer et al., 2004; Fig 1.1). The Cenozoic was the main era of diversification of mammals and angiosperms and has witnessed both hothouse and icehouse conditions. Much of life therefore evolved in climates very different from today or over periods of substantial climate change. We are only just beginning to unravel how such great climatic fluctuations influenced evolution.

1.1.2 Causes of climate change and interactions with life

Climate changes because the global energy budget of the earth varies over time (Caballero and Lynch, Chapter 2). The energy budget is mainly determined by

changes in solar irradiance and atmosphere and by changes in the properties of the earth's surface. Climate forcing is an imposed, natural or anthropogenic perturbation of the earth's energy balance with space (IPCC, 2007b). The overall response of global climate to forcing factors is complex, however, due to a number of positive and negative feedbacks that can have a strong influence on the climate system (Meehl et al., 2007; Trenberth et al., 2007). Coupled global circulation models used to model climate change, starting with the early attempts of Phillips (1956), attempt to provide detailed description of the dynamics and physics of the atmosphere and ocean (Caballero and Lynch, Chapter 2).

Solar irradiance, including orbital forcing (Milancovitch cycles), and greenhouse gases, especially CO₂, methane (CH₄) and nitrous oxide (N₂O), are known to be major forcing factors (Archer, 2007; Trenberth et al., 2007). Astronomical calculations demonstrate that periodic changes in characteristics of the earth's orbit around the sun, including its tilt, control the seasonal and latitudinal distribution of incoming solar radiation at the top of the atmosphere (insolation). Orbital factors have been linked closely with glaciation cycles of the Quaternary and other climate shifts in the past (EPICA, 2004; Wunsch, 2004; Caballero and Lynch, Chapter 2). Galactic solar ray flux has also been implicated in climate change (Shaviv and Veizer, 2003; Svensmark and Calder, 2007; Trenberth et al., 2007).

The role of atmospheric greenhouse gases in climate change is well accepted, with evidence from both theoretical and empirical studies. Greenhouse gases act primarily to change the atmospheric absorption of outgoing radiation and consequently influence the temperature. The scientific basis of greenhouse theory was developed in the late nineteenth and early twentieth centuries by various researchers such as Tyndall (1865), who discovered the greenhouse properties of gases and water, and Arrhenius (1908), who was the first to model the effects of changes in the concentration of atmospheric CO₂ on climate and develop the 'hot-house theory'. CO₂ has been linked to major extremes of climate in recent history (IPCC, 2007a) and the deep past (Caldeira and Kasting, 1992; Hoffman et al., 1998; Donnadieu et al., 2004; Pierrehumbert, 2004; DeConto et al., 2008). Evidence for the influence of greenhouse gases on climate comes from ancient air and other matter such as dust trapped in ancient ice. Records cover much of the Quaternary (Fig 1.2). Stable water isotopic fractions ($\delta^{18}\text{O}$ and deuterium) in snowfall are temperature-dependent and can be used to record past temperature. It is also possible to collect several other sources of data such as greenhouse gases in these cores. Deuterium excess is considered as a proxy for past ocean surface temperature at the moisture source region. The $\delta^{18}\text{O}$ record is a proxy for past air temperatures at the ice-core site. Size of ice crystals is also of value (EPICA, 2004).

Impressive data sets from ice cores have been collected in Antarctica and Greenland. An ice-core record from the Russian Vostok station in central east Antarctica reached a depth of 3623 metres, corresponding to a time

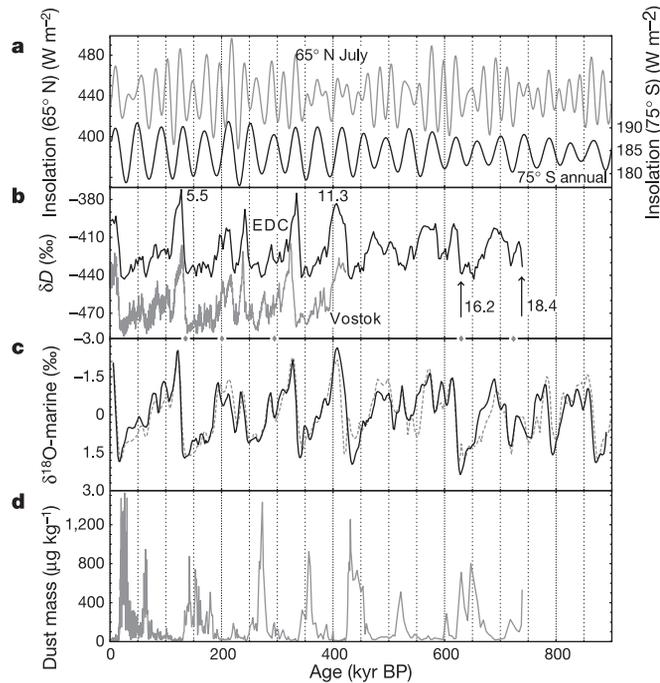


Figure 1.2 Antarctic ice-core data from EPICA Dome C and Vostok with other palaeoclimatic records. (A) Insolation records. Upper curve (left axis), mid-July insolation at 65° N; lower curve (right axis), annual mean insolation at 75° S, the latitude of the ice core at Dome C. (B) Upper curve, δD from EPICA Dome C (EDC; 3000-year averages). Lower curve, Vostok δD ; arrows indicate marine isotope stage numbers. (C) Marine oxygen isotope. The solid line is the tuned low latitude stack of site MD900963 and ODP6773. The dashed line is a stack of seven sites for the last 400 kyr but consisting only of ODP site 677 for the earlier period. (D) Dust from EPICA Dome C. Reproduced with permission from EPICA (2004).

of approximately 420 000 years before present (Fig 1.2; Petit et al., 1999). More recently, a deuterium record has been extracted from an ice core taken at Dome C in the Antarctic by the European Project for Ice Coring (EPICA, 2004). It gives a 750 000 year record including the last eight glaciations (Fig 1.2; EPICA, 2004). The Vostok cores also show a close association between greenhouse gases and climate. CO_2 and CH_4 measurements closely mirrored temperate proxy data: as temperature rose in the interglacials so too did the greenhouse gases. Ocean sediment cores show similar variation and the same glacial cycles over the Quaternary, indicated by the isotope ratios of buried microfossil shells (such as foraminifera – McManus, 2004).

Evidence for the association of greenhouse gases and Quaternary climate is strong, but a number of publications based on other palaeontological and

geochemical proxy data sets (ice cores do not exist at this timescale) indicate that the relationship between climate and atmospheric CO₂ may be less clear for pre-Quaternary time (Pagani et al., 1999, 2005; Pearson and Palmer, 2000; Veizer et al., 2000; McElwain, 2002; Royer et al., 2004). Studies of ocean sediment profiles assessing the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ record of deep-sea benthic taxa (belemnites, brachiopods, conodonts and foramanifera) during the last 80 million years (Zachos et al., 2001, 2008; Cramer et al., 2009) or during the Phanerozoic (Veizer et al., 2000; Shaviv and Veizer, 2003) have revealed the complexity of factors contributing to climate change including earth boundary conditions/tectonics, orbital factors, cosmic ray fluxes and greenhouse gases. However, the role of greenhouse gases in palaeoclimates should not be underestimated or dismissed (Royer et al., 2004).

The role of the earth's surface, its geology and biological life (the climate-biogeosphere interaction) is important in regulating climate and atmosphere. Both biophysical (e.g. albedo) and biogeochemical (e.g. weathering and carbon cycle) processes are important (Berner, 1997, 2004; Kump and Pollard, 2008). The carbon cycle and abundance of greenhouse gases are tightly coupled with biological life. CO₂ levels are controlled by geological activity such as supply from volcanoes and metamorphic degassing and removal by chemical weathering of calcium and magnesium silicate rocks (Beerling and Berner, 2005). There are several destabilising positive and stabilising negative feedbacks between life (especially plants) and greenhouse gas levels. Aquatic and terrestrial photosynthetic organisms act as major carbon sinks and regulate excess CO₂ in the atmosphere (Beerling and Woodward, 2001; Beerling and Berner 2005). CO₂ levels have also greatly influenced biological evolution and diversification, so the coevolutionary feedbacks on CO₂ and climate are complex (Beerling and Berner, 2005; Woodward and Kelly, 2008; Beerling, 2009). The history of oxygen is also complex, tightly coupled not only with biological evolution but also with the geosphere via recycling of the earth's crust (Copley, 2001; Berner, 2004; Lenton, 2004).

Climate change can occur relatively quickly and be stimulated by various tipping elements that may push the earth system past critical states into qualitatively different modes of operation and climate phases (Archer, 2007; Lenton et al., 2008). For example, changes in global ocean currents are believed to be important (Masson-Delmotte et al., 2005; Steffensen et al., 2008). The global ocean circulation responsible for large interhemispheric and interocean exchanges of mass, heat and fresh water is known as the meridional overturning circulation (MOC; also related to the thermohaline circulation). Rapid and large climate changes (2–4 °C from one year to the next) have been linked to abrupt circulation changes in the Atlantic component of the MOC (NGRIP, 2004; Steffensen et al., 2008). Such warming can also result in massive iceberg discharges known as Heinrich events (Heinrich, 1988; Broecker, 1994), and these may themselves trigger global climate

change (Broecker, 1994). Another tipping element involves critical changes in regulatory carbon sinks (Beerling and Woodward, 2001; Beerling and Berner, 2005) that may accelerate the rate of climate change (Cox et al., 2000; Cramer et al., 2001). The role of forests might decline over this century as their ability to absorb CO₂ and synthesise biomass saturates is overtaken by the release of CO₂ by respiration in a hotter, drier future climate (Cramer et al., 2001).

1.2 Adaptation, speciation and extinction

We shall best understand the probable course of natural selection by taking the case of a country undergoing some slight physical change, for instance, of climate. The proportional numbers of its inhabitants will almost immediately undergo a change, and some species will probably become extinct (Darwin, 1859).

Darwin and his influential contemporary Wallace laid the foundations for our understanding of adaptation, speciation, extinction and biogeography (Darwin and Wallace, 1858; Darwin, 1859; Wallace, 1869, 1876). The diversity of life is influenced by a complex interaction of abiotic (temperature, water, light, nutrients/poison, wind, fire), biotic (competition, herbivory, predation) and historical (plate tectonics) factors. These factors structure species and populations into forms that we recognise in several ways. They can for example be classified ecologically into biomes or niches, or taxonomically into realms or other units of species diversity (Wallace, 1876, 1880; Walther et al., 2002; Breckle, 2002; Engelbrecht et al., 2007; Cox et al., 2010).

1.2.1 Biomes and niches

At a global scale, species are adapted to their biome. Biomes are ecological species formations, usually on an intercontinental scale, defined by distinct life forms, characteristic physiognomy (stature, habitat etc.) and similar taxonomic diversity (Campbell et al., 2008). Aquatic biomes include coral reefs, oceanic pelagic and benthic zones, estuaries and intertidal zones. They are determined mainly by chemical and physical differences such as salt concentration and temperature. For example, coral reefs are sensitive to temperatures below c. 18–20 °C and above 30 °C (Campbell et al., 2008) and are therefore found primarily in the tropics. However, global zonation of aquatic biome types is not as obvious as vegetation type. This is because terrestrial biomes (Fig 1.3) are influenced primarily by climate, and especially water availability and temperature (Breckle, 2002). Vegetation biomes therefore show latitudinal zones, because there are latitudinal patterns to climate (Breckle, 2002). Biome zones have also shifted through geological time with fluctuating climate and global positioning of the continental plates (Fig 1.4; Ziegler et al., 2003).

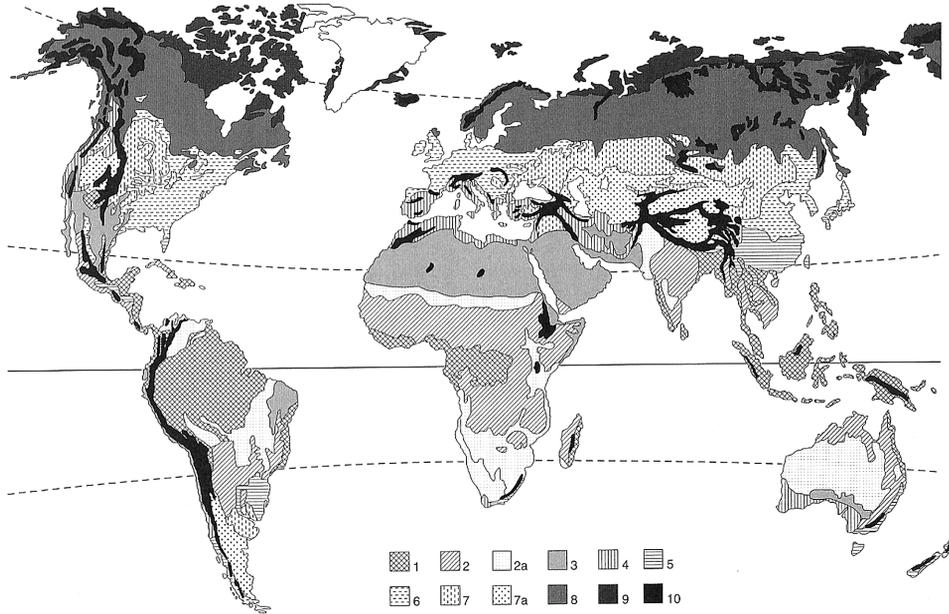


Figure 1.3 Major biomes of the world. Map shows simplified vegetation zones. 1, evergreen rainforests; 2, semi-evergreen and wet season green forests; 2a, savannas, grasslands, dry woodlands; 3, hot deserts and semi-deserts; 4, sclerophyllic woodlands and winter rain; 5, moist warm temperate woodlands; 6, deciduous forests; 7, steppes; 7a, semi-deserts and deserts with cold winters; 8, boreal coniferous zone; 9, tundras, 10, mountains. Reproduced with permission from Breckle (2002).

At a finer geographical scale, organisms are adapted to their ecological niche. The niche is often more informative than the biome for ecological study of individual species, because organisms do not respond to the approximated global averages that are used to define biomes (Walther et al., 2002). Regional changes that are highly spatially heterogeneous are thus of critical importance. Furthermore, biotic as well as abiotic factors determine the ecological niche of an organism (Grinnell, 1917). Because of this, Hutchinson (1957, 1978) made the distinction between the fundamental and realised niche (Rödder et al., Chapter 11). The fundamental niche is defined by the abiotic conditions in which a species is able to persist, whereas the realised niche describes the conditions in which a species persists given the presence of other species.

Some groups of organisms have evolved to occupy highly different ecological niches. In other groups ecological niches have remained more or less conserved. The tendency of species to retain ancestral ecological characteristics is known as 'niche conservatism' (Peterson et al., 1999; Wiens and Graham, 2005). This can be contrasted with 'niche lability', which describes the tendency of species to change their ancestral ecological niche characteristics (Hardy, 2006; Pearman et al.,

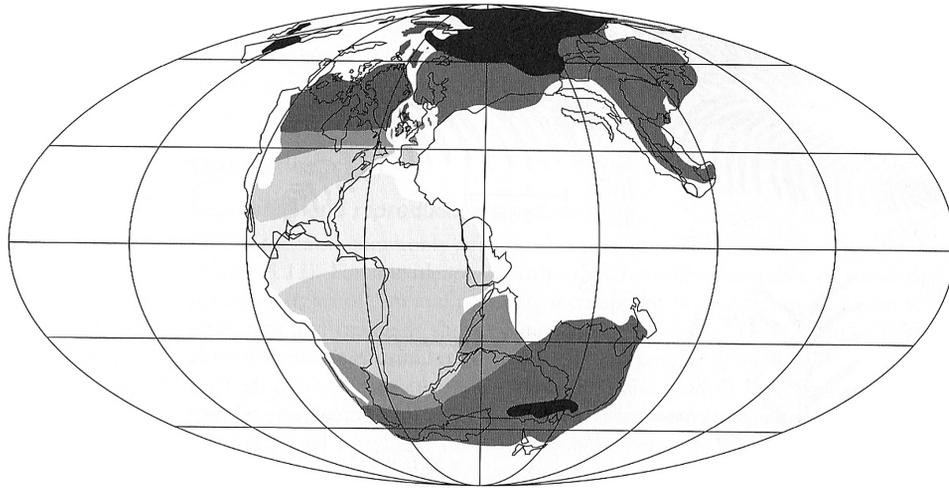


Figure 1.4 Geological distribution of the continents in the early Jurassic, with global vegetation biomes. White, tropical summerwet; light grey, subtropical desert; grey, winterwet; dark grey, warm temperate; black, cool temperate. Reproduced with permission from Willis and McElwain (2002).

2007). Examples of niche conservation in relation to climate include Tethyan laurels (Rodríguez-Sánchez and Arroyo, Chapter 13), *Cyclamen* (Yesson and Culham, Chapter 12), amphibians (Rödger et al., Chapter 11), and grasses (Bouchenak-Khelladi and Hodkinson, Chapter 7).

1.2.2 Realms and species diversity

It has been long known that species diversity and taxonomic groupings are non-randomly distributed across the globe and, as a consequence, taxonomic realms have been described (Wallace, 1876; Schmidt, 1954; Wnuk, 1996). Realms are areas with distinct suites of taxa, each area including a significant proportion of endemic families. Realms are strongly influenced by geographic and tectonic history, climate and dispersal ability of species. The major floristic realms broadly match the major faunal zones (Fig 1.5). The breakup of Pangea during the past 200 million years (Mesozoic and Cenozoic - Fig 1.4) resulted in the isolation of continents and has left an evolutionary/taxonomic footprint. The unique terrestrial faunas and floras of South America and Australia exist because these continents have been islands for much of the last 100 million years and because many species have limited dispersal ability. There are large differences between the tropical floras and faunas of the Old and New World. These have been termed the Palaeotropics and Neotropics, respectively (Fig 1.5). Thus although suitable climate exists for many species in different areas of the world, they may not occupy those areas because

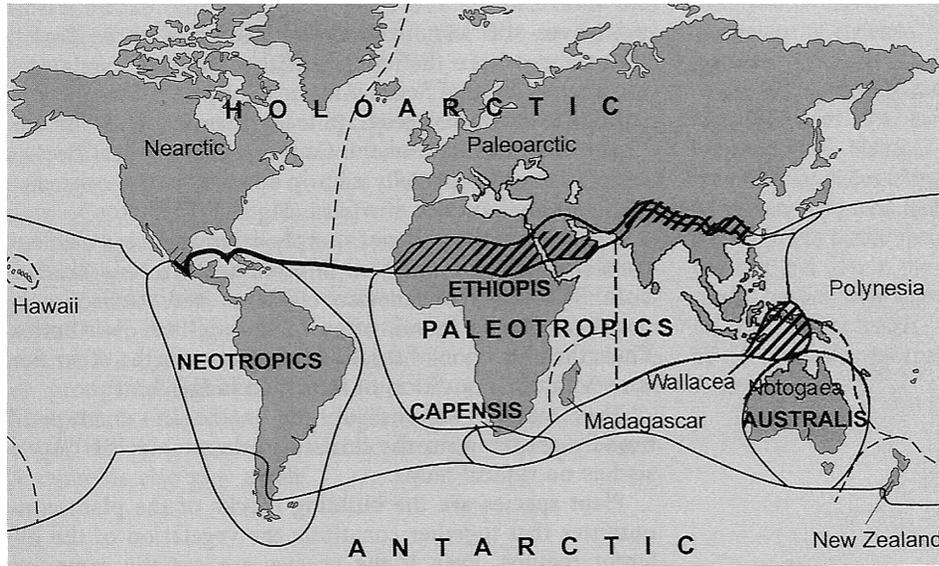


Figure 1.5 Floristic and faunal realms of the world: floristic realms shown in uppercase letters, faunal realms in lowercase. Reproduced with permission from Breckle (2002).

they are restricted by dispersal ability. Where there has been more opportunity for dispersal, larger latitudinal realms prevail. For example, Greenland and North America separated from Eurasia relatively recently, and hence floristic differences between them are smaller than between the tropical continents. Therefore, the Holarctic is often considered as a realm instead of the Nearctic and Palearctic that are recognised for fauna (Fig 1.5; Schmidt, 1954). Clear patterns can also be seen between hemispheres, such as amongst gymnosperm families. Taxodiaceae and Pinaceae have a largely northern hemisphere distribution, and many Podocarpaceae such as *Araucaria* have a largely southern hemisphere distribution (Breckle, 2002).

The geographical distribution of species diversity is also closely linked to climate and latitude (Jablonski et al., 2006). The tropics have much higher species diversity than other areas (Woodward and Kelly, 2008). There are two major explanations for the latitudinal patterns in species diversity, known as the 'time area hypothesis' and 'diversification rate hypothesis' (Willig et al., 2003; Benton, 2009). In the former, time and area interact to influence diversification. For example, the tropical clades have had longer to speciate and have done so in a larger geographical area because the tropical belt is larger and older than comparatively large belts elsewhere. In the diversification rate hypothesis, it is assumed that there are higher rates of speciation and lower rates of extinction in the tropics than elsewhere. Studies have also shown a positive correlation between primary

productivity and species diversity (Woodward and Kelly, 2008). Primary productivity shows a climatic and latitudinal pattern, being higher in the tropics than in temperate regions. Biodiversity hotspots have recently received much attention (Myers et al., 2000; Crawford, 2008), and climate seems to be critical to their existence. In some cases, such as the South African fynbos and the southwestern Australia hotspot, they have remained relatively climatically stable for long periods of time, allowing the accumulation of high biodiversity. Given the evidence for the diversification rate hypothesis, we would also expect rates of speciation to vary with time, because climate has changed over time. The fossil record should, therefore, be able to offer clues to the interaction of diversity and climate (Mayhew, Chapter 4; McElwain et al., Chapter 5).

The fossil record shows several periods of global extinction and origination of higher taxonomic groups at rates and magnitudes greatly exceeding background levels (Alroy et al., 2008; Mayhew et al., 2008). There have been major cycles in fossil diversity (Rohde and Muller, 2005; Mayhew, Chapter 4; McElwain et al., Chapter 5). The 'big five' recorded megaextinctions, based largely on marine records, include the end-Ordovician (446 mya), the Frasnian-Famennian (late Devonian – 371 mya), the Permian-Triassic (251 mya), the Triassic-Jurassic (200 mya) and the Cretaceous-Palaeogene (65 mya) (Raup and Sepkoski, 1982; Sheehan, 2001; Sepkoski, 2002; Benton and Twitchett, 2003). Although there is no clear consensus on the precipitating causes of such extinctions, there is evidence they may have been forced by abiotic change including meteorites, volcanism, euxinia and greenhouse gases (Peters and Foote, 2002; Benton, 2003; Benton and Twitchett, 2003; Wignall, 2005; Meyer and Kump, 2008; Peters, 2008). Large-scale extinctions of plants, for example, were all characterised by large excursions in stable carbon isotopic composition, indicating major disturbance of the global carbon cycle between atmosphere, biosphere and rock reservoirs (McElwain et al., 1999; McElwain and Punyasena, 2007; van de Schootbrugge et al., 2009; McElwain et al., Chapter 5). See Mayhew (Chapter 4) for a perspective on fauna. Global-scale analyses demonstrate that extinction rates are generally elevated during hothouse phases and biodiversity is depressed. There is also evidence for delayed biological recovery in terms of diversity origination rates after extinctions (Kirchner and Weil, 1990; Cornette et al., 2002; Alroy, 2008).

To understand the cycles of diversity over time it is useful to again consider abiotic (Court Jester model – Barnosky, 2001) and biotic factors (Red Queen model – van Valen, 1973) and a mixture of the two (Mayhew, Chapter 4). They operate over different geographical and temporal scales. For example, biotic factors involved in the Red Queen model, such as competition, herbivory and predation, occur over short time spans and are relatively predictable. Abiotic factors involved in the Court Jester model operate over thousands and millions of years (Benton, 2009), as they involve climate and tectonic events that shape larger-scale patterns

regionally and globally, and are less predictable. Mayhew (Chapter 4) argues that the fossil evidence suggests that abiotic factors such as climate are a major influence on biodiversity through time, but relatively predictably so (unlike the paradigm of the Court Jester). To accommodate this he suggests a third paradigm, the Ace of Spades, where there is abiotic but predictable extinction.

1.2.3 Phylogeny and key innovations

Phylogenetic approaches are becoming increasingly useful for the study of biological diversification and its link with climate change (Donoghue, 2005, 2008; Edwards et al., 2007). The tree of life is not balanced, and some groups are much more species-rich than others (Hodkinson and Parnell, 2007). For example, the largest five orders of insects, representing just 6% of all insect orders, contain 83% of their species. One order, Coleoptera, contains a staggering *c.* 350 000 species (which is 35% of all insect species). The same can be seen in the flowering plants, where five families, representing just 1% of all angiosperm families, contain 32% of its species (Hodkinson and Parnell, 2007). Some groups of organisms have therefore been winners and others losers in terms of the evolution of high numbers of species. Many lineages have gone extinct (Hodkinson and Parnell, 2007). It is a challenge to discover the biological attributes of these groups and their key innovations that have enabled them to become so successful. Phylogenetic approaches can highlight shifts in diversification of clades and date when they occurred (Hodkinson et al., 2007; Bouchenak-Khelladi and Hodkinson, Chapter 7). Sister clade comparisons can also be used for assessing the significance of contrasting biological traits on the success of those clades (Purvis, 1996).

Several key innovations, facilitating extensive species diversification, have been linked to climate change. In plants, these innovations need to be interpreted with care (Donoghue, 2005), but nevertheless they include the initial evolution of their leaves (Beerling et al., 2001), their photosynthetic abilities under climatic stress (Bouchenak-Khelladi and Hodkinson, Chapter 7) and their wood anatomy (Baas and Wheeler, Chapter 6). These innovations have, in turn, accelerated the diversification of animals such as insects (Kenrick and Crane, 1997) and mammals (Bouchenak-Khelladi et al., 2009).

The evolution of leaves is closely linked to climatic and atmospheric change (Beerling, 2005). Leaves have evolved at least twice (microphylls in lycophytes and megaphylls in ferns, gymnosperms and angiosperms). Megaphylls originated from the developmental modification of lateral branches, and this innovation greatly increased the ability of the terrestrial vegetation to fix CO₂ at a global scale (Beerling, 2005). Megaphylls became widespread at the close of the Devonian (360 mya) but their rise seems tightly linked to climate and CO₂. They began to dominate during the late Palaeozoic, which witnessed a 90% drop in CO₂ (Berner, 2004). This corresponded with a rise in stomatal density. Increased stomatal density allowed

the evolution of larger leaves by permitting greater evaporative cooling and alleviating the requirement for convective heat loss. The large leaves gradually appeared as CO₂ levels declined and stomatal numbers rose to increase evaporative cooling and ease the thermal burden of observed solar energy (Beerling et al., 2001).

Leaves are held above the ground to capture light, sometimes higher than 100 metres in the tallest trees such as the coastal redwoods of California (Pakenham, 2003), but increased height produces a hydraulic problem, as they need to transport water to their leaves against gravity (Baas and Wheeler, Chapter 6). Dixon and Joly (1895) proposed a solution to this problem: they recognised the chemical properties of water (the cohesion–tension theory), and that transpiration (evaporation at the leaf) allows water to travel up the water-conducting elements (xylem tracheids and vessels) to the leaf. Wood clearly provides the support needed for a tree to reach the required height to compete with other trees for light. There is growing evidence that xylem evolution has been driven by functional adaptations to climate change (Baas and Wheeler, Chapter 6). Climate change has contributed to multiple parallelisms and reversals in vessel, fibre, parenchyma and ray modifications. For example, scalariform perforations add to the flow resistance in vessels, putting selective pressure on their elimination in environments demanding high conductive efficiency such as lowland tropics or drought-stressed environments, but can be of high value in trapping gas bubbles in thawing xylem sap at frost-prone latitudes and altitudes (Baas and Wheeler, Chapter 6).

There is also strong evidence that the evolution of photosynthesis and its variants such as C₃ and C₄ metabolism are linked to climate change. C₄ photosynthesis is found in several taxonomic groups but is particularly common in the grass family Poaceae (Bouchenak-Khelladi et al., 2008, 2009; Bouchenak-Khelladi and Hodkinson, Chapter 7) and the sedge family Cyperaceae (Besnard et al., 2009; Simpson et al., Chapter 19). Temperature and precipitation largely determine the geographical distribution of the predominantly tropical C₄ and predominantly temperate C₃ grasses (Poorter and Navas, 2003; Sage, 2004). There is good evidence from dated phylogenetic trees and fossils to show that C₄ photosynthesis in grasses first evolved in the hot conditions of the Eocene (at *c.* 30 mya) during periods of declining CO₂, and that it has done so independently on approximately 20–30 occasions depending on the analysis performed (Christin et al., 2008; Bouchenak-Khelladi et al., 2009). Although there is an association of C₄ evolution with declining CO₂, and good physiological evidence to show C₄ plants are more efficient under hot dry conditions with limited CO₂ than their C₃ counterparts (the CO₂ starvation hypothesis), we must be careful not to confuse correlation with cause (Roalson, 2008). Grasses did not rise to dominance until the Miocene, and not earlier than 10 million years ago. It is clear that a whole system of factors has contributed to their success, including climatic and atmospheric tolerance, fire resistance, competitive ability and nutrient efficiency. The evolution of C₄ photosynthesis undoubtedly

facilitated the expansion of tropical grasslands and savannas (Edwards and Still, 2008; Osborne and Freckleton, 2009; Bouchenak-Khelladi et al., 2010; Bouchenak-Khelladi and Hodkinson, Chapter 7). In these ecosystems, grasses were coevolving with ungulate herbivores, and some evidence points to an evolutionary arms race between the two (Bouchenak-Khelladi et al., 2009; Bouchenak-Khelladi and Hodkinson, Chapter 7).

1.2.4 Adaptation

Species have limits to their distribution and possess populations that occupy marginal habitats. These populations demarcate an endpoint in adaptation to a changing environment (Crawford, 2008). The margins of a species can sometimes be abrupt and easily visible, such as the interface between one vegetation type and another (e.g. *Nothofagus* forest in the Andes). However, they can also be diffuse, such as the interface (ecotones) between southern limits of the boreal forest and northern limits of the deciduous broadleaved forest (Crawford, 2008). When the limits of distribution are reached, populations need to either adapt or migrate. Different species will respond in different ways, and in practice there is an interaction between adaptation, migration and plasticity in response to climate change (Bradshaw, 1965; Davis and Shaw, 2001). Evidence of widespread niche conservatism would indicate that there might be more potential to migrate than to evolve to cope with short- or long-term climatic change. Forest trees provide a good example of this interaction and are therefore discussed in some detail below.

As trees tracked the shifting climate during the Holocene, evidence suggests that it was easier for species to disperse seed and establish in new environments than to evolve a new range of climatic preferences. Such niche conservatism is common in other groups of organism (Wiens and Graham, 2005). However, this does not mean that the populations are undifferentiated. Migration is not an alternative to adaptation.

Widespread temperate and boreal trees that shifted latitudes during the Holocene display much genetic variability in their nuclear DNA, but little geographical differentiation (Davis and Shaw, 2001). This indicates a high degree of gene flow among populations. Much of this occurs through pollen, as the species are generally wind-pollinated outbreeders. Chloroplast DNA (cpDNA) markers (maternally inherited and useful for tracking seed dispersal) show greater differentiation. For example, Petit et al. (2002), in a wide-ranging European-scale study of neutral oak cpDNA haplotypes, showed that populations are genetically differentiated in geographical space. The haplotypes also reflect the postglacial history when populations migrated from glacial refugia. One lineage expanded from an Iberian refugium throughout northwest Europe in an oceanic distribution (Kelleher et al., 2004) while others are continental, expanding from other refugia such as in Italy or the Balkans. Some forest trees in the northern hemisphere

show a decline in genetic variability from south to north due to several factors including stochastic loss through repeated founder effects (Davis and Shaw, 2001). These postglacial migration and diversity patterns can also be seen with animal populations such as brown bears in Europe (Hewitt, 2000; Lowe et al., 2004).

Even though diversity analyses can indicate the potential for evolution, studies of adaptation or studies on the adaptive genes themselves are required to directly study adaptive variation. Common garden experiments (provenance trials) have long been used in forest research to help growers select populations with particular growth traits. These provenance trials have also offered a powerful tool for studying climate tolerance and response. The studies have demonstrated that modern populations that have shifted ranges in the past are adapted to the climatic conditions where they now grow (Davis and Shaw, 2001; Jump et al., 2009). For example, Scots pine (*Pinus sylvestris* L.) migrated across central Europe from the south as temperatures warmed about 15 000 years ago. Transplant trials throughout northern Sweden showed striking differentiation with respect to survival (Eriksson et al., 1980). At each site, mortality was higher for trees transplanted there from lower latitudes than for trees native to the site.

Selection and gene flow are important processes in range shifts (Excoffier et al., 2009). Natural selection will sieve out genotypes less suited to local conditions. For northward range shifts (in the northern hemisphere), the arrival of seed (e.g. from southern populations) may contribute to adaptation, and selection will also promote new genetic combinations. Studies are teasing apart the population dynamics and genetics of advancing and retracting ranges (Pauli et al., 2006; Sexton et al., 2009). For example, populations at the leading edge of the migrating front may be enhanced by gene transfer from the middle of the range. In contrast, populations at the trailing edge of the range receive less pollen from better adapted populations (Davis and Shaw, 2001; Excoffier et al., 2009). Adaptation at the trailing edge of a species' range depends largely on variation in the local population and may be slower than at the advancing edge (Davis and Shaw, 2001).

Range shifts also offer new conditions for hybridisation (Rieseberg and Carney, 1998; Rieseberg et al., 2003; Soltis and Soltis, 2009). Major ecological transitions can be facilitated by hybridisation. In the tree genus *Fraxinus*, for example, hybrid zones occur in various parts of Europe and facilitate gene flow between otherwise largely climatically separated species. Ecological niche modelling has shown that climate change will cause a change in the potential size and distribution of hybrid-zone populations and their parental species (Thomasset et al., Chapter 15). Similar studies on the influence of climate on the fate of hybridising species have been undertaken on hybrid zones between eastern and western species of north American birds (Swenson, 2006). The hybrid zones are geographically clustered and associated with the sharp temperature gradient of the Great Plains to the Rocky Mountain ecotone. The range borders of the parental species are thus

maintained by strong selection against the hybrids; the distinction of the parental species is therefore likely to be maintained.

Recently, phylochronological studies using ancient DNA have been used to study the genetic response of species to climate change (Hadly et al., 2004). Advances in sequencing, especially emulsion-based clonal amplification, assist in producing sequence information from small fragments of DNA that it is possible to retrieve from fossil material of differing ages (Ramakrishnan and Hadly, 2009). This approach allows us to link population genetics and evolution, changes in phenotypic traits, the genes that govern them and changes in the environment. This is made possible by serially taking DNA genotype data from fossils. Serially sampled genetic data permit the chronologic testing of the reconstructed population. Using this phylochronological approach, Hadly et al. (2004) investigated the effect of changing population size of the montane vole and northern pocket gopher during times of climatic change (including the little ice age and the medieval warm period) in mountain habitats of western North America. Their studies could track gene diversity during that time and showed that the two species responded differently to climate change; their response was linked to life-history strategy and gene flow.

Organisms may deal with a variable environment by evolving the capacity for phenotypic plasticity. Plasticity is the ability of an organism to change its phenotype in response to environmental change. It is, in itself, an adaptive trait (Bradshaw, 1965). Phenotypic plasticity can be seen in the phenology of plants and animals. Phenology refers to the timing of recurring lifecycle events (Donnelly et al., Chapter 8). Climate change has caused several phenological changes in a wide range of organisms (Hall et al., 2007). Warmer spring temperatures in recent years have influenced bud burst in trees (Fitter and Fitter, 2002; Cleland et al., 2007), appearance and abundance of insects and migration of birds (Cotton, 2003; Menzel et al., 2006; Huntley et al., Chapter 16). Phenotrends have also been observed in marine pelagic environments (Edwards and Richardson, 2004). Some of these changes can be attributed to phenotypic plasticity. For example, bud burst in trees has changed in response to climate change within the same individual trees (Donnelly et al., Chapter 8). Furthermore, long-term genetic studies of American red squirrels in the Arctic indicated that a high proportion (62%) of the change in breeding dates occurring over a 10 year period was the result of phenotypic plasticity and 13% due to population genetic change (Berteaux et al., 2004). However, sometimes changes in phenology require adaptation. Donnelly et al. (Chapter 8) discuss the relationship between adaptation and plasticity for phenological traits in plants, butterflies and birds.

Studies of genes involved in adaptation are required for the study of adaptation at a molecular level. Some attempts have been made with neutral markers (Jump and Peñuelas, 2005; Jump et al., 2006, 2008) or candidate genes of adaptive

traits (Neale and Ingvarsson, 2008). Genes controlling complex adaptive traits are usually discovered via approaches such as quantitative trait loci or association mapping (Neale and Savolainen, 2004). Once discovered, it is possible, via resequencing of different populations, to assess variation in these target genes and test the presence of selection using modern population genetic approaches (mutation rates and departures from neutrality to indicate they might be under some form of natural selection). For example, roughly 20% of the *c.* 300 forest tree genes that have been tested showed departure from neutrality (but demographic processes may also account for such a departure – Neale and Ingvarsson, 2008). Genes for biotic (e.g. disease resistance) and abiotic (water-use efficiency, cold tolerance, bud set) have been investigated (Neale and Ingvarsson, 2008; Donnelly et al., Chapter 8).

One of the earliest studies on genotypic and phenotypic variation in forest trees using the candidate gene approach was by Ingvarsson et al. (2006). They studied a phytochrome gene (*phyB2*) involved in dormancy induced by shortening of the photoperiod (short day induced bud set) in *Populus*. A resequencing study in European aspen (*P. tremula* L.) found several DNA sequence variants (single nucleotide polymorphisms, SNPs) that showed significant clinal variation with latitude (Donnelly et al., Chapter 8). Hall et al. (2007) also report adaptive population differentiation across a latitudinal gradient in aspen. Other species and candidate genes have been investigated in the study of genes of ecological and adaptive significance, including bud burst genes in oak (Derory et al., 2010), drought stress genes in pine (Eveno et al., 2008) and stem cold hardiness and wood formation genes in Douglas-fir (Krutovsky and Neale, 2005). Studies on other organisms such as corals and algae are also finding evidence for genetic adaptation of populations to climate change (Parmesan, 2006; Bradshaw and Holzapfel, 2006). Rindi (Chapter 9) discusses adaptation in terrestrial algae in response to climate change and outlines evidence of genetic adaptation at the molecular level. These studies are therefore confirming the conclusions of common garden experiments that suggest strong adaptive differentiation within species. They are also identifying the specific genes involved in those traits, and characterising their variation.

1.3 Biogeography, migration and ecological niche modeling

It is notorious that each species is adapted to the climate of its own home: species from an arctic or even from a temperate region cannot endure a tropical climate, or conversely (Darwin, 1859).

It is essential to know how the geographic distribution of species has been affected by climate change and how it will be influenced in the future. Range

shifts often entail niche shifts (Parmesan and Yohe, 2003; Wiens and Graham, 2005). Palaeoecological studies on the glacial history of habitat types, especially in Europe and North America (Lowe and Walker, 1997), have produced thousands of pollen and macrofossil diagrams compiled in databases. These have provided records of species' abundances as they changed through space and time (at regional and continental scales) and at high taxonomic detail. These records of species distribution therefore provide a palaeoecological way of tracking how species have migrated in response to climate change and how their population sizes have varied. This evidence has been supported by recent DNA studies of extant and ancient samples (Hewitt, 2000; Petit et al., 2002).

Range shifts associated with recent climate change are clearly seen with altitude. Empirical studies have shown how changing temperatures can drive upward or downward range shifts of species in mountains. Lowland birds have started breeding in montane cloud forest in Costa Rica (Pounds et al., 1999). The range of Edith's checkerspot butterfly has shifted upward by 105 m in Mexico and North America (Parmesan, 2006). Similarly, the lower altitudinal limits of 16 Spanish butterfly species have increased by an average of 212 m in 30 years (concurrent with a 1.3°C rise in temperature – Wilson et al., 2005). Several shifts have been recorded for the elevation of mountain tree lines (Parmesan and Yohe, 2003; Crawford, 2008; Jump et al., 2009).

Species in mountain regions are typically restricted to relatively narrow altitudinal bands, and change in their distribution is easy to observe (Crawford, 2008). In contrast, latitudinal range shifts are less easy to document because of the geographical scale involved (Jump et al., 2009). For recent global change, there is less evidence for range shifts with latitude than with altitude. There is approximately a 1°C change in temperature with a 167 m change in altitude (5–6.5°C per 1000 m) or a 145 km change in latitude (6.9°C per 1000 km at 45° N). Thus stratification of ecosystems can be much more readily seen in mountain regions than across latitudes (Jump et al., 2009). Recent changes in plant distribution in mountains have been reported for a range of species (tropical epiphytes, alpine plants and forest species), and mountain tree lines have shifted upwards (forwards) by up to 130 m over the past 50 years (Jump et al., 2009). The shift seems to be biased to the leading edge, but some studies also show similar-magnitude retractions of the trailing edge (due to elevated mortality and reproductive decline – Jump et al., 2009).

Given the strong evidence of range shifts in mountains, we can predict what should occur over latitude (Jump et al., 2009). We would expect latitudinal shifts of tens to hundreds of kilometres (based on the altitude-to-latitude model). Reports of latitudinal range shifts are rare, because of lack of research and methodological issues, but some reports have been made in several groups of organisms. For example, in plants, there has been an expansion of forest over the Alaskan tundra over the last 50 years (and increase in the latitudinal position and density of

trees and shrubs such as white spruce and green alder. For butterflies, Parmesan et al. (1999) found that nearly two-thirds of 35 non-migratory European species had shifted their ranges north by 35–240 km and only two species had shifted south. In the most extreme cases, such as the sooty copper, the southern edge contracted concurrent with the northern-edge expansion. For birds, a mean northward shift of *c.* 20 km over a 20-year period has been recorded in UK populations (Thomas and Lennon, 1999). For lichens, 77 new epiphytic lichens colonised the Netherlands from the south between 1979 and 2001 (van Herk et al., 2002; Ellis and Yahr, Chapter 20). Finally, for mammals, red fox expansion of range has been recorded, with a simultaneous retreat of arctic fox range (Hersteinsson and MacDonald, 1992).

At lower latitudes, shifts are associated with movements of tropical species into more temperate areas (Parmesan, 2006). North African species are moving into Spain and France, and Mediterranean species are moving up into the continental interior. For example, large populations of the African plain tiger butterfly have established in Spain (Haeger, 1999). In the Americas, the rufous hummingbird has shown a large shift in its winter range, expanding from Mexico into southern USA (Parmesan, 2006). Over this time winter temperatures rose by approximately 1 °C.

1.3.1 Ecological niche and distribution modelling

It is possible to use modelling approaches to understand the distribution of species and their ecological niches in relation to climate change, and to make inferences about past distributions (hindcasting) and future distributions (forecasting). These approaches use a variety of statistical methods to model species' geographic distributions and their ecological niches in relation to climatic and topographic variables. They are variously known as climate envelope models, climatic niche models, species distribution models, ecological niche models, or statistical niche models (Peterson, 2006; Wake et al., 2009; Rödder et al., Chapter 11). Niche modelling applies powerful computational tools to species' locality data assembled through fieldwork and specimens in herbaria and museum collections. The modelling approach involves (1) georeferenced localities for the study species (collection localities and their latitude/longitude coordinates); (2) climatic variable data (e.g. temperature and precipitation variables) at the collection sites and surrounding areas; and (3) algorithms for estimating the climatic niche envelope of those species, based on the distribution of climatic variables where they occur and do not occur within a region (Wiens and Graham, 2005; Rödder et al., Chapter 11).

A range of modelling resources are available (Soberón and Peterson, 2004; Culham and Yesson, Chapter 10; Rödder et al., Chapter 11). Georeferenced localities are available on the internet. The Global Biodiversity Information Facility provides such records for free (www.gbif.org). Fine-scale climatic data sets such as WorldClim are also freely available, based on information from a large number

of weather stations and statistical and modelling extrapolations to locations without weather stations (Beaumont et al., 2005; Hijmans and Graham, 2006). There is also a diverse range of methods to construct ecological niche models and model species distributions, including environmental envelopes, ordination approaches, generalised regression models, genetic algorithms and Bayesian methods (Guisan and Thuiller, 2005; Araújo and Guisan, 2006; Elith et al., 2006; Heikkinen et al., 2006; Peterson, 2006; Phillips et al., 2006; Elith and Leathwick, 2009). In general the statistical model establishes a relationship between point locality data and environmental layers that describe the variation in a climatic variable over space (Peterson, 2006).

The model is then used to create a map of predicted species distribution, given these environmental variables (Wiens and Graham, 2005). When this map of predicted range is overlaid on the actual species distribution map it is possible to see how well the climatic variables predict the species' range limits. Matching distributions support the hypothesis that the specialised climatic tolerances of a species may limit its geographical spread. If a range is overpredicted, the climate variables indicate that the species should have a wider distribution than its distribution data suggest. Overprediction may indicate that climate is not the primary factor that limits the species' geographical distribution (Wiens and Graham, 2005).

It is also possible with different approaches to determine which climatic variables are the most important for limiting geographical distribution of the species (Wiens and Graham, 2005). These data can be used in various ways, such as in conservation biology. They are commonly used for forecasting and hindcasting (Pearman et al., 2008). Several studies have incorporated distribution models and geographical information systems (GIS) in phylogenetic studies, an approach known as phyloclimatic modelling (Kozak et al., 2008; Culham and Yesson, Chapter 10).

1.3.2 Phyloclimatic modelling

Evolutionary processes, such as speciation and genetic divergence of populations, are heavily influenced by environmental variables. Therefore, phyloclimatic modelling approaches can help establish the ecological causes of evolutionary processes. A growing number of evolutionary and systematic studies are making use of climate envelope models and the extensive data sets available in geographical information systems (Kozak et al., 2008; Rödder et al., Chapter 11). This is an improvement over previous studies that would have used only a limited set of environmental variables because of lack of data availability. For example, phylogeographic studies often only considered geographic distance to explain their results and did not analyse complex environmental data. GIS-based data tools are now making it relatively simple to include such information in evolutionary research (Kozak et al., 2008; Culham and Yesson, Chapter 10). Applications are

numerous and include speciation (Graham et al., 2004b; Rödder et al., Chapter 11), phylogeography (Yesson and Culham, Chapter 12) and character evolution (Kozak et al., 2008).

Rödder et al. (Chapter 11) use climatic envelope models to delimit the potential palaeodistribution (sympatry and allopatry) of taxa belong to the Afrotropical reed frog genus *Hyperolius*, and hence use these distribution data to help interpret speciation and species delimitation in the group. In another approach of phyloclimatic modelling, the limiting climatic variables obtained from ecological niche modelling can be assessed phylogenetically (e.g. mapped onto a phylogenetic tree or compared to genetic distances) to see how they change during the evolutionary history of the group (Graham et al., 2004a, 2004b; Davis, 2005; Yesson and Culham, 2006a, 2006b; Edwards et al., 2007; Kozak et al., 2008; Jakob et al., 2009). This will determine if they are conserved over the evolutionary history of the group or if they are labile. Examples include Yesson and Culham (Chapter 12) for *Cyclamen* evolution and Chatrou et al. (Chapter 14) for the study of the impact of climate change on the origin and future of East African rainforest trees. Chatrou et al. (Chapter 14) use a phyloclimatic approach to identify the environmental variables associated with the origin of East African endemics of the genus *Monodora*. Yesson and Culham (Chapter 12) review phyloclimatic work undertaken on the Mediterranean *Cyclamen* protected by CITES legislation and provide new results on the palaeogeography and palaeoclimate of the genus.

Many of the phyloclimatic approaches use GIS data sets and tools (e.g. DIVA GIS) to obtain environmental data for each locality and then analyse these statistically. They can test for correlations between environmental variables and spatial patterns of phenotypic divergence. Ruegg et al. (2006) used GIS to study the relationship between genetic differentiation and climatic differentiation on song evolution in Swainson's thrush. They quantified temperature and precipitation across the species' range and found that the acoustic divergence of the populations was not correlated with genetic distance but was correlated with geographical distances in climate. Climate was shown to be an indirect cause because song was closely related to the acoustic differences in climatically determined forest type (rainforest versus coniferous). It is clear that there is great potential to use GIS approaches to help establish an evolutionary framework to estimate how species respond to climate change.

1.4 Conservation

There can be no purpose more enspiriting than to begin the age of restoration, reweaving the wondrous diversity of life that still surrounds us (Wilson, 1992).

1.4.1 Impacts

Despite uncertainty in climate predictions there is compelling evidence for rapid recent human-driven climate change (Ruddiman, 2003; Juckes et al., 2007; Meehl et al., 2007). Even if the cause is not anthropogenic, there is serious reason to be concerned about the impacts of climate change, because of escalating global population growth and habitat loss and fragmentation. Several studies have reported the impacts of climate change on individual species and habitats. Declining populations have already been recorded in several groups of organisms including amphibians (McMenamin et al., 2008), birds (Both et al., 2006; Møller et al., 2008), mammals (Moritz et al., 2008) and several other groups (Parmesan and Yohe, 2003; Parmesan, 2006). Climate change can also influence species' interactions by, for example, introducing potentially invasive species (Vila et al., 2000; Broennimann et al., 2007; Broennimann and Guisan, 2008; Rödder and Lötters, 2009; Thomasset et al., Chapter 15; Simpson et al., Chapter 19), and can influence interactions with pests and diseases (Parmesan, 2006). However, meta-analyses have been necessary to show broad-scale patterns of the impacts of recent climate change on populations and ecosystems. These studies have shown a 'coherent fingerprint' of climate on life (Parmesan and Yohe, 2003). In their meta-analyses of 1700 species, Parmesan and Yohe (2003) defined a diagnostic biological fingerprint of temporal and spatial 'sign switching' responses uniquely predicted by climate trends of the last century. Meta-analyses therefore confirmed predictions based on individual species or habitats.

1.4.2 Prediction

Predicting the response of organisms to future climates is a serious challenge to conservationists and ecologists (Pearson and Dawson, 2003; Parmesan, 2006; Sutherland, 2006; Huntley, 2007a). There is a requirement to forecast many things including range shifts, extinction risks, population sizes, biome shifts, disturbance regimes and biogeochemical weathering (Williams et al., 2007). There is also a pressing need to be able to do this at local as well as international scales (Walther et al., 2002). Progress with climate-change predictions at regional and local levels is discussed by Meehl et al. (2007) and Caballero and Lynch (Chapter 2).

The risk of population decline and extinction is not even across taxonomic groups or across geographical space. Species' responses to climate change are likely to depend on interactions between population processes, between species, and between demographic and landscape dynamics (Keith et al., 2008). Dispersal ability and habitat preference of species are crucial. Studies predict that risks of extinctions are particularly high in mountainous regions, high-latitude areas and in areas with high endemism (IUCN, 2001; Hannah et al., 2008). Species become increasingly threatened with extinction as suitable habitat becomes reduced and

new areas remain unreachable due to natural and anthropogenic barriers to dispersal (Hannah et al., 2007). Conservation strategies need to consider the results of such studies (Hannah et al., 2008). Hodd and Sheehy Skeffington (Chapter 21) discuss the threat of climate change to mountain plant communities. They provide a case study of mountain bryophyte species that occur in scarce communities of hyperoceanic montane heath in Ireland. These communities are clearly vulnerable to climate change and require careful monitoring and management. A further case study is provided by Ellis and Yahr (Chapter 20), who discuss lichens in arctic–alpine ecosystems.

The first extinctions of species attributed to recent global warming were of mountain- or ocean-restricted species. Many cloud-forest-dependent amphibians have declined or gone extinct on a mountain in Costa Rica (Pounds et al., 2006) due to the indirect impact of climate change. An estimated 67% of harlequin frogs in Central and South American tropics have disappeared over the last 20–30 years due to climate shifts, especially in precipitation, favouring the pathogenic chytrid fungus *Batrachochytrium dendrobatidis* Longcore, Pessier and D. K. Nichols, 1999 (Pounds et al., 2006). Sharp population declines of frogs have also been linked to this epidemic disease in western USA (Walther et al., 2002). Similar temperature factors are significant for extinctions in range-restricted coral reefs. Several periods of mass coral bleaching have occurred since 1979, and these events are increasing in frequency and intensity. Up to 16% of the world's reef-building corals died during the most severe bleaching and extreme temperate period in the El Niño event of 1997–98 (Parmesan, 2006). The problem was exasperated by poor dispersal of symbionts between reefs.

Making predictions about extinction probability is shrouded in uncertainty, but some approaches have been useful. Thomas et al. (2004, 2006) used an approach combining climate envelope modelling and statistics that estimated the probability of extinction. Using projections of species' distributions for future climate scenarios, they assessed extinction risks for sample regions covering some 20% of the earth's terrestrial surface. Methods to estimate extinction were based on the species–area relationship, which is a well-established empirical power-law relationship describing how the number of species relates to area (MacArthur and Wilson, 1967; Rosenzweig, 1995). This relationship predicts adequately the numbers of species that become extinct or threatened when the area available to them is reduced. They predicted, on the basis of mid-range climate warming scenarios for 2050, that 15–37% of species in their sample of regions and taxa will be 'committed to extinction'.

Conservationists have established networks of protected areas and other designated sites. These are static, fixed geographical locations, and there is concern amongst both governmental and non-governmental conservation bodies that such sites may, in the future, fail to provide suitable conditions for the species

and ecosystems for whose protection they were established (Araújo et al., 2004; Hannah, 2008). Huntley et al. (Chapter 16) used *c.* 1700 bird species breeding in sub-Saharan Africa and a network of 803 important bird areas (IBAs) identified and designated in that region as a model to explore this issue. They used climate envelope models fitted to current climate to predict the future occurrences of the species in the IBAs. They showed that the networks have the potential to maintain most species under future climate-change scenarios, but the outcome depends on substantial species turnover. This and other studies have shown that the effectiveness of the networks will depend on their connectivity and sympathetic management of the wider landscape (Hannah et al., 2008; Hole et al., 2009, in press). Range shifts are limited by habitat fragmentation (Hijmans and Graham, 2006). In Madagascar, for example, there is 90% endemism amongst plants, mammals, reptiles and amphibians. The impacts of current and future climate change are likely to be high because suitable habitat for most of these is much reduced and fragmented due to deforestation that has claimed approximately 90% of the island's natural forest (Hannah et al., 2008), providing a poor environment for large-scale range shifts of species. Changes in atmospheric gases also need to be considered. Future life will potentially experience novel atmospheres and novel environments (Williams and Jackson, 2007, Williams et al., 2007). We need to make predictions about the impact of future climate change on communities, but no analogue communities may exist. It will be a challenge for ecologists to study ecosystems they have never seen (Williams et al., 2007). Models need to incorporate net primary productivity (NPP) that is predicted to increase with increased CO₂ (Korner, 2006). Woodward and Kelly (2008) show that rising NPP should potentially increase species' diversity but suggest that the effect will not be enough to offset the damage caused by habitat loss.

Models can also be limited because they are often based on the assumption of niche conservatism (Huntley, 2007b). It seems that some species may have undergone rapid niche shifts while others experienced long periods of niche stability. This casts doubt on the prediction of climate-change impacts by species distribution models that do not consider adaptation. There is a need to know how the potential for niche change varies amongst species, and to take this into account in the modelling, or it may be necessary to choose species more carefully for modelling (Pearman et al., 2008). There is also a need for models to make predictions about population size (Green et al., 2008). It is clear that ecological niche models will need to become more complex (Thuiller, 2004; Pearson et al., 2006; Thuiller et al., 2008; Huntley et al., 2010; Rödder et al., Chapter 11).

1.4.3 Conservation and primary taxonomic data

The ability to study the response of life to climate change, to make predictive conclusions about its fate, and to provide strategies for its conservation, is entirely

dependent on the quality of primary data. For many studies the primary data are taxonomic. Most studies are dependent on accurate species identification, some rely on accurate taxon inventories (species lists), and some rely on location data of predefined taxa (species occurrence data). The taxonomic and systematic community therefore has the responsibility to provide accurate and informative data to all biologists. However, progress in the world's oldest science, taxonomy, is unacceptably slow given the biodiversity crisis (Hodkinson and Parnell, 2007). Only *c.* 1.7 million species, from a conservative estimate of four million species, have been described, and at current rates the process could take several more centuries to near completion (Hodkinson and Parnell, 2007). There is thus a serious taxonomic impediment to progress in ecological and climate-change research (Hall and Miller, Chapter 17). Taxonomy is an enabling science, and there is an urgent need to better characterise species when they are first described. For example, ecological information is generally lacking when species are described. To make taxonomy predictive, Bateman (Chapter 3) argues that much stricter requirements should be placed on species descriptions. The taxonomic community is probably far from meeting that logical aspiration because of ideological, historical and practical constraints. Furthermore, systematic studies are required to better define species. It is clear that we have underestimated species diversity because many species are cryptic and have thus far gone unnoticed. Bernardo (Chapter 18) provides a thorough review of species concepts and cryptic diversity and gives examples of where ecological studies such as ecological niche modelling can fail to reach accurate conclusions because of such shortcomings. There is also a pressing need to speed up taxonomic discovery and provide more useful taxonomic resources to end users such as ecologists (Hall and Miller, Chapter 17). Several innovations offer huge potential to reduce the taxonomic impediment, including digital literature, DNA barcoding and improved field guides (Hall and Miller, Chapter 17; Bateman, Chapter 3).

Ecologists and systematists need to communicate the implications of their science for improved conservation planning, policy, research and management. Conservation biology is a complex multidisciplinary field, and it will be important to develop robust principles and detailed recommendations (Barnard and Thuiller, 2008; Carnaval and Moritz, 2008). Significant care will be necessary to test the predictive science using theoretical and empirical studies.

1.5 Conclusions: crisis upon crisis

It is alarming to note that the current climate crisis has coincided with a biodiversity crisis, which in turn has been met by a taxonomic crisis. There is, therefore, an urgent need to deal with all these issues, and ecological and systematic

research are central to these efforts. Ecological and systematic research interact powerfully to explain the impact of climate and other aspects of environmental change on ecological niches and species diversity through space and time. They help us understand the past and allow us to make meaningful predictions about the future. It is the aim of this book to demonstrate how these research fields are at their most useful for climate-change research when fully integrated. Results from such research are vital for policy and conservation work at a time when life on earth faces an unprecedented threat from many factors, including climate change, which must not be ignored.

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