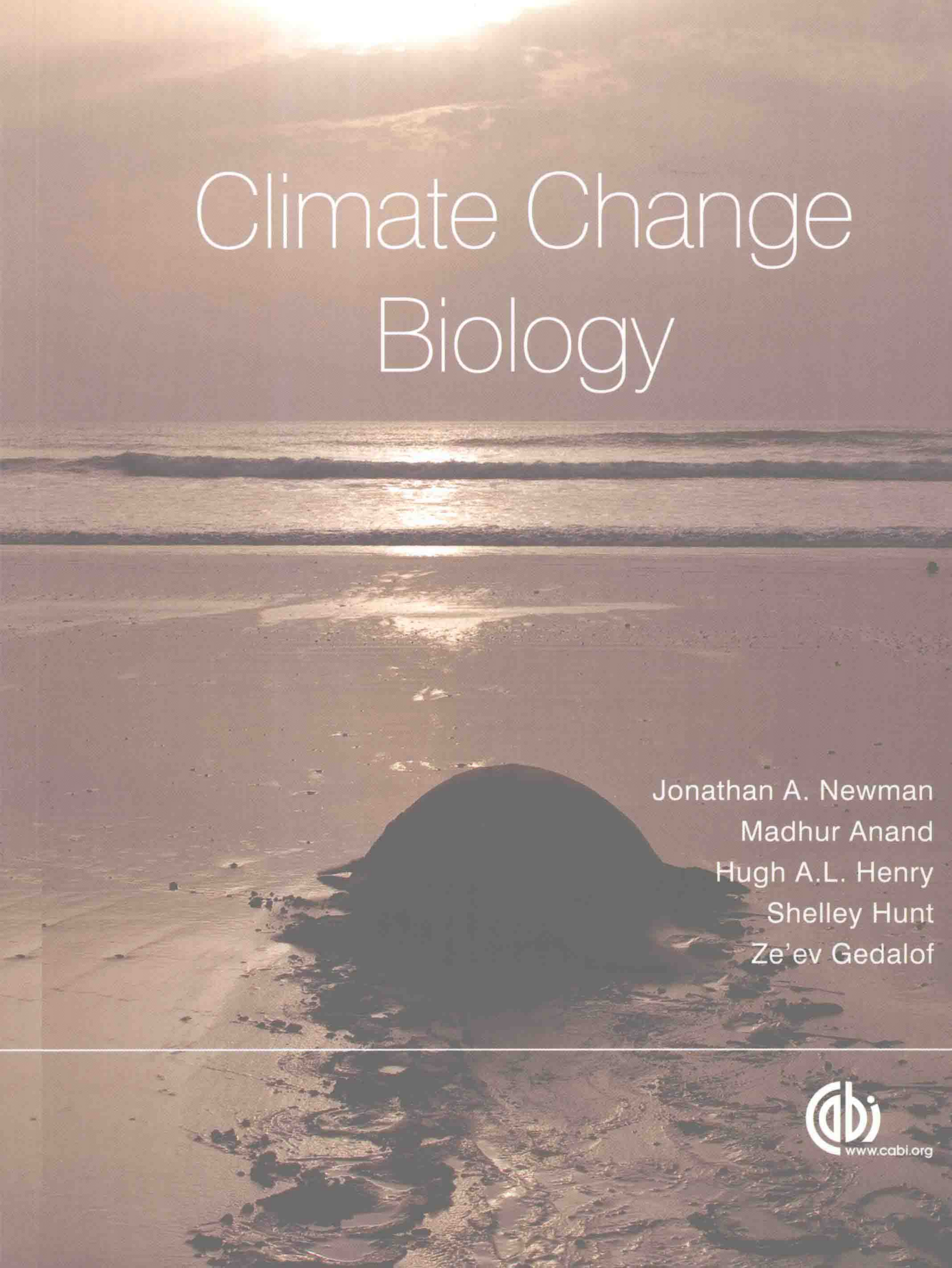

Climate Change Biology

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Preface

We authors all feel that climate change is an important and pressing political issue and that action on our part is warranted and urgently needed, but this is not a book about policy, ethics, economics or environmental activism; it is a book about biology. We are biologists who study the impacts of climate change; this is a book about research into those impacts. Climate change biology is a big subject. Climate change influences all levels of biological organization from biochemistry to ecosystems. While we have tried to be comprehensive in concepts, we have certainly not been comprehensive in examples, in coverage of the variety of ecosystems, taxa, biogeographical areas, etc. We aimed to provide an introduction to the study of the biological impacts of climate change, leaving the more advanced topics for further study.

This book is organized around the basic outline of a 12-week undergraduate course that one of us (J.A.N.) designed in 2006. That course was difficult for undergraduates for two principal reasons. First, there was no suitable textbook available. There are many edited volumes written with a specialist audience in mind (see e.g. Newton *et al.*, 2007) and there are many texts about climate change aimed at undergraduates, but they have little or nothing to do with biology. Our book is intended to fill this gap. The second difficulty that undergraduates have with this topic is the general lack of synthesis. Climate change biology is a relatively new field of research and the questions asked within this field are large and difficult. We have tried to provide some synthesis of the field where that is possible, and to point out the open questions where it is not.

We hope that the book will provide a good survey introduction to climate change biology that can be covered comfortably in a single semester. We have aimed the text at third- and fourth-year undergraduates, but properly supplemented it should work well as a second-year undergraduate text or even a first-year graduate text. We generally assume students are familiar with first-year biology and general ecology, although we try to remind the reader of basic concepts where appropriate.

We appreciate all of the help and support we received from our colleagues throughout the process of writing and assembling this book. Colleagues provided us with images, photos and in some cases data so that we could re-graph them as needed. We also benefited from many discussions with our colleagues. The remaining faults are entirely our own. The literature on climate change biology is increasing at what seems to be an exponential rate, and it was impossible to keep up with everything. We could not provide a comprehensive literature review due to space constraints, and we apologize if we have not cited important papers.

Glossary

Acclimation. When plants reduce their rate of photosynthesis in response to long-term exposure to elevated CO_2. Sometimes used more generically to mean a reduction in a plant's growth rate response to elevated CO_2. See also **Down Regulation**.

Adaptation. Used in two different contexts in this book. (1) *Evolutionary adaptation* is a population's change in gene frequency through time in response to a specific selection pressure. (2) *Climate change adaptation* refers to the process of altering management options or behaviour to reduce the impacts of climate change on a process or metric of interest.

Bioclimatic Envelop Model. A mathematical/statistical model where the observed distribution of a species is correlated with the observed climate. These models can be used to predict changes in the potential observed distribution in the future under climate change. Compare with **Ecological Niche Model.**

C_3 Plants. These plants have a form of photosynthesis where they use the Calvin Cycle directly, catalysing the primary uptake of CO_2 with the enzyme Rubisco. Compare with **C_4 Plants.**

C_4 Plants. These plants have a form of photosynthesis where they catalyse the primary uptake of CO_2 with the enzyme PEP carboxylase. CO_2 taken up in this way is then transported deeper into the leaf tissue where it enters the Calvin Cycle. Because of this carbon concentrating mechanism, C_4 plants generally have greater **Water Use Efficiency** than **C_3 Plants.**

Carbon Sequestration. Carbon can basically be in three places in a terrestrial ecosystem: the atmosphere, the soil or living organisms. In general sequestration occurs when the rate of carbon entering a carbon pool occurs faster than the rate of carbon leaving that pool. In particular, we only really use the term 'sequester' when referring to either the soil or some longer-lived organisms such as trees, in the stemwood. Some subpools of carbon in the soil turn over very slowly (e.g. humic substances) and so are able to keep that particular carbon out of the atmosphere for very long periods of time. Another term for a pool that sequesters carbon is a *carbon sink* (as compared to a *carbon source*).

Climate Proxy. A measure of something biological or physical that is correlated with contemporary climate. Measuring that variable is not a *direct* measure of climate, it is a *proxy* measure of climate. Classic examples of climate proxies are tree ring widths (see **Dendroclimatology**), deuterium concentrations, or fossilized organisms or parts such as diatoms and pollen. Climate proxies are used in climate reconstructions that allow us to infer what the climate would have been like in a particular place either where direct measurements were not taken, or before such measurements existed.

CO_2 Fertilization Effect. Sometimes referred to as simply the *fertilization effect*. Since photosynthetic rates of **C_3 Plants** are often not saturated at ambient CO_2, adding additional CO_2 tends to stimulate photosynthesis and hence plant growth. This effect is commonly exploited in the greenhouse industry where commercial greenhouses are flooded with additional CO_2 to produce better yields and faster plant growth. The effect is also commonly seen in climate change experiments where CO_2 is manipulated, at least for C_3 plants. **C_4 Plants** tend to be less limited by CO_2 concentrations at ambient CO_2 concentrations and are therefore less likely to show this effect.

Community. A group of **Populations** that coexist in the same geographic area and that interact with each other. Sometimes this term is used with a more restrictive adjective such as *grass community* or *bacterial community*. It is rare to see community used in its most inclusive forms in the context of experiments. See also **Succession.**

Dendroclimatology/Dendroecology. 'Dendro' refers to tree rings (from the Greek word *dendron*, meaning tree limb). *Dendroclimatology* is the process of using known relationships between tree-ring widths and contemporary climate to reconstruct past climates (i.e. the tree ring record is a form of climate proxy). *Dendroecology* is the process of using tree-ring widths through time to infer something about the local ecology at the time the rings were deposited. For example, tree rings can be used to reconstruct the pattern of fire disturbance in a forest.

Diversity Index. There are many *diversity indices*. They are ways of reducing diversity, which is essentially a multi-dimensional quality, into a single dimensional metric. In general, ecologists tend to think of diversity as a function of both the number of species present (*richness*) and the *evenness* with which individuals are distributed between different species. Diversity indices are mathematical means of combining these two dimensions (richness and evenness) into a single dimension. A common metric is *Shannon Diversity* (H).

Down Regulation. In the context of climate change this term is usually used synonymously with **Acclimation.** More broadly in biology, the term usually refers to when a gene is not as active as it usually is. There are occasions in the climate change biology literature where down regulation takes on this latter meaning.

Ecological Niche Model. A model that uses experimental information about the climate tolerances of a species, and then maps those tolerances to observed or future climate to identify geographical regions where a species might be found. These models are used in studies of species ranges. See also **Bioclimatic Envelop Model.**

Ecosystem. An ecosystem is an entire biotic **Community** along with its physical environment. It can be difficult to define the boundaries of an ecosystem since individuals interact across almost any boundary used as a definition. It is common to see ecosystems defined in terms of a watershed or body of water, both of which would seem to have relatively clear boundaries, but even in these cases energy and material certainly flow back and forth across the shoreline or the topological boundary of the watershed. In many cases the boundary of an ecosystem is not much more than a human construct used for descriptive and accounting purposes. Also notice that *ecosystem* has come to be used much more broadly over the past 10 years or so. It is sometimes used synonymously with *nature*, *habitat* and *community*.

Ecosystem Functioning. Ecosystem functioning usually refers to things that ecosystems do that benefit humans, although it need not be so restrictive. Typical functions include productivity (e.g. **NPP**), nutrient cycling, **Carbon Sequestration**, pest management, water purification, pollination services, and so on.

Evapotranspiration. Abbreviated ET, evapotranspiration is the sum of two different processes: evaporation and transpiration. ET is one of the important sources of moisture loss from an ecosystem or watershed. Along with surface runoff and ground water recharge, ET helps account for the level of soil moisture, which can be key in some ecosystems for plant productivity. See also **Transpiration.**

External Validity. A term that refers to the similarity between the conditions of an experiment and those of the real system to which the experiment is meant to be relevant. External validity must often be traded off against considerations of experimental control and experimental replication.

Extirpation. When a species becomes *locally* extinct. Also applies to subspecies and populations.

FACE. An acronym standing for *Free Air Carbon dioxide Enrichment*. FACE is a technique for experimentally enriching the CO_2 concentration over a plot of ground. It is widely considered to be the most **Externally Valid** method for conducting CO_2-enrichment experiments, but the method tends to suffer from low levels of experimental replication and so is vulnerable to a **Type II Error.**

Functional Traits. These are phenotypic characteristics possessed by individual organisms within an ecosystem. They usual distinguish those traits that are relevant for ecosystem functioning such as **NPP, Trophic**

Level, nitrogen fixation, and so on. Functional traits tend to ignore characteristics that we think have little to do with ecosystem functioning (e.g. colour). Functional traits are often discussed in the context of **Ecosystem Functioning**, where it is hypothesized that the greater the diversity of functional traits within an ecosystem, the higher the level of function. If functional trait diversity is to be a useful concept, it must do some work that 'species diversity' does not. Individuals from different species may share the same, or similar, functional traits, leading to the conclusion that, from an ecosystem perspective, these species are 'redundant'. Objectively defining functional traits is not easy. If traits are defined too narrowly, then there will be as many traits as species and the concept becomes useless. Defined too broadly, nearly all species will appear to be the same from the perspective of ecosystem functioning.

GCM (AOGCM). Stands for *Global Circulation Model*, although it is also commonly used in a more generic sense to mean Global *Climate* Model. AOGCM is the more technically correct term and stands for Atmosphere–Ocean coupled GCM. However, since these days nearly all GCMs are AOGCMs, it is common to see them all referred to simply as GCMs. GCMs are large mathematical models of the entire Earth that represent the physical processes that determine weather and hence climate. These models are told what the current and future concentrations of greenhouse gases will be, and they then project the climate into the future. See also **SRES Scenario** and **RCM.**

GPP. Stands for *Gross Primary Productivity*. This is the rate at which carbon (CO_2) is captured by an ecosystem. It is measured in kg/m^2/year. Much of this captured carbon is quickly respired by the autotrophs and this difference is known as **NPP.** Note: GPP also stands for Gross Primary *Production* where the units are simply kg/m^2 and the time period is understood to be 1 year.

Holocene Epoch. A geological time period that began about 12,000 years ago. It is part of the **Quaternary Period** that began about 2.5 million years ago.

Interaction. This term is commonly used when discussing the results of experimental studies. Two treatments or factors are said to interact if the overall effect of the two is greater or lesser than the sum of the two individual effects. Suppose that doubling the level of soil nitrogen doubled the growth of a particular plant species, and that doubling the level of CO_2 increased the growth of that same plant species by 50%. Then presented in combination we would expect that doubled nitrogen *and* doubled CO_2 would result in a 2.5-fold stimulation of growth. If we observed more than 2.5-fold stimulation then we could conclude that CO_2 and nitrogen interacted positively in this experiment. Less than a 2.5-fold increase would cause us to conclude that CO_2 and nitrogen were antagonistic (or perhaps growth becomes limited by some third factor) in their effects. Either conclusion would be an example of two factors or treatments interacting with each other.

Invasive Species. Sometimes also referred to as *non-native* species or *exotic* species, these are species that did not evolve in the particular habitat in which they are now present. Some ecologists make distinctions among these different terms, with *invasive* referring to species that are both non-native and in some sense harmful to either humans (usually in the sense of economically harmful) or native species. Other ecologists use the terms interchangeably.

IPCC. Stands for the *Intergovernmental Panel on Climate Change*. The IPCC is convened under the auspices of the United Nations Environment Program (UNEP) and the World Meterological Organization (WMO). The IPCC is not a policy-making organization. Its job is to provide information to policy makers about climate change and its consequences. The IPCC is the most authoritative body speaking about climate change. Since 1990 the IPCC has been producing assessment reports every 6 years (the most recent, fourth, assessment report, AR4, was published in 2007).

Meta-analysis. This is a statistical technique for combining the results of multiple experiments that all ask similar questions. It has become a widely used technique in ecology since the early 1990s and is now fairly common in the field of climate change biology. It can help overcome the problem of low **Statistical Power,** but can be biased by the general tendency for journals to not publish negative results.

Multitrophic. Many or most climate change biology studies concentrate on the response of organisms at a single **Trophic Level** to some climate change variable. *Multitrophic* refers to considerations regarding the response of multiple interacting trophic levels at the same time and to the same environmental variables. For example, how do C_3 grasses respond to elevated CO_2? Asking this question in isolation from those grasses' herbivores, parasites and viruses might give a very different view than if we examined the entire *multitrophic* response.

NEP. Stands for *Net Ecosystem Productivity*. NEP is **NPP** minus heterotrophic respiration (i.e. respiration by the organisms that eat the plants). It is measured in $kg/m^2/year$. Note: NEP also stands for Net Ecosystem *Production* where the units are simply kg/m^2 and the time period is understood to be 1 year.

NPP. Stands for *Net Primary Productivity*. NPP is **GPP** minus the rate of autotrophic respiration. It is measured in $kg/m^2/year$. Because NPP includes all the belowground growth, and because that growth can be very difficult to measure in practice, it is not uncommon to see estimates of NPP restricted to aboveground NPP, either reported as such, or reported as total NPP after multiplying by a constant fraction used as a stand-in for actual estimates of belowground NPP. Note: NPP also stands for Net Primary *Production* where the units are simply kg/m^2 and the time period is understood to be 1 year.

NUE. Stands for *Nutrient Use Efficiency*. Sometimes refers to the more specific *nitrogen use efficiency* with the same abbreviation. NUE can be a more general measure, but sometimes refers to the more specific **PNUE**. There are many definitions of NUE and so the precise meaning in any given circumstance can sometimes be difficult to determine. Generally NUE means mass gained per unit mass of the nutrient. The confusion arises from both halves of this concept. Where is the mass being gained? Is it leaf mass, whole plant mass, grain mass, etc.? Where is the nutrient? Is it in the plant, in the soil, or in the form of fertilizer, etc.? For any specific application of the concept, one or more of these definitions might make more sense.

Phenological/Phenology. Phenology refers to the timing of critical life history events such as seed set, germination, moulting, egg laying, etc.

Phenotypic Plasticity. A *phenotype* is an observable characteristic of an organism that results from both its *genotype* and its environment. Phenotypic plasticity refers to the range of values the phenotype can display as the environment changes. Phenotypic plasticity is what allows individual organisms to tolerate (or perhaps thrive) across a range of some environmental variable.

PNUE. Stands for *Photosynthetic Nutrient Use Efficiency*. This is the photosynthetic rate per unit of leaf nitrogen. See also **NUE**.

Population. A group of organisms all belonging to the same species that coexist in the same geographic area and interact with each other.

ppm. Stands for 'parts per million'. ppm is a dimensionless measure of concentration commonly used to talk about the concentration of CO_2 in the atmosphere. Commonly used too is the mole fraction expression (number of moles of carbon per mole of air, expressed in μmol/mol, where micro (μ) is 10^{-6}, hence parts per million). Both expressions are commonly seen in the literature. We have standardized on ppm throughout this text.

Quaternary Period. This is the current geological period that began approximately 2.5 million years ago. It encompasses two geological epochs, the Pleistocene (2.5 million years ago to about 12,000 years ago) and the **Holocene** (12,000 years ago to present) Epochs.

RCM. Stands for *Regional Climate Model*. RCMs cover small parts of the globe and simulate climate at a much finer level of detail than **GCMs**.

Rubisco. Stands for *Ribulose-1,5-bisphosphate carboxylase oxygenase*. Also commonly abbreviated RuBisCO. Rubisco is the enzyme responsible for catalysing the uptake of CO_2 at the start of the Calvin Cycle. Rubisco and its activity is the subject of much research in the field of climate change biology because of its role in the primary uptake of CO_2 for **C_3 Plants**, and because it often represents a significant amount of the total nitrogen in a plant and is therefore a major player in our understanding of **NUE**.

Scenario. Also called *climate change scenario* and **SRES Scenario**. This is a coherent, self-consistent 'story' about what levels of future greenhouse gas emissions might look like. They are stories about how population growth will change, the pace of economic development, the pace of technological change, the mixture of fuels used in the future, and so on. These assumptions are then 'interpreted' through mathematical models that produce greenhouse gas emissions. These emissions are then fed into **GCMs** that are then used to project climate into the future. Scenarios are not *predictions*, since they depend on processes that can only be predicted with great uncertainty; so, for example, there are no *most likely* or *least likely* scenarios. Equally, scenarios are meant to be *value neutral*; for example, there is no *best case* or *worst case* scenario.

Species Diversity. See **Diversity Index**.

Species-specific Responses. The conclusion from many climate change experiments. Species-specific responses refer to the situation where similar species did not respond in the same way to one or more climate change variables. Such a conclusion is often the same as saying that there was not a general response observed across all species. Sometimes the term *idiosyncratic* will be used, which can mean the same thing, but more commonly means that the responses are not only species-specific, but also specific to the particular set of species combinations. That is, not only do species X and species Y not respond to higher temperatures in the same way, their responses also depend of whether species A, B, C, etc. are present and, in which combinations.

SRES Scenario. The subset of climate scenarios developed under the **IPCC**'s Special Report on Emissions Scenarios. This report developed a standard set of scenarios used by all of the climate modelling groups for the IPCC's third and fourth assessment reports. New emissions scenarios are being developed for the IPCC's fifth assessment report, due out in 2013. These new emissions scenarios and related climate change projections will probably start to appear in the scientific literature by early 2012.

Successional/Succession. The change in **Community** membership through time. Most areas have one or a few possible *climax* communities that would arise if not for disturbance, either anthropogenic or natural. We can talk about a successional stage (e.g. early, mid, late) or type (e.g. primary, secondary, bog, etc.).

Trophic Level. Refers to the position occupied by a species within the foodweb of a specific ecosystem. For example, producers (autotrophs, e.g. plants), primary consumers (herbivores) and secondary and tertiary consumers, etc. (predators, parasitoids, detritovores) are descriptions of different trophic levels.

Trophic Structure. One way of describing how a biological community is structured. Trophic structure can refer to the number of organisms at different **Trophic Levels**, or the ratio between the numbers of organisms at two different trophic levels (e.g. predators to herbivores).

Type II Error. A Type II Error occurs when we conclude that an experimental treatment has no effect when it actually does. The smaller our sample size or the smaller the effect size we are trying to detect, the more vulnerable will our experiments be to the occurrence of Type II Errors.

WUE. Stands for *Water Use Efficiency*. In general, WUE is a measure of the number of kilograms of biomass produced by a plant per kilogram of water. Confusion can arise as to whether we are talking about water available in the soil or water in the leaf/plant.

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PART I
Preliminaries

Open-topped chambers for studying the impacts of elevated CO_2. These chambers are located in a scrub oak ecosystem at the Kennedy Space Center in the Merritt Island National Wildlife Refuge. They were established by Bert Drake, of the Smithsonian Environmental Research Center, in 1996. This is an example of one of several methods for manipulating the concentration of CO_2 in the atmosphere to study the potential impact of climate change. This and other methods are discussed in Chapter 3. (Photo courtesy of the Smithsonian Environmental Research Center.)

Overview

In this section we explore the following questions: How do we know about past climates? How do we know about future climates? How do we study the biological impacts of climatic change? In Chapter 1 we introduce the methods of studying past climates and climatic changes. We also provide some insight into the climatic history of the Earth and the causes of non-anthropogenic climatic variation.

In Chapter 2 we explain that future climatic change is projected in three main steps. First we construct stories about how the Earth may change in the coming years in terms of things like population growth, availability and use of various sources of energy, the pace of economic development, and the pace of technological change. Next, these stories are interpreted via 'scenario models'. These models yield quantitative projections of the magnitude and dynamics of greenhouse gas emissions. Finally, these quantitative greenhouse gas emissions are used in large computer simulations of atmospheric and ocean physics which yield not only the climate projections that we readily encounter in the popular press, but much more detailed projections by region and year for many more variables than simply temperature.

In Chapter 3 we turn our attention to the methods that we use to study and predict the biological impacts of climatic change. These methods range from the laboratory, to the greenhouse, to the field. They involve theory, observation and experimentation. We have come a long way in our study of the biological impacts of climatic change, but there are limits to what we can show and what we have shown. In this chapter we identify and discuss some of these limitations. To become intelligent consumers of such impact studies, we need to appreciate their limitations. This chapter is particularly important as the ideas within apply to nearly all of the remainder of the book.

1 Putting it in Perspective: The Palaeorecord and Climate Reconstructions

The climate of the Earth has not been static at any scale of variability. Variations in the brightness of the Sun, fluctuations in the Earth's orbital properties, the changing geometry of the continents, the impacts of meteorites and the eruptions of volcanoes, and the activities of organisms all interact to produce a constantly changing climate. By examining the history of the Earth's climate we can answer questions such as: How unusual are the recent and anticipated changes in the Earth's climate? What have the effects of climatic changes been on species' distributions? How sensitive is the climate system to changes in atmospheric chemistry? How have patterns of variability and climatic extremes varied with changes in mean temperature? Because instrumental records of climate are available for barely 100 years of the Earth's approximately 4.5 billion year history, to see anything more than the briefest snapshot of its climate history it is necessary to make use of natural archives of climate information. In this chapter we examine the types of proxy records available for reconstructing the pre-instrumental climate of the Earth; we explore the history of the Earth's climate over the past 300 million years, with a particular focus on the climate of the last 15,000 years.

1.1 Methods of Palaeoclimatic Reconstruction

Many biological and geophysical processes are sensitive to variations in climate and thus record in their structures information that may be used to reconstruct the climate at their time of formation. These sources of information are generally termed 'proxy records of climate', since they are not direct measurements of the climate system itself, but rather indirect measurements of associated processes. There is a wide range of potential sources of proxy climate data (Table 1.1), but they all share a few common characteristics. First, they all contain non-climatic signals (or noise) as well as a climate signal. Second, they are sensitive only to particular features of the climate system, such as growing season moisture or mean annual water temperature. Lastly, they are sensitive to climate only at specific frequencies – above which it is not possible to resolve a signal and below which the climate signal may be confounded by other, non-climatic signals.

To extract the climate signal from these proxy records four main steps are necessary.

1. The chronology of the archive must be determined. That is, dates must be assigned to the components of the system that will be measured. There is a wide range of tools and techniques for doing this, some of which are addressed in more detail below, but two of the more commonly used techniques include radiocarbon dating – which allows the dating of organic material, within some range of uncertainty, that is up to 60,000 years old – and tree-ring cross-dating, which uses unique patterns of wide and narrow growth rings to assign specific calendar years to individual tree-ring measurements.
2. The parameter of interest must be measured. For some proxy records this step is relatively straightforward – as with the width of a tree ring or the particle size distribution for a sediment sample – but very often the measurement of proxy records is technically challenging, expensive and time-consuming.

Table 1.1. Common sources of palaeoclimatic data, their typical temporal properties and their commonly extracted climate signals.

Proxy record	Minimum resolution (years)	Typical time span (years)	Optimal frequency (years)	Main climate signals
Historical records	0.001–1	100s–1,000s	Variable	T, P, D, E, V, S
Tree rings	0.1–1	100–1,000	1–100	A, D, E, L, T, P
Sedimentary pollen	1–10	1,000–10,000	10–100	D, T, P, V
Sedimentary charcoal	1–10	1,000–10,000	10–100	D, E, V
Lake sediments	1–10	1,000–10,000	10–100	E, L
Diatoms	1–10	1,000–10,000	10–1,000	T, P, D, W
Chironomids	1–10	1,000–10,000	10–1,000	T, P, D, W
Ice cores	1–100	1,000–10,000+	10–100	A, D, E, P, T, S
Bivalve shells	0.1–1	10–100	1–10	T, W
Speleothems	1–10	100–1,000+	10–1,000+	T, P, W
Coral chemistry	0.1–1	10–100	1–100	T, L, P
Packrat middens	10–100	100–10,000	~100	D, V
Borehole temperature profiles	~10	500–1,000	10–100, decreasing with age/depth	T
Marine sediments	10–100	10,000–1,000,000	100–1,000	T, W, E, L

A, atmospheric composition; D, drought; E, events (e.g. volcanic eruptions, wildfires, storms); T, temperature; P, precipitation; V, vegetation change; S, solar variability; L, sea level; W, water chemistry.

For example, the measurement of gas concentrations in air bubbles trapped in ice cores requires that the core remains solidly frozen, isolated from potential contaminants (including the air in the laboratory itself), and the use of highly specialized equipment.

3. Once the parameter of interest has been dated and measured it must be calibrated to the climate signal being reconstructed. For some types of proxy record there is a direct physical relationship between the climate system and the measured properties of the proxy record. This is the case with many isotopic measurements made on geophysical proxy records (although they present other challenges to climate reconstruction). More commonly, a statistical relationship is calculated between the measured variable and the climate signal of interest, using the modern period for which instrumental data are available to calibrate the reconstruction model.

4. The resulting reconstruction must be verified against independent sources of climate information in order to establish its quality. For highly resolved proxy records such as tree rings, coral skeletal chemistry and varied sediments (see Section 1.3), the instrumental record may be used. A portion of the available data is usually withheld from the calibration and is used to quantify the quality of the reconstruction. For more poorly resolved proxies, and for those that do not overlap with the instrumental record, other means must be found to verify them, such as comparisons with other palaeoclimatic reconstructions or with global circulation models (GCMs; Chapter 2).

While there is an almost bewildering array of biological and geophysical records that can be used to reconstruct elements of the climate system, these records can generally be placed into one of four categories (Bradley, 1999): glaciological, geological, biological or historical. Within each of these categories there are many potential records available. For example, glaciological records include such measures as maximum extent (as evidenced by the formation of moraines), rates of ice accumulation (measured from core samples), atmospheric composition (measured from air bubbles trapped in these cores), the isotopic composition of the ice itself, the amount and source area of dust entrained within glaciers, and structural properties of the ice itself. Because many palaeoclimatic records are assigned dates using similar techniques, we begin our examination of palaeoclimatic records with a discussion of the main tools available for dating these samples.

1.2 Methods of Chronology Determination

One of the greatest challenges facing palaeoclimatologists lies in assigning dates to samples. Accurate dating is essential for comparing different records with each other, for determining the sequence of changes around the Earth, for evaluating rates of change and for disentangling the many chains of cause and effect in the Earth's climate system. A wide range of tools and techniques is available for dating samples of interest. They vary in their precision and accuracy, the materials to which they may be applied and the time scales over which they are useful. There are three main groups of techniques that are most commonly used for dating palaeoclimatic data: radioisotopic, palaeomagnetic and biological.

Radioisotopic techniques rely on the fact that under certain conditions unstable isotopes of a given element may be formed. If these initial conditions occur as a discrete event in time, and the decay rate of the element is known and appropriate to the age of the material being dated, these relationships can be used to determine the age of the material. The most common radioisotopic technique is radiocarbon dating, but there are other tools available to palaeoclimatologists including potassium–argon dating, uranium-series dating and cosmogenic dating. Palaeomagnetic techniques make use of episodic reversals in the Earth's magnetic field and movement of the position of the magnetic poles and the Earth's plates that result in predictable variations in the orientation of magnetic particles in rocks and sediments. Biological dating techniques make use of the growth rates and growth patterns of organisms to estimate their age and, by extension, the age of the surfaces on which they are growing. Very often these organisms also contain natural archives that can also be used to reconstruct properties of the climate system directly (see Section 1.3).

Radiocarbon dating

Radiocarbon dating is undoubtedly the workhorse of palaeoclimatic dating techniques. It can be applied to any organic compound, is useful for material up to approximately 50,000 years in age and is relatively inexpensive to perform. Radiocarbon dating is possible because carbon atoms occur in three distinct forms or isotopes. Carbon-12 atoms (denoted ^{12}C) contain six protons and six neutrons, and are the most common carbon isotope, accounting for about 98.9% of the Earth's atmosphere. The other important isotope is carbon-14 (^{14}C), which represents only 0.0000000001% of the Earth's atmosphere. The remaining isotope, carbon-13 (^{13}C), accounts for the remaining approximately 1.1% of the Earth's atmosphere, but is not used for dating purposes. ^{14}C is formed in the Earth's upper atmosphere when a nitrogen atom is struck by a neutron energized by cosmic radiation. This neutron displaces one proton, leaving the atom with only six protons but eight neutrons – converting it from ^{14}N to ^{14}C. A hydrogen atom is also produced during this process. ^{14}C is an unstable isotope of carbon, though, and episodically a neutron in the atom will decay into a proton and an electron, converting the carbon atom back into nitrogen. The rate of this decay is relatively constant, such that, in a given sample, half of the ^{14}C will decay in approximately 5730 years. This interval, termed the 'half-life' of the isotope, means that, for example, a 100 g sample of wood might initially contain 5.0×10^{-9} g ^{14}C, and would contain only 9.8×10^{-12} g ^{14}C after ten half-lives.

Newly produced carbon atoms oxidize rapidly to form carbon dioxide (CO_2) and are readily mixed throughout the atmosphere. Because plants assimilate CO_2 during photosynthesis, plant tissues contain a proportion of ^{14}C similar to the atmosphere. This radioactive carbon cascades through the food web as herbivores consume plants, and as carnivores consume herbivores. Thus, all living organisms contain a small proportion of ^{14}C in their tissues. The fact that ^{14}C is assimilated only by living organisms, coupled with the fact that it decays over time, allows scientists to measure the relative abundance of ^{14}C to ^{12}C to determine the length of time that has passed since the organism died. The accuracy of dates determined by radiocarbon dating is complicated by several factors. First, the decay rate of ^{14}C is slightly variable, meaning that the half-life is more correctly stated as 5730±40 years. Second, as samples age, the amount of ^{14}C present decreases to the point where it is difficult to measure the decay rate accurately. Several other issues are worth discussing in more detail.

One of the main assumptions behind radiocarbon dating is that the total amount of ^{14}C in the atmosphere has been constant over time. It is now widely recognized that this assumption is not valid