

# Relict Species

Jan Christian Habel • Thorsten Assmann  
Editors

# Relict Species

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*Editors*

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# Foreword

Mankind has evolved both genetically and culturally to become a most successful and dominant species. But we are now so numerous and our technology is so powerful that we are having major effects on the planet, its environment, and the biosphere. For some years prophets have warned of the possible detrimental consequences of our activities, such as pollution, deforestation, and overfishing, and recently it has become clear that we are even changing the atmosphere (e.g. ozone, carbon dioxide). This is worrying since the planet's life systems are involved and dependent on its functioning. Current climate change – global warming – is one recognised consequence of this larger problem.

To face this major challenge, we will need the research and advice of many disciplines – Physics, Chemistry, Earth Sciences, Biology, and Sociology – and particularly the commitment of wise politicians such as US Senator Al Gore.

An important aspect of this global problem that has been researched for several decades is the loss of species and the impoverishment of our ecosystems, and hence their ability to sustain themselves, and more particularly us! Through evolutionary time new species have been generated and some have gone extinct. Such extinction and regeneration are moulded by changes in the earth's crust, atmosphere, and resultant climate. Some extinctions have been massive, particularly those associated with catastrophic meteoric impacts like the end of the Cretaceous Period 65Mya. Each time, new species and ecosystems have evolved subsequently over millions of years. The rate of species loss today due to Man's activities is great, and has been classed as the next major extinction.

One way to study this problem is to focus on Relict Species. As species become rare through natural processes, they are reduced to few populations in few locations and are considered as threatened or endangered. Numerous species are now placed in this dangerous situation because of Man's expansion. This leads to great public concern and efforts for their conservation. To better inform these efforts, it is most valuable to study the origins, history, and status of such Relict Species.

For this, one clearly needs research on the species habitat requirements and ecological limits, particularly with the growing concern for current climate change. There is pertinent research on the last 2My, the Quaternary Period, with its cycles of increasingly severe ice ages that caused great changes in species abundance and distribution as seen in the fossil record. Our understanding of the origins and

history of species have been greatly advanced by new DNA methods that allow the genetic relations and diversity across a species range to be revealed and analysed. This Phylogeographic approach is informing and sometimes challenging the views in Biogeography and Conservation, and permeating most areas of Evolutionary Biology.

A symposium on Relict Species seemed a good way forward. This would bring together the people studying the various relevant aspects, including topics in Ecology, Phylogeography, Climate Change, and Conservation. And so one was organised in Luxembourg in 2007. Europe was the theatre concerning many participants, where there is considerable interest in ice age refugia and postglacial colonisation to produce our present biota. Studies from Africa, North and South America, and Asia were also included, and the range of organisms covered fungi, plants, many insects, reptiles, and mammals. The relevance of phylogeography and climate change to the conservation of species was addressed in many contributions.

Museums were often considered as dusty shrines. But today the major ones are concerned in modern research in the evolution and management of biodiversity and in educating the next generation in such important matters. They also serve as rich archives and sources of material for such studies. The organisation of this symposium by the Luxembourg Museum is a signal example of such farsighted and crucial involvement.

April 2009

Godfrey Hewitt

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# Relict Species: From Past to Future

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and John C. Avise

## 1 What Are Relicts?

Dictionaries define a “relict” as something that has survived, usually as a trace, from the past. In biology, relicts are distinctive populations or species that typically are small in size or severely restricted in geographic range. Biologists distinguish between taxonomic and biogeographic relicts. Taxonomic relicts are a few or sole survivors of a once diverse taxonomic assemblage, whereas biogeographic relicts are descendants of once widespread taxa (or populations) that now have a narrow geographic distribution (Lomolino et al. 2006). Both categories sometimes coincide, as for example in the case of “living fossils” (such as ginko, lungfishes, crossopterygians, or marsupials) that closely resemble their ancient ancestors in overall phenotype (Futuyma 2005; Lomolino et al. 2006; Beierkuhnlein 2007). In the following, we focus on biogeographic relicts.

Climatic and other large-scale environmental changes can have fundamental impact on the distributional patterns of species and alter the composition of communities and ecosystems (e.g. Hewitt 1999; Schweiger et al. 2009). Species react by range shifts, or by local or regional extinctions when their *adaptive capacity* is exceeded (Agarwal 2001). The origins and distributions of modern-day relicts can often be related to environmental changes of the past. Glacial periods and warm interglacial periods of the Quaternary, in particular, often help us to understand how relict species and

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populations arise and sometimes have served as important sources for re-colonizing much larger areas (de Lattin 1967). For example, many thermophilic species survived the last ice age in relatively small refugia on Europe's Southern peninsulas. During interglacial periods, these species often colonized large areas. Thus, many temperate species that are widespread today existed as small relict populations just a few thousand years ago (cf. Schmitt 2007). Conversely, many cold-adapted species show evidence of formerly wide distributions, followed by severe range restrictions during postglacial warming. Prominent examples of the latter are the butterflies *Procllossiana eunomia* pictured on this book (front side) and *Lycaena helle* (small picture on the back side), which currently resides only in high-elevation mountain enclaves and at more Northern latitudes that have been shown to coincide with distinctive genetic clusters in this species (Habel et al. 2009). Although such species today (and during the other warm periods between glacial periods) are restricted to small areas, they may have the potential to recolonize larger areas if and when the climate cools again. In general, the assumption that relict species inevitably are on their way to extinction may be erroneous; at least some relict populations undoubtedly retain the potential to adapt to a broad spectrum of environmental conditions (Hampe and Petit 2005).

Range restrictions and expansions are also known to result from human-mediated landscape changes. For example, woodlands covered large areas of Central Europe prior to anthropogenic deforestation. Especially during the Middle Ages and early modern times, these extensive woodlands were degraded to a few small remnants. After the establishment of modern forestry and changes in land use, woodland coverage again increased enormously. The former woodland remnants preserved forest-inhabiting plants and animals, some of which still show relict-like distributions but others of which were able to re-colonize large areas (e.g. Assmann 1999; Drees et al. 2008). Comparable changes are known for numerous habitat types and regions. These alternating scenarios of range expansions and restrictions remind us that species with relict-like versus wide distributions are *not* necessarily contradictory indicators of past environmental changes.

## 2 Conservation of Relict Species and Populations

Why focus special conservation attention on relict as opposed to non-relict taxa? One explanation may reside in the connotation for relict that appears from the word "trace" in the dictionary definition. Typically, little remains of any relict, implying in the current biological context that extant populations of a relict species are few in number or small in size. Thus, populations of a relict taxon might occupy disjunct mountain peaks or perhaps a few isolated lakes, for example. Rarity and restricted distributions obviously place relict species in special demographic jeopardy of extinction, especially in the face of ongoing climatic changes and other ecological perturbations.

Another more subtle connotation in the dictionary definition is that relicts are unchanged or "left behind" relative to their non-relict counterparts. It seems doubtful,



however, that evolutionary genetic change has ceased or even slowed substantially in relict species. Indeed, if genetic drift is a potent evolutionary force (as expected for small populations), then the genetic differences of extant relicts from their ancestors or from their modern sister taxa might even be greater than the genetic differences of non-relict species from their respective ancestors or extant relatives. One of the most robust discoveries from the field of molecular evolution is that genetic change proceeds inexorably through time, in essentially all species, and sometimes at surprisingly steady mean rates. An interesting scientific question is whether relict species (as defined by small population size or restricted geographic distribution) tend to evolve at the genotypic or phenotypic levels at rates that differ consistently from those of their non-relict counterparts (García-Ramos and Kirkpatrick 1997).

Another set of scientifically interesting questions stems from the fact that various relict species and populations can have strikingly different ages, thus making them excellent objects for comparative evolutionary and ecological studies (Lesica and Allendorf 1995). In particular, phylogeographic surveys can give great insights into historical, ecological and evolutionary processes related to past shifts (restrictions and expansions) in the distributions of species (Avice 2000; Hewitt 2000, 2004; Schmitt 2007). Moreover, by helping to identify evolutionarily significant units (ESUs) and management units (MUs), phylogeographic and population genetic analyses can help to identify relict populations of special importance for conservation and management (cf. Moritz 1994; Avice and Hamrick 1996; Pérez-Tris et al. 2004; De Guia and Saitoh 2006). Finally, there is a huge scientific interest in stochastic processes as well as inbreeding in relict species that consist either of single populations or structured metapopulations (cf. Melbourne and Hastings 2008). These processes can reduce genetic variability (Petit et al. 2003; Chang et al. 2004) and diminish genetic fitness (cf. Berger 1990; Reed and Frankham 2003) within relict populations of both plants (Oostermeijer et al. 1996) and animals (Wynhoff et al. 1996; Madsen et al. 1999).

Many relict species are already endangered and referenced in *Red Lists*. Conservation must not ignore relicts, as they form an essential component of overall biodiversity. Relict populations and species are, almost by definition, “survivors”. Thus, it is both sad and ironic that conservation biologists must now be concerned about the survival into the future of relict species that, by definition, are proven survivors from the evolutionary past. Nonetheless, such conservation concern is merited, because human actions are precipitating global climatic and other environmental changes that may fall outside the adaptive scope of many relict (and other) living species.

### 3 The Scope of This Book

This book focuses on relict species and describes their history, current status, and future trends. It presents a compilation of case studies representing different methodological approaches and different temporal and spatial scales, all meant to

illustrate evolutionary processes and ecological traits of isolated remnant populations. The book is structured into five sections. Section 1 deals with the basics of climate change and the responses of species and ecosystems. Sections 2 and 3 deal with the effects of pre-glacial and glacial phenomena, and postglacial range expansions, on relict species. Section 4 includes conservation approaches to protect and preserve relict species. Finally, in Section 5, future trends of relict species and their projected distributional patterns are discussed. The book also includes four mini-reviews that highlight molecular techniques, the biogeography of Europe, cave species, and ecological niche modelling.

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**Part I**  
**Climate and Ecosystems**

# The Changing Climate: Past, Present, Future

Markus Quante

**Abstract** Over the 4.6 billion years of its existence, the Earth has seen a large variety of climate states. During the evolution of our planet, its climate was characterized by periods of enhanced climate variability or even swings and some more or less stable – almost quiet – periods. Natural climate variability was the rule rather than an exception and the evolution of life on Earth was closely linked to climate and its change.

For about 250 years, mankind has interfered stronger with the climate system via the release of radiative gases and particles in substantial amounts into the atmosphere. A global mean near surface temperature increase – global warming – can be deduced from instrumental observations, which started in about 1860. The pace and amount of this temperature increase is unprecedented at least the past 1600 years, as reconstructions from proxy data indicate. The observed warming can be attributed to a large extent to human activities as the most recent report of Intergovernmental Panel on Climate Change states. The atmospheric temperature increase is accompanied by an increase in sea surface temperature and a rise of the sea level. Evidence is building that human-induced climate change has also a direct influence on changes in precipitation and the hydrological cycle.

Climate projection driven by socio-economic scenarios indicate that the global temperature and sea level rise will continue throughout the twenty-first century and beyond, the amount of which is strongly dependent on the underlying emission assumptions.

There are a few climate elements that may be sensitive to sudden, abrupt changes, when a set of conditioning parameters is overstepped or certain thresholds are passed; a prominent example is a possible collapse of the thermohaline circulation in the North Atlantic. Here, further research is necessary to quantify thresholds, effects and time horizons.

Overall it can be said that a certain amount of future climate change is unavoidable regardless which route of emission reductions mankind will follow and that emissions from the twenty-first century will noticeably affect climate over the entire millennium.

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## 1 Introduction

About 4.6 billion years ago the solar system, including planet Earth, was formed. During the evolution of our planet its climate was characterized by periods of enhanced variability or even swings and some more or less stable – almost quiet phases. The history of the Earth is a story of the co-development of the oceans, the atmosphere, crustal rocks, climate and life in a cosmic perspective (Cloud 1978). From the viewpoint of us human beings, one of the most striking questions in this context is: what is needed and in what quality and quantity to enable planets to support life? Whether planets are suitable for life depends to a large extent on their volatile abundances, especially water, and, as a precondition for their climate which is strictly determined by the availability of energy, on the distance from their central star.

The Earth's climate has remained conducive to life for at least the past 3.5 billion years, despite a much lower solar luminosity at the beginning of this time span (about 30% less, Gough 1981), which is known as faint young sun (Kasting et al. 1988; Kasting and Catling 2003). The fact that the global temperature varied only between values which allowed for liquid water during the early phase (faint young sun paradox) is most probably due to elevated concentrations of the greenhouse gases carbon dioxide ( $\text{CO}_2$ ) and/or methane ( $\text{CH}_4$ ), which are involved in long-term feedback loops, which stabilize climate in such a way as to allow a water cycle to be maintained (Broecker 1985; Pavlov et al. 2000; Kasting 2005).

The main external and internal natural drivers for climate variability which had more or less an influence over the entire time span of the Earth's history are related to changes in the sun's output on different time scales (e.g. Haigh 2007), orbital changes with different periodicities (e.g. Berger 1988), plate tectonics (Raymo and Ruddiman 1992), and volcanism (Lamb 1970; Robock 2000). After a purely physicochemical determined phase at the very beginning of the evolution of life, the climate started to be strongly influenced by the biosphere. With the emergence of photosynthesis in the oceans and on land, the biosphere contributed essentially to the high oxygen concentration in the atmosphere and thereby gained an important influence on the chemistry of trace gases. The biosphere started to become involved in many of the cycles of matter, and with the water cycle and the carbon cycle established the strongest signature in the climate system. The development and expansion of vegetation on land substantially changed the albedo of the Earth's surface, thereby impacting on the energy budget of the planet.

The stability of climate over several recent millennia has allowed land to be cleared, developed and activated to allow for the production of food needed by a growing population. With the development of agriculture some 1,000 years ago and the related release of greenhouse gases, mainly  $\text{CO}_2$  and  $\text{CH}_4$ , and changes in land cover affecting the Earth's albedo and biogeophysical cycles, humans started to influence the global climate (Ruddiman 2003). With the advent of coal-burning factories and power plants in modern times, industrial societies began to release  $\text{CO}_2$  on a large scale into the atmosphere. The development of the mobile society with an ever increasing number of motorised vehicles (locomotives, ships and cars)

added to the emission portfolio. Crutzen and Stoermer (2000) called the industrial era with humans massively altering the greenhouse gas concentration in the atmosphere as the “Anthropocene”; the year 1800 has been assigned as the beginning of this epoch (see also Steffen et al. 2007). All relevant greenhouse gas concentrations have increased considerably over the last 200 years and the global mean temperature is rising and projected to rise throughout the next centuries (IPCC 2007a). Today, mankind finds itself in a position where urgent decisions need to be made and address the issues - in what form and amount emissions related to its activity have to be reduced - in order to *avoid* dangerous interferences with the climate system, as is postulated by the United Nations Framework Convention on Climate Change (UN 1992).

Stabilizing the carbon dioxide component of climate change is strongly related to changing *how* we produce our energy. Stabilization will require carbon emission-free primary energy sources in addition to a reduced end-use energy demand and improvements in energy efficiency. In a widely recognized paper, Pacala and Socolow (2004) build up a scenario with a target value of 500 ppm CO<sub>2</sub> over a 50-year-time scale, which relies entirely on current technologies. In contrast, Hoffert et al. (2002) conclude from their assessment that only an advanced technology path can lead to a stabilized climate and that intensive research and development on this sector is urgently needed. Besides mitigation, adaptation measures (IPCC 2007b) are also being discussed, given the prospect that a certain change of the global climate is almost unavoidable (IPCC 2007a). In recent years, an essentially different and older idea to address global warming has been reanimated, it concentrates on an active, deliberate *interference* with the climate system in order to reduce the risks associated with climate change. The proposed measures for an attempt to transform the Earth climate on planetary scale are generally summarised by the expression *geoengineering* (Keith 2000; Schneider 2001; Weart 2008). *Geoengineering* is currently being broadly but controversially discussed, since many consequences of the proposed concepts are highly uncertain, and might stay uncertain for a long time, and the ethical, political and legal aspects are only barely touched upon (Fleming 2007; Robock 2008; Schneider 2008).

Most probably, climate change *is* and *will be* affecting the physiology, phenology and the distribution of plant and animal species all over the world. Observational and modelling studies are supporting this statement, with details being still under discussion. Plants and animals are responding in an overall unsurprising way, as they did at the end of the last ice age. Mainly in an effort to keep the temperature zone they are adapted to (but other parameters might also be important), they are shifting their range towards the higher latitudes and, if possible, towards higher altitudes such as mountainous regions. Such shifts have been observed in a wide range of species. European butterflies can serve as a well-documented example, and Parmesan et al. (1999) found that more than 2/3 of the species they followed had shifted their range Northward during the twentieth century. In the Alps and the rocky mountains, trees and grasses have been migrating upslope. Details on this topic can not be presented in the frame of this overview; however, some relevant information regarding species, biodiversity and climate change can be extracted

from the following publications and the many cited references therein: Hughes 2000; Sala et al. 2000; Walther et al., 2002; Parmesan and Yohe 2003; Walther 2003; Parmesan 2006; Botkin et al. 2007; Fischlin et al. 2007; Hoegh-Guldberg et al. 2007, 2008; Kerr et al. 2007; Midgley et al. 2007; Thuiller 2007; Bonan 2008; Lee and Jetz 2008; Rosenzweig et al. 2008; Thuiller et al. 2008.

The science of climate change is touching upon a huge number of topics with many facets, which can not be fully accounted for here, and the selected aspects can not be elaborated in depth. Hence, an attempt has been made in the following sections to provide an extended selection of relevant references for further study, many of them in easily attainable journals. In the subsequent sections and after a short summary of the principal scientific fundamentals, the story of the Earth's climate over the past is recapitulated with enhanced emphasis on the Holocene. The section on the present-day climate builds on observations based on direct measurements of climate parameters, mainly temperature and precipitation. Finally, the outlook into the future reports on modelling studies of global and regional climate change assessments based on scenario-driven simulations. The limitations of model predictions, especially with respect to regionalisation, will also be touched upon. Regarding present and future climate, the results of the latest assessment report (AR4) published by the Intergovernmental Panel on Climate Change (IPCC 2007a) are used as a baseline. As the IPCC AR4 considers only published scientific papers up to 2005, for some aspects more recent work has been considered, in addition.

## 2 Scientific Basis

### 2.1 *The Climate System and Relevant Processes*

The usual definition of climate is that it encompasses the slowly varying aspects of the atmosphere–hydrosphere–land surface system. In some sense, climate is the average condition of the weather over several years to tens of years (averaging times need to be carefully chosen), as exemplified by the parameters viz., temperature, wind velocity, relative humidity, cloudiness and the amount of precipitation. Modern climate definitions include higher order statistics beyond mean values, such as the magnitudes of day-to-day or year-to-year variations, standard deviations or measures of shapes of parameter distributions.

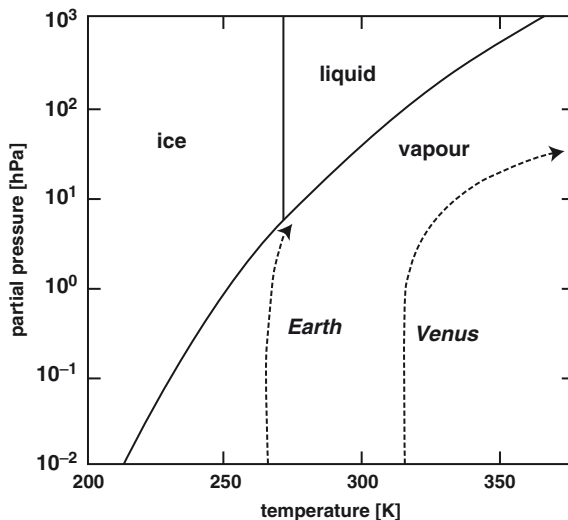
Climate depends not only on atmospheric processes and composition, but also physical, chemical, and biological processes involving other components of the Earth system play a crucial role. In order to understand what the factors are which control the evolution of climate, the interactions among the different components of the Earth system need to be assessed (e.g. Brasseur et al. 1999). This adds to the complexity of the topic since the evolution and feedbacks involved run on a variety of different time scales. The atmosphere, the hydrosphere, the biosphere,



the cryosphere and the lithosphere are the five different Earth system regimes with widely varying impacts and time scales which make up the climate system.

The *abundance of water* in its three states of aggregation and a functioning global water cycle is of utmost importance for the climate system (e.g. Pagano and Sorooshian 2006; Quante and Matthias 2006). The phase of water depends on the temperature and pressure it is exposed to. At the normal range of atmospheric pressures and temperatures on Earth water can exist in all three of its basic states, as is evident from its phase diagram in Fig. 1, which shows the phase transition curves as a function of temperature and partial pressure (see Webster 1994). The Earth’s trajectory in Fig. 1, driven by an increasing water vapour greenhouse effect, intercepts the phase curves in the vicinity of the triple point of water (273.16 K), allowing the formation of a complex hydrological cycle. In contrast, because Venus is a star with a considerably warmer primitive surface temperature, the curve for Venus does not intercept any of the water phase transition lines at all. Water stays in the gaseous phase on this planet. The state curve for Mars starts at a relatively low temperature (~240 K; not shown here) and rapidly intercepts the vapour-ice phase transition.

All subcomponents of the climate system are involved in or maintain processes which can have a huge impact on climate. The interplay between radiation and convection in the atmosphere regulates the temperature at the Earth’s surface. The oceans, which cover about 72% of the surface area of our planet, influence climate by their large thermal inertia and their important role in taking up carbon dioxide from the atmosphere. If present, the cryosphere with extensive snow and



**Fig. 1** Phase diagram of water illustrating the possible occurrence of the three states of water for the range of temperatures observed at the Earth’s surface and in the lower atmosphere; ~190 K–325 K and 0–50 hPa partial pressure range at the surface. Figure adapted from Quante and Matthias (2006)

ice covered areas has a strong influence on the planetary albedo (Parkinson 2006). Besides their large influence on the Earth's albedo with a corresponding net cooling effect, the clouds are also contributing to a warming of the surface by absorbing infrared radiation and emitting it partly back towards the ground (e.g. Quante 2004). Clouds cover at any given time between 60 and 70% of the globe. Living organisms on land and in the oceans are involved in liberating oxygen and sequestering carbon in the Earth's crust and thereby reducing the CO<sub>2</sub> concentration of the atmosphere. The evolution of vegetation is strongly coupled with that of soil and climate, and there is a myriad of interactions involved (e.g. Berry et al. 2005; Barth et al. 2005). Plate tectonics exerts an influence on climate on time scales of more than millions of years through continental drift, creation of mountains (Turcotte and Schubert 2002) and volcanism (Robock 2000). Of all the biogeochemical cycles, the hydrological (e.g. Quante and Matthias 2006; Oki and Kanae 2006) and the carbon cycle (e.g. Houghton 2007; Doney and Schimel 2007) are the most relevant for climate and its evolution.

The major external forcing of the climate system comes from the sun. Everything on Earth relies on a steady energy flow provided by our central star. The amount of radiation produced by the sun is not constant, especially in the short, ultraviolet wavelengths. Due to changes in the magnetic structure of the gaseous sun, the solar activity shows variations, which are manifested in an 11-year cycle. Although attempts have been made, a firm theoretical coupling of this short-term solar activity fluctuations with climate changes could not be found. A slightly enhanced energy deposition in the stratosphere is among the most recognized effects. Some evidence for the influence of solar activity variations on the lower atmosphere and climate is critically assessed by Bard and Frank (2006), Foukal et al. (2006) and Haigh (2007). These variations play some role in the discussion on modern global warming, since if climate changes due to the sun were significantly large, it would be more difficult to extract the anthropogenic signal from the climate record (see Sect. 4.4). The story is different, however, when dealing with the long-term evolution of the sun; in its infancy, the sun's intensity was about 30% less than what is observed today (Gough 1981), the relatively moderate climate under these conditions is generally referred to as "faint young sun paradox" (e.g. Sagan and Chyba 1997). A further possible external forcing of Earth's climate might come via galactic cosmic rays and their influence on clouds (Marsh and Svensmark 2000; Carlsaw et al. 2002; Kristjánsson et al. 2004; Kirkby 2008). The related science and the potential magnitude of postulated effects is currently being debated and planned experiments at the Conseil Européen pour la Recherche Nucléaire (CERN) should, at least, provide some insight into underlying cloud microphysical processes.

In summary, Fig. 2 sketches the Earth system and its interactions, encompassing the physical climate system, biogeochemical cycles, external forcing, and the effects of human activities. For a more rigorous treatment of the different aspects concerning the climate system and underlying processes, the books by Peixoto and Oort 1992; Graedel and Crutzen 1993; Hartmann 1994; Brasseur et al. 1999; Seinfeld and Pandis 2006; Ruddiman 2008; and Pierrehumbert 2009 are recommended.

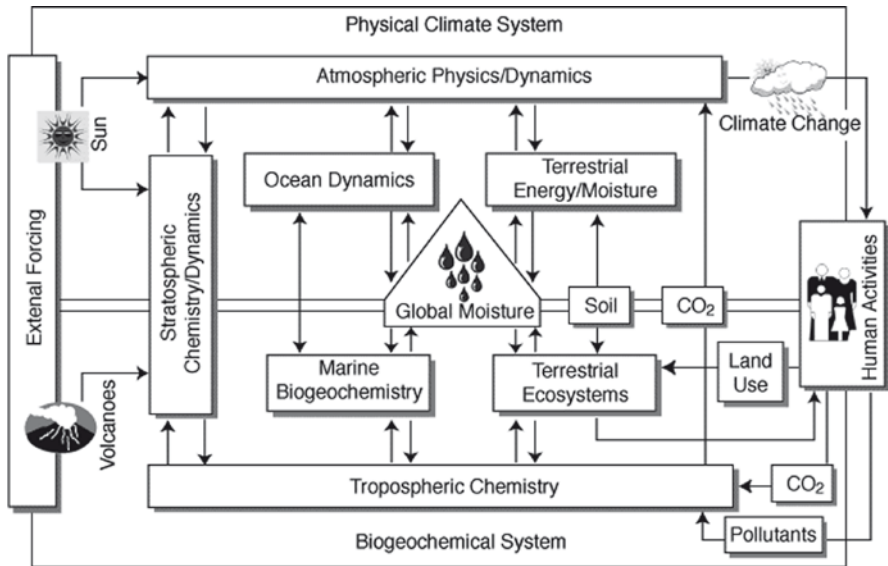


Fig. 2 Schematic diagram of the climate system and its interactions among different components of the Earth system (from Earth System Science: Overview, NASA)

## 2.2 Climate Variability

Climate varies on all time scales longer than its definition limit and on a wide range of spatial scales, from regional to global. The variability of climate can be expressed in terms of two basic modes: the forced mode with variations which are the response of the climate system to changes in external forcing, which themselves are not influenced by the climatic variables themselves, and the free mode variations due to internal instabilities and feedbacks leading to non-linear interactions among the various compounds of the climate system (Peixoto and Oort 1992; Ghil 2002a). Also, stochastic forcings could produce sudden impulses to the climate variables (Hasselmann 1976). It is due to this complex nature of the variability that a reliable identification of an anthropogenic influence on climate and especially its quantification turns out to be so difficult.

The temporal variability of the climate system over the last 10 million years can be visualized by reproducing a power spectrum for temperature near the surface (Fig. 3), which is a composite of several climatic time series. The sharp lines in the spectrum correspond to periodically forced variations (daily and yearly cycles), broader peaks arise from internal modes of variability, and the continuous segments of the spectrum reflect stochastically forced variations, as well as deterministic chaos resulting from the interplay of non-linear feedbacks (Ghil 2002b).

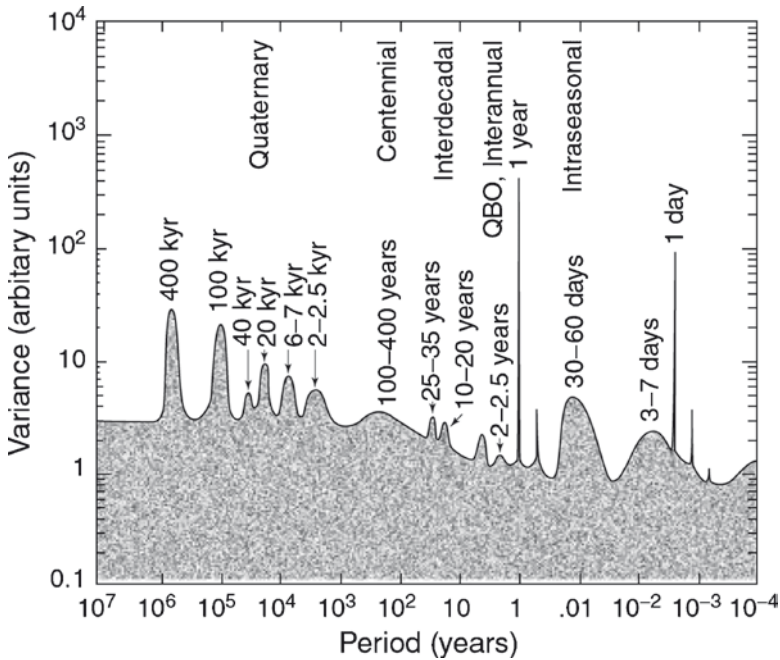


Fig. 3 Composite power spectrum of climate variability over the last 10 Myr (after Ghil 2002b)

The signature immediately to the left of the peak at the 1-year-period reflects the influence of an interannual variability, which is known as El Niño-Southern Oscillation (ENSO) (Neelin et al. 1998) and involves internal modes of the tropical Pacific ocean-atmosphere variability. Periods of several decades as they occur in the spectrum are the subject of ongoing research. As the interdecadal variability is related to climate system internal processes this part of the spectrum might hold some clues for the extension of the predictability of the ocean-atmosphere system.

The spectrum part with periods between 1,000 years (1 kyr) to about 1 million years (1 Myr) in Fig. 3 represents the paleoclimatic variability. The temperature data underlying the spectrum far outside the instrumental record come from proxy indicators such as coral reef records, tree rings, marine sediment cores, and ice core records. The time span captured by the spectrum is called *ice age era* with its main glaciation cycles (Imbrie and Imbrie 1979), it occupies no more than about one-tenth of the documented Earth history. The past 2.5 Myr with the marked climatic swings are called Quaternary period.

The external forcings comprise variations caused by smaller fluctuations in the sunlight reaching the Earth, which occur over longer timescales. These involve changes in the shape of the Earth's orbit around the sun and changes in the Earth-sun distance at the time of the equinoxes. Early in the twentieth century, in Belgrade, Milutin Milankovic' produced a mathematical theory that became the basis for a general

explanation of the dynamical behaviour of the climate system, i.e. the major changes in past and future (Berger 1988). In particular, the theory which builds on deterministic astronomical variations in the orbital parameters of the Earth should explain the recent ice ages on Earth. The theory was not fully accepted by his contemporary scholars, and today we know that orbits are *not* everything (Broecker and Kunzig 2008), but basic orbit variability can be used to reconstruct climate records.

The prominent peaks around 20, 40 and 400 kyr in the spectrum in Fig. 3 are a result of quasi periodic variations in the Earth's orbit (Berger 1988), which affect the summer insolation at high latitudes. In intervals with relatively weak summer insolation snow deposited during winter does not melt completely, so over thousands of years thick ice sheets can be accumulated (enforced by the ice-albedo-feedback). The cycle of about 100,000 years is due to changes in the eccentricity of the orbit (ellipticity), variations of the tilt of the Earth's axis of rotation relative to the orbit plane (the obliquity) leads to the 41,000-year-cycle and the 23,000-year- (19,000 year) cycle marks the changing axial precession. Details of the orbital theory of climate variation are still under investigation (Paillard 2006).

Overall, it can be said that climate variability results from complex interactions of forced and free variations because the climate system is a highly non-linear, dissipative system with many sources of instabilities (Peixoto and Oort 1992). Feedback mechanisms act as internal controls of the system, they originate from special couplings between the open subcomponents and are of particular importance for the Earth's climate system. Feedbacks may either amplify or dampen the original distortions of the system. Important feedbacks are the water vapour-, cloud-, snow/ice-albedo-feedbacks, and the carbon-silicate cycle/carbon dioxide feedback (Held and Soden 2000; Stephens 2005; Kasting and Catling 2003).

### 2.3 Energy Balance and Greenhouse Effect

The Earth receives the overwhelming amount of its energy from the sun in the form of visible and near-infrared radiation; it is mainly this latter energy which warms its surface. Our planet is cooled by the emission of thermal infrared radiation into space. Treating the Earth as a blackbody radiator with an effective temperature  $T_e$ , the balance of incoming radiation and outgoing radiation leads to the following relationship (e.g. Wallace and Hobbs 2006):  $\sigma T_e^4 = S/4(1 - A)$ , where  $\sigma$  is the Stefan-Boltzmann constant, where  $S$  is the solar flux at the distance Sun-Earth, and  $A$  is the planetary albedo. Using the appropriate numerical constants and quantities, solving the equation yields an effective emission temperature of 255 K. Reality is, however, slightly more complex, in that the Earth together with its atmosphere is *not* a perfect blackbody. The atmosphere warms the surface by the so-called greenhouse effect; parts of the infrared radiation emitted from the surface is selectively absorbed and re-emitted by infrared-active gases within the atmosphere. With the present-day incoming solar flux ( $\sim 1,368 \text{ Wm}^{-2}$ ), albedo ( $\sim 0.3$ ) and atmospheric

composition, a global mean surface temperature of 288 K results. The difference between the effective emission temperature and this surface temperature of 33 K is the magnitude of the actual greenhouse effect. A more complete treatment of the involved energy fluxes with emphasis on the energy budget resolved for additional processes is given in Kiehl and Trenberth (1997). The most difficult factor in the quantification of the energy fluxes through the atmosphere is the planetary albedo, which is determined by ocean and land surface characteristics (soil type, soil moisture, vegetation) and the three-dimensional cloud distribution in the atmosphere, which is responsible for the largest fraction. The relevant cloud (and aerosol) properties are difficult to predict. Thus, calculations of past or future climates based on energy principles (radiative and turbulent fluxes) are subject to high uncertainties, i.e. since clouds are involved in several feedback loops (Stephens 2005).

In the present-day atmosphere the most important greenhouse gases are water vapour and carbon dioxide, of which the former contributes about two-thirds of the associated warming. Lesser contributions come from methane, nitrous oxide, ozone and various chlorofluorocarbons. It is important to distinguish between long-lived greenhouse gases, which are removed slowly from the atmosphere on a time scale of hundreds to thousands of years, and short-lived greenhouse gases, which are removed within weeks to a year by condensation or fast chemical reactions. The short-lived greenhouse gases act primarily as a feedback mechanism. In the eighteenth century, the atmospheric concentration of most of these gases (with the exception of water vapour) began to be significantly altered due to emissions from power plants, industry, agriculture and animal farming as well as the mobility sector. The ongoing greenhouse effect discussion is driven by the anthropogenic emissions of  $\text{CO}_2$ ,  $\text{CH}_4$ ,  $\text{N}_2\text{O}$ ,  $\text{O}_3$  and CFC which show strong increases, especially over the last decades. It has to be noted that all of these gases have a relatively long residence time in the atmosphere and therefore, a high greenhouse warming potential.

Water vapour as the major player in the Earth's energy budget is buffered by the huge oceans on a time scale of a few weeks. This gas adjusts its atmospheric concentration in response to climate changes, and it has a strong positive feedback in the climate system, thus amplifying global warming caused by other forcings (Held and Soden 2000). Water vapour, although an important greenhouse gas, is not a prime driver of modern climate change (it plays an essential role via its positive feedback). As there are no significant anthropogenic emissions, water vapour has not become the subject of political regulatory protocols.

Of course human beings started influencing the atmospheric composition, and greenhouse gas concentrations, well before the massive industrialisation began. About 11,000 years ago stone-age farmers may have already altered Earth's climate by clearing forests and irrigating fields to grow crops. Besides resulting in changes to the albedo, these activities may have led to considerable amounts of  $\text{CO}_2$  and  $\text{CH}_4$  being emitted. It should be mentioned that some scholars have even put forward the hypothesis that this early interference with the climate system could possibly have averted the start of a new ice age (Ruddiman 2003, 2005). This controversial hypothesis is discussed, for example, by Claussen et al. (2005), since