

MICHAEL BEGON  
COLIN R. TOWNSEND

# ECOLOGY

FROM INDIVIDUALS TO ECOSYSTEMS

FIFTH EDITION



WILEY Blackwell



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This fifth edition first published 2021 © 2021 by John Wiley & Sons Ltd

*Edition History*

4e, Wiley, 2006; 3e, Wiley, 1996; 2e, Wiley 1990; 1e, Wiley, 1986

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John Wiley & Sons Ltd, The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

*Editorial Office*

9600 Garsington Road, Oxford, OX4 2DQ, UK

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*Library of Congress Cataloging-in-Publication Data*

Names: Begon, Michael, author. | Townsend, Colin R., author.

Title: Ecology : from individuals to ecosystems / Michael Begon, The University of Liverpool, Liverpool, UK, Colin Townsend, University of Otago, Dunedin, New Zealand.

Description: Fifth edition. | Hoboken, NJ : Wiley, 2021. | Includes bibliographical references and index.

Identifiers: LCCN 2020012775 (print) | LCCN 2020012776 (ebook) | ISBN 9781119279358 (paperback) | ISBN 9781119279372 (adobe pdf) | ISBN 9781119279310 (epub)

Subjects: LCSH: Ecology.

Classification: LCC QH541 .B415 2020 (print) | LCC QH541 (ebook) | DDC 577-dc23

LC record available at <https://lcn.loc.gov/2020012775>

LC ebook record available at <https://lcn.loc.gov/2020012776>

Cover Design: Wiley

Cover Credit: Decorators painting wall © Dougal Waters/Getty Images

Panel of Native American Newspaper Rock petroglyphs © milehightraveler/Getty Image

Set in 10.5/13pt Dante by SPi Global, Pondicherry, India

*This book is dedicated to our families, and especially to our children and grandchildren,  
who will inherit the ecosystems we hand on to them –  
by Mike to Linda, Jessica, Robert, Carl, Ria and Erica,  
and by Colin to Dominic, Brennan, Amelie and Ella*



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# Preface

## A science for everybody – but not an easy science

This book is about the distribution and abundance of living organisms, and about the physical, chemical and especially the biological features and interactions that determine these distributions and abundances.

Unlike some other sciences, the subject matter of ecology is apparent to everybody: most people have observed and pondered the natural world. In this sense most people are ecologists of sorts. But ecology is not an easy science. It must deal explicitly with three separate levels of the biological hierarchy – the individual organisms, the populations of organisms, and the communities of populations. What's more, as we shall see, it can't ignore the detailed biology of individuals, or the pervading influences of historical, evolutionary and geological events. It feeds on advances in our knowledge of biochemistry, behaviour, climatology, plate tectonics and so on, but it feeds back to our understanding of vast areas of biology too. One of the fathers of modern evolutionary biology, T. H. Dobzhansky famously claimed, in the middle of the 20th century, that 'Nothing in biology makes sense, except in the light of evolution'. But equally, very little in evolution, and hence in biology as a whole, makes sense, except in the light of ecology.

Ecology, too, has the distinction of being peculiarly confronted with uniqueness: millions of different species, countless billions of genetically distinct individuals, all living and interacting in a varied and ever-changing world. Imagine doing chemistry if water molecules were not precisely the same, always and everywhere – or physics if the speed of light was different at different field sites. The challenge for ecologists, therefore, is to seek patterns and predictions in a way that recognises this uniqueness and complexity,

rather than being swamped by it. The mathematician and philosopher Alfred North Whitehead's advice for scientists, offered 100 years ago, is never more apposite than when applied to ecology: 'Seek simplicity – and distrust it'.

## Thirty-four years on: the urgent problems facing us

This fifth edition comes fully 14 years after its immediate predecessor and 34 years after the first edition. Much has changed over that time – in ecology, in the world around us, and also, unsurprisingly, in us authors. The first edition had a cave painting as its cover, which we justified in the Preface by arguing that 'ecology, if not the oldest profession, is probably the oldest science', since the most primitive humans had to understand, as a matter of necessity, the dynamics of the environment in which they lived. We pursued that cave painting theme for two further editions, but for the fourth edition, replaced it with its modern equivalent, urban graffiti. This captured the idea that we, as a species, are still driven to broadcast our feelings graphically and publicly, but the cave painting's celebration of nature's bounty had been replaced by an impassioned plea for its protection. Now, 14 years on, the image on our cover, and its message, are darker and more desperate. Instead of focusing on those who are pleading, on nature's behalf, for respect, this time we shine our light on man the destroyer – obliterating the heritage in our cave painting as he is threatening our natural heritage (the inspiration coming from graffiti artist Banksy, who used a similar idea in an art work involving a water blaster). The ecosystem on our front cover is still there – but it is disappearing.

This evolving image reminds us, too, that 34 years ago it seemed acceptable for ecologists to hold a comfortable, detached position, from which the ecological communities around us were simply material for which we sought a scientific understanding. Now, we must accept the immediacy of the environmental problems that threaten us and the responsibility of ecologists to come in from the sidelines and play their full part in addressing these problems. Applying the principles that emerge from the study of ecology is not only a practical necessity, but also as challenging as deriving those principles in the first place. Thus, in this edition, two whole chapters and one half of another are devoted entirely to applied topics, and examples of how ecological principles have been applied to problems facing us appear, and are highlighted, throughout the remaining 19 chapters. Nonetheless, we remain wedded to the belief that environmental action can only ever be as sound as the ecological principles on which it is based. Hence, while we have tried harder than ever to help improve preparedness for addressing the environmental problems of the years ahead, the book remains, in its essence, an exposition of the *science* of ecology.

## About this fifth edition

Hence, we have aimed to make this fifth edition an up-to-date guide to ecology *now*. To this end, the results from around 1000 studies have been newly incorporated into the text, most of them published since the fourth edition. Nonetheless, we have resisted the temptation to lengthen the text, mindful that, clichéd as it may be, less is often more. We have also consciously attempted, while including so much modern work, to avoid bandwagons that seem likely to have run into the buffers by the time many will be using the book. Of course, we may also, sadly, have excluded bandwagons that go on to fulfil their promise.

Having said this, we hope, still, that this edition will be of value to all those whose degree programme includes ecology and all who are, in some way, practicing ecologists. Certain aspects of the subject, particularly the mathematical ones, will prove difficult for some, but our coverage is designed to ensure that wherever our readers' strengths lie – in the field or laboratory, in theory or in practice – a balanced and up-to-date view should emerge.

Different chapters of this book contain different proportions of descriptive natural history, physiology, behaviour, rigorous laboratory and field experimentation, careful field monitoring and censusing, and mathematical modelling (a form of simplicity that it is essential to seek but equally essential to distrust). These varying proportions to some

extent reflect the progress made in different areas. They also reflect intrinsic differences in various aspects of ecology. Whatever progress is made, ecology will remain a meeting-ground for the naturalist, the experimentalist, the field biologist and the mathematical modeller. We believe that all ecologists should to some extent try to combine all these facets.

## Technical and pedagogical features

An important technical feature is the incorporation of marginal notes as signposts throughout the text. These, we hope, will serve a number of purposes. In the first place, they constitute a series of subheadings highlighting the detailed structure of the text. However, because they are numerous and often informative in their own right, they can also be read in sequence along with the conventional subheadings, as an outline of each chapter. They should act too as a revision aid for students – indeed, they are similar to the annotations that students themselves often add to their textbooks. Finally, because the marginal notes generally summarise the take-home message of the paragraph or paragraphs that they accompany, they can act as a continuous assessment of comprehension: if you can see that the signpost is the take-home message of what you have just read, then you have understood.

To highlight the link between the pure science of ecology and the application of this knowledge to the many environmental problems that now face us we have introduced a new feature – a systematic presentation of ecological applications, highlighted in special boxes throughout the text.

## Acknowledgments

This is the second major revision we have written as a two-some rather than a trio, and this time the authorship reflects this. Nonetheless, while little remains of the original text, we are deeply conscious of the debt we owe to John Harper, who sadly died in 2009. We cannot promise to have absorbed or, to be frank, to have accepted, every one of his views, but we hope, in this fifth edition, that we have not strayed too far from the paths along which he guided us. If readers recognise any attempts to stimulate and inspire rather than simply to inform, to question rather than to accept, to respect our readers rather than to patronise them, and to avoid unquestioning obedience to current reputation while acknowledging our debt to the masters of the past, then they will have identified John's intellectual legacy still firmly imprinted on the text.

In previous editions we thanked the great many friends and colleagues who helped us by commenting on various drafts of the text. The effects of their contributions are still strongly evident in the present edition. This fifth edition was also read by a series of reviewers, and we are delighted to be able to acknowledge their help. Thanks to David Atkinson, Richard Bardgett, Rob Brooker, Dylan Childs, Tim Coulson, Hans de Kroon, Andy Fenton, Rob Freckleton, Cristina Garcia, Sue Hartley, Andy Hector, Alan Hildrew, Marcel Holyoak, Dave Hooper, Tony Ives, Xavier Lambin, Steve Long, Michel Loreau, Peter Morin, Asko

Noormets, Ilik Saccheri, Ross Thomson, Jake Weiner and Rob Whittaker.

At our publisher Wiley, we are grateful to Ward Cooper (now moved on), who brought us back within the fold, and throughout the writing and production to Sarah Keegan, Jane Andrew, Jane Grisdale and Debbie Maizels.

Mike Begon  
Colin Townsend

## About the Companion Website

This book is accompanied by a website, with resources for Instructors and Students.

**[www.wiley.com/go/begon/ecology5](http://www.wiley.com/go/begon/ecology5)**

The Instructor resources include:

- Figures as Powerpoint and jpgs

The Student resources include:

- Glossary of terms

# Introduction: Ecology and its Domain

## Definition and scope of ecology

The word 'ecology' was first used by Ernest Haeckel in 1866. Paraphrasing Haeckel we can describe ecology as the scientific study of the interactions between organisms and their environment. The word is derived from the Greek *oikos*, meaning 'home'. Ecology might therefore be thought of as the study of the 'home life' of living organisms. A less vague definition was suggested by Krebs (1972): 'Ecology is the scientific study of the interactions that determine the distribution and abundance of organisms'. Notice that Krebs' definition does not use the word 'environment'; to see why, it is necessary to define the word. The environment of an organism consists of all those factors and phenomena outside the organism that influence it, whether these are physical and chemical (abiotic) or other organisms (biotic). The 'interactions' in Krebs' definition are, of course, interactions with these very factors. The environment therefore retains the central position that Haeckel gave it.

Krebs' definition has the merit of pinpointing the ultimate subject matter of ecology: the distribution and abundance of organisms – *where* organisms occur, *how many* occur there and *why*. This being so, it might be better still to define ecology as:

the scientific study of the distribution and abundance of organisms and the interactions that determine distribution and abundance.

As far as the subject matter of ecology is concerned, 'the distribution and abundance of organisms' is pleasantly succinct. But we need to expand it. The living world can be viewed as a biological hierarchy that starts with subcellular particles, and continues up through cells, tissues and organs.

Ecology deals with the next three levels: the individual *organism*, the *population* (consisting of individuals of the same species) and the *community* (consisting of a greater or lesser number of species populations). At the level of the organism, ecology deals with how individuals are affected by (and how they affect) their environment. At the level of the population, ecology is concerned with the presence or absence of particular species, their abundance or rarity, and with the trends and fluctuations in their numbers. Community ecology then deals with the composition and organisation of ecological communities. Ecologists also focus on the pathways followed by energy and matter as these move among living and non-living elements of a further category of organisation: the *ecosystem*, comprising the community together with its physical and chemical environment.

There are two broad approaches that ecologists can take at each level of ecological organisation. First, much can be gained by building from properties at the level below: physiology when studying organismal ecology; individual clutch size and survival probabilities when investigating the dynamics of individual populations of species; food consumption rates when dealing with interactions between predator and prey populations; limits to the similarity of coexisting species when researching communities, and so on. An alternative approach deals directly with properties of the level of interest – for example, niche breadth at the organismal level; relative importance of density-dependent processes at the population level; species diversity at the level of community; rate of biomass production at the ecosystem level – and tries to relate these to abiotic or biotic aspects of the environment. Both approaches have their uses, and both will be used throughout the book.

## Explanation, description, prediction and control

At all levels of ecological organisation we can try to do a number of different things. In the first place we can try to *explain* or *understand*. This is a search for knowledge in the pure scientific tradition. Obviously, though, in order to understand something, we must first have a *description* of whatever it is that we wish to understand. This, in itself, adds to our knowledge of the living world. Note, however, that the most valuable descriptions are those carried out with a particular problem or 'need for understanding' in mind. All descriptions are selective: but undirected description, carried out for its own sake, is often found afterwards to have selected the wrong things.

Ecologists also often try to *predict* what will happen to an organism, a population, a community or an ecosystem under a particular set of circumstances: and on the basis of these predictions we may try to *control* the situation. We may try to minimise the effects of locust plagues by predicting when they are likely to occur and taking appropriate action. We may try to protect crops by predicting when conditions will be favourable to the crop and unfavourable to its enemies. We may try to maintain endangered species by predicting the conservation policy that will enable them to persist. And we may try to conserve biodiversity in order to maintain ecosystem 'services' such as the protection of chemical quality of natural waters. Some prediction and control can be carried out without explanation or understanding. But confident predictions, precise predictions and predictions of what will happen in unusual circumstances can be made only when we can explain what is going on. Mathematical modelling has played, and will continue to play, a crucial role in the development of ecology, particularly in our ability to predict outcomes. But it is the real world we are interested in, and the worth of models must always be judged in terms of the light they shed on the working of natural systems.

Note, too, that there are two different classes of explanation in biology: proximal and ultimate explanations. For example, the present distribution and abundance of a particular species of bird may be 'explained' in terms of the physical environment that the bird tolerates, the food that it eats and the parasites and predators that attack it. This is a *proximal* explanation. However, we may also ask how this species of bird comes to have these properties that now appear to govern its life. This question has to be answered by an explanation in evolutionary terms. The *ultimate* explanation of the present distribution and abundance of this bird lies in the ecological experiences of its ancestors. There are many problems in ecology that

demand evolutionary, ultimate explanations: 'How have organisms come to possess particular combinations of size, developmental rate, reproductive output and so on?' (Chapter 7), 'What causes predators to adopt particular patterns of foraging behaviour?' (Chapter 9) and 'How does it come about that coexisting species are often similar but rarely the same?' (Chapters 8 and 16). These problems are as much part of modern ecology as are the prevention of plagues, the protection of crops and the preservation of rare species. Our ability to control and exploit ecosystems cannot fail to be improved by an ability to explain and understand. And in the search for understanding, we must combine both proximal and ultimate explanations.

## Pure and applied ecology

Ecologists are concerned not only with ecosystems, communities, populations and organisms *in nature*, but also with man-made or human-influenced environments (plantation forests, wheat fields, grain stores, nature reserves and so on), and with the consequences of human influence *on* nature (pollution, overharvesting, the spread of invasive species, global climate change, etc.). Our influence is so pervasive that we would be hard pressed to find an environment that was totally unaffected by human activity. Indeed, moves are afoot to designate a new geological epoch – the Anthropocene – the latest slither of geological history during which people have become a major geological force and the major ecological force around the globe. Environmental problems are now high on the political agenda and ecologists clearly have a central role to play: a sustainable future depends fundamentally on ecological understanding and our ability to predict or produce outcomes under different scenarios.

When the first edition of this text was published in 1986, the majority of ecologists would have classed themselves as pure scientists, defending their right to pursue ecology for its own sake and not wishing to be deflected into narrowly applied projects. The situation has changed dramatically in the past three and a half decades, partly because governments have shifted the focus of grant-awarding bodies towards ecological applications, but also, and more fundamentally, because ecologists have themselves responded to the need to direct much of their research to the many environmental problems that have become ever more pressing. This is recognised in this new edition by a systematic treatment of ecological applications throughout the text. We believe strongly that the application of ecological theory must be based on a sophisticated understanding of the pure science. Thus, our treatment of ecological applications is organised alongside the theory in each chapter.







## Chapter 1

# Organisms in their Environments: the Evolutionary Backdrop

### 1.1 Introduction: natural selection and adaptation

From our definition of ecology in the Preface, and even from a layman's understanding of the term, it is clear that at the heart of ecology lies the relationship between organisms and their environments. In this opening chapter we explain how, fundamentally, this is an evolutionary relationship. The great Russian–American biologist Theodosius Dobzhansky famously said: 'Nothing in biology makes sense, except in the light of evolution'. This is as true of ecology as of any other aspect of biology. Thus, we try here to explain the processes by which the properties of different sorts of species make their life possible in particular environments, and also to explain their failure to live in other environments. In mapping out this evolutionary backdrop to the subject, we will also be introducing many of the questions that are taken up in detail in later chapters.

#### the meaning of adaptation

The phrase that, in everyday speech, is most commonly used to describe the match between organisms and environment is: 'organism X is adapted to' followed by a description of where the organism is found. Thus, we often hear that 'fish are adapted to live in water', or 'cacti are adapted to live in conditions of drought'. In everyday speech, this may mean very little: simply that fish have characteristics that allow them to live in water (and perhaps exclude them from other environments) or that cacti have characteristics that allow them to live where water is scarce. The word 'adapted' here says nothing about how the characteristics were acquired. For an ecologist or

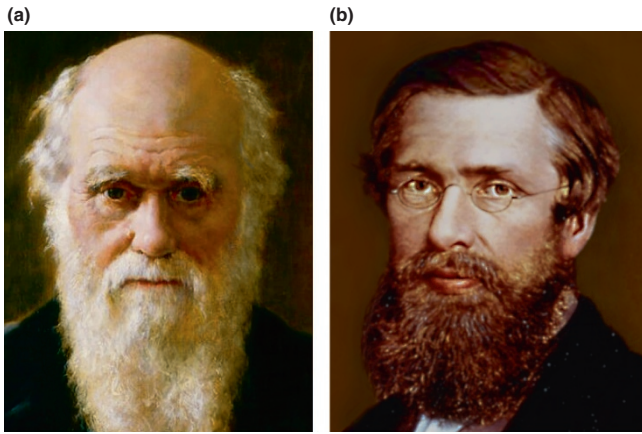
evolutionary biologist, however, 'X is adapted to live in Y' means that environment Y has provided forces of natural selection that have affected the life of X's ancestors and so have moulded and specialised the evolution of X. 'Adaptation' means that genetic change has occurred.

Regrettably, though, the word '*adaptation*' implies that organisms are matched *to* their present environments, suggesting 'design' or even 'prediction'. But organisms have not been designed for, or fitted to, the present: they have been moulded (by *natural selection*) by past environments. Their characteristics reflect the successes and failures of ancestors. They appear to be apt for the environments that they live in at present only because present environments tend to be similar to those of the past.

The theory of evolution by natural selection is an ecological theory. It was first elaborated by Charles Darwin (1859), though its essence was also appreciated by a contemporary and correspondent of Darwin's, Alfred Russell Wallace (Figure 1.1). It rests on a series of propositions.

#### evolution by natural selection

- 1 The individuals that make up a population of a species are *not identical*: they vary, although sometimes only slightly, in size, rate of development, response to temperature, and so on.
- 2 Some, at least, of this variation is *heritable*. In other words, the characteristics of an individual are determined to some extent by its genetic make-up. Individuals receive their genes from their ancestors and therefore tend to share their characteristics.



**Figure 1.1 The fathers of evolution.** (a) Charles Darwin. Detail from painting by John Collier 1883 (National Portrait Gallery RPG 1024). (b) Alfred Russell Wallace. Detail from photograph by Thomas Sims 1869, colourised by Paul Edwards, copyright G. W. Beccaloni.

- 3 All populations have the *potential* to populate the whole earth, and they would do so if each individual survived and each individual produced its maximum number of descendants. But they do not: many individuals die prior to reproduction, and most (if not all) reproduce at a less than maximal rate.
- 4 Different ancestors leave *different numbers of descendants*. This means much more than saying that different individuals produce different numbers of offspring. It includes also the chances of survival of offspring to reproductive age, the survival and reproduction of the progeny of these offspring, the survival and reproduction of their offspring in turn, and so on.
- 5 Finally, the number of descendants that an individual leaves depends, not entirely but crucially, on *the interaction between the characteristics of the individual and its environment*.

In any environment, some individuals will tend to survive and reproduce better, and leave more descendants, than others. If, because of this, the heritable characteristics of a population change from generation to generation, then evolution by natural selection is said to have occurred. This is the sense in which nature may loosely be thought of as *selecting*. But nature does not select in the way that plant and animal breeders select. Breeders have a defined end in view – bigger seeds or a faster racehorse. But nature does not *actively* select in this way: it simply sets the scene within which the evolutionary play of differential survival and reproduction is played out.

fitness: it is all relative

The fittest individuals in a population are those that leave the greatest number of descendants.

In practice, the term is often applied not to a single individual, but to a typical individual or a type. For example, we may say that in sand dunes, yellow-shelled snails are fitter than brown-shelled snails. *Fitness*, then, is a relative not an absolute term. The fittest individuals in a population are those that leave the greatest number of descendants *relative to* the number of descendants left by other individuals in the population.

When we marvel at the diversity of complex specialisations, there is a temptation to regard each case as an example of evolved perfection. But this would be wrong. The evolutionary process works on the genetic variation that is available. It follows that natural selection is unlikely to lead to the evolution of perfect, ‘maximally fit’ individuals. Rather, organisms come to match their environments by being ‘the fittest available’ or ‘the fittest yet’: they are not ‘the best imaginable’. Part of the lack of fit arises because the present properties of an organism have not all originated in an environment similar in every respect to the one in which it now lives. Over the course of its evolutionary history (its phylogeny), an organism’s remote ancestors may have evolved a set of characteristics – evolutionary ‘baggage’ – that subsequently constrain future evolution. For many millions of years, the evolution of vertebrates has been limited to what can be achieved by organisms with a vertebral column. Moreover, much of what we now see as precise matches between an organism and its environment may equally be seen as constraints: koala bears live successfully on *Eucalyptus* foliage, but, from another perspective, koala bears cannot live without *Eucalyptus* foliage.

evolved perfection? no

## 1.2 Specialisation within species

The natural world is not composed of a continuum of types of organism each grading into the next: we recognise boundaries between one type of organism and another. Nevertheless, within what we recognise as *species* (defined below), there is often considerable variation, and some of this is heritable. It is on such intraspecific variation, after all, that plant and animal breeders – and natural selection – work.

The word ‘*ecotype*’ was first coined for plant populations (Turesson, 1922a, 1922b) to describe genetically determined differences between populations within a species that reflect local matches between the organisms and their environments. But evolution forces the characteristics of populations to diverge from each other only if: (i) there is sufficient heritable variation on which selection can act; and (ii) the forces favouring divergence are strong enough

to counteract the mixing and hybridisation of individuals from different sites. Two populations will not diverge completely if their members (or, in the case of plants, their pollen) are continually migrating between them and mixing their genes.

Local, specialised populations become differentiated most conspicuously amongst organisms that are immobile for most of their lives. Motile organisms have a large measure of control over the environment in which they live; they can recoil or retreat from a lethal or unfavourable environment and actively seek another. Sessile, immobile organisms have no such freedom. They must live, or die, in the conditions where they settle. Populations of sessile organisms are therefore exposed to forces of natural selection in a peculiarly intense form.

This contrast is highlighted on the seashore, where the intertidal environment continually oscillates between the terrestrial and the aquatic. The fixed algae, sponges, mussels and barnacles all tolerate life somewhere along the continuum. But the mobile shrimps, crabs and fish track their aquatic habitat as it moves; whilst the shore-feeding birds track their terrestrial habitat. The mobility of such organisms enables them to match their environments to themselves. The immobile organism must match itself to its environment.

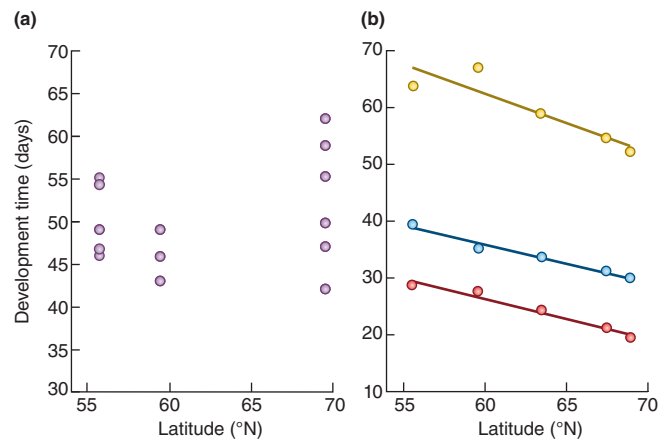
### 1.2.1 Geographic variation within species: ecotypes

geographic  
variation on a  
small scale

Differentiation within a species can occur over a remarkably small geographic scale. In the case of sweet vernal grass, *Anthoxanthum odoratum*, growing along a 90 m transition zone between mine and pasture soils at the Trelogan zinc and lead mine in Wales, there was a striking increase in evolved tolerance to zinc, at otherwise toxic concentrations, over a distance of only 3 m within the zone. In this case, any counteracting mixing and hybridisation of the ecotypes was reduced because plants growing on the mine soil tended to flower later than their counterparts in the pasture (Antonovics, 2006).

.... and a large scale

In a study with a much broader geographic range, common frogs (*Rana temporaria*) were monitored over a latitudinal gradient encompassing Sweden and Finland. Geographic variation within species is generally studied both *in situ* and using a 'common garden' approach, where individuals from different sites are transplanted and grown together, thus eliminating any influence of immediate environments. In this case, while there was considerable variation in tadpole development time (from complete gill absorption to emergence of



**Figure 1.2 At a given temperature, tadpoles from higher latitudes developed faster than those from lower latitudes.**

(a) Tadpoles from ponds in two areas of Sweden, in the south, and from Finland, in the north, showed variation in development times but no consistent trend with latitude.

(b) When tadpoles from sites at various latitudes were reared in the laboratory at different temperatures, those from higher latitudes consistently developed fastest. Temperatures: 14°C (yellow circles), 18°C (blue circles), and 22°C (red circles).

Source: From Laugen *et al.* (2003).

the first foreleg), no consistent trend with latitude was evident (Figure 1.2a). However, when tadpoles from different sites were reared in a common environment, at a range of temperatures, those from higher latitudes developed significantly faster. There had clearly been local adaptation, and frogs experiencing colder temperatures (at higher latitudes) had evolved compensatory increases in development rate. The net result was that development times were similar at different latitudes.

On the other hand, local selection by no means always overrides hybridisation. In a study of *Chamaecrista fasciculata*, an annual legume from disturbed habitats in eastern North

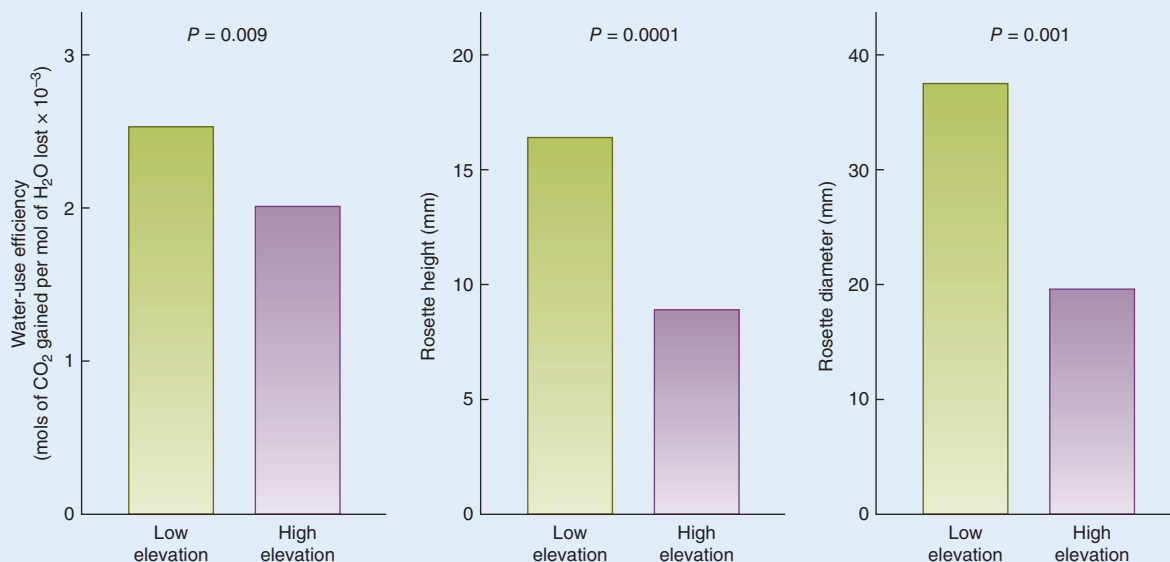
the balance  
between local  
adaptation and  
hybridisation

America, plants were grown in a common garden that had been derived from the 'home' site or were transplanted from distances of 0.1, 1, 10, 100, 1000 and 2000 km (Galloway & Fenster, 2000). The study was replicated three times: in Kansas, Maryland and northern Illinois. Five characteristics were measured: germination, survival, vegetative biomass, fruit production and the number of fruit produced per seed planted. But for all characters in all replicates there was little or no evidence for local adaptation except for transplant distances of 1000 km or more. There is 'local adaptation' – but in this case it was clearly not *that* local.

### APPLICATION 1.1 Selection of ecotypes for conservation

The sapphire rockcress, *Arabis fecunda*, is a rare perennial herb restricted to calcareous soil outcrops in western Montana (USA) – so rare, in fact, that there are just 19 existing populations separated into two groups ('high elevation' and 'low elevation') by a distance of around 100 km. Whether there is local adaptation is of practical importance for conservation: four of the low-elevation populations are under threat from spreading urban areas and may require reintroduction from elsewhere if they are to be sustained. Reintroduction may fail if local adaptation is too marked. Observing plants in their own habitats and checking for differences between them would not tell us if there was local adaptation in the evolutionary sense. Differences may

simply be the result of immediate responses to contrasting environments made by plants that are essentially the same. But once again, the 'common garden' approach circumvents this problem. The low-elevation sites were more prone to drought – both the air and the soil were warmer and drier – and the low-elevation plants in the common garden were indeed significantly more drought tolerant (Figure 1.3). More generally, we need to improve our understanding of local adaptation, and its genetic basis, because of their importance for the conservation and restoration of genetic resources, and for crop and animal production, and this is of particular significance in a changing climate (McKay *et al.*, 2005; Savolainen *et al.*, 2013).

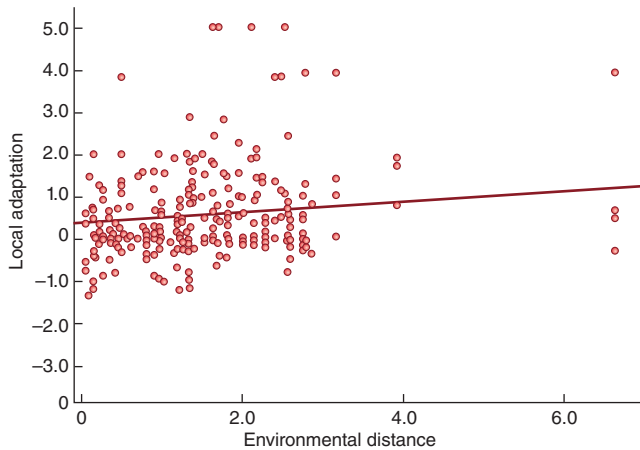


**Figure 1.3** Local adaptation of rare sapphire rockcress plants. When plants of the rare sapphire rockcress from low-elevation (drought-prone) and high-elevation sites were grown together in a common garden, there was local adaptation: those from the low-elevation site had significantly better water-use efficiency as well as having both taller and broader rosettes. *Source:* From McKay *et al.* (2001).

We can also test whether organisms have evolved to become specialised to life in their local environment in *reciprocal transplant* experiments: comparing their performance when they are grown 'at home' (i.e. in their original habitat) with their performance 'away' (i.e. in the habitat of others). In his meta-analysis of 74 reciprocal transplant studies (50 concerning plants, 21 animals, two fungi and one protist), Hereford (2009) reported that local adaptation was common (71% of studies) but not ubiquitous. On average, local populations

had 45% greater fitness than non-local populations. And crucially, there was a small but significant positive association between fitness differences and the magnitude of environmental differences between parental sites ('environmental distance' measured using composite values for up to four environmental variables, such as soil moisture, annual rainfall, elevation and frequency of predation) (Figure 1.4). The magnitude of local adaptation does not seem to be correlated with geographic distance (Leimu & Fischer, 2008), so





**Figure 1.4 Meta-analyses reveal generalities about local adaptation.** Regression of local adaptation on environmental distance between sites in a meta-analysis of reciprocal transplant experiments ( $P = 0.003$ ). Local adaptation is the difference in relative fitness between a native population and a non-native population in the native's environment. To standardise measures of environmental difference between sites, Euclidean distances from the means of environmental variables were calculated for all sites in each study. *Source:* From Hereford (2009).

Hereford's results emphasise the role of ecological factors, not separation itself, as drivers of adaptive differentiation.

### 1.2.2 Genetic polymorphism

#### transient polymorphisms

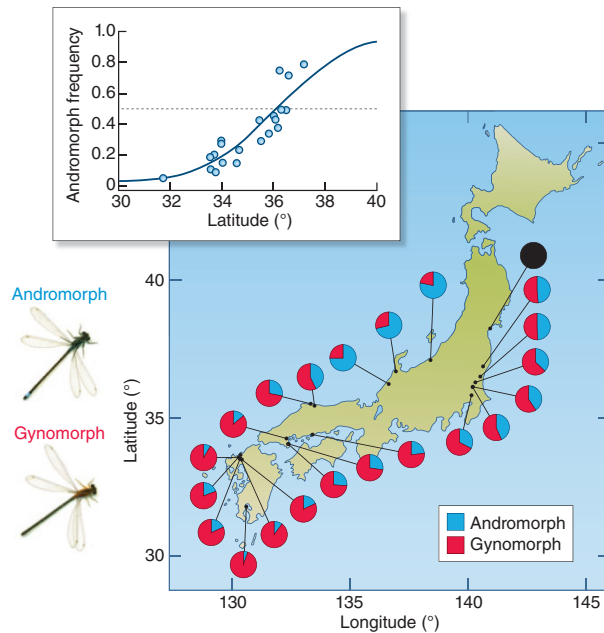
On a finer scale than ecotypes, it may also be possible to detect levels of variation *within* populations.

Such variation is known as polymorphism. Specifically, genetic polymorphism is 'the occurrence together in the same habitat of two or more discontinuous forms of a species in such proportions that the rarest of them cannot merely be maintained by recurrent mutation or immigration' (Ford, 1940). Not all such variation represents a match between organism and environment. Indeed, some of it may represent a mismatch, if, for example, conditions in a habitat change so that one form is being replaced by another. Such polymorphisms are called transient. As all communities are always changing, much polymorphism that we observe in nature may be transient, representing the extent to which the genetic response of populations to environmental change will always be out of step with the environment and unable to anticipate changing circumstances.

Many polymorphisms, however, are actively maintained in a population by natural selection, and there are a number of ways in which this may occur.

#### the maintenance of polymorphisms

- 1 *Heterozygotes may be of superior fitness*, but because of the mechanics of Mendelian genetics they continually generate less fit homozygotes within the population. Such 'heterosis' is seen in human sickle-cell anaemia where malaria is prevalent. The malaria parasite attacks red blood cells. The sickle-cell mutation gives rise to red cells that are physiologically imperfect and misshapen. However, sickle-cell heterozygotes are fittest because they suffer only slightly from anaemia and are little affected by malaria, but they continually generate homozygotes who are either dangerously anaemic (two sickle-cell genes) or susceptible to malaria (no sickle-cell genes). Nonetheless, the superior fitness of the heterozygote maintains both types of gene in the population (that is, a polymorphism).
- 2 *There may be gradients of selective forces* favouring one form (morph) at one end of the gradient, and another form at the other. This can produce polymorphic populations at intermediate positions in the gradient. Females of some damselfly species come in distinct colour morphs: gynomorphs and male-mimicking andromorphs. The andromorph form may provide benefit by reducing harassment of the females by males, allowing more time for foraging, but this may be at the expense of being more obvious to predators (Huang & Reinhard, 2012). Takahashi *et al.* (2011) have described a geographic cline in this polymorphism in *Ischnura senegalensis* over a latitudinal range of 1100 km in Japan (Figure 1.5). Such clines suggest that the fitness advantage of each morph changes differentially along an environmental gradient such that the balance of advantage switches around a mid-point where each phenotype has equal fitness. In this case, Takahashi *et al.* (2011) determined that the reproductive potential of gynomorphs (related to ovariole number, body size and egg volume) was indeed higher in the south and lower in the north compared with andromorphs.
- 3 *There may be frequency-dependent selection* where each of the morphs of a species is fittest when it is rarest (Clarke & Partridge, 1988). This is believed to be the case when rare colour forms of prey are fit because they go unrecognised and are therefore ignored by their predators.
- 4 *Selective forces may operate in different directions within different patches* in the population. A striking example of



**Figure 1.5** The frequency of andromorphs of local damselfly populations in Japan increases with latitude. The inset shows the logistic regression with latitude ( $t = 8.15$ ,  $df = 21$ ,  $P < 0.001$ ), excluding the northernmost population (solid black plot). This population had been recently established in a newly created pond by gynomorphs, and showed 100% gynomorph frequency because of the founder effect. Source: From Takahashi *et al.* (2011).

this is provided by a reciprocal transplant study of white clover (*Trifolium repens*) in a field in north Wales. To determine whether the characteristics of individuals matched local features of their environment, Turkington and Harper (1979) removed plants from marked positions in the field and multiplied them into clones in the common environment of a greenhouse. They then transplanted samples from each clone into the place in the sward of vegetation from which it had originally been taken (as a control), and also to the places from where all the others had been taken (a transplant). The plants were allowed to grow for a year before they were removed, dried and weighed. The mean weight of clover plants transplanted back into their home sites was 0.89 g but at away sites it was only 0.52 g, a statistically highly significant difference. This provides strong, direct evidence that clover clones in the pasture



**Figure 1.6** Contrasting ecotypes of the periwinkle *Littorina saxatilis* from Sweden and Spain. Swedish crab ecotype (top left) and wave ecotype (top right), and Spanish wave ecotype (bottom left) and crab ecotype (bottom right). Source: From Johannesson (2015).

had evolved to become specialised, such that they performed best in their local environment. But all this was going on within a single population, which was therefore polymorphic.

In fact, the distinction between local ecotypes and polymorphic populations is not always a clear one, as illustrated by a study involving the marine snail *Littorina saxatilis*.

no clear distinction between local ecotypes and a polymorphism

This common inhabitant of North Atlantic shores is remarkably polymorphic with reproductively isolated ecotypes in microhabitats where crabs are either present and wave action is weak (crab ecotype), or on wave-swept rocky surfaces where waves are strong and crabs are absent (wave ecotype) (Johannesson, 2015). The crab ecotype is large and robust, with a thick shell, a high spire and a relatively small aperture, while the wave ecotype is only about half the size of its crab counterpart, has a thin shell, a relatively large aperture and a low spire (Figure 1.6). The same pattern is observed in different parts of the snail's range and, for example, in both Sweden and Spain, snails of each ecotype are fitter in their native microhabitat than if moved to the other microhabitat. In contact zones, however, snail morphologies represent a continuum from one morph to the other, with all possible intermediate stages. Even though the spatial scale of distribution of the two ecotypes may be very small, the forces of selection are clearly able to outweigh the mixing forces of hybridisation – but it is a moot point whether we should describe this as a small-scale series of local ecotypes or a polymorphic population maintained by a gradient of selection.



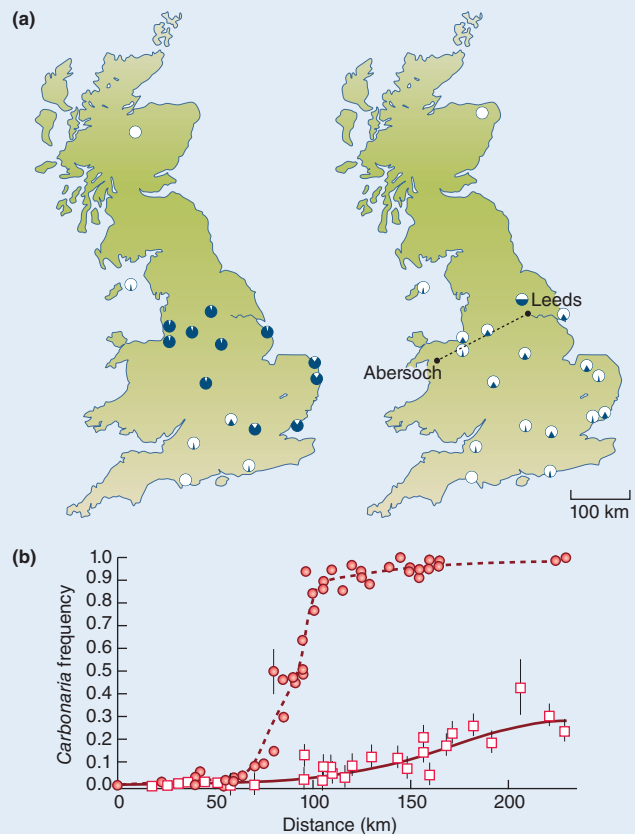
## APPLICATION 1.2 Variation within a species with man-made selection pressures

It is, perhaps, not surprising that some of the most dramatic examples of local specialisation within species (indeed of natural selection in action) have been driven by man-made ecological forces, especially those of environmental pollution. These can provide rapid change under the influence of powerful selection pressures. *Industrial melanism*, for example, is the phenomenon in which black or blackish forms of species have come to dominate populations in industrial areas. In the dark individuals, a dominant gene is typically responsible for producing an excess of the black pigment melanin. Industrial melanism has been reported in most industrialised countries and in more than 100 species of moth.

industrial melanism  
in the  
peppered moth

The earliest recorded species to evolve in this way was the peppered moth (*Biston betularia*); the first black specimen in an otherwise pale population was caught in Manchester (UK) in 1848. The mutation event giving rise to industrial melanism is reported to have been the insertion of a transposable element (a DNA sequence that can change its position in the genome) into a gene called *cortex*, which plays a role in early wing development, and is estimated to have occurred in about 1819 (van't Hof *et al.*, 2016). By 1895, about 98% of the Manchester peppered moth population was melanic. Following many more years of pollution, a large-scale survey of pale and melanic forms of the peppered moth in Britain recorded more than 20 000 specimens (Figure 1.7). The winds in Britain are predominantly westerlies, spreading industrial pollutants (especially smoke and sulphur dioxide) toward the east. Melanic forms were concentrated toward the east and were completely absent from the unpolluted western parts of England and Wales, northern Scotland and Ireland. Notice from the figure, though, that many populations were polymorphic: melanic and non-melanic forms coexisted. Thus, the polymorphism seems to be a result both of environments changing (becoming more polluted) – to this extent the polymorphism is transient – and of there being a gradient of selective pressures from the less polluted west to the more polluted east.

The overriding selective pressure appears to be applied by birds that prey on the moths. In field experiments, large numbers of melanic and pale ('typical') moths were reared and released in equal numbers. In a rural and largely



**Figure 1.7** The frequency of melanic forms of the peppered moth in western Britain was high during the height of pollution from the burning of coal, but that frequency declined after the passing of smoke-free legislation. (a) The distribution of melanic (*carbonaria*) and pale forms (blue and white portions of the pie diagrams, respectively) of the peppered moth, *Biston betularia*, for 1952–56 (left) and 1996 (right), for sites where a comparison between the two periods could be made. The dotted line shows the transect examined in (b). (b) Clines in the frequency of the melanic form along a transect running WSW to NSE from Abersoch in Wales to Leeds in England for the periods 1964–75 (filled circles) and 2002 (open squares). Bars are SEs. Source: (a) After Grant *et al.* (1998). (b) After Saccheri *et al.* (2008).

unpolluted area of southern England, most of those captured by birds were melanic. In an industrial area near the city of Birmingham, most were typicals (Kettlewell, 1955). Any idea, however, that melanic forms were favoured simply because they were camouflaged against smoke-stained backgrounds in the polluted areas (and typicals were favoured in

[Continued]

## APPLICATION 1.2 (Continued)

unpolluted areas because they were camouflaged against pale backgrounds) may be only part of the story. The moths rest on lateral branches or tree trunks during the day, and non-melanic moths are well hidden against a background of mosses and lichens, especially on tree trunks. Industrial pollution has not just blackened the moths' background; sulphur dioxide, especially, has also destroyed most of the moss and lichen on the tree trunks. Thus, sulphur dioxide pollution may have been as important as smoke in selecting melanic moths. The distribution patterns are probably also influenced to some extent by migration between sites that differ in pollution levels (male moths can move 2 km in a night while newly emerged larvae spin threads that might carry them away from the oviposition sites over even greater distances) and there may be some non-visual advantage of melanics over typicals, but this must be weaker than the

visual disadvantage associated with predation in a polluted environment (Cook & Saccheri, 2013).

In the 1960s, industrialised environments in Western Europe and the USA started to change again, as oil and electricity began to replace coal, and legislation was passed to impose smoke-free zones and to reduce industrial emissions of sulphur dioxide. The frequency of melanic forms then fell back to near preindustrial levels with remarkable speed (Figure 1.7). Again, there was transient polymorphism – but this time populations were heading in the other direction as pollution was declining.

It is heartening to note that sometimes the consequences of anthropogenic pressures can be reversed if appropriate action is taken.

reversing man-made selection pressures

## 1.3 Speciation

It is clear, then, that natural selection can force populations of plants and animals to change their character – to evolve. But none of the examples we have considered so far has involved the evolution of a new species. What, then, justifies naming two populations as different species? And what is the process – 'speciation' – by which two or more new species are formed from one original species?

### 1.3.1 What do we mean by a 'species'?

biospecies: the Mayr–Dobzhansky test

Cynics have said, with some truth, that a species is what a competent taxonomist regards as a species.

On the other hand, back in the 1930s two American biologists, Mayr and Dobzhansky, proposed an empirical test that could be used to decide whether two populations were part of the same species or of two different species. They recognised organisms as being members of a single species if they could, at least potentially, breed together in nature to produce fertile offspring. They called a species tested and defined in this way a *biological species* or *biospecies*. In the examples that we have used earlier in this chapter, we know that melanic and normal peppered moths can mate and that the offspring are fully fertile; this is also true of *Anthoxanthum* plants from different positions along the gradient at the

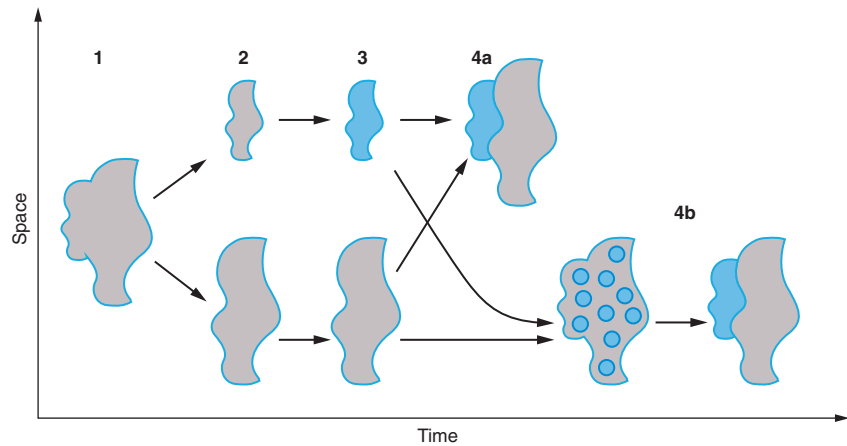
Trelogan mine. They are all variations within species – not separate species.

In practice, however, biologists do not apply the Mayr–Dobzhansky test before they recognise every species: there is simply not enough time or resources, and in any case, there are vast portions of the living world – most microorganisms, for example – where an absence of sexual reproduction makes a strict interbreeding criterion inappropriate. What is more important is that the test recognises a crucial element in the evolutionary process that we have met already in considering specialisation within species. If the members of two populations are able to hybridise, and their genes are combined and reassorted in their progeny, then natural selection can never make them truly distinct. Although natural selection may tend to force a population to evolve into two or more distinct forms, sexual reproduction and hybridisation mix them up again.

### 1.3.2 Allopatric speciation

Allopatric speciation is speciation driven by divergent natural selection in distinct subpopulations in different places. The most orthodox scenario for this comprises a number of stages (Figure 1.8). First, two subpopulations become geographically isolated and natural selection drives genetic adaptation to their local environments. Next, as a *byproduct* of this genetic differentiation, a degree of reproductive isolation builds up between the two. This may be 'pre-zygotic', tending to prevent mating in the first place (e.g. differences

**Figure 1.8 The orthodox picture of ecological speciation.** A uniform species with a large range (1) differentiates (2) into subpopulations (for example, separated by geographic barriers or dispersed onto different islands), which become genetically isolated from each other. (3) After evolution in isolation they may meet again, when they are either already unable to hybridise (4a) and have become true biospecies, or they produce hybrids of lower fitness (4b), in which case evolution may favour features that prevent interbreeding between the ‘emerging species’ until they are true biospecies.



in courtship ritual), or ‘post-zygotic’: reduced viability, perhaps inviability, of the offspring themselves. Then, in a phase of ‘secondary contact’, the two subpopulations re-meet. The hybrids between individuals from the different subpopulations are now of low fitness, because they are literally neither one thing nor the other. Natural selection will then favour any feature in either subpopulation that *reinforces* reproductive isolation, especially pre-zygotic characteristics, preventing the production of low-fitness hybrid offspring. These breeding barriers then cement the distinction between what have now become separate species.

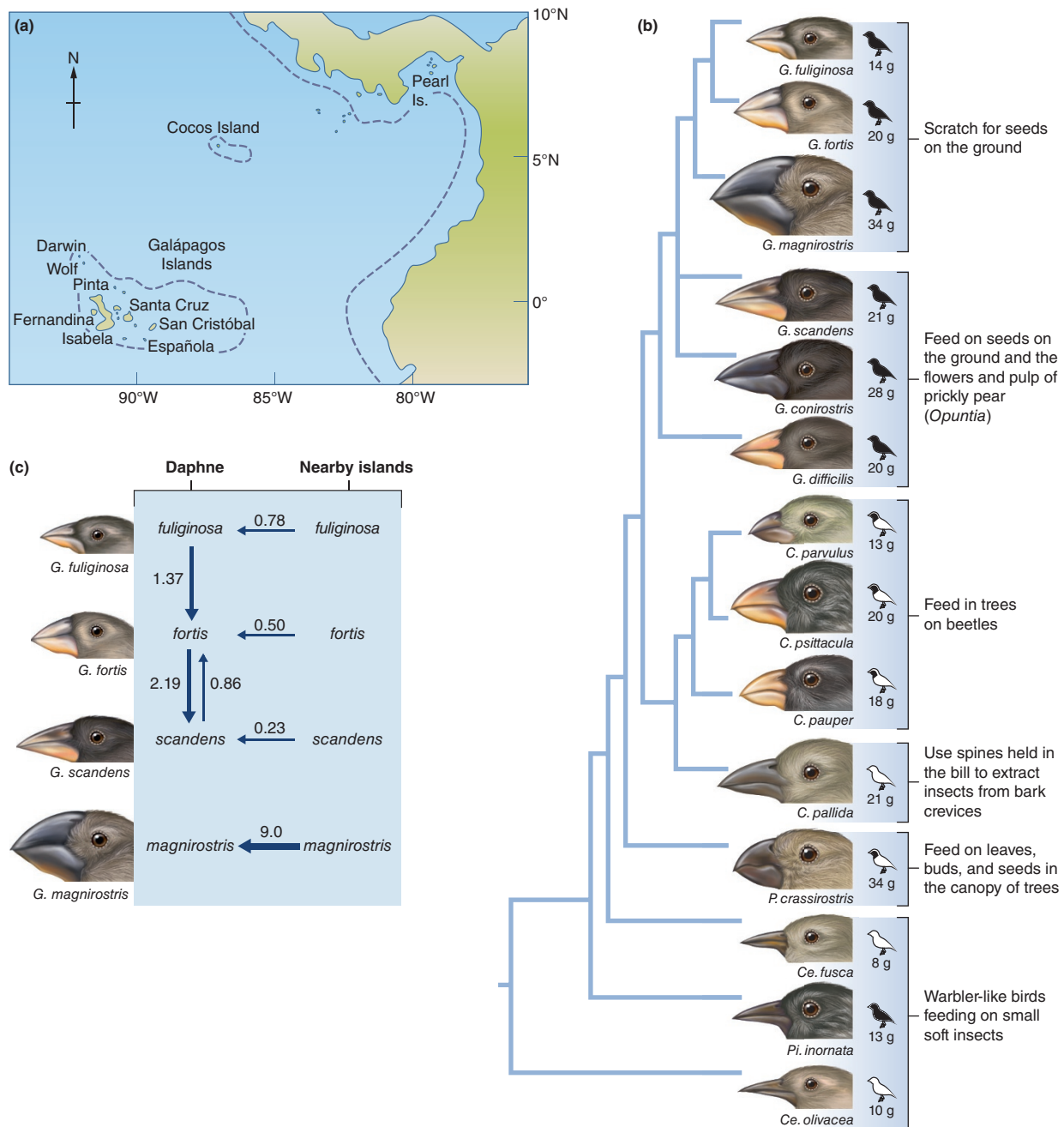
#### Darwin's finches

The isolation of islands provides arguably the most favourable scenario for populations to diverge into distinct species. The most celebrated example is the case of Darwin's finches in the Galápagos archipelago, a group of volcanic islands isolated in the Pacific Ocean about 1000 km west of Ecuador and 750 km from the island of Cocos, which is itself 500 km from Central America (Figure 1.9). At more than 500 m above sea level the vegetation is open grassland. Below this is a humid zone of forest that grades into a coastal strip of desert vegetation with some endemic species of prickly pear cactus (*Opuntia*). Fourteen species of finch are found on the islands. The evolutionary relationships amongst them have been traced by molecular techniques using microsatellite DNA that have confirmed the long-held view that the family tree of the Galápagos finches radiated from a single trunk: a single ancestral species that invaded the islands from the mainland of Central America. The molecular data also provide strong evidence that the warbler finch (*Certhidea olivacea*) was the first to split off from the founding group and is likely to be the most similar to the original colonist ancestors. The entire process of

evolutionary divergence of these species appears to have happened in less than 3 million years.

Isolation – both of the archipelago itself and of individual islands within it – has led to an original evolutionary line radiating into a series of species, each matching its own environment. Populations of ancestor species became reproductively isolated, most likely after chance colonisation of different islands within the archipelago, and evolved separately for a time. Secondary contact phases subsequently occurred as a result of movements between islands that brought non-hybridising biospecies together that then evolved to fill different niches that elsewhere in the world are filled by quite unrelated species. Members of one group, including *Geospiza fuliginosa* and *G. fortis*, have strong bills and hop and scratch for seeds on the ground. *G. scandens* has a narrower and slightly longer bill and feeds on the flowers and pulp of the prickly pears as well as on seeds. Finches of a third group have parrot-like bills and feed on leaves, buds, flowers and fruits, and a fourth group with a parrot-like bill (*Camarhynchus psittacula*) has become insectivorous, feeding on beetles and other insects in the canopy of trees. A so-called woodpecker finch, *Camarhynchus* (*Cactospiza*) *pallida*, extracts insects from crevices by holding a spine or a twig in its bill, while yet a further group includes the warbler finch, which flits around actively and collects small insects in the forest canopy and in the air.

However, the biospecies compartments are not watertight. A study of the four species on the small island of Daphne Major, and of their possible interbreeding with birds from larger nearby islands, again using molecular techniques, is summarised in Figure 1.9c. The two most abundant species, *Geospiza fortis* and *G. scandens*, were subject to a greater flow of genes between one another than they were



**Figure 1.9** Many different species of Darwin's finches have evolved on the Galápagos Islands. (a) Map of the Galápagos Islands showing their position relative to Central America; on the equator 5° equals approximately 560 km. (b) A reconstruction of the evolutionary history of the Galápagos finches based on variation in the length of microsatellite DNA. (A microsatellite is a tract of repetitive DNA in which certain DNA motifs, ranging in length from 2 to 5 base pairs, are repeated, with the number of repeats varying in alleles of individuals.) A measure of the genetic difference between species is shown by the length of the horizontal lines. The feeding habits of the various species are also shown. Drawings of the birds' heads are proportional to actual body size. The maximum amount of black colouring in male plumage and the average body mass are shown for each species. *C*, *Camarhynchus*; *Ce*, *Certhidea*; *G*, *Geospiza*; *P*, *Platyspiza*; *Pi*, *Pinaroloxias*. (c) Gene flow for the four species on Daphne Major, through interbreeding with other species on the island and with immigrants of the same and other species from the nearby islands. Flow is measured as the effective number of individuals per generation. For genes to flow, the first-generation hybrid offspring must themselves mate with one of the parental species. Genes flow from *G. fortis* to *G. scandens* when the hybrid sings the *G. scandens* song (because its father did) and vice versa for genes flowing from *G. scandens* to *G. fortis*. The population of *G. fuliginosa* on Daphne Major is very small, and hence the flow of genes into *G. fortis* comes from immigrants from other islands. Source: (b) After Petren *et al.* (1999). (c) After Grant & Grant (2010).

to genes from immigrants of their own species from other islands. Indeed, in the case of *G. fortis*, there was also a substantial flow of genes from *G. fuliginosa* immigrants from other islands. Thus, the ‘ideal’ of gene flow within a species but not between them is not borne out by the data. But the fact that there are ‘grey areas’ partway through the process does not diminish the importance of either the process of speciation or the concept of biospecies.

ring species –  
perfect examples of  
speciation in action,  
but why so rare?

That speciation is a process rather than an event is beautifully illustrated by the existence of ring species. In these, races or subspecies of a species that fall short of being full species themselves (i.e. distinct forms that are nonetheless capable of producing fertile hybrids) are arranged along a geographic gradient in such a way that the two ends of the gradient themselves meet, hence forming a ring, and where they do, they behave as good species despite being linked, back around the ring, by the series of interbreeding races. Thus, what would normally be a temporal sequence of events, that we can only presume to have happened, becomes frozen in space. That the phenomenon is theoretically feasible has been demonstrated using mathematical models (e.g. de Brito Martins & de Aguiar, 2016). But actual examples are rare, and several that have been proposed in the past have been called into question by modern molecular studies, leading Pereira and Wake (2015) to wonder whether ring species are an unfulfilled promise or, worse still, wish-fulfilment fantasy.

The classic example is the extraordinary case of two species of sea gull. The lesser black-backed gull (*Larus fuscus*) originated in Siberia and colonised progressively to the west, forming a chain or *cline* of different forms, spreading from Siberia to Britain and Iceland. The neighbouring forms along the cline are distinctive, but were assumed to hybridise readily in nature. Neighbouring populations are regarded as part of the same species and taxonomists give them only ‘subspecific’ status (e.g. *L. fuscus graellsii*, *L. fuscus fuscus*). Populations of the gull have, however, also spread east from Siberia, again forming a cline of freely hybridising forms. Together, the populations spreading east and west encircle the northern hemisphere. They meet and overlap in northern Europe. There, the eastward and westward clines have diverged so far that it is easy to tell them apart, and they are recognised as two different *species*, the lesser black-backed gull (*L. fuscus*) and the herring gull (*L. argentatus*). Moreover, the two species do not hybridise: they have become true biospecies. In this remarkable example, then, we can see how two distinct species seem to have evolved from one primal stock, and that the stages of their divergence remain frozen in the cline that connects them.

However, modern molecular techniques to determine genetic relationships have revealed a more complex picture. Thus, while ancestral populations expanded in a roughly circular fashion, there have been intermittent periods of allopatric fragmentation and subsequent range expansion, leading to areas of secondary contact where hybridisation currently occurs. Population divergence, therefore, proceeded at least partly in allopatry, not exclusively through isolation by distance throughout a contiguous range, as the ring species concept requires. Moreover, adjacent subspecies have been found not necessarily to be each other’s closest relatives and evidence is lacking of closure of the circumpolar ring by colonisation of Europe by North American herring gulls, a cornerstone of the ring species concept (Martens & Packert, 2007).

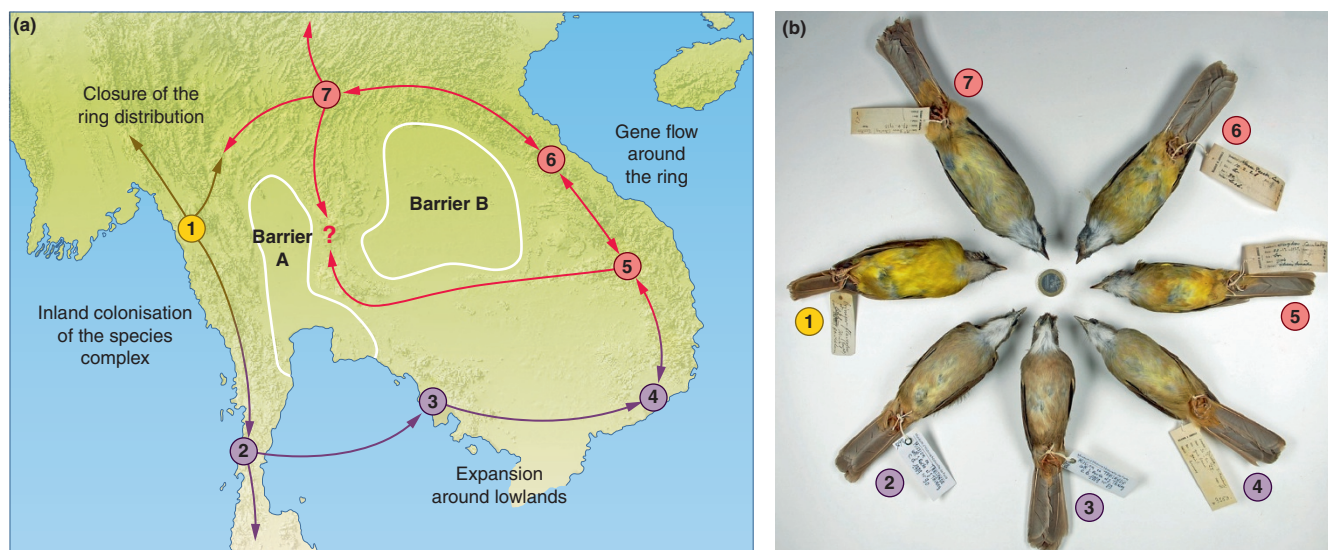
A more convincing example involves bulbuls in the genus *Alophoixus* in montane habitats of the Indo-Malayan bioregion. Fuchs *et al.* (2015) have shown that diversification is consistent with most criteria expected for ring species (Figure 1.10a). First, molecular analysis shows that the seven taxa (Figure 1.10b) are all descendants of a single ancestral species, and probably derive from a single colonisation from Sundaland. Second, neighbouring taxa are most closely related, suggesting that taxa have diverged from a stepping stone colonisation of the high-elevation forest around Thailand’s lowlands (lowland ‘barriers’ A and B in Figure 1.10a). The current distribution suggests that divergence can be explained by isolation by distance, as assumed by the ring species concept (but also, partly, by periods of geographic isolation that probably occurred during climatic cycles following initial diversification of the complex). Third, gene flow between neighbouring taxa suggests that divergence and secondary contact between taxa around the ring have resulted in genetic intergradation. And fourth, demographic analyses indicate a recent expansion and geographic overlap of the oldest taxon (1) and its most distant relative (7), leading to closure of the ring. However, hybrids sampled at the terminus of the ring (where taxon 1 meets taxon 7) indicate that divergence has not been sufficient for complete reproductive isolation to evolve.

It would be wrong to imagine that all examples of speciation conform fully to the orthodox picture described in Figure 1.8. In fact,

allopatric speciation  
without secondary  
contact

there may never be secondary contact. This would be pure ‘allopatric’ speciation; that is, with all divergence occurring in subpopulations in *different* places. This seems particularly likely for island populations and helps explain the preponderance of endemic species (those found nowhere else) on remote islands.





**Figure 1.10 Closure of a ring distribution of bulbul morphotypes.** (a) Distribution of *Alophoixus* bulbuls in the Indo-Malayan bioregion. Taxa composing the *Alophoixus* ring are represented by circles (colours distinguish three currently recognised species); single arrows represent colonisation around the barrier; double arrows represent zones of genetic intergradation; closure of the ring (involving taxa 1 and 7) is shown at the top left (the question mark indicates a possible secondary contact at the mid-ring involving taxa 5 and 7). (b) Eco-morphotypes: (1) *A. flaveolus*, (2) *A. ochraceus ochraceus*, (3) *A. o. cambodianus*, (4) *A. o. hallae*, (5) *A. pallidus khmerensis*, (6) *A. p. annamensis* and (7) *A. p. henrici*. Source: From Fuchs *et al.* (2015), after Pereira & Wake (2015). (b) Photo credit: A. Previato, MNHN.

### 1.3.3 Sympatric speciation

Furthermore, the advent of modern molecular techniques has spurred interest in the view that an allopatric phase may not be necessary: that is, ‘sympatric’ speciation is possible, with subpopulations diverging despite not being geographically separated from one another. Sympatric speciation has long fascinated evolutionary biologists because it sets diversifying selection against the tendency of sexual reproduction to homogenise populations. There are few truly convincing cases in nature, and indeed it is to be expected that examples of such a process will be difficult to identify because, for most groups, range maps are incomplete, the patterns of habitat use are poorly known and phylogenies do not include all species (Santini *et al.*, 2012). Once again, however, mathematical models provide a way of testing the viability of alternative speciation scenarios and suggest the criteria that need to be satisfied (Bird *et al.*, 2012). There are at least five criteria for inferring that a particular case is best explained by sympatric speciation – four proposed by Coyne and Orr (2004): (1) the two species must have largely overlapping geographical distributions; (2) speciation must be complete; (3) the two species must be sister species (descended from a common ancestor); and (4) the biogeographic and evolutionary history of the groups must make the existence of an allopatric phase ‘very

unlikely’; and a fifth, based on a population genetics rather than biogeographic perspective: (5) evidence must support panmixia of the ancestral population (i.e. mating must have been possible between all potential partners) (Fitzpatrick *et al.*, 2008).

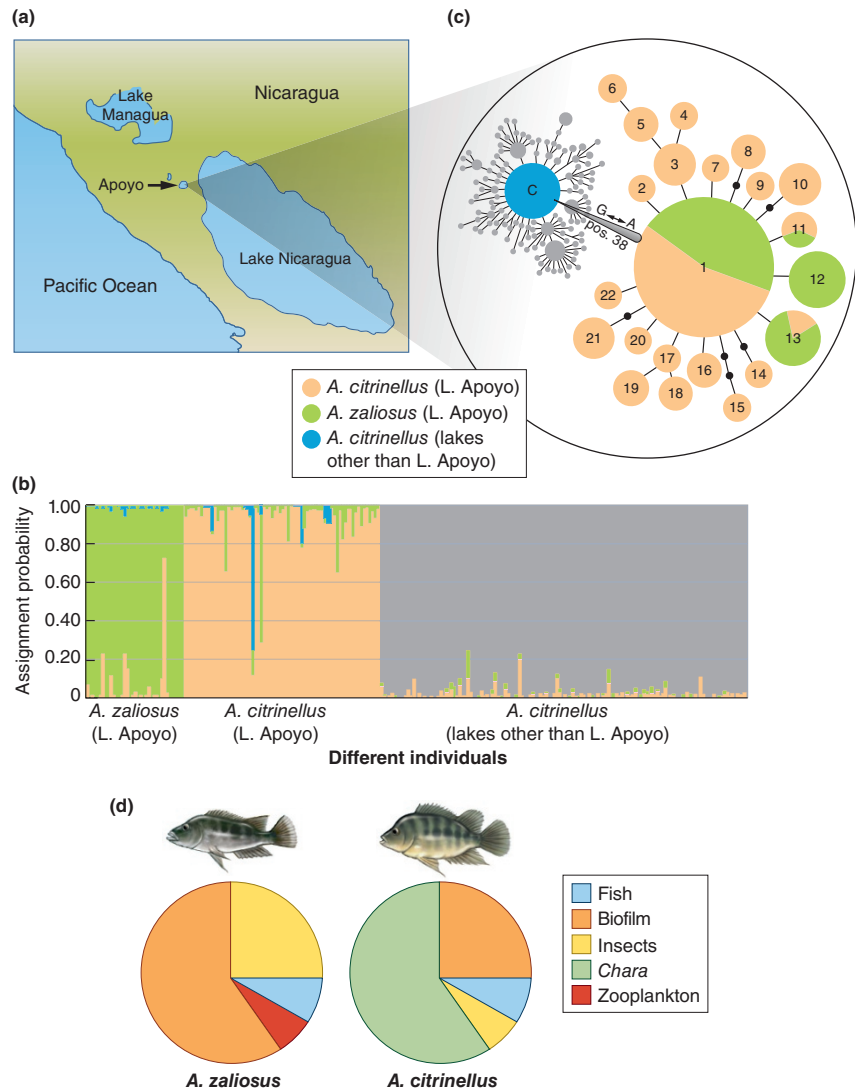
A good example is provided by two species of cichlid fish in Nicaragua: the Midas cichlid *Amphilophus citrinellus* and the arrow cichlid *A. zaliosus* (Figure 1.11a) (Barluenga *et al.*, 2006). These species coexist in the small, isolated Lake Apoyo (satisfying criterion 1), which is relatively homogeneous in terms of habitat, and of recent origin (less than 23 000 years). *A. zaliosus* is found nowhere else, while *A. citrinellus* occurs in many water bodies in the region, including the largest. A variety of behavioural (mate choice) and genetic evidence, including that from microsatellite DNA, indicates that the two species in Lake Apoyo are reproductively isolated from one another (satisfying criterion 2) and indeed from *A. citrinellus* in other lakes (Figure 1.11b). Further genetic evidence from mitochondrial DNA (passed by mothers to their offspring) indicates that the cichlids of Lake Apoyo, of both species, had a single common ancestor arising from the much more widespread stock of *A. citrinellus* (Figure 1.11c) (satisfying criteria 3 and 5). The common ancestor was a high-bodied benthic species but *A. zaliosus*, the new elongated pelagic species, has evolved in less than 10 000 years. Now *A. citrinellus* and *A. zaliosus* in Lake



**Figure 1.11 Sympatric speciation in the cichlid fish *Amphilophus citrinellus* and *A. zaliosus*.** (a) The location of Lake Apoyo in Nicaragua.

(b) The assignment of individuals to populations based on variation at 10 microsatellite DNA loci: *A. zaliosus* (green) and *A. citrinellus* (orange) from Lake Apoyo and *A. citrinellus* (blue) from other lakes. The clear separation of colours is indicative of partial or total reproductive isolation between them.

(c) The relatedness network of 637 'haplotypes' of mitochondrial DNA sequences from individual fish using the same colour coding as in (b). (A haplotype is a set of markers on a single chromosome that tend to be inherited together from a single parent.) The size of a circle reflects the frequency with which a particular haplotype was found. The most common haplotype in Lake Apoyo ('1') is distinguished from the most common *A. citrinellus* haplotype from elsewhere ('C') by a single mutation (base substitution of guanine by adenine at position 38), but all Lake Apoyo haplotypes, of both species, share this mutation, indicating their origin from a single common ancestor. (d) Stomach content analyses of the two species in Lake Apoyo. (*Chara* is a multicellular alga.). Source: After Barluenga *et al.* (2006).



Apoyo are morphologically distinct from one another and have substantially different diets: both feed on biofilm but *A. citrinellus* feeds more from the benthic environment (algae, insects and fish along the lake shore and bed) while *A. zaliosus* feeds more from open water and the surface (including winged insects; Figure 1.11d). There seems little doubt, therefore, that this speciation must have occurred sympatrically, presumably driven by the divergent selection to specialise on bottom-feeding in the one case and on open water-feeding in the other.

where is sympatric speciation most likely?

Examples of species groups most likely to satisfy Coyne and Orr's (2004) criteria are organisms with a strong, genetically determined fidelity to a habitat in which mating will occur, such as insects that feed on more than one species of host plant, where each requires specialisation by the insects to overcome the plant's

defenses, fish on coral reefs (and perhaps marine animals more generally; Bird *et al.*, 2012) and parasites (Santini *et al.*, 2012). And we have already seen how two lake fish conform to the scenario. Indeed, one of the most staggeringly rich examples of endemism has also been provided by cichlid fish: those of the East African Great Lakes, with more than 1500 endemic species in a relatively small, isolated geographic region. It remains to be discovered how important a role sympatric speciation plays in that case, and whether divergent selection to different niches is the main driving force.

A final critical question is whether a case thought to have arisen by sympatric speciation is truly a result of species diverging while gene flow was occurring (sympatric) or merely 'microallopatric' speciation. A small-scale geographic barrier (analogous

sympatric speciation – divergence with gene flow or microallopatric speciation?

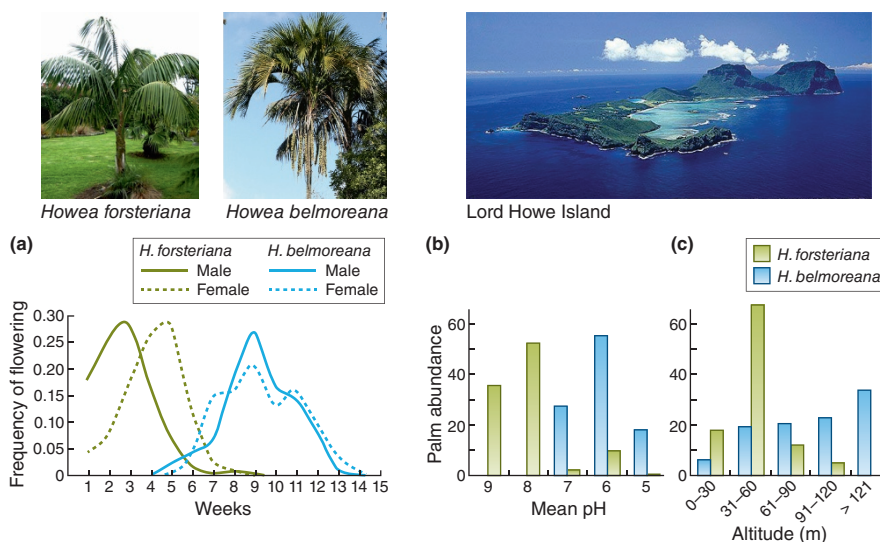
to ocean habitat between islands) may occur, for example, as an underwater ridge in a lake. Moreover, host-specific parasites and phytophagous insects might also have broadly overlapping geographic ranges and yet never encounter one another because of their distinct ecological niches. In other words, populations might overlap at a coarse grain if they occupy the same geographic region, but not co-occur at a finer grain if they occupy different habitats within that region. Thus, whether populations are described as sympatric is somewhat at the discretion of the observer (Fitzpatrick *et al.*, 2008).

a mechanism for sympatric speciation: AITs?

It is easy to see how geographically isolated populations have diverged, because they are also reproductively isolated, but not so straightforward to conceive how assortative mating can evolve sympatrically in populations that are not geographically isolated but experience divergent selective pressures. This may occur via ‘automatic isolating traits’ (AITs). An example would be where a particular locus or set of loci interacts with the environment to express different mating behaviours under different environmental conditions, regardless of genotype, such as the timing of flowering in

plants. For example, the most recent common ancestor of two sympatric sister *Howea* palms on the tiny Lord Howe Island, 600 km off the coast of Australia, may have exhibited different flowering times when growing in different soil types so that a difference in physiology elicited by environmental differences, rather than a difference in genotype, could have enforced mating fidelity by soil type rather than genotype and increased the likelihood that divergence was possibly despite broad-scale sympatry (Figure 1.12). Papadopoulos *et al.* (2011) describe other examples of sympatric speciation of plants in the genera *Metrosideros* and *Coprosma* on Lord Howe Island. Further possible cases where AITs may operate include fish with colour polymorphisms, genes responsible for insect hybrid male sterility, and cases involving chemical signalling (Bird *et al.*, 2012).

While allopatric speciation is generally accepted to be much more common than sympatric speciation, sympatric lineage divergence due to selection has certainly come of age in the wake of the molecular biology revolution, which has allowed hypotheses that were once untestable to be critically evaluated. Evolutionary ecologists are not so focused now on whether or not sympatric speciation can happen, but rather how often and under what conditions.



**Figure 1.12 Sympatric speciation in *Howea* palms.** Two species of *Howea* palm on the tiny and isolated Lord Howe Island off the coast of Australia. *Howea forsteriana* has straight leaves with drooping leaflets, while *H. belmoreana* has recurved leaves with ascending leaflets. (*H. forsteriana* is now one of the world’s most widely traded house plants.) A comprehensive DNA-based phylogenetic tree indicates that these are sister species with their closest relative, *Laccospadix*, on the Australian mainland. Molecular dating methods show the two *Howea* species diverged 1–1.92 million years ago, long after Lord Howe Island was formed by volcanic activity 6.4–6.9 million years ago. *H. forsteriana* diverged from its sister species (an ancestor of *H. belmoreana*) by colonising widespread lowland calcarenite deposits. Extensive molecular evidence is consistent with Coyne and Orr’s criteria for sympatric speciation (see earlier). (a) *H. forsteriana* (green lines) flowers early in the flowering season, with male flowering (solid line) peaking 2 weeks before female receptivity (dashed line); *H. belmoreana* male and female flowering is synchronous but later in the season. (b) *H. forsteriana* occurs in soils of higher pH and (c) lower altitude than *H. belmoreana*. Source: After Savolainen *et al.* (2006).

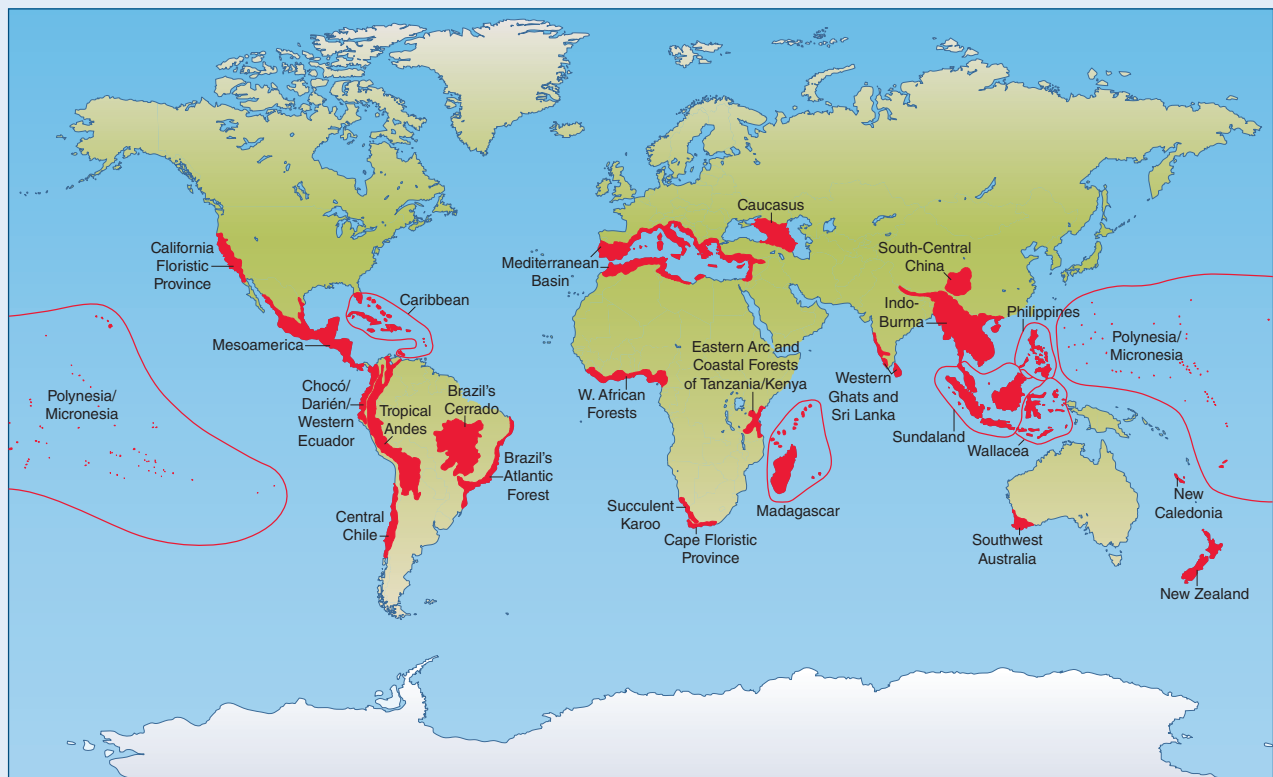
### APPLICATION 1.3 Conservation significance of hot spots of endemism

Conservationists have to make hard decisions in their quest to preserve biological diversity. Given limited resources, how can the most species be supported at minimum cost? One way is to focus attention on 'biodiversity hot spots' of species that are found nowhere else. Myers *et al.* (2000) took this approach when mapping the entire globe in terms of exceptional concentrations of endemic species coupled with exceptional loss of habitat (and therefore subject to a greater degree of threat to biodiversity than areas without such habitat loss). Hot-spot boundaries were set according to the characteristic biotas they contain: examples include island groups such as the Galápagos (Section 1.3.2) and Hawaii (Section 1.4.2), and 'ecological' islands such as the East African Great Lakes (Section 1.3.3) or clearly defined continental units such as the Cape Floristic Province in South Africa. The taxa included in the analysis consisted of vascular plants, mammals, birds, reptiles and amphibians. Figure 1.13 shows 25 identified hot spots that between them contain 133 149 plant species (that is, 44% of the world's plants) and 9645 vertebrate species (35% of the world's total). Or to put it in another way that emphasises their importance, we can say that this set

of hot spots provide the sole remaining habitats of 44% of the world's plant species (and 35% of animals).

The five most prominent hot spots, the tropical Andes, Sundaland, Madagascar, Brazil's Atlantic Forest and the Caribbean, contain 20% of the world's vascular plants and 16% of vertebrate species but together they comprise only 0.4% of the world's surface. Moreover, they are subject to some of the heaviest levels of habitat loss: the Caribbean retains only 11.3% of its primary vegetation, Madagascar 9.9%, Sundaland 7.8% and Brazil's Atlantic Forest 7.5%. There was reasonable congruence between levels of endemism of plants and vertebrates in the hot spots, but note that no invertebrates were included in the analysis. In a geographically more restricted study in South Africa, Bazelet *et al.* (2016) showed that there was congruence between hot spots of the rather circumscribed diversity of katydids (bush crickets) and the biodiversity hot spots already recognised for much wider groupings, indicating that the conservation of biodiversity hot spots may often also protect non-target organisms.

Myers *et al.* (2000) called for a more than 10-fold increase in annual funding from governmental and international agencies to safeguard these hot spots.



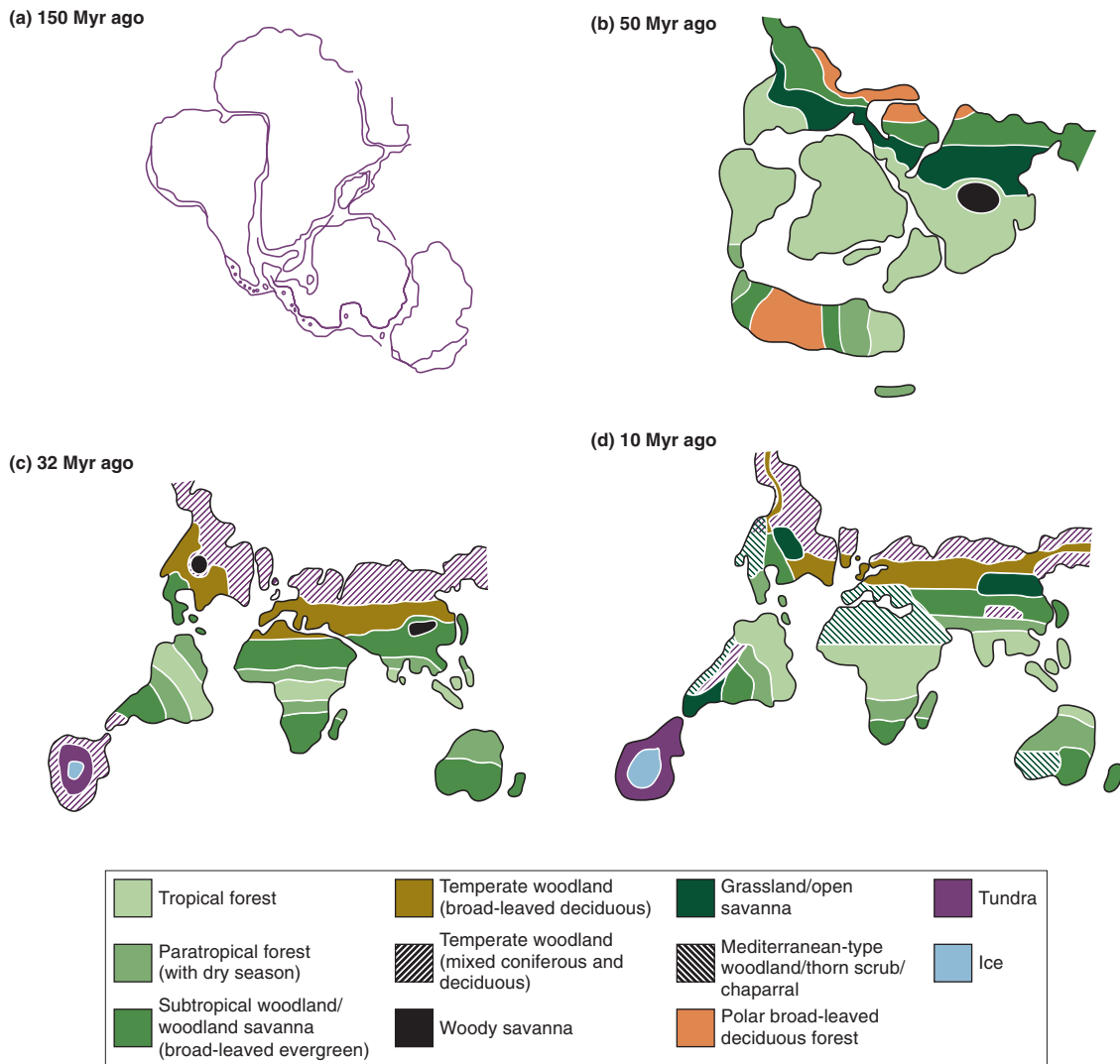
**Figure 1.13 Biodiversity hot spots.** Twenty-five biodiversity hot spots identified because of their exceptional concentrations of endemic species that are undergoing exceptional levels of human induced habitat loss. *Source:* From Myers *et al.* (2000).

## 1.4 The role of historical factors in the determination of species distributions

Our world has not been constructed by someone taking each species in turn, testing it against each environment, and moulding it so that every species finds its perfect place. It is a world in which species live where they do for reasons that are often, at least in part, accidents of history. We illustrate this first by considering continental drift, a process that operates over a timescale of tens of millions of years.

### 1.4.1 Movements of landmasses

Long ago, the curious distributions of species between continents, seemingly inexplicable in terms of dispersal over vast distances, led biologists, especially Wegener (1915), to suggest that the continents themselves must have moved. This was vigorously denied by geologists, until geomagnetic measurements required the same, apparently wildly improbable explanation. The discovery that the tectonic plates of the earth's crust move and carry with them the migrating continents, reconciles geologist and biologist (Figure 1.14). Thus,



**Figure 1.14** Continental drift means that continents that are now separate were once joined to one another. (a) The ancient supercontinent of Gondwanaland began to break up about 150 million years (Myr) ago. (b) About 50 Myr ago (early Middle Eocene) recognisable bands of distinctive vegetation had developed, and (c) by 32 Myr ago (early Oligocene) these had become more sharply defined. (d) By 10 Myr ago (early Miocene) much of the present geography of the continents had become established but with dramatically different climates and vegetation from today; the position of the Antarctic ice cap is highly schematic.

Source: After Norton & Sclater (1979), Janis (1993) and other sources.

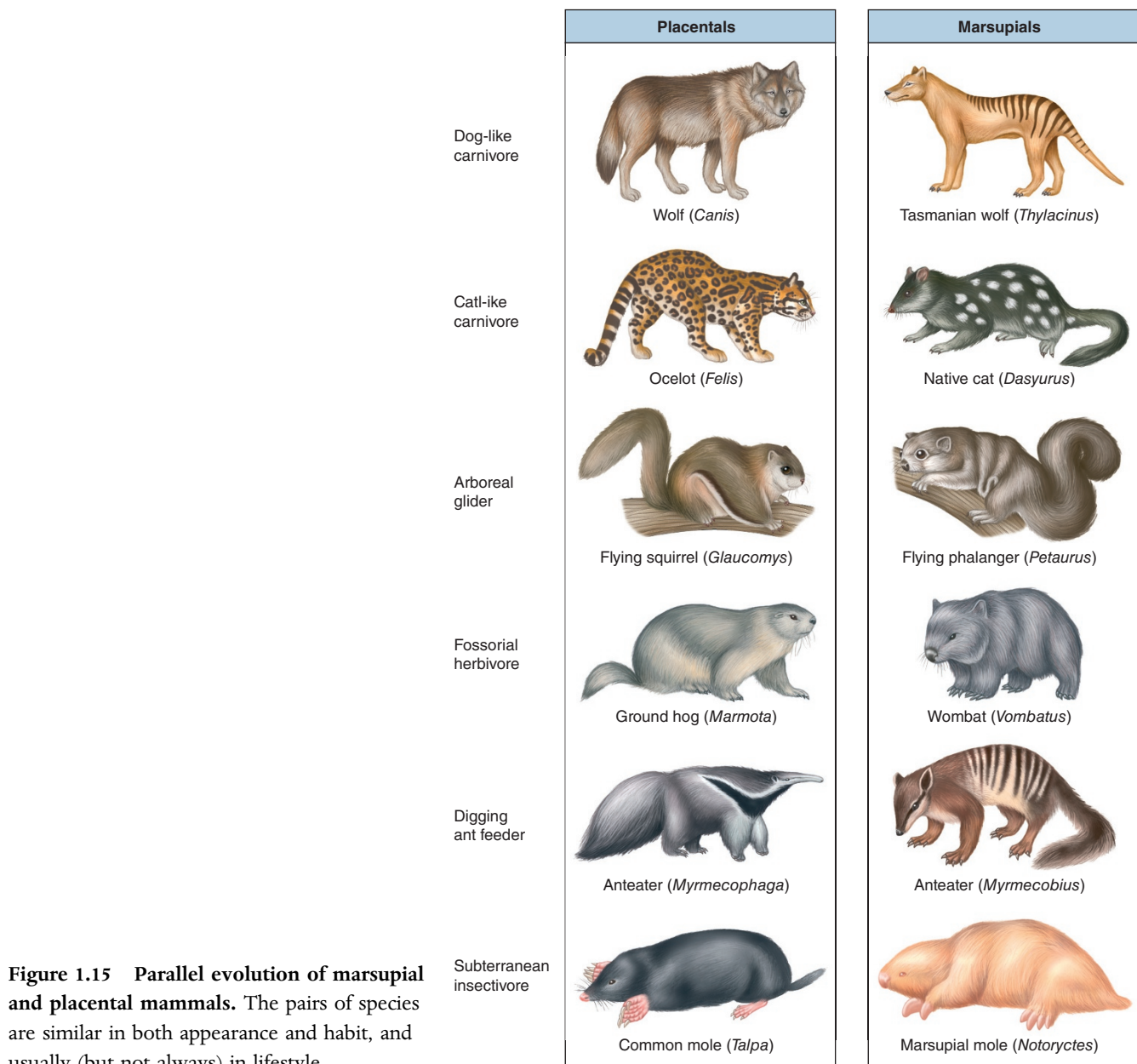


whilst major evolutionary developments were occurring in the plant and animal kingdoms, populations were being split and separated, and land areas were moving across climatic zones.

placental and marsupial mammals

The drift of large landmasses over the face of the earth explains many patterns in the distribution of species that would otherwise be difficult to understand. A classic example is provided by the placental and marsupial mammals. Marsupials arrived on what would become the Australian continent about 90 million years ago (in the Cretaceous period), when the only other mammals present were the curious egg-laying

monotremes (now represented only by the spiny anteaters (*Tachyglossus aculeatus*) and the duckbill platypus (*Ornithorhynchus anatinus*)). An evolutionary process of radiation then occurred that in many ways paralleled that of placental mammals on other continents (Figure 1.15). The subtlety of the parallels in both the form of the organisms and their lifestyle is so striking that it is hard to escape the view that the environments of placentals and marsupials provided similar opportunities to which the evolutionary processes of the two groups responded in similar ways. Because they started to diversify from a common ancestral line, and both inherited a common set of potentials and constraints, we refer to this as *parallel evolution* (as opposed to *convergent*



**Figure 1.15 Parallel evolution of marsupial and placental mammals.** The pairs of species are similar in both appearance and habit, and usually (but not always) in lifestyle.

*evolution*, where structures are analogous (similar in superficial form or function) but not homologous (i.e. not derived from an equivalent structure in a common ancestry), such as the wings of birds and bats). The important point here, though, is that the marsupials are found where they are not simply because they are the best fitted to those particular environments but also because of an accident of history – in this case, geological history.

### 1.4.2 Island history

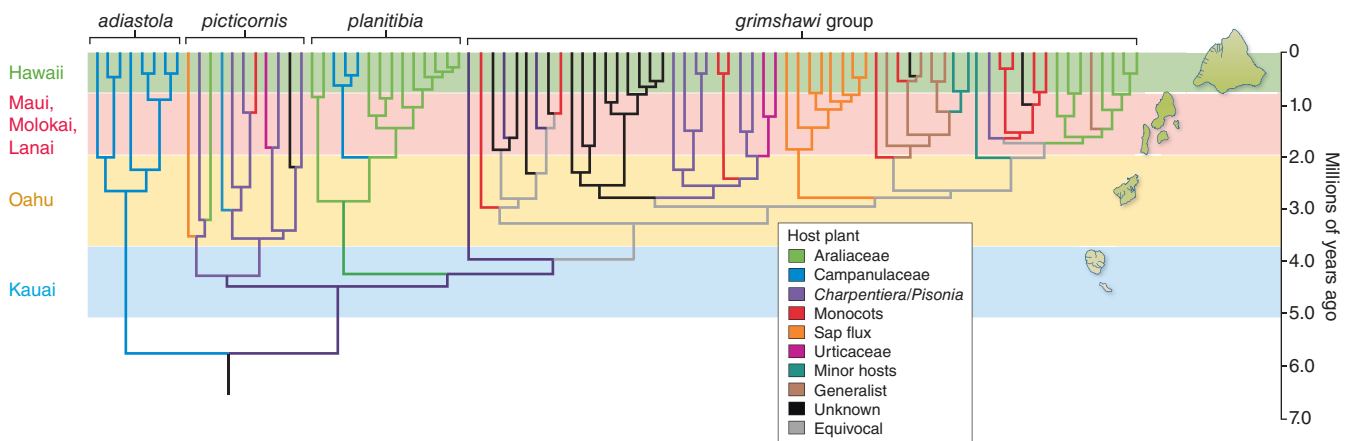
Hawaii provides another remarkable example of a historical process that depends on the movement of a tectonic plate, but in this case in relation to volcanism and in a restricted geographic area. The Hawaiian chain of islands is volcanic in origin, having been formed gradually over the last 40 million years, as the centre of the Pacific tectonic plate moved steadily over a volcanic ‘hot spot’ in a south-easterly direction. Thus, Niihau and Kauai are the most ancient of the islands, and Hawaii itself the most recent.

#### Hawaiian *Drosophila*

The *Drosophila* ‘fruit-flies’ of Hawaii provide an especially spectacular example of species formation and endemism on islands.

There are several thousand species of *Drosophila* worldwide (not all named yet) of which up to 1000 are found only in the Hawaiian Islands (Kang *et al.*, 2016). Of particular interest are the 120 or so endemic species of ‘picture-winged’ *Drosophila*, very few of which occur on more than one island. The majority of the picture-winged species are specialised to oviposit and develop in the decaying bark of native trees in particular families. The lineages through which these species have evolved can be traced by analysing their DNA sequences, in this case using five nuclear genes with a total of 4260 nucleotides, to produce a comprehensive phylogeny of 93 of the species (Magnacca & Price, 2015). The evolutionary tree that emerges is shown in Figure 1.16, with each estimated species divergence date lined up alongside the island on which it occurred.

The standard view for the biogeographic evolution of Hawaiian taxa is a ‘progression-rule pattern’, with the most basal species occurring on ancient Kauai and each lineage dispersing to younger islands as these emerged and matured to a deeply eroded topography with forests and well-developed soils. Historical elements in ‘what lives where’ are plainly apparent for many of the species groups in the figure. The earliest split within the picture-wing clade occurred prior to the emergence of the mature Kauai, with separation of the basal *adiastola* group (Figure 1.16). The



**Figure 1.16** An evolutionary tree linking 93 species of picture-winged *Drosophila* on the Hawaiian Islands, traced by the analysis of DNA sequences on five nuclear genes, with species groups indicated. The shaded areas denote the time periods when the labelled island was the youngest available for colonisation. Species’ divergence dates are lined up against the island on which they occurred. The islands of Maui, Molokai and Lanai are grouped together because they were recently linked by a land bridge. The earliest split (with separation of the *adiastola* group) occurred prior to the emergence of the mature Kauai, with subsequent splits into the other three species groups occurring on the ancient Kauai, and later dispersal to the younger islands as these emerged and matured. Speciation often involved specialisation on particular host plant families, indicated by different colours in the tree (‘sap flux’ is fermenting sap as it oozes from trees; ‘minor hosts’ are individual plant species, not in the families in the list, and used by only one or two species). *Source:* From Magnacca & Price (2015).

figure also shows that the basal species of the *picticornis*, *planitibia* and *grimshawi* groups are found on the ancient island of Kauai, with these groups separating 3.8–4.7 million years ago (mya). A second stage of diversification can be seen when the *grimshawi* subgroups split at 2.1–3.1 mya on Oahu. The *planitibia* group provides a particularly clear example of progression-rule dispersal, with a split into two lineages on Kauai, followed by a split into three lineages on Oahu and subsequent dispersal to the younger islands. But such clear patterns are not always discernible, particularly in the *grimshawi* group. As new islands have been formed, rare dispersers have reached them and eventually evolved into new species, usually by becoming specialised on particular host plants. The arrival on Oahu around 3 mya of new plants upon which *grimshawi* species specialise (including *Charpentiera* and *Pisona* spp.) may have triggered a burst of speciation in the group. At least some of the picture-winged species appear to match the same environment as others on different islands. Of two closely related species, for example, *D. adiasstola* is only found on Maui and *D. setosimentum* only on Hawaii, but the environments that they live in are apparently indistinguishable (Heed, 1968). What is most noteworthy, of course, is the power and importance of isolation (coupled with natural selection) in generating new

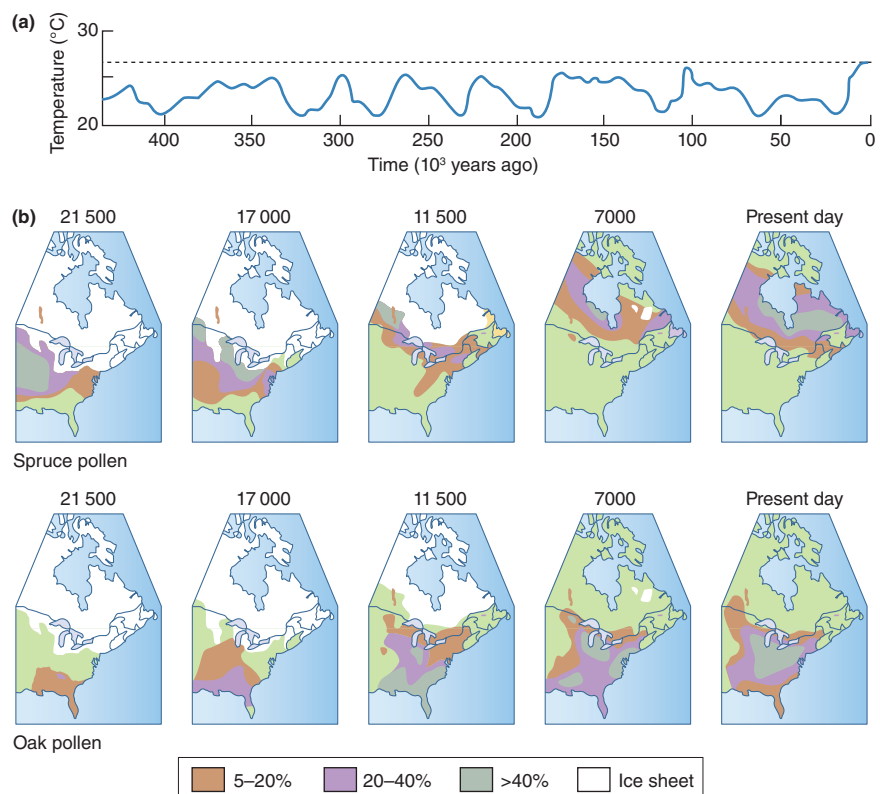
species. Thus, this island biota illustrates two important, related points: (i) that there is a historical element in the match between organisms and environments; and (ii) that there is not just one perfect organism for each type of environment.

### 1.4.3 Climatic history

Climatic variations have occurred on shorter timescales than the movements of landmasses. Changes in climate during the Pleistocene ice ages, in particular, bear a lot of the responsibility for the present patterns of distribution of plants and animals. Techniques for analysing and dating biological remains (particularly buried pollen) increasingly allow us to detect just how much of the present distribution of organisms is a precise locally evolved match to present environments, and how much is a fingerprint of the hand of history. As climates have changed, species populations have advanced and retreated, been fragmented into isolated patches, and may then have rejoined. Much of what we see in the present distribution of species represents a phase in the recovery from past climatic change (Figure 1.17).

**Figure 1.17** Contrasting changes in the distribution of spruce and oak species in relation to the waning of an ice age.

(a) Estimates of temperature during glacial cycles over the past 400 000 years, obtained by comparing oxygen isotope ratios in fossils taken from ocean cores in the Caribbean. Periods as warm as the present have been rare events, and the climate during most of the past 400 000 years has been glacial. The dotted line represents the temperature 10 000 years ago at the beginning of the present period of warming (b) Ranges in eastern North America, as indicated by pollen percentages in sediments, of spruce species (above) and oak species (below) from 21 500 years ago to the present. Note how the ice sheet contracted during this period. *Source:* (a) After Emiliani (1966) and Davis (1976). (b) After Davis & Shaw (2001).



the Pleistocene  
glacial cycles ...

Techniques for the measurement of oxygen isotopes in ocean cores indicate that there may have been as many as 16 glacial cycles in the Pleistocene, each lasting for about 125 000 years (Figure 1.17a). Each cold (glacial) phase may have lasted for as long as 50 000–100 000 years, with brief intervals of only 10 000–20 000 years when the temperatures rose to, or above, those of today. From this perspective, present floras and faunas are unusual, having developed at the warm end of one of a series of unusual catastrophic warm periods.

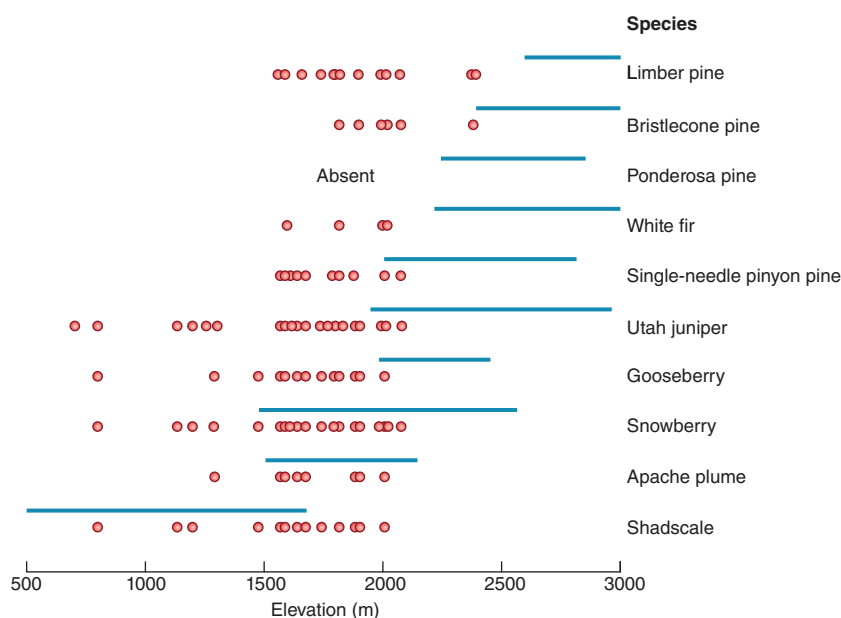
During the 20 000 years since the peak of the last glaciation, global temperatures have risen by about 8°C. The analysis of buried pollen – particularly of woody species, which produce most of the pollen – can show how vegetation has changed (Figure 1.17b). As the ice retreated, different forest species advanced in different ways and at different speeds. For some, like the spruce of eastern North America, there was displacement to new latitudes; for others, like the oaks, the picture was more one of expansion.

We do not have such good records for the postglacial spread of animals associated with the changing forests, but it is certain that many species could not have spread faster than the trees on which they feed. Some of the animals may still be catching up with their plants, and tree species are still returning to areas they occupied before the last ice age. It is quite wrong to imagine that our present

vegetation is in some sort of equilibrium with (adapted to) the present climate.

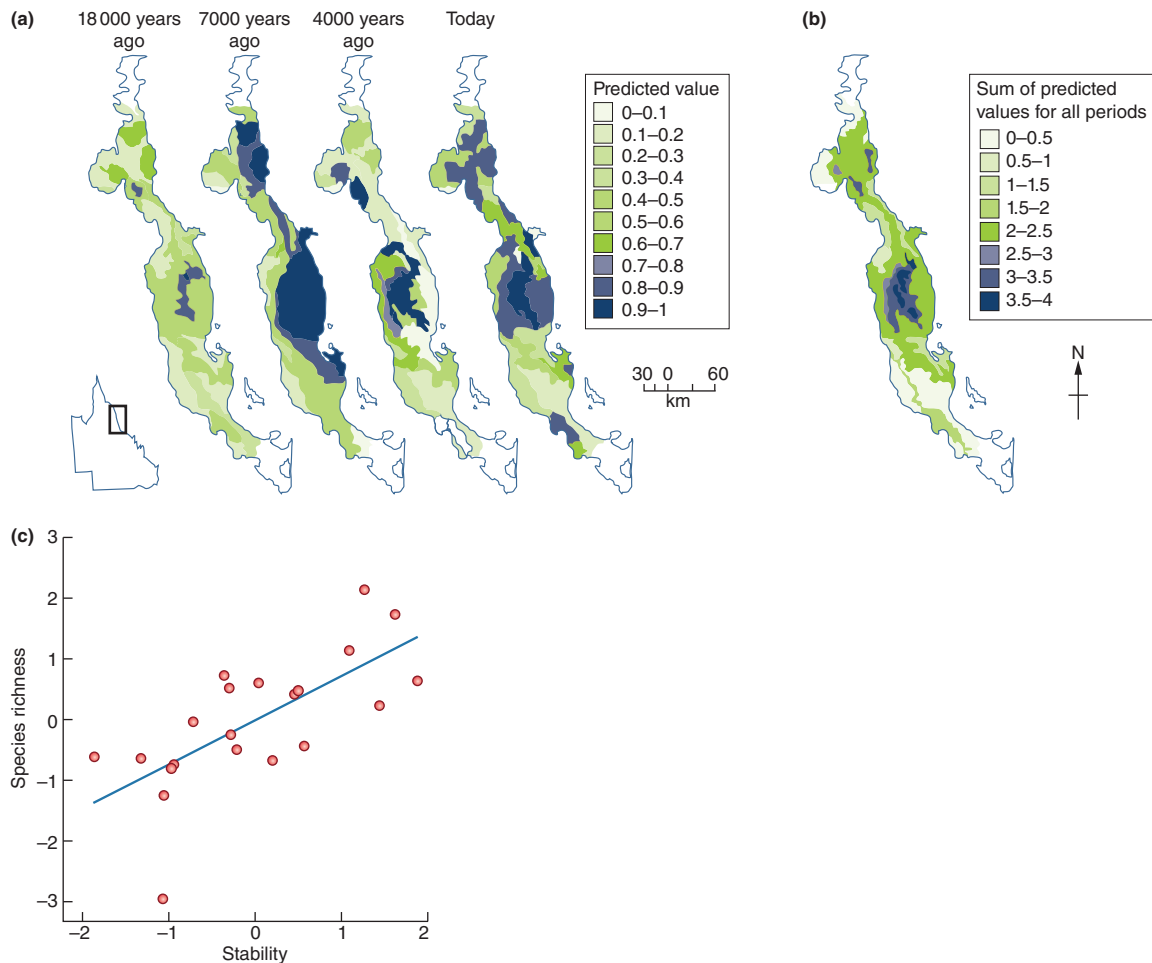
Even in regions that were never glaciated, pollen deposits record complex changes in distributions. In the mountains of the Sheep Range, Nevada, for example, different woody species of plant show different patterns of change in the ranges of elevations that they have occupied as climate has changed (Figure 1.18). The species composition of vegetation has continually been changing and is almost certainly still doing so.

The records of climatic change in the tropics are far less complete than those for temperate regions. It has been suggested, though, that during cooler, drier glacial periods, the tropical forests retreated to smaller patches, surrounded by a sea of savanna, within which speciation was intense, giving rise to present-day 'hot spots' of endemism. Evidence for this in, for example, the Amazonian rainforest now seems less certain than it once did, but there is support for the idea in other regions. In the Australian wet tropics of Queensland, north-eastern Australia, it has been possible to use present-day distributions of forest to predict distributions in the cool-dry climate of the last glacial maximum when forest contraction was greatest (about 18 000 years ago), the cool-wet period around 7000 years ago when a massive expansion was likely, and the warm-wet period around 4000 years ago when there was likely to have been another contraction (Figure 1.19a) (Graham *et al.*, 2006).



**Figure 1.18** Contrasting changes between fossil and current distributions of 10 species of woody plant from the mountains of the Sheep Range, Nevada. The red dots represent fossil records, while the blue lines show current elevational ranges. Source: After Davis & Shaw (2001).





**Figure 1.19 Forest species richness is positively related to forest 'stability' in north-east Australia.** (a) A predictive study of the distribution of Australian 'wet forest' in Queensland (see inset), based on climatic conditions at 2000 random points in the current forested region. From left to right are the predicted overall distribution of forest across the region in cool-dry (18 000 years ago), cool-wet (7000 years ago), warm-wet (4000 years ago) and current climatic conditions. The values between 0 and 1 indicate the probability, according to the model, of forest being found at a given point. (b) Forest 'stability', which is calculated simply as the sum of the values in the four figures in (a). (c) Current species richness in 21 forest subregions (of mammals, birds, reptiles and frogs) increases with estimated 'stability'. The axes are scaled around zero because both stability and species richness were standardised to take account of the fact that both increase with subregion area. *Source:* After Graham *et al.* (2006).

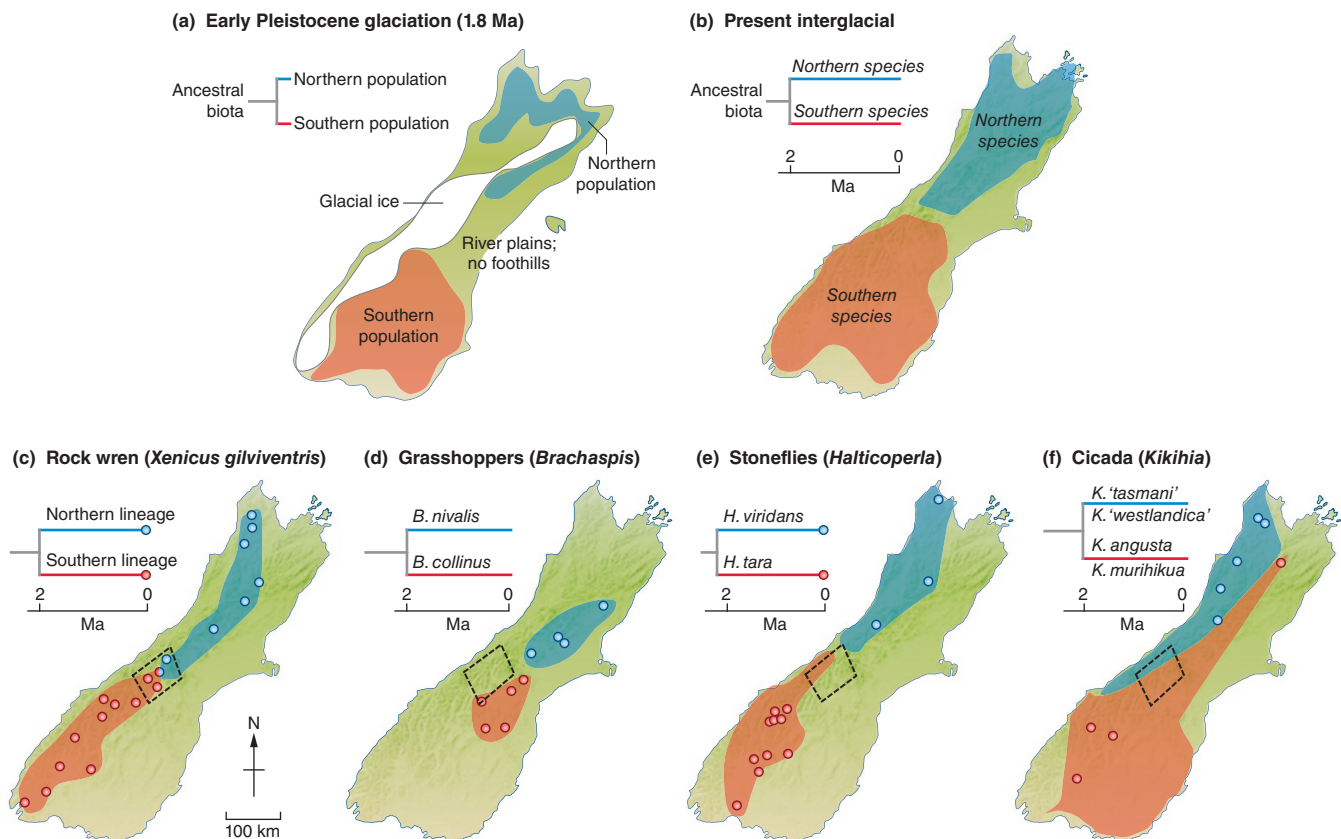
Putting the distributions together, then, allows each subregion of the forest to be assigned a 'stability' (Figure 1.19b) – the most stable being the one in which forest has been most constantly present – and these stabilities can in turn be compared with the species richness today, in each subregion, of mammals, birds, reptiles and frogs. Richness tends to be greatest where stability has been highest (Figure 1.19c), that is, where the forest refuges were in the past. On this interpretation, the present distributions of species may again be seen as largely accidents of history (where the refuges were) rather than precise matches between species and their differing environments.

The Pleistocene ice ages undoubtedly eliminated biota from many mid- to high-latitude areas of the planet. However, in the case of alpine species of the Pyrenees, Himalayas, Andes and Southern Alps, evidence is accumulating that glaciation may sometimes have promoted allopatric speciation by severing continuously distributed populations along the length of mountain ranges (Wallis *et al.*, 2016). In the Southern Alps of New Zealand, for example, comparative phylogeographic analysis, based on mitochondrial and nuclear DNA, has revealed a phylogenetic split 2 mya (the date of the first major glacial epoch), found in both insect and bird biotas, that bisects each into northern and southern assemblages (Figure 1.20).

## APPLICATION 1.4 Global warming and species distributions and extinctions

Evidence of changes in vegetation that followed the last retreat of the ice provides clues about the likely consequences of global warming associated with the continuing increases of carbon dioxide and other greenhouse gases in the atmosphere. Warming of  $0.7^{\circ}\text{C}$  in average global mean surface temperature was recorded between 1970 and 2010. Future climate will depend on warming still to occur but as a result of past anthropogenic emissions, future emissions, natural climate variability and whether or not major volcanic eruptions occur. Models that take into account various scenarios indicate that, relative to 1850–1900, global surface temperature increase by the end of the 21st century is likely to exceed  $2^{\circ}\text{C}$  (IPCC, 2014). But note that the scale of current temperature change is dramatically different from that which has

occurred since the last ice age. Postglacial warming of  $8^{\circ}\text{C}$  over 20 000 years, or  $0.04^{\circ}\text{C}$  per century, must be compared with the current rate of global warming of about  $1.75^{\circ}\text{C}$  per century. It is disturbing to note that changes in the vegetation failed to keep pace even with a rise of  $0.04^{\circ}\text{C}$  per century. Projections for the 21st century require range shifts for trees at rates of 300–500 km per century compared with typical rates in the past of 20–40 km per century (and exceptional rates of 100–150 km). It is striking that the only precisely dated extinction of a tree species in the Quaternary period, that of *Picea critchfeldii*, occurred around 15 000 years ago at a time of especially rapid post-glacial warming (Jackson & Weng, 1999). Clearly, even more rapid change in the future could result in extinctions of many additional species (Davis & Shaw, 2001).



**Figure 1.20** A phylogenetic split bisecting insect and bird biotas into northern and southern assemblages in New Zealand. (a, b) Glaciation of the alpine region of the South Island of New Zealand which is hypothesised to be responsible for fracturing the ancestral biota into north and south lineages that have subsequently diverged. Green shading represents lowlands. (c–f) North–south phylogeographic breaks for alpine birds and insects with dendrograms showing phylogenetic relationships and approximate divergence times. Sampling sites are shown as circles, the shading shows approximate taxon ranges, and the dotted square represents a particularly highly glaciated narrow alpine neck. *Source:* After Wallis *et al.* (2016).

## APPLICATION 1.5 Human history and species invasions

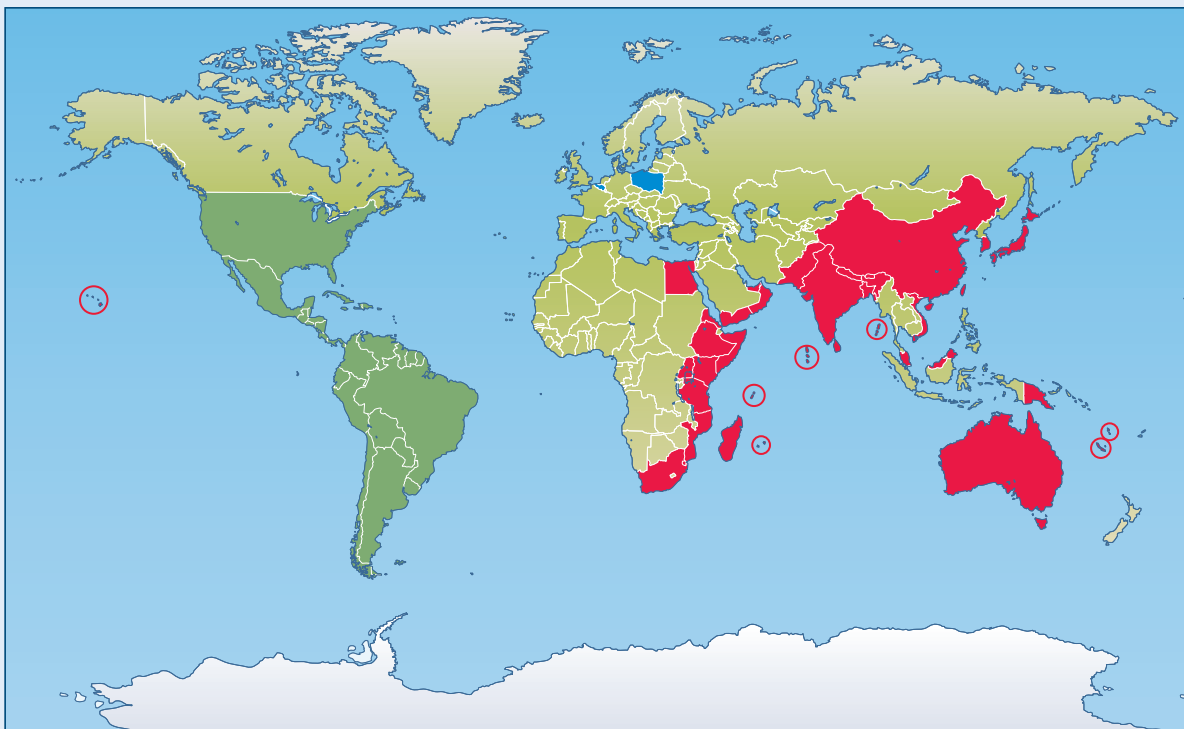
In this section on the role of history in the determination of species distributions, it would be misleading only to consider 'natural' historical factors. Human history has had equally profound effects on the distribution of species around the globe. The world has shrunk as travel has boomed and, just like us, animals, plants and microorganisms have become globetrotters, introduced to new locations on purpose or as accidental tourists.

Only about 10% of invaders become established, and of these, about 10% spread and have significant, sometimes disastrous, consequences (Townsend, 2008). The introduction in the 1950s of Nile perch (*Lates niloticus*) to establish a commercial fishery in Lake Victoria in East Africa, for example, is held responsible for the extinction or near-extinction of several hundred native fish species. An equally striking plant example is provided by the neotropical *Parthenium* weed (*Parthenium hysterophorus*) that has invaded large areas of a number of continents (Figure 1.21), generally by accident, and is responsible for the degradation of grasslands and of many cropping and livestock systems.

Its success as an invader can be attributed to tolerance of a wide range of physicochemical conditions, escape from natural predators in non-native regions, high competitiveness against other plants (including the release of allelopathic chemicals into the soil) and high genetic diversity, among other factors (Bajwa *et al.*, 2016). Finally, prominent among imported human disease organisms are HIV, influenza and Zika viruses.

A profound consequence of global transport and past colonialism has been homogenisation of the biota. The same set of human camp followers now occur in widely separated regions – house sparrows, cockroaches, rats and mice, salmonid fish and game animals, domestic animals and crop plants (with their associated pests and diseases) (Townsend, 2008). Because native species often fare badly in the face of this onslaught, many parts of North America and the southern hemisphere now reflect a European legacy more closely than their native heritage. A graphic example of biotic homogenisation is provided

homogenisation of the biota



**Figure 1.21 The invasion of *Parthenium* weed.** This weed is invasive in the countries shaded or circled in red. Blue-shaded countries represent populations of the weed that may be establishing in Europe. Countries shaded green are considered to be within its invasive range. Source: From Bajwa *et al.* (2016).

[Continued]

## APPLICATION 1.5 (Continued)

at both ends of the trade link between the Great Lakes of North America and the Baltic Sea. Often spread in the ballast water of ships moving along this route, a third of the 170 species of invasive fish, molluscs and crustaceans in the Great Lakes are from the Baltic, and a third of the 100 invaders in the Baltic Sea come from the Great Lakes. Furthermore, enhanced shipping promoted by recent expansions of the Suez and Panama Canals can be expected to escalate marine invasions at regional and continental scales, while increases in internet-based trade in pets and other exotic organisms is providing novel pathways that will be difficult to regulate (Ricciardi *et al.*, 2017). We take this case up again in Section 6.6.2.

### economic consequences of invasions

Invaders can have far-reaching economic as well as ecological consequences. Table 1.1 categorises the tens of thousands of exotic invaders in the USA into taxonomic groupings

and lists these in order of their estimated annual costs (in terms of economic damage done and costs of control). Overall, pests of crop plants, including weeds, insects and pathogens are the most expensive, with rats some way behind but responsible for the destruction of stored grains, starting fires by gnawing through electrical wires, polluting foodstuffs, spreading diseases and preying on native animals. Imported human disease organisms are also very expensive to treat and result in 40 000 deaths per year. Ecological knowledge is needed to predict future invasions that are likely to have damaging consequences so that the invaders can be confronted, particularly via biosecurity at national borders. Despite their obvious deleterious effects, the importance of biological invasions seems not to be well understood by the public or fully accepted by decision makers (Courchamp *et al.*, 2017). Ecologists have much to contribute in this arena.

**Table 1.1** Estimated annual costs (billions of US dollars) associated with damage caused and management costs of invaders in the USA. Taxonomic groupings are ordered in terms of the total costs associated with them. *Source:* After Pimentel *et al.* (2000).

Type of organism	Number of invaders	Major culprits	Loss and damage	Control costs	Total costs
Microbes (pathogens)	>20 000	Crop pathogens	32.1	9.1	41.2
Mammals	20	Rats and cats	37.2	Na	37.2
Plants	5 000	Crop weeds	24.4	9.7	34.1
Arthropods	4 500	Crop pests	17.6	2.4	20.0
Birds	97	Pigeons	1.9	NA	1.9
Molluscs	88	Asian clams, zebra mussels	1.2	0.1	1.3
Fishes	138	Grass carp, etc.	1.0	NA	1.0
Reptiles, amphibians	53	Brown tree snake	0.001	0.005	0.006

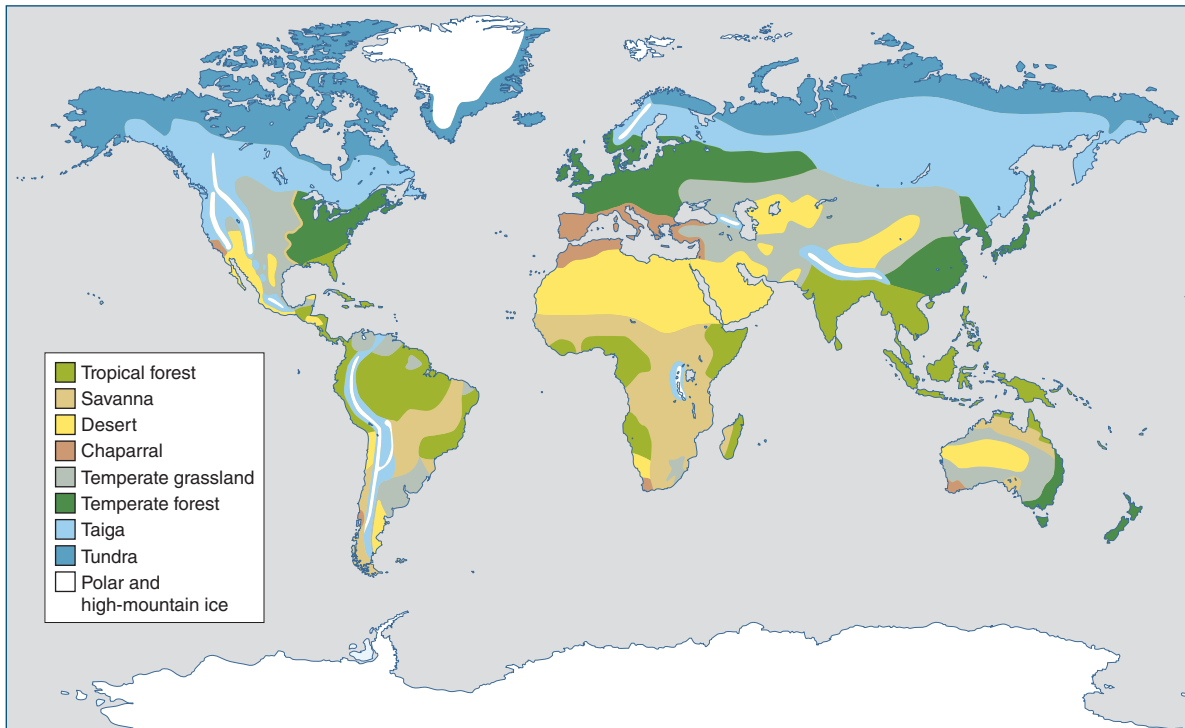
NA, data not available

## 1.5 The match between communities and their environments

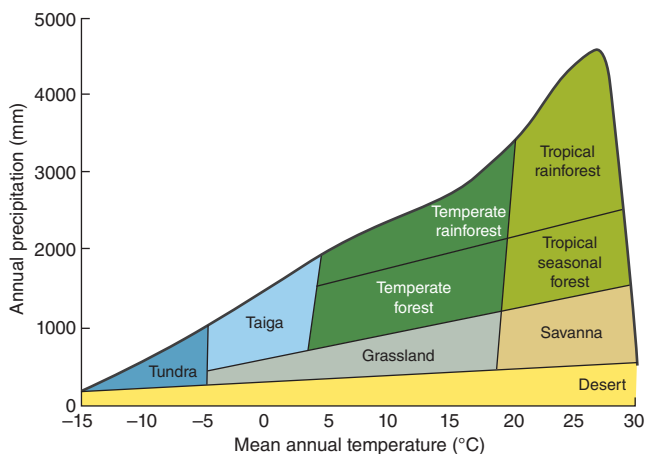
### 1.5.1 Terrestrial biomes of the earth

Before we examine the differences and similarities between communities, we need to consider the larger groupings, 'biomes', in which biogeographers recognise marked differences in the flora and fauna of different parts of the world. The number of terrestrial biomes that are distinguished is a

matter of taste. They certainly grade into one another, and sharp boundaries are a convenience for cartographers rather than a reality of nature. We describe eight terrestrial biomes and illustrate their global distribution in Figure 1.22, and show how they may be related to annual temperature and precipitation (Figure 1.23). Apart from anything else, understanding the terminology that describes and distinguishes these biomes is necessary when we come to consider key questions later in the book. Why are there more species in some communities than in others? Are



**Figure 1.22 World distribution of the major biomes of vegetation.** Source: From <http://www.zo.utexas.edu/faculty/sjasper/images/50.24.gif>.



**Figure 1.23 Biomes in relation to rainfall and temperature.** The variety of environmental conditions experienced in terrestrial biomes can be described in terms of their annual rainfall and mean annual temperatures. Source: After Woodward & Lomas (2004).

some communities more stable in their composition than others, and if so why? Do more productive environments support more diverse communities? Or do more diverse communities make more productive use of the resources available to them?

*Tundra* occurs around the Arctic Circle, beyond the tree line.

tundra

Small areas also occur on sub-Antarctic islands in the southern hemisphere. 'Alpine' tundra is found under similar conditions but at high altitude. The environment is characterised by the presence of permafrost – water permanently frozen in the soil – while liquid water is present for only short periods of the year. The typical flora includes lichens, mosses, grasses, sedges and dwarf trees. Insects are extremely seasonal in their activity, and the native bird and mammal fauna is enriched by species that migrate from warmer latitudes in the summer. In the colder areas, grasses and sedges disappear, leaving nothing rooted in the permafrost. Ultimately, vegetation that consists only of lichens and mosses gives way, in its turn, to the polar desert. The number of species of higher plants (i.e. excluding mosses and lichens) decreases from the Low Arctic (around 600 species in North America) to the High Arctic (north of 83°, e.g. around 100 species in Greenland and Ellesmere Island). In contrast, the flora of Antarctica contains only two native species of vascular plant and some lichens and mosses that support a few small invertebrates. The biological productivity and diversity of Antarctica are concentrated at the coast and depend almost entirely on resources harvested from the sea.



**taiga**

*Taiga* or northern coniferous forest occupies a broad belt across North America and Eurasia. Liquid water is unavailable for much of the winter, and plants and many of the animals have a conspicuous winter dormancy in which metabolism is very slow. Generally, the tree flora is very limited. In areas with less severe winters, the forests may be dominated by pines (*Pinus* species, which are all evergreens) and deciduous trees such as larch (*Larix*), birch (*Betula*) or aspens (*Populus*), often as mixtures of species. Farther north, these species give way to single-species forests of spruce (*Picea*) covering immense areas. The overriding environmental constraint in northern spruce forests is the presence of permafrost, creating drought except when the sun warms the surface. The root system of spruce can develop in the superficial soil layer, from which the trees derive all their water during the short growing season.

**temperate forests**

*Temperate forests* range from the mixed conifer and broad-leaved forests of much of North America and northern Central Europe (where there may be 6 months of freezing temperatures), to the moist, dripping forests of broad-leaved evergreen trees found at the biome's low-latitude limits in, for example, Florida and New Zealand. In most temperate forests, however, there are periods of the year when liquid water is in short supply, because potential evaporation exceeds the sum of precipitation and water available from the soil. Deciduous trees, which dominate in most temperate forests, lose their leaves in the autumn and become dormant. On the forest floor, diverse floras of perennial herbs often occur, particularly those that grow quickly in the spring before the new tree foliage has developed. Temperate forests also provide food resources for animals that are usually very seasonal in their occurrence. Many of the birds of temperate forests are migrants that return in spring but spend the remainder of the year in warmer biomes.

**grassland**

*Grassland* occupies the drier parts of temperate and tropical regions. Temperate grassland has many local names: the steppes of Asia, the prairies of North America, the pampas of South America and the veldt of South Africa. Tropical grassland or savanna is the name applied to tropical vegetation ranging from pure grassland to some trees with much grass. Almost all of these temperate and tropical grasslands experience seasonal drought, but the role of climate in determining their vegetation is almost completely overridden by the effects of grazing animals that limit the species present to those that can recover from frequent defoliation. In the savanna, fire is also a common hazard in the dry season and, like grazing animals, it tips the balance in the

vegetation against trees and towards grassland. Nonetheless, there is typically a seasonal glut of food, alternating with shortage, and as a consequence the larger grazing animals suffer extreme famine (and mortality) in drier years. A seasonal abundance of seeds and insects supports large populations of migrating birds, but only a few species can find sufficiently reliable resources to be resident year-round.

Many of these natural grasslands have been cultivated and replaced by arable annual 'grasslands' of wheat, oats, barley, rye and corn. Such annual grasses of temperate regions, together with rice in the tropics, provide the staple food of human populations worldwide. At the drier margins of the biome, many of the grasslands are 'managed' for meat or milk production, sometimes requiring a nomadic human lifestyle. The natural populations of grazing animals have been driven back in favour of cattle, sheep and goats. Of all the biomes, this is the one most coveted, used and transformed by humans.

**chaparral**

*Chaparral* or *maquis* occurs in Mediterranean-type climates (mild, wet winters and summer drought) in Europe, California and north-west Mexico, and in a few small areas in Australia, Chile and South Africa. Chaparral develops in regions with less rainfall than temperate grasslands and is dominated mainly by a drought-resistant, hard-leaved scrub of low-growing woody plants. Annual plants are also common in chaparral regions during the winter and early spring, when rainfall is more abundant. Chaparral is subject to periodic fires; many plants produce seeds that will only germinate after fire while others can quickly resprout because of food reserves in their fire-resistant roots.

**desert**

*Deserts* are found in areas that experience extreme water shortage: rainfall is usually less than about  $25 \text{ cm year}^{-1}$ , is usually very unpredictable and is considerably less than potential evaporation. The desert biome spans a very wide range of temperatures, from hot deserts, such as the Sahara, to very cold deserts, such as the Gobi in Mongolia. In their most extreme form, the hot deserts are too arid to bear any vegetation; they are as bare as the cold deserts of Antarctica. Where there is sufficient rainfall to allow plants to grow in arid deserts, its timing is always unpredictable. Desert vegetation falls into two sharply contrasted patterns of behaviour. Many species have an opportunistic lifestyle, stimulated into germination by the unpredictable rains. They grow fast and complete their life history by starting to set new seed after a few weeks. These are the species that can occasionally make a desert bloom. A different pattern of behaviour is to be long-lived with sluggish physiological

processes. Cacti and other succulents, and small shrubby species with small, thick and often hairy leaves, can close their stomata (pores through which gas exchange takes place) and tolerate long periods of physiological inactivity. The relative poverty of animal life in arid deserts reflects the low productivity of the vegetation and the indigestibility of much of it.

#### tropical rainforest

*Tropical rainforest* is the most productive of the earth's biomes – a result of the coincidence of high solar radiation received throughout the year and regular and reliable rainfall. The productivity is achieved, overwhelmingly, high in the dense forest canopy of evergreen foliage. It is dark at ground level except where fallen trees create gaps. Often, many tree seedlings and saplings remain in a suppressed state from year to year and only leap into action if a gap forms in the canopy above them. Apart from the trees, the vegetation is largely composed of plant forms that reach up into the canopy vicariously; they either climb and then scramble in the tree canopy (vines and lianas, including many species of fig) or grow as epiphytes, rooted on the damp upper branches. Most species of both animals and plants in tropical rainforest are active throughout the year, though the plants may flower and ripen fruit in sequence. Dramatically high species richness is the norm for tropical rainforest, and communities rarely if ever become dominated by one or a few species. The diversity of rainforest trees provides for a corresponding diversity of resources for herbivores, and so on up the food chain.

#### aquatic biomes?

All of these biomes are terrestrial. Aquatic ecologists could also come up with a set of biomes, although the tradition has largely been a terrestrial one. We might distinguish springs, rivers, ponds, lakes, estuaries, coastal zones, coral reefs and deep oceans, among other distinctive kinds of aquatic community. For present purposes, we recognise just two aquatic biomes, *marine* and *freshwater*. The oceans cover about 71% of the earth's surface and reach depths of more than 10 000 m. They extend from regions where precipitation exceeds evaporation to regions where the opposite is true. There are massive movements within this body of water that prevent major differences in salt concentrations developing (the average concentration is about 3%). Two main factors influence the biological activity of the oceans. Photosynthetically active radiation is absorbed in its passage through water, so photosynthesis is confined to the surface region. Mineral nutrients, especially nitrogen and phosphorus, are commonly so dilute that they limit the biomass that can develop. Shallow waters (e.g. coastal regions and estuaries) tend to have high biological activity because they receive mineral input from the land and less incident

radiation is lost than in passage through deep waters. Intense biological activity also occurs where nutrient-rich waters from the ocean depths come to the surface; this accounts for the concentration of many of the world's fisheries in Arctic and Antarctic waters.

Freshwater biomes occur mainly on the route from land drainage to the sea. The chemical composition of the water varies enormously, depending on its source, its rate of flow and the inputs of organic matter from vegetation that is rooted in or around the aquatic environment. In water catchments where the rate of evaporation is high, salts leached from the land may accumulate and the concentrations may far exceed those present in the oceans; brine lakes or even salt pans may be formed in which little life is possible. Even in aquatic situations liquid water may be unavailable, as is the case in the polar regions.

Differentiating between biomes allows only a very crude recognition of the sorts of differences and similarities that occur between communities of organisms. Within biomes there are both small- and large-scale patterns of variation in the structure of communities and in the organisms that inhabit them. Moreover, as we see next, what characterises a biome is not necessarily the particular species that live there.

### 1.5.2 The 'life form spectra' of communities

We pointed out earlier the crucial importance of geographic isolation in allowing populations to diverge under selection. The geographic distributions of species, genera, families and even higher taxonomic categories of plants and animals often reflect this geographic divergence. All species of lemurs, for example, are found on the island of Madagascar and nowhere else. Similarly, 230 species in the genus *Eucalyptus* (gum tree) occur naturally in Australia (and two or three in Indonesia and Malaysia). The lemurs and the gum trees occur where they do because they evolved there – not because these are the only places where they could survive and prosper. Indeed, many *Eucalyptus* species grow with great success and spread rapidly when they have been introduced to, for example, California, Spain and Kenya. A map of the natural world distribution of lemurs tells us quite a lot about the evolutionary history of this group. But as far as its relationship with a biome is concerned, the most we can say is that lemurs happen to be one of the constituents of the tropical rainforest biome in Madagascar.

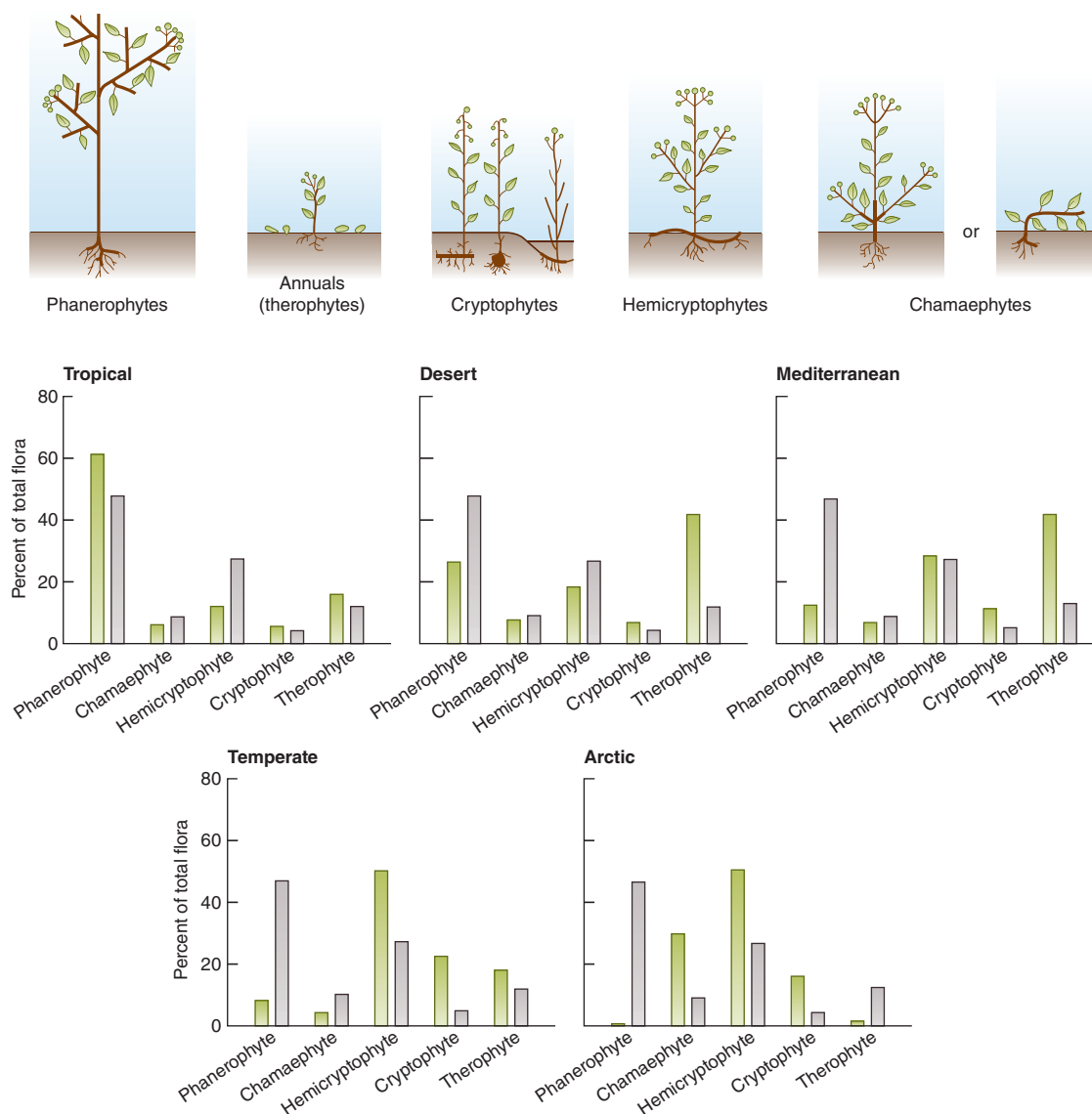
Similarly, particular biomes in Australia include certain marsupial mammals, while the *same* biomes in other parts of the world are home to their placental counterparts.



A map of biomes, then, is not usually a map of the distribution of species. Instead, we recognise different biomes and different types of aquatic community from the *types* of organisms that live in them. How can we describe their similarities so that we can classify, compare and map them? In addressing this question, the Danish biogeographer Raunkiaer developed, in 1934, his idea of 'life forms', a deep insight into the ecological significance of plant forms (Figure 1.24). He then used the spectrum of life forms present in different types of vegetation as a means of describing their ecological character.

Plants grow by developing new shoots from the buds that lie at the apices (tips) of existing shoots and in the leaf axils. Within the buds, the meristematic cells are the most sensitive part of the whole shoot – the 'Achilles' heel' of plants. Raunkiaer argued that the ways in which these buds are protected in different plants are powerful indicators of the hazards in their environments and may be used to define the different plant forms (Figure 1.24). Thus, trees expose their buds high in the air, fully exposed to the wind, cold and drought; Raunkiaer called them

Raunkiaer's plant classification



**Figure 1.24 Raunkiaer's life forms.** The drawings above depict the variety of plant forms distinguished by Raunkiaer on the basis of where they bear their buds (shown as green circles). Below are life form spectrums for five different biomes. The green bars show the percentage of the total flora that is composed of species with each of the five different life forms. The grey bars are the proportions of the various life forms in the world flora for comparison. *Source:* From Crawley (1986).

*phanerophytes* (Greek *phanero*, 'visible'; *phyte*, 'plant'). By contrast, many perennial herbs form cushions or tussocks in which buds are borne above ground but are protected from drought and cold in the dense mass of old leaves and shoots (*chamaephytes*: 'on the ground plants'). Buds are even better protected when they are formed at or in the soil surface (*hemicyptophytes*: 'half hidden plants') or on buried dormant storage organs (bulbs, corms and rhizomes – *cryptophytes*: 'hidden plants'; or *geophytes*: 'earth plants'). These allow the plants to make rapid growth and to flower before they die back to a dormant state. A final major category consists of annual plants that depend wholly on dormant seeds to carry their populations through seasons of drought and cold (*therophytes*: 'summer plants'). Thero-phytes are the plants of deserts (they make up nearly 50% of the flora of Death Valley, USA), sand dunes and

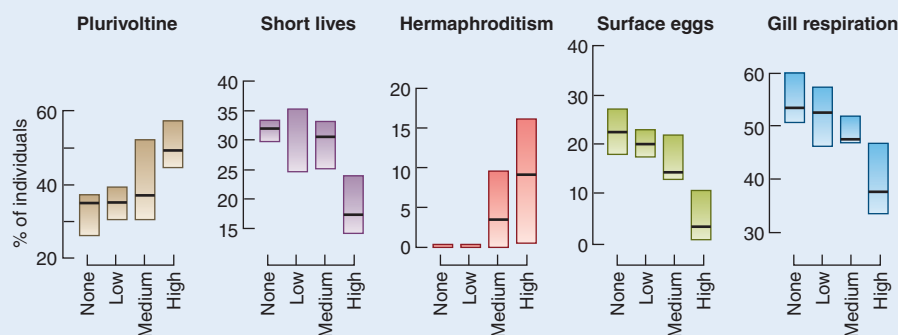
repeatedly disturbed habitats. They also include the annual weeds of arable lands, gardens and urban wastelands.

But there is, of course, no vegetation that consists entirely of one growth form. All vegetation contains a mixture, a spectrum, of Raunkiaer's life forms. The composition of the spectrum in any particular habitat is as good a short-hand description of its vegetation as ecologists have yet managed to devise. Raunkiaer compared these with a 'global spectrum' obtained by sampling from a compendium of all species known and described in his time (the *Index Kewensis*), biased by the fact that the tropics were, and still are, relatively unexplored. Thus, for example, we recognise a chaparral type of vegetation when we see it in Chile, Australia, California or Crete because the life form spectrums are similar. Their detailed taxonomies would only emphasise how different they are.

### APPLICATION 1.6 Stream invertebrate species traits and agricultural pollution

While plant scientists have tended to be keener on classifying floras than animal scientists on classifying faunas, an analogous approach can be of use to resource managers. For example, agriculture in the catchment area of streams can have profound impacts on the invertebrate communities they contain, and just as with Raunkiaer's classification of plants, the patterns may be more closely related to species traits (paralleling Raunkiaer's life form spectra) than to taxonomic composition. Doledec *et al.* (2006) found that traits associated with population resilience (the ability to bounce back following perturbations), including short generation time and

hermaphroditic reproduction, became more prevalent with increasing agricultural intensity in the catchment, reflecting more frequent and intense variations in stream nutrient concentrations (Figure 1.25). There was also a shift away from laying eggs at the water surface and a decrease in gill respiration, reflecting the increasing likelihood of smothering by sediment introduced as a result of ploughing or disturbance of soil and stream banks by grazing animals. The representation of these and other species traits can be used to devise indexes and thresholds of stream health that managers can aspire to attain or restore (Serra *et al.*, 2017).



**Figure 1.25 Species traits in streams.** Relationships between the representation of species traits of stream invertebrates (% of individuals possessing the trait in the multispecies community as a whole) and the intensity of agriculture in the catchment area of the stream. None, ungrazed native tussock grassland; low, grazed native tussock grassland; medium, extensively grazed pasture; high, dairy or deer farming. Plurivoltine, more than one generation per year; short lives, 10–30 days; hermaphroditism, one individual possessing both sexes; surface eggs, laying unattached eggs at the stream surface; gill respiration, having external gills.

Source: From Doledec *et al.* (2006).

## 1.6 The diversity of matches within communities

Although a particular type of organism is often characteristic of a particular ecological situation, it will almost inevitably be only part of a diverse community of species. A satisfactory account, therefore, must do more than identify the similarities between organisms that allow them to live in the same environment – it must also try to explain why species that live in the same environment are often profoundly different. To some extent, this ‘explanation’ of diversity is a trivial exercise. It comes as no surprise that a plant utilising sunlight, a fungus living on the plant, a herbivore eating the plant and a parasitic worm living in the herbivore should all coexist in the same community (food webs will be discussed in Chapter 17 and the flow of energy and nutrients through ecosystems in Chapters 20 and 21). On the other hand, most communities also contain a variety of different species that are all constructed in a fairly similar way and all living (at least superficially) a fairly similar life. We have seen excellent examples among the finches of the Galápagos (Figure 1.9), the cichlid fish of Lake Apoyo (Figure 1.11), the *Howea* palms of Howe Island (Figure 1.12), and the picture-winged fruit-flies of Hawaii (Figure 1.16). There are several elements in an explanation of this diversity.

environments are heterogeneous

A completely homogeneous environment might well become dominated by one or a very few species that are well adapted to the conditions and resources there. But there are no homogeneous environments in nature. Even a continuously stirred culture of microorganisms is heterogeneous because it has a boundary – the walls of the culture vessel – and cultured microorganisms often subdivide into two forms: one that sticks to the walls and the other that remains free in the medium.

The extent to which an environment is heterogeneous depends on the scale of the organism that senses it. To a mustard seed, a grain of soil is a mountain; and to a caterpillar, a single leaf may represent a lifetime’s diet. A seed lying in the shadow of a leaf may be inhibited in its germination while a seed lying outside that shadow germinates freely. What appears to the human observer as a homogeneous environment may, to members of species within it, be a mosaic of the intolerable and the adequate.

There may also be gradients in space (e.g. altitude) or gradients in time, and the latter, in their turn, may be rhythmic (like daily and seasonal cycles), directional (like the accumulation of a pollutant in a lake) or erratic (like fires, hailstorms and typhoons).

Heterogeneity crops up again and again in later chapters – in part because of the challenges it poses to organisms in

moving from patch to patch (Chapter 6), in part because of the variety of opportunities it provides for different species (Chapters 2 and 3), and in part because heterogeneity can alter communities by interrupting what would otherwise be a steady march to an equilibrium state of a few species (Chapters 8 and 18).

It is important to note that the existence of one type of organism in an area immediately diversifies it for others. Over its lifetime, an organism may increase the diversity of its environment by contributing dung, urine, dead parts (e.g. skin or leaves) and ultimately its dead body. During its life, its body may serve as a place in which other species find homes. Indeed, some of the most strongly developed matches between organisms and their environment are those in which one species has developed a dependence upon another. This is the case in many relationships between consumers and their foods. Whole syndromes of form, behaviour and metabolism constrain the animal within its narrow food niche, and deny it access to what might otherwise appear suitable alternative foods. Similar tight matches are characteristic of the relationships between parasites and their hosts. The various interactions in which one species is consumed by another are the subject matter of Chapters 8–10 and 12.

Where two species have evolved a mutual dependence, the fit may be

pairs of species

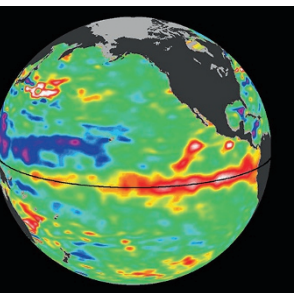
even tighter. We examine such ‘mutualisms’ in detail in Chapter 13. The association of nitrogen-fixing bacteria with the roots of leguminous plants, and the often extremely precise relationships between insect pollinators and their flowers, are two good examples. When a population has been exposed to variations in the physical factors of the environment, for example a short growing season or a high risk of frost or drought, a once-and-for-all tolerance may ultimately evolve. The physical factor cannot itself change or evolve as a result of the evolution of the organisms. By contrast, when members of two species interact, the change in each produces alterations in the life of the other, and each may generate selective forces that direct the evolution of the other. In such a coevolutionary process the interaction between two species may continually escalate. What we then see in nature may be pairs of species that have driven each other into ever-narrowing ruts of specialisation – an ever closer match.

While it is no surprise that species with rather different roles coexist within the same community, it is also generally the case that communities support a variety of species performing apparently rather similar roles. Do these species compete with one another? Do competing species need to be different if

coexistence of similar species

they are to coexist? If so, how different do they need to be: is there some limit to their similarity? Do species like Darwin's finches interact with one another at the present time, or has evolution in the past led to the absence of such interactions in contemporary communities? We return to these questions about coexisting, similar species in Chapter 8, and take them up again in Chapters 16–19.

Even at this stage, though, we may note that coexisting species, even when apparently very similar, commonly differ in subtle ways – not simply in their morphology or physiology but also in their responses to their environment and the role they play within the community of which they are part. The 'ecological niches' of such species are said to be differentiated from one another. The concept of the ecological niche is itself explained in the next two chapters.



## Chapter 2

# Conditions

### 2.1 Introduction

In order to understand the distribution and abundance of a species we need to know its history (Chapter 1), the resources it requires (Chapter 3), the individuals' rates of birth, death and migration (Chapters 4 and 6), their interactions with their own and other species (Chapters 5 and 8–13) and the effects of environmental conditions. This chapter deals with the limits placed on organisms by environmental conditions.

conditions may be altered – but not consumed

A condition is an abiotic environmental factor that influences the functioning of living organisms.

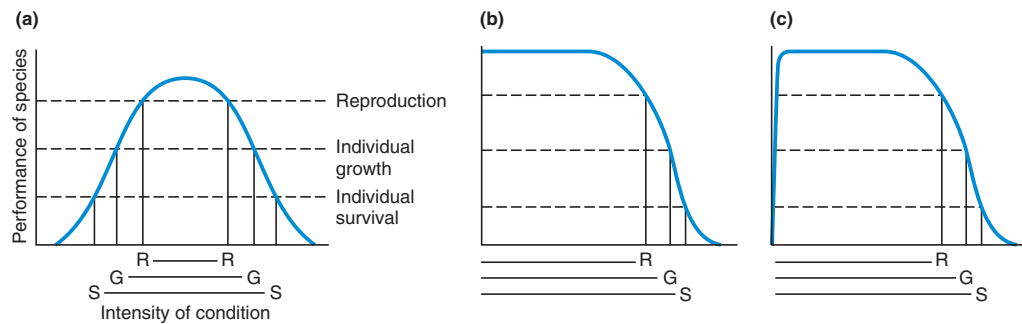
Examples include temperature, relative humidity, pH, salinity and the concentration of pollutants. A condition may be modified by the presence of other organisms. For example, temperature, humidity and soil pH may be altered under a forest canopy. But unlike resources, conditions are not consumed or used up by organisms.

For some conditions we can recognise an optimum concentration or level at which an organism performs best, with its activity tailing off at both lower and higher levels (Figure 2.1a). But what is meant by 'performs best'? From an evolutionary point of view, 'optimal' conditions are those under which individuals leave most descendants (are fittest), but these are often impossible to determine in practice because measures of fitness should be made over several generations. Instead, we more often measure the effect of conditions on some key property like the activity of an enzyme, the respiration rate of a tissue, the growth rate

of individuals or their rate of reproduction. However, the effect of variation in conditions on these various properties will often not be the same; organisms can usually survive over a wider range of conditions than permit them to grow or reproduce (Figure 2.1a).

The precise shape of a species' response will vary from condition to condition. The generalised form of response, shown in Figure 2.1a, is appropriate for conditions like temperature and pH in which there is a continuum from an adverse or lethal level (e.g. freezing or very acid conditions), through favourable levels of the condition to a further adverse or lethal level (heat damage or very alkaline conditions). There are, though, many environmental conditions for which Figure 2.1b is a more appropriate response curve: for most toxins, including radioactive emissions and chemical pollutants, a low-level intensity or concentration of the condition has no detectable effect, but an increase begins to cause damage and a further increase may be lethal. There is also a different form of response to conditions that are toxic at high levels but essential for growth at low levels (Figure 2.1c). This is the case for sodium chloride – an essential resource for animals but lethal at high concentrations – and for the many elements that are essential micronutrient resources in the growth of plants and animals (e.g. copper, zinc and manganese), but that can become lethal at the higher concentrations sometimes caused by industrial pollution.

In this chapter, we consider responses to temperature in much more detail than other conditions, because it is the single most important condition that affects the lives of



**Figure 2.1** Response curves illustrating the effects of a range of environmental conditions on individual survival (S), growth (G) and reproduction (R). (a) Extreme conditions are lethal, less extreme conditions prevent growth, and only optimal conditions allow reproduction. (b) The condition is lethal only at high intensities; the reproduction–growth–survival sequence still applies. (c) Similar to (b), but the condition is required by organisms, as a resource, at low concentrations.

organisms, and many of the generalisations that we make have widespread relevance. We move on to consider a range of other conditions, before returning, full circle, to temperature because of the way that other conditions interact with it. We begin, though, by explaining the framework within which each of these conditions should be understood: the ecological niche.

## 2.2 Ecological niches

The term *ecological niche* is frequently misunderstood. It is often misused to describe the sort of place in which an organism lives, as in the sentence: ‘Woodlands are the niche of woodpeckers’. Strictly, however, where an organism lives is its *habitat*. A niche is not a place but an idea: a summary of the organism’s tolerances and requirements. The habitat of a gut microorganism would be an animal’s alimentary canal; the habitat of an aphid might be a garden; and the habitat of a fish could be a whole lake. Each habitat, however, provides many different niches: many other organisms also live in the gut, the garden or the lake – and with quite different lifestyles. The word *niche* began to gain its present scientific meaning when Elton wrote in 1933 that the niche of an organism is its mode of life ‘in the sense that we speak of trades or jobs or professions in a human community’. The niche of an organism started to be used to describe how, rather than just where, an organism lives.

### niche dimensions

The modern concept of the niche was proposed by Hutchinson in 1957 to address the ways in which tolerances and requirements interact to define the conditions (this chapter) and resources (Chapter 3) needed by an individual of a species in order to practice its way of life. Temperature, for

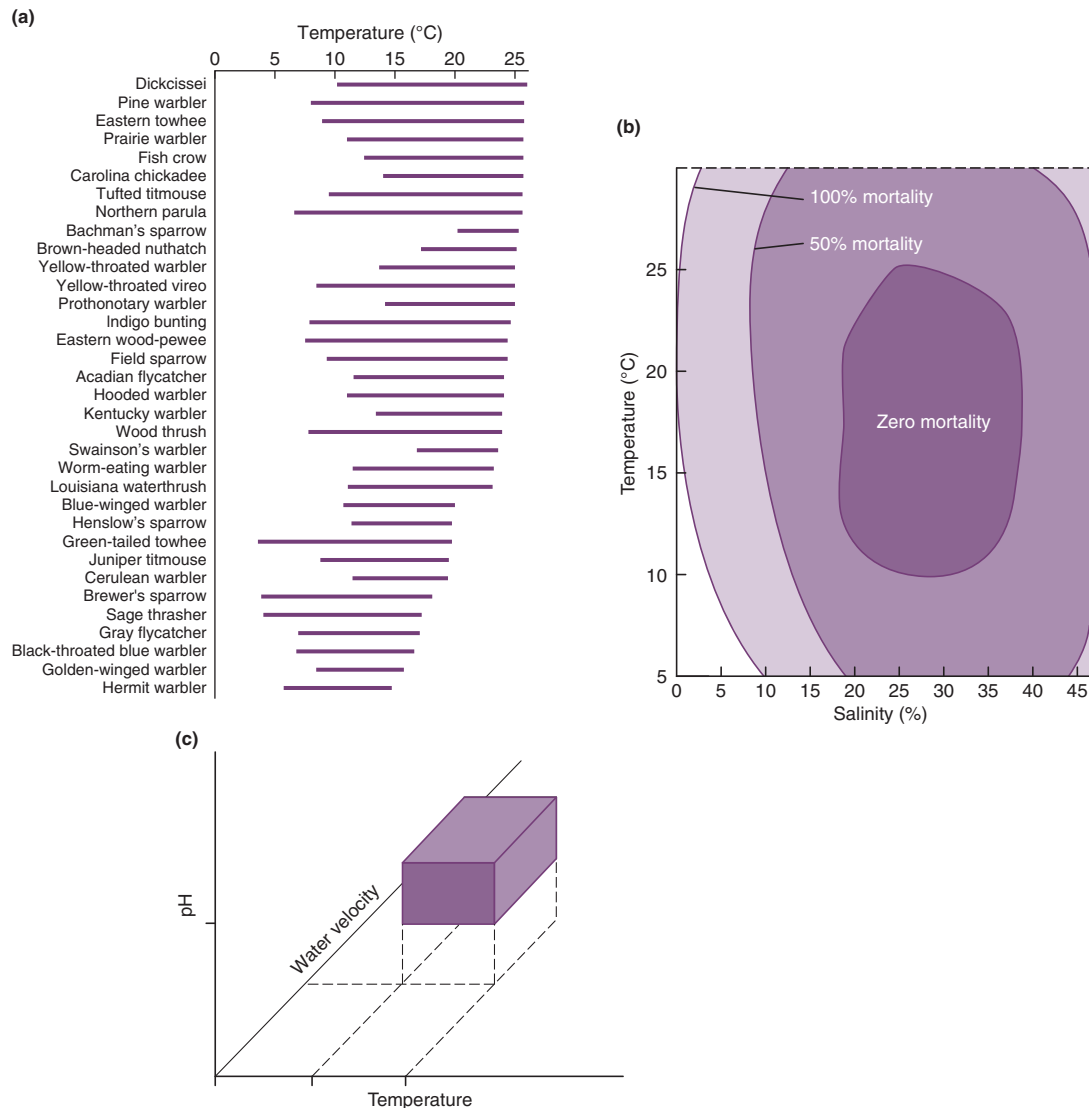
instance, limits the growth and reproduction of all organisms, but different organisms tolerate different ranges of temperature. This range is one *dimension* of an organism’s ecological niche. Figure 2.2a shows how species of passerine birds in North America vary in this dimension of their niche. But there are many such dimensions of a species’ niche – its tolerance of various other conditions (relative humidity, pH, wind speed, water flow and so on) and its need for various resources. Clearly the real niche of a species must be *multidimensional*.

It is easy to visualise the early stages of building such a multidimensional niche. Figure 2.2b illustrates the way in which two niche dimensions (temperature and salinity) together define a two-dimensional area that is part of the niche of a sand shrimp. Three dimensions, such as temperature, pH and current velocity in a stream, may define a three-dimensional niche volume of a stream alga (Figure 2.2c). In fact, we consider a niche to be an *n-dimensional hypervolume*, where *n* is the number of dimensions that make up the niche. It is hard to imagine (and impossible to draw) this more realistic picture. Nonetheless, the simplified three-dimensional version captures the idea of the ecological niche of a species. It is defined by the boundaries that limit where it can live, grow and reproduce, and it is very clearly a concept rather than a place. The concept has become a cornerstone of ecological thought.

the *n*-dimensional hypervolume

The difficulties of interpreting the multiplicity of relevant niche dimensions can be reduced by a mathematical technique called *ordination*. This is one of several methods used by ecologists to condense information from many dimensions into a much smaller, more manageable number, in this case allowing us to simultaneously display species and several influential environmental variables along one or more ‘ordination axes’.

ordination as an aid to conceiving the *n*-dimensional niche

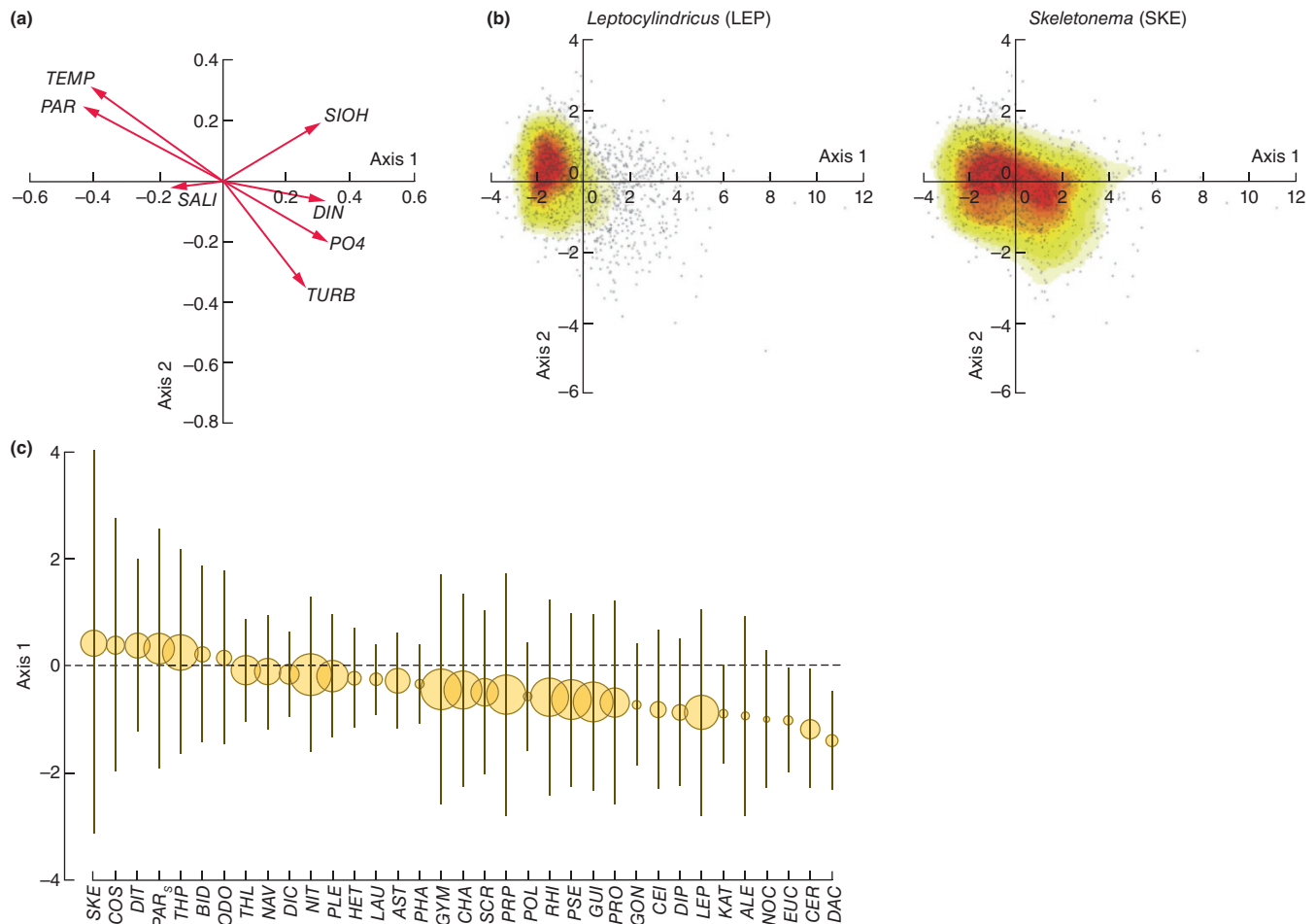


**Figure 2.2 The ecological niche in one, two and three dimensions.** (a) A niche in one dimension showing the thermal range of passerine birds in southern Canada and the contiguous USA recorded during the North American Breeding Bird Survey 2002–06 in relation to minimum and maximum thermal limits of an average of 10 occurrence locations for each species (measured in each case as mean springtime breeding season temperature). (b) A niche in two dimensions for the sand shrimp (*Crangon septemspinosa*) showing the fate of egg-bearing females in aerated water at a range of temperatures and salinities. (c) A diagrammatic niche in three dimensions for a stream-dwelling alga showing a volume defined by temperature, pH and water velocity; in reality, the niche would not appear as a neat cuboid defined by the three tolerance ranges because, for example, temperature tolerance may be reduced when pH is low. *Source:* (a) Data from Coristine & Kerr (2015). (b) After Haefner (1970).

Species with the most similar niches appear closest together, and the direction of increase or decrease of environmental variables along each axis reveals how the species' niches are arranged in relation to these variables. In their study of marine phytoplankton along the French coast, Farinas *et al.* (2015) related abundance data for 35 taxa to seven environmental factors: temperature, salinity and turbidity (conditions), and photosynthetically active radiation and the concentrations of three inorganic nutrient concentrations

(resources for phytoplankton). The relationships of these variables along two ordination axes derived by the method are displayed in Figure 2.3a. Note, for example, that nutrient concentrations are positively related to the first axis, while salinity, solar radiation and temperature are negatively related to this axis. Figure 2.3b illustrates for two taxa, *Leptocylindrus* spp. and *Skeletonema* spp., the space occupied along the first and second axes of the ordination. *Leptocylindrus* has a narrower niche than *Skeletonema*, and *Leptocylindrus* is





**Figure 2.3 The use of ordination to facilitate understanding of the multidimensional niche.** (a) Weights along two ordination axes of seven environmental factors (*TEMP*, water temperature; *PAR*, photosynthetically active radiation; *SALI*, salinity; *TURB*, turbidity; *PO4*, phosphates; *DIN*, dissolved inorganic nitrogen; *SIOH*, silicates) used to characterise the ecological niche of 35 phytoplankton taxa in French coastal seas. (b) Space occupied by two of the taxa, *Leptocylindricus* (LEP) and *Skeletonema* (SKE) spp., along the first and second axes of the ordination analysis. The yellow to red colour gradient represents phytoplankton density from low to high. (c) Space occupied by each taxon along axis 1 of the ordination. The diameter of the circle is proportional to the total occurrence frequency of each taxon. Axis 1 is positively related to nutrient concentrations and negatively related to temperature, salinity and photosynthetically active radiation. *Source:* From Farinas *et al.* (2015).

displaced towards the negative end of axis 1 and the positive end of axis 2, being more strongly related than *Skeletonema* to temperature and photosynthetically active radiation. Figure 2.3c shows the space occupied by all 35 taxa along axis 1: those with more negative positions are associated with higher temperatures, salinity and photosynthetically active radiation levels; those with more positive positions are associated with higher nutrient concentrations. While a hypervolume with more than three dimensions cannot be visualised, ordination allows it to be more readily comprehended, and hence allows us to see how much species' niches overlap, which of them are quite distinct, and so on.

Another approach to characterising a multidimensional niche makes use of *ecological niche models* (also known as *climate matching* or *climate envelope models*) (Jeschke & Strayer, 2008). A species' niche characteristics, defined largely by its physiology, are fairly constant, so that it is not unreasonable to expect that the details of a species' niche in one location may be broadly transferable to another. This is the basis for *ecological niche modelling* (Peterson, 2003), where occurrence patterns in a species' native range are used to build a model that can be projected to identify other areas that are

ecological niche  
modelling approach  
to the multi-  
dimensional niche

potentially habitable, using one of several available software packages: BIOCLIM, GARP, MAXENT and others (Elith & Graham, 2009). The basic process of niche modelling is outlined in Figure 2.4. As much environmental information as possible is taken from all of the locations where a species is currently found and from a range of locations where the species has not been recorded, allowing those locations to be identified that meet the species' requirements even though the species is currently absent. The ability to project into geographic space can be used to predict species distributions in previously unexplored parts of the native range (checking how good the model is) or in new, often quite distant locations of interest (e.g. predicting places where a potentially invasive species may prove problematic; Figure 2.5).

#### fundamental and realised niches

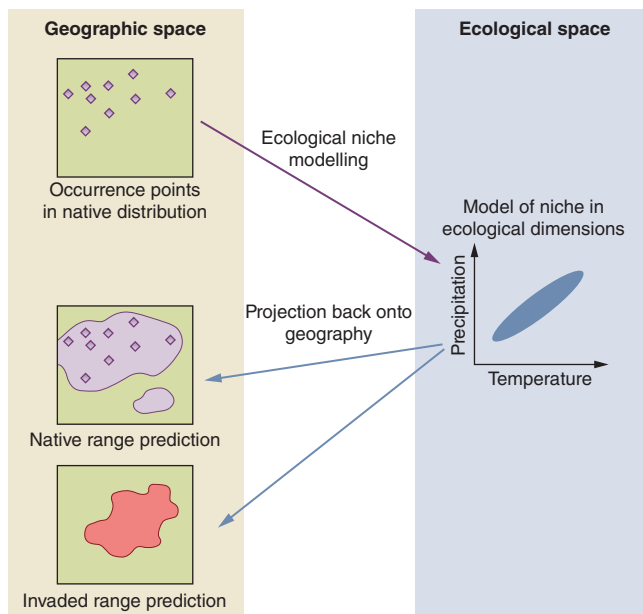
Provided that a location is characterised by conditions within acceptable limits for a given species, and provided also that it contains all the necessary resources, then the species can, potentially, occur and persist there. Whether or not it does so depends on two further factors. First, as we have just seen, it must be able to reach the location, and this

depends in turn on its powers of colonisation and the remoteness of the site, or on human agency in spreading invasive species from one area to another. Second, its occurrence may be precluded by the action of individuals of other species that compete with, prey upon or parasitise it.

Usually, a species has a larger ecological niche in the absence of enemies than it has in their presence. In other words, there are certain combinations of conditions and resources that can allow a species to maintain a viable population, but only if it is not being adversely affected by enemies. This led Hutchinson to distinguish between the *fundamental* and the *realised* niche. The former describes the overall potentialities of a species; the latter describes the more limited spectrum of conditions and resources that allow it to persist, even in the presence of competitors, predators and parasites. One of the acknowledged shortcomings of the modelling of niches based on distributions in species' native ranges, described earlier, is that it is the realised niche that is under consideration (on the assumption that competitors, predators and parasites are present and exert an effect). When a species invades a new area, there is every possibility that some or all of its native enemies will be absent, so that it may be able to occupy an expanded niche, closer to its fundamental niche. Modellers need to beware this possibility (Jeschke & Strayer, 2008).

Just as negative interactions can play a role in determining species' distributions (leading to a realised niche smaller than the fundamental niche), so can the positive effects of mutualists that we discuss in more detail in Chapter 13 (potentially producing a realised niche larger than the fundamental niche). Take, for example, the tropical anemone fish *Amphiprion chrysopterus*, which retreats between the stinging tentacles of the sea anemone *Heteractis magnifica* when predators threaten, but protects the anemone against its grazers, increasing anemone survivorship, growth and reproduction (Holbrook & Schmitt, 2005). Either species may tolerate the conditions at a location, but their success also depends on the presence of the other. In similar vein, most higher plants have intimate mutualistic associations between their roots and fungi (mycorrhiza; Section 13.9) that capture nutrients from the soil and transfer them to the plants, as well as improving water uptake and disease resistance, while receiving photosynthetic products from the plant (Delavaux *et al.*, 2017). Many plants can live without their mycorrhizal associates in soils when water and nutrients are in good supply, but in the highly competitive world of plant communities the presence of the fungi is often necessary if the plant is to prosper.

The remainder of this chapter looks at some of the most important condition dimensions of species' niches, starting with temperature; the following chapter examines resources, which add further dimensions of their own.



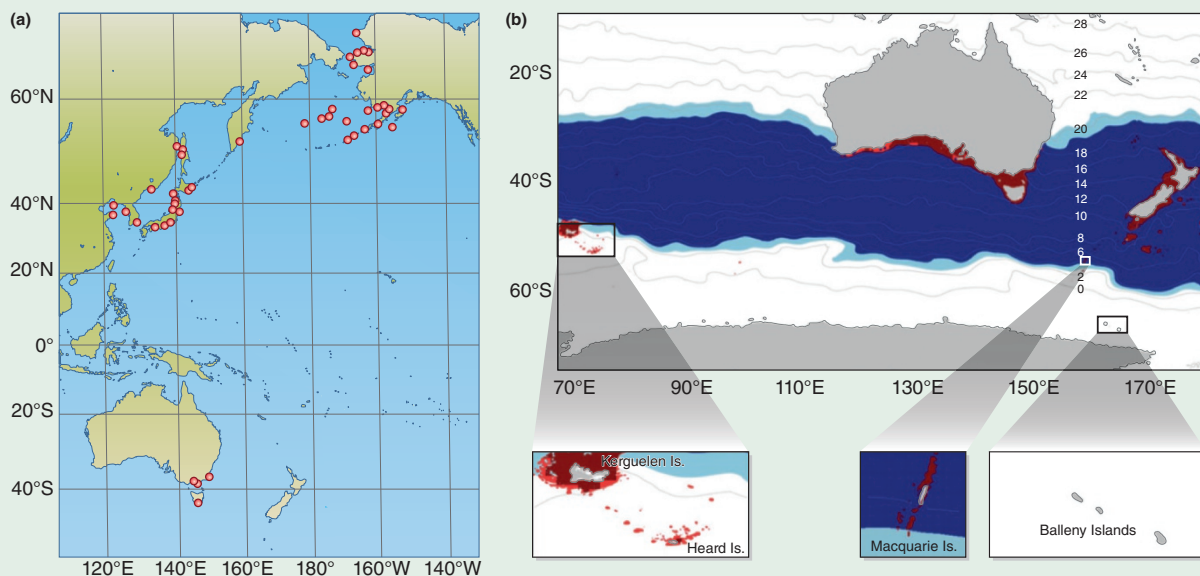
**Figure 2.4 Ecological niche modelling.** The first step is to characterise a species' distribution in two-dimensional geographic space. Then the niche is modelled in ecological space, in terms of a number of influential dimensions of the  $n$ -dimensional hypervolume (such as temperature, precipitation, humidity, soil pH, etc.). Finally, the occupation of ecological space is projected back into geographic space. Source: After Peterson (2003).

## APPLICATION 2.1 Ecological niche modelling and ordination as management tools

Managers are frequently confronted by problems associated with invasive species and make use of *climate envelope models* or *ordination* to develop solutions.

The Arctic sea star, *Asterias amurensis*, is among the most ecologically influential of marine invertebrates, being a voracious predator with a particular affinity for bivalves (frequently putting it in conflict with bivalve fishers) and capable of dramatically affecting local biodiversity. Its native range extends in the North Pacific from the Arctic to southern Japan (Figure 2.5a). Accidentally introduced in the early 1980s to Tasmania (probably through the release of pelagic larvae in ship's ballast water), adults became established on the seabed where they caused the extinction of many species. *A. amurensis* has since

spread to Victoria along the coast of mainland Australia (Figure 2.5a) but so far it has not invaded New Zealand or the sub-Antarctic Islands. One critical dimension of its multidimensional niche is water depth: the species cannot survive below a depth of 200 m. Both summer and winter temperature ranges are also fundamentally important to the success of the sea stars, and so to assess the potential for range expansion, Byrne *et al.* (2016) used the climate envelope model MaxEnt to characterise the thermal niche of both adults and the dispersive larval stages. Figure 2.5b shows the predicted invasive range, which includes much of New Zealand, together with the sub-Antarctic Macquarie, Heard and Kerguelen Islands. The red areas are considered suitable for adult sea stars (dark red highly suitable), while



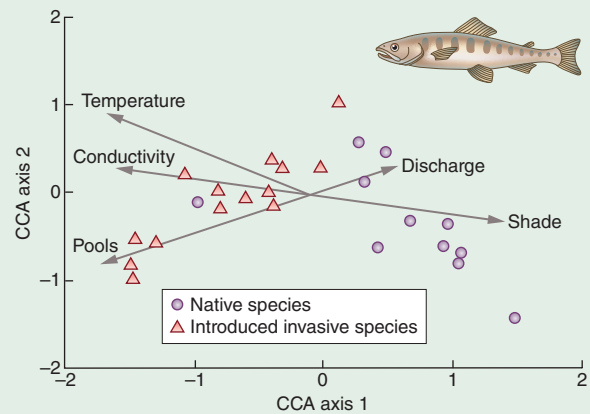
**Figure 2.5 Modelling the potential range of an invasive starfish.** (a) Current distribution records for the sea star *Asterias amurensis* in its native (northern hemisphere) and invasive (southern hemisphere) range. (b) Modelled distribution in its invasive range. Red regions represent areas with suitable mean winter and summer seafloor temperatures for the benthic adult stage (light red suitable, dark red highly suitable). Blue regions represent areas where the sea surface temperature is suitable for the pelagic larval stages (dark blue optimal). Isotherms represent mean sea surface temperature (°C) during winter. Boxes show islands that might provide a stepping-stone habitat for invasion of *A. amurensis* into Antarctica, especially the Macquarie, Heard and Kerguelen Islands, which are ice-free year-round. Currently the Balleny Islands are only ice-free in summer but this may change with global warming. Source: From Byrne *et al.* (2016).

(Continued)

### APPLICATION 2.1 (Continued)

the blue zones are suitable for the development of dispersing larval stages (dark blue optimal). That the species may spread to many new locations is alarming enough, but there is also a strong possibility that global warming will put much of the Antarctic coastline in peril. Results of such analyses highlight the importance of vigilance and border biosecurity.

Marchetti and Moyle (2001) used an *ordination* technique to define how a suite of fish species, 11 native and 14 invaders, are related to environmental factors in a Californian river (Figure 2.6). The native and invasive species clearly occupy different parts of the multidimensional niche space. Most of the natives were associated with higher mean discharge ( $\text{m}^3 \text{s}^{-1}$ ), good canopy cover (higher levels of % shade), lower concentrations of plant nutrients (lower conductivity,  $\mu\text{S}$ ), lower temperatures and a greater percentage of fast-flowing, riffle habitat (less pool habitat). These are all features of the natural, undisturbed state of streams. The invaders, on the other hand, are favoured by the present combination of conditions where water regulation and damming have reduced discharge and riffle habitat, shady riparian vegetation has been removed leading to higher stream temperatures, and nutrient concentrations have increased because of agricultural and domestic runoff. Restoration of more natural flow regimes and riparian planting will be needed to halt the continued decline of native fish, and it is heartening to note that



**Figure 2.6 Ordination contrasts the multidimensional niches of native and invasive fish.** Plot of results of an ordination technique called canonical correspondence analysis (CCA) showing native species of fish (purple circles), introduced invasive species (red triangles) and five influential environmental variables. Note how the native and invasive species occupy different parts of multidimensional niche space. *Source:* After Marchetti & Moyle (2001).

hundreds of dams across the USA, whether originally built for public or private benefit, have been removed in river restoration projects in recent years.

### APPLICATION 2.2 Judging the fundamental niche of a species driven to extreme rarity

The takahe (*Porphyrio hochstetteri*), one of only two remaining species of large, herbivorous, flightless birds that dominated the pre-human New Zealand landscape, was itself believed extinct until rediscovery in 1948 of a small population in the remote and climatically extreme Murchison Mountains in the south-west of the South Island (Figure 2.7). Intense conservation efforts have involved captive breeding, habitat management, predator control, wild releases into the Murchison Mountains and nearby ranges as well as translocations to offshore islands that lack the introduced mammals that are now widespread on the mainland (Lee & Jamieson, 2001). From just a handful of

individuals, there are now more than 300 in existence. Some ecologists believed that because the takahe is a grassland specialist, feeding mainly on tussock grasses in the genus *Chionocloa*, and adapted to the alpine zone, they would not fare well elsewhere. Others noted that fossil evidence indicated that takahe were once widespread in New Zealand and occurred at altitudes below 300 m, including coastal areas that were a mosaic of forest, shrubland and grassland (Figure 2.7), and that they might therefore be well suited to life on offshore islands that lack the mammals that have caused their demise. Indeed, they have formed self-sustaining populations after introduction to

## APPLICATION 2.2 (Continued)

**Figure 2.7 Location of fossil bones of the takahe in the South Island of New Zealand.** The population had become restricted to a single site in the Murchison Mountains, but was this a true reflection of its niche requirements? *Source:* After Treweek & Worthy (2001).



four offshore islands, although the island habitat may not be optimal (with poorer hatching and fledging success in island than mountain populations) (Jamieson & Ryan, 2001). The fundamental niche of takahe probably encompasses much of the South Island, but it became confined to a much smaller realised niche because of the effects of

predators (human hunters and introduced stoats, *Mustela erminea*) and competitors for food (introduced red deer, *Cervus elaphus scoticus*). The removal of these mammalian interlopers would enable takahe to occupy something closer to their fundamental niche, as they did before humans and the other invaders arrived in New Zealand.

## 2.3 Responses of individuals to temperature

### 2.3.1 What do we mean by 'extreme'?

It seems natural to describe certain environmental conditions as 'extreme', 'harsh', 'benign' or 'stressful'. It may seem obvious when conditions are 'extreme': the midday heat of a desert, the cold of an Antarctic winter, the salinity of the Great Salt Lake. But this only means that these conditions are extreme *for us*, given our particular physiological characteristics and tolerances. To a cactus there is nothing extreme about the desert conditions in which cacti have evolved; nor are the icy fastnesses of Antarctica an extreme environment for penguins. It is lazy and dangerous for the ecologist to

assume that all other organisms sense the environment in the way we do. Rather, the ecologist should try to gain a worm's-eye or plant's-eye view of the environment: to see the world as others see it. Emotive words like harsh and benign, even relativities such as hot and cold, should be used by ecologists only with care.

### 2.3.2 Metabolism, growth, development and size

Individuals respond to temperature essentially in the manner shown in Figure 2.1a: impaired function and ultimately death at the lower and

exponential effects  
of temperature on  
metabolic reactions



upper extremes (discussed in Sections 2.3.4 and 2.3.6), with a functional range between the extremes, within which there is an optimum. This is accounted for, in part, simply by changes in metabolic effectiveness. For each  $10^{\circ}\text{C}$  rise in temperature, for example, the rate of biological enzymatic processes often roughly doubles, and thus appears as an exponential curve on a plot of rate against temperature (Figure 2.8a, b). The increase is brought about because a higher temperature increases the speed of molecular movement and speeds up chemical reactions. The factor by which a reaction changes over a  $10^{\circ}\text{C}$  range is referred to as  $Q_{10}$ : a rough doubling means that  $Q_{10} \approx 2$ , and animals generally conform quite closely to this value (Figure 2.8c) as do microbial organisms (Kirchman, 2012) and plants (Lange *et al.*, 2012).

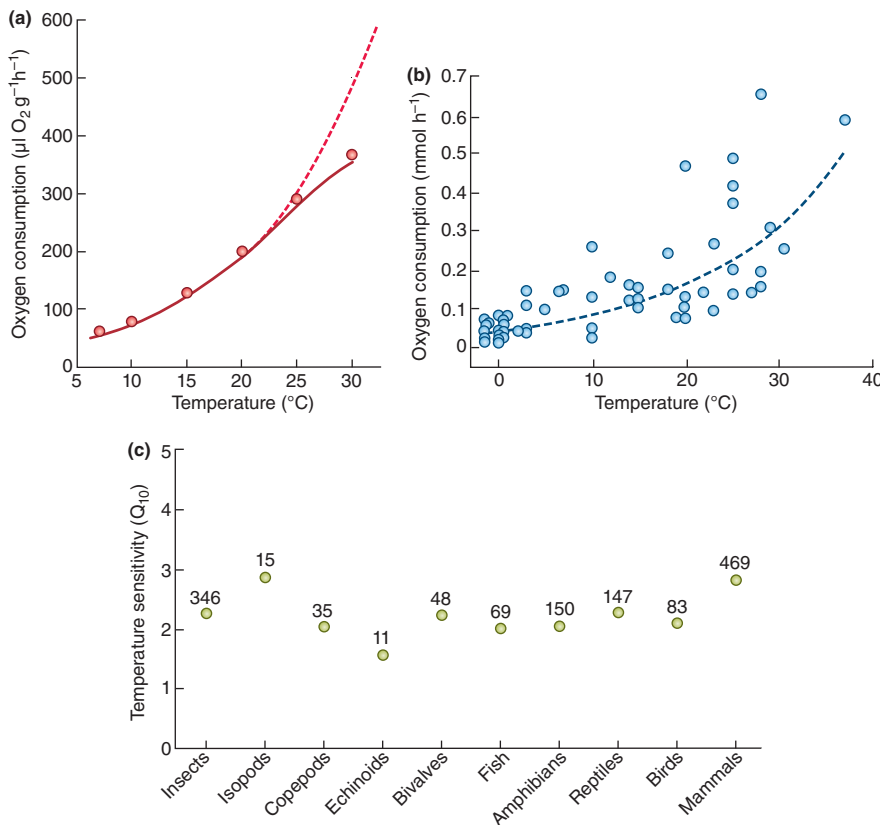
effectively linear effects on rates of growth and development

For an ecologist, however, effects on individual chemical reactions are likely to be less important than effects on rates of growth (increases in mass), on rates of development (progression through lifecycle stages) and on final body size, since, as we shall discuss much more fully in Chapter 4, these tend to drive the core ecological activities of survival, reproduction and movement. And when rates of growth and development

of whole organisms are plotted against temperature, there is quite commonly an extended range over which there are, at most, only slight deviations from linearity (Figure 2.9).

When the relationship between growth or development is effectively linear, the temperatures experienced by an organism can be summarised in a single very useful value, the number of ‘day-degrees’. For instance, Figure 2.9c shows that at  $15^{\circ}\text{C}$  ( $5.1^{\circ}\text{C}$  above a development threshold of  $9.9^{\circ}\text{C}$ ) the predatory mite, *Amblyseius californicus*, took 24.22 days to develop (i.e. the proportion of its total development achieved each day was  $0.041 (= 1/24.22)$ ), but it took only 8.18 days to develop at  $25^{\circ}\text{C}$  ( $15.1^{\circ}\text{C}$  above the same threshold). At both temperatures, therefore, development required 123.5 day-degrees (or, more properly, ‘day-degrees above threshold’), i.e.  $24.22 \times 5.1 = 123.5$ , and  $8.18 \times 15.1 = 123.5$ . This is also the requirement for development in the mite at other temperatures within the non-lethal range. Such organisms cannot be said to require a certain length of time for development. What they require is a combination of time and temperature, often referred to as ‘physiological time’.

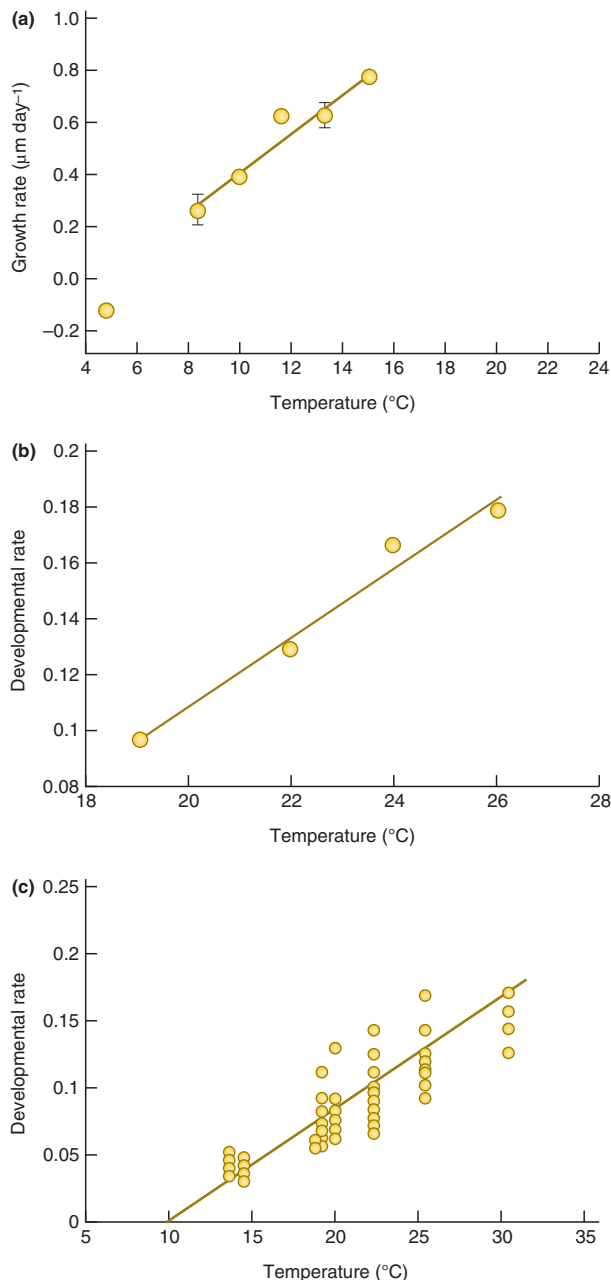
day-degree concept



**Figure 2.8 Exponential effects of temperature on metabolic reactions.**

(a) The rate of oxygen consumption of the Colorado beetle (*Leptinotarsa decemlineata*), which doubles for every  $10^{\circ}\text{C}$  rise in temperature up to  $20^{\circ}\text{C}$ , but increases less fast at higher temperatures. (b) Relationship between resting oxygen consumption of teleost fish, plotted for a variety of species as oxygen consumption at their typical environmental temperature for a standardized 50 g fish. (c)  $Q_{10}$  values for oxygen consumption of various invertebrate and vertebrate animal taxa, averaged across multiple published studies (numbers shown). Source: (a) After Marzusch (1952). (b, c) Data compiled from various sources by Clarke (2017).





**Figure 2.9 Effectively linear relationships between rates of growth and development and temperature.** (a) Growth of the protist *Strombidinopsis multiauris*. (b) Egg development in the beetle *Oulema duftschmidi*. (c) Egg to adult development in the mite *Amblyseius californicus*. The vertical scales in (b) and (c) represent the proportion of total development achieved in one day at the temperature concerned. Source: (a) After Montagnes *et al.* (2003). (b) After Severini *et al.* (2003). (c) After Hart *et al.* (2002).

Together, the rates of growth and development determine the final size of an organism. For

temperature–  
size rule

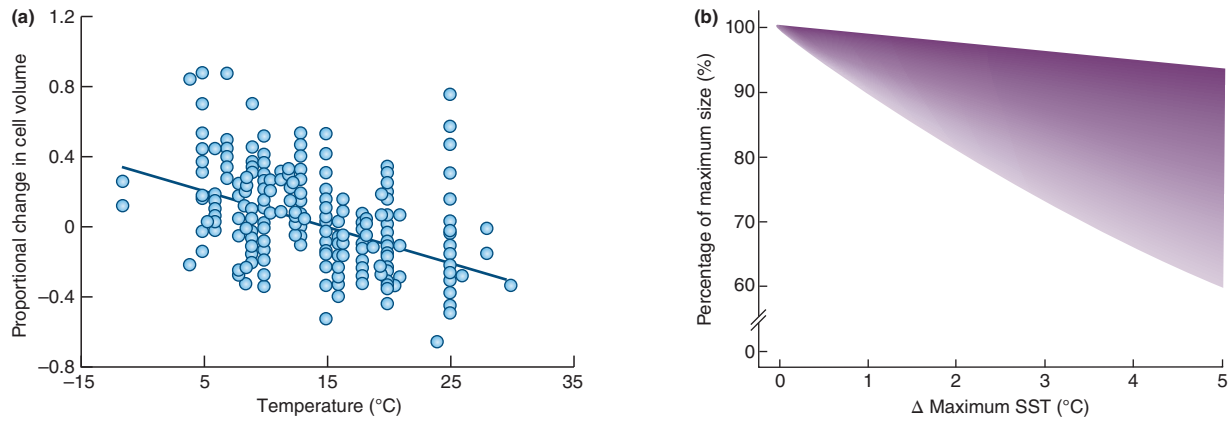
instance, for a given rate of growth, a faster rate of development will lead to smaller final size. Hence, if the responses of growth and development to variations in temperature are not the same, temperature will also affect final size. In fact, development usually increases more rapidly with temperature than does growth, such that, for a very wide range of organisms, final size tends to decrease with increasing temperature: the ‘temperature–size rule’ (see Atkinson *et al.*, 2003). An example for single-celled protists (72 datasets from marine, brackish and freshwater habitats) is shown in Figure 2.10a: for each  $1^{\circ}\text{C}$  increase in temperature, final cell volume decreased by roughly 2.5%.

These links can equally be seen from the viewpoint of how metabolism co-varies with temperature and size. We pick this up again in Section 3.9 when we look at the so-called metabolic theory of ecology.

### 2.3.3 Ectotherms and endotherms

Many organisms have a body temperature that differs little, if at all, from their environment. A parasitic worm in the gut of a mammal, a fungal mycelium in the soil and a sponge in the sea acquire the temperature of the medium in which they live. Terrestrial organisms, exposed to the sun and the air, are different because they may acquire heat directly by absorbing solar radiation or be cooled by the latent heat of evaporation of water (typical pathways of heat exchange are shown in Figure 2.11). Various fixed properties may ensure that body temperatures are higher (or lower) than the ambient temperatures. For example, the reflective, shiny or silvery leaves of many desert plants reflect radiation that might otherwise heat the leaves. Organisms that can move have further control over their body temperature because they can seek out warmer or cooler environments, as when a lizard chooses to warm itself by basking on a hot sunlit rock or escapes from the heat by finding shade.

Amongst insects there are examples of body temperatures raised by controlled muscular work, as when bumblebees raise their body temperature by shivering their flight muscles. Social insects such as bees and termites may combine to control the temperature of their colonies and regulate them with remarkable thermostatic precision. Even some plants (e.g. *Philodendron*) use metabolic heat to maintain a relatively constant temperature in their flowers; and, of course, birds and mammals use metabolic heat almost all of the time to maintain an almost perfectly constant body temperature.



**Figure 2.10 The temperature–size rule (final size decreases with increasing temperature).** (a) Reduction in protist cell volume (65 datasets combined) with increasing rearing temperature. The vertical scale measures the proportional change from cell volume at 15°C. (b) Maximal size of 74 fish species generally declines across a steep temperature gradient in the Mediterranean Sea. The figure presents the best model based on the whole dataset, plotting percent of maximum size observed with an increase in maximum sea surface temperature (SST) of up to 5°C. The species vary in their activity levels: lighter shading corresponds to more active pelagic species and darker shading to more sedentary benthic species. The active species show a steeper decline in maximum size with increasing temperature. *Source:* (a) After Atkinson *et al.* (2003). (b) After van Rijn *et al.* (2017).

### APPLICATION 2.3 Getting predictions right in the face of climate change

The effects of temperature on growth, development and size may be of practical rather than simply scientific importance. Increasingly, ecologists are called upon to predict. We may wish to know what the consequences would be, say, of a 2°C rise in temperature resulting from global warming (Section 2.9.2), or to understand the role of temperature in seasonal, interannual and geographic variations in the productivity of, for example, marine ecosystems. We cannot afford to assume exponential relationships with temperature if they are really linear, nor to ignore the effects of changes in organism size on their role in ecological communities. Figure 2.10b shows for

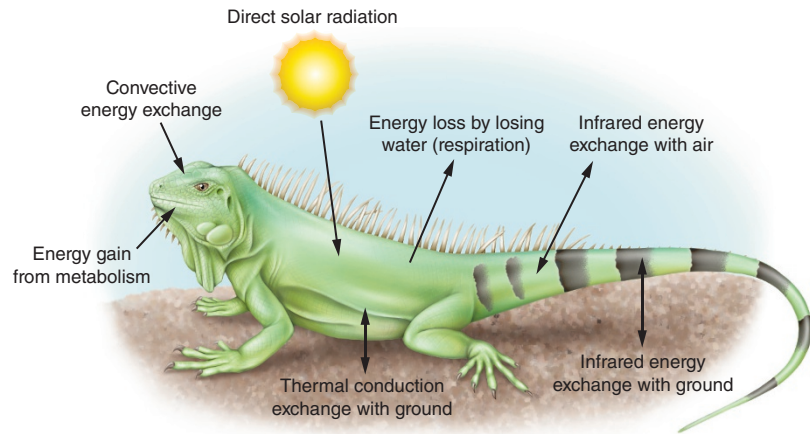
74 fish species how maximum size varies across a steep sea surface temperature gradient in the Mediterranean Sea. If the reason for this pattern is the temperature–size rule (rather than genetic differences between locations) there could be important implications for fishery yields in a warmer climate. Van Rijn *et al.* (2017) suggest that the most pronounced size reductions will occur in large, active, non-migratory species that are often the major source of economic revenue, while elevated temperatures may have smaller effects on benthic, less active, and often less valuable, species. To optimise their catch, fishers may have to adapt their fishing strategies.

An important distinction, therefore, is between *endotherms* that regulate their temperature by the production of heat within their own bodies, and *ectotherms* that rely on external sources of heat. But this distinction is not entirely clear-cut. As we have noted, apart from birds and mammals, there are also other taxa that use heat generated in their own bodies to regulate body temperature, but only for limited periods; and there are some birds and mammals that relax or suspend their endothermic abilities at the

most extreme temperatures. In particular, many endothermic animals escape from some of the costs of endothermy by hibernating during the coldest seasons: at these times they behave almost like ectotherms.

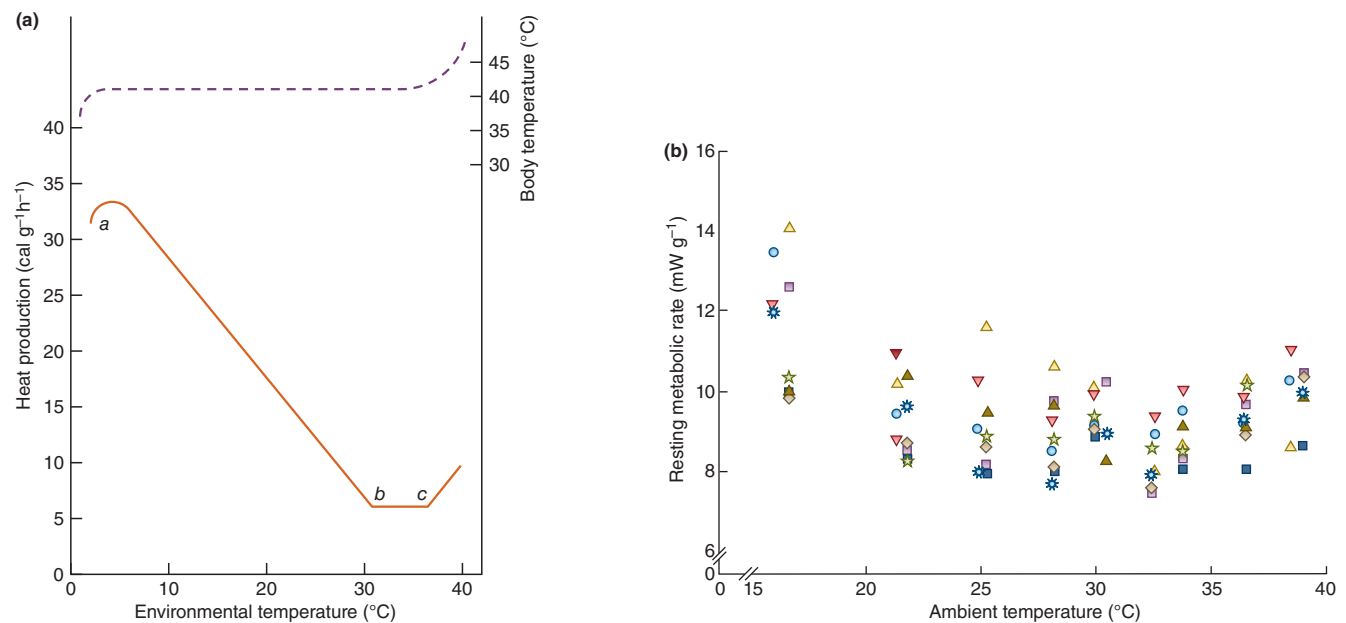
Birds and mammals usually maintain a constant body temperature between 35 and 42°C, and they therefore tend to lose heat in most environments; but this loss is

endotherms:  
temperature  
regulation – but at  
a cost



**Figure 2.11** The avenues of heat exchange between an ectotherm and its environment.

Source: After Fei *et al.* (2012).



**Figure 2.12** Examples of the thermoneutral zone. (a) Thermostatic heat production by an endotherm is constant in the thermoneutral zone, between *b*, the lower critical temperature, and *c*, the upper critical temperature. Heat production rises, but body temperature remains constant, as environmental temperature declines below *b*, until heat production reaches a maximum possible rate at a low environmental temperature. Below *a*, heat production and body temperature both fall. Above *c*, metabolic rate, heat production and body temperature all rise. Hence, body temperature is constant at environmental temperatures between *a* and *c*. (b) Mean resting metabolic rate (measured in units of power) versus ambient temperature in nine Japanese quail, *Coturnix japonica* (each bird has a different symbol). The thermoneutral zone extends between 23.2 and 36.0°C and the birds' minimum body temperature within this zone was 40.7°C. Source: (a) After Hainsworth (1981). (b) After Ben-Hamo *et al.* (2010).

moderated by insulation in the form of fur, feathers and fat, and by controlling blood flow near the skin surface. When it is necessary to increase the rate of heat loss, this too can be achieved by the control of surface blood flow and by a number of other mechanisms shared with ectotherms like panting and the simple choice of an appropriate habitat. Together, all these mechanisms and properties give endotherms a

powerful (but not perfect) capability for regulating their body temperature, and the benefit they obtain from this is a constancy of near-optimal performance. But the price they pay is a large expenditure of energy (Figure 2.12), and thus a correspondingly large requirement for food to provide that energy. Over a certain temperature range (the *thermoneutral zone*) an endotherm consumes energy at a basal rate. But at

environmental temperatures further and further above or below that zone, the endotherm consumes more and more energy in maintaining a constant body temperature. Even in the thermoneutral zone, though, an endotherm typically consumes energy many times more rapidly than an ectotherm of comparable size.

ectotherms and endotherms coexist: both strategies 'work'

The responses of endotherms and ectotherms to changing temperatures, then, are not so different as they may at first appear to be.

Both are at risk of being killed by even short exposures to very low temperatures and by more prolonged exposure to moderately low temperatures. Both have an optimal environmental temperature and upper and lower lethal limits. There are also costs to both when they live at temperatures that are not optimal. For the ectotherm these may be slower growth and reproduction, slow movement, failure to escape predators and a sluggish rate of search for food. But for the endotherm, the maintenance of body temperature costs energy that might have been used to catch more prey, produce and nurture more offspring or escape more predators. There are also costs of insulation (e.g. blubber in whales, fur in mammals) and even costs of changing the insulation between seasons. Temperatures only a few degrees higher than the metabolic optimum are liable to be lethal to endotherms as well as ectotherms (Section 2.3.6).

It is tempting to think of ectotherms as 'primitive' and endotherms as having gained 'advanced' control over their environment, but it is difficult to justify this view. Most environments on earth are inhabited by mixed communities of endothermic and ectothermic animals. This includes some of the hottest – e.g. desert rodents and lizards – and some of the coldest – penguins and whales together with fish and krill at the edge of the Antarctic ice sheet. Rather, the contrast is between the high cost–high benefit strategy of endotherms and the low cost–low benefit strategy of ectotherms. But their coexistence tells us that both strategies, in their own ways, can 'work'.

### 2.3.4 Life at low temperatures

The greater part of our planet is below 5°C. More than 70% of the planet is covered with seawater: mostly deep ocean with a remarkably constant temperature of about 2°C. If we include the polar ice caps, more than 80% of earth's biosphere is permanently cold.

chilling injury

By definition, all temperatures below the optimum have adverse effects, but there is usually a wide

range of such temperatures that cause no physical damage and over which any effects are fully reversible. There are, however, two quite distinct types of damage at low temperatures that can be lethal, either to tissues or to whole organisms: chilling and freezing. Many organisms, particularly tropical and subtropical plants, are damaged by exposure to temperatures that are low but above freezing point – so-called 'chilling injury'. The fruits of the banana blacken and rot after exposure to chilling temperatures and many rainforest species are sensitive to chilling. Many insects also succumb to the effects of chilling at temperatures well above the freezing point of their body fluids. In these chill-sensitive insects, including the majority of temperate, subtropical and tropical species, chilling causes a loss of homeostasis that leads to paralysis, injury and ultimately death (Bale, 2002).

Temperatures below 0°C can have lethal physical and chemical consequences even though ice may not be formed. Water may 'supercool' to temperatures at least as low as –40°C, remaining in an unstable liquid form in which its physical properties change in ways that are certain to be biologically significant: its viscosity increases, its diffusion rate decreases and its degree of ionisation decreases. In fact, ice seldom forms in an organism until the temperature has fallen several degrees below 0°C. Body fluids remain in a supercooled state until ice forms suddenly around particles that act as nuclei. The concentration of solutes in the remaining liquid phase rises as a consequence. It is rare for ice to form within cells and it is then inevitably lethal, but the freezing of extracellular water is one of the factors that prevents ice forming within the cells themselves (Wharton, 2002), since water is withdrawn from the cell, and solutes in the cytoplasm (and vacuoles) become more concentrated. The effects of freezing are therefore mainly osmoregulatory: the water balance of the cells is upset and cell membranes are destabilised. The effects are essentially similar to those of drought and salinity.

temperatures below 0°C

Plants inhabiting high latitudes and altitudes are particularly exposed to frost damage. Woody alpine plants, for example, can experience

frost resistance of plants and their parts

frost damage at any time of year (Neuner, 2014). In summer, the most frost-susceptible organs are reproductive shoots (–4.6°C), followed by immature leaves (–5.0°C), fully expanded leaves (–6.6°C), vegetative buds (–7.3°C) and xylem tissue (–10.8°C). These levels of resistance can be insufficient to survive frost events in summer and it may be that the most frost-susceptible parts define the upper limit of elevation for the distribution of such woody species. The same plant

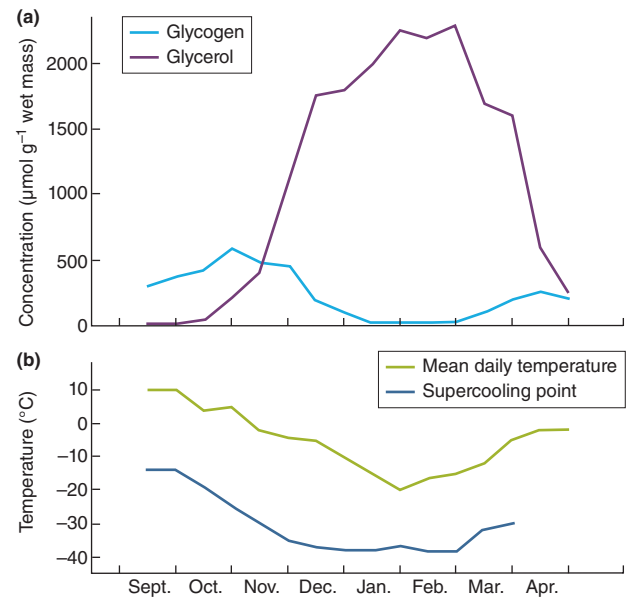
tissues are much less sensitive to frost damage in winter, the reproductive buds being most susceptible ( $-23.4^{\circ}\text{C}$ ), but with greater levels of freezing resistance in vegetative buds ( $-30$  to  $-50^{\circ}\text{C}$ ), leaves ( $-25$  to  $-58.5^{\circ}\text{C}$ ) and stems ( $-30$  to  $-70^{\circ}\text{C}$ ). Mechanisms of frost resistance include the production of cryoprotectant proteins, which appear to protect membranes and proteins against the severe dehydration stress associated with freezing, and the rapid accumulation of soluble carbohydrates, including sucrose, that serve to reduce cellular dehydration during freezing (Wisniewski *et al.*, 2014).

#### metabolic strategies of cold hardiness

Insects, and other taxa, have two main metabolic strategies that allow survival through the low temperatures of winter. A 'freeze-avoiding' strategy uses the synthesis of antifreeze proteins and the accumulation of extremely high levels of carbohydrate cryoprotectants (most often glycerol) so that body fluids can supercool to temperatures well below those normally encountered. A contrasting 'freeze-tolerant' strategy involves the regulated freezing of up to about 65% of total body water in extracellular spaces. Ice formation outside the cells is often triggered by the action of specific ice-nucleating agents or proteins, whereas low molecular weight cryoprotectants are used to maintain a liquid intracellular space and to protect membrane structure. Storey and Storey (2012) list two further strategies discovered more recently. The first, described for soil-dwelling invertebrates and particularly polar species, is 'cryoprotective dehydration', which combines extreme dehydration, in which virtually all freezable water is lost, together with high cryoprotectant levels that stabilise macromolecules. And more recently still, Sformo *et al.* (2010), in a study of the Alaskan bark beetle (*Cucujus clavipes*), showed that larvae at lower temperatures did not freeze but transitioned into a vitrified state (a non-crystalline amorphous solid) in which they could survive down to  $-100^{\circ}\text{C}$ . The 'vitrification' strategy is accompanied by extensive dehydration and accumulation of antifreeze proteins and high concentrations of polyols.

#### acclimation and acclimatisation

The tolerances of organisms to low temperatures are not fixed but are preconditioned by the experience of temperatures in their recent past. This process is called *acclimation* when it occurs in the laboratory and *acclimatisation* when it occurs naturally. Acclimatisation may start as the weather becomes colder in the autumn, stimulating the conversion of almost the entire glycogen reserve of animals into polyols such as glycerol (Figure 2.13), but this can be an energetically costly affair: about 16% of the carbohydrate reserve may be consumed in the conversion of the glycogen reserves.



**Figure 2.13 Acclimatisation involves conversion of glycogen to glycerol in a caterpillar.** (a) As a result of cooling autumn temperatures, larvae of the goldenrod gall moth, *Epiblema scudderiana*, convert their stores of glycogen to glycerol, which eventually constitutes over 19% of the caterpillar's body mass. (b) The high levels of glycerol plus antifreeze proteins suppress the larval supercooling point from  $-14^{\circ}\text{C}$  in late summer to  $-38^{\circ}\text{C}$  by mid-winter, values well below environmental temperature extremes. Source: (a, b) From Storey & Storey (2012), after Rickards *et al.* (1987).

Acclimatisation aside, individuals commonly vary in their temperature response depending on the stage of development they have reached. Probably the most extreme form of this is when an organism has a dormant stage in its life cycle. Dormant stages are typically dehydrated, metabolically slow and tolerant of extremes of temperature.

### 2.3.5 The genetics of cold tolerance

Cold tolerance and acclimatisation have long been recognised as being controlled by many genes, and the advent of technology that allows us to identify these and recognise their function has led to significant advances in the understanding of cold hardiness. In plants, for example, perception of cold temperatures seems to occur at the plasma membrane and is associated with an increase in calcium concentration that sets in train the activation of a wide variety of genes responsible for the biochemical changes already described (Wisniewski *et al.*, 2014). And in insects, Zhang



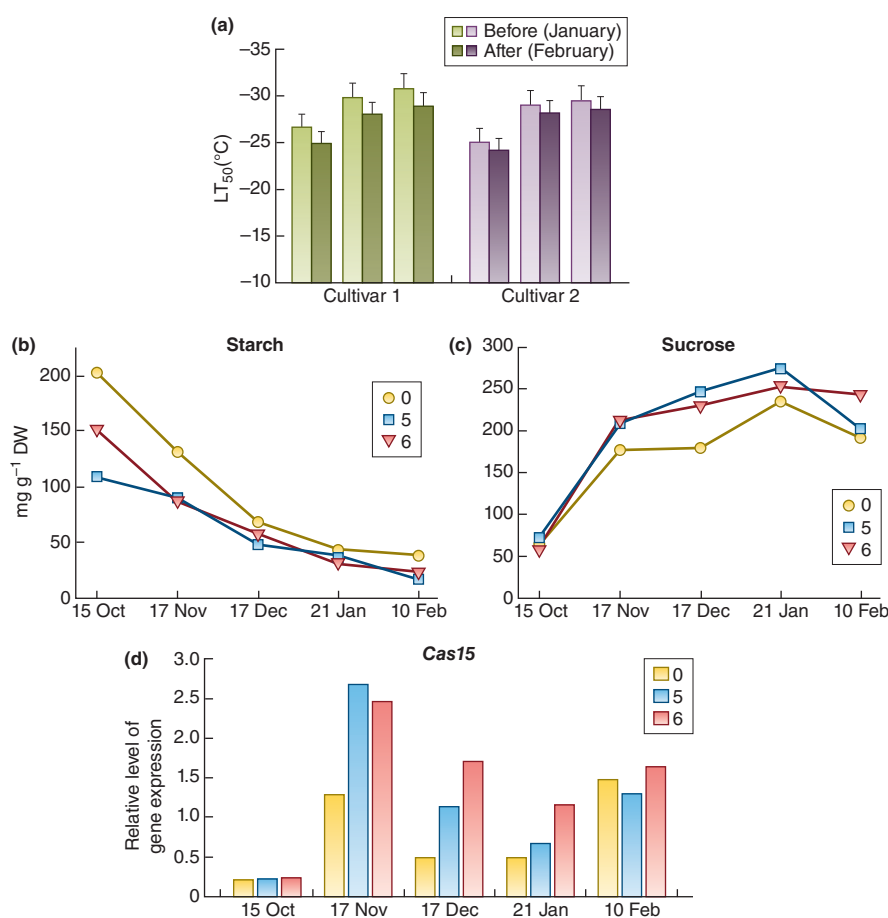
*et al.* (2011) identified cold-responsive genes in the fruit-fly *Drosophila melanogaster* associated with muscle structure and function, immune and stress responses and carbohydrate metabolism.

In a laboratory 'selection' experiment involving plants of alfalfa (*Medicago sativa*, an important animal forage species), Castonguay *et al.* (2011) investigated whether the plant could be selected for improved freezing tolerance. Five weeks after sowing 1500 genotypes of a particular alfalfa cultivar used in eastern Canada, the plants were moved to low-temperature chambers for two week's acclimation at 2°C before being transferred to -2°C for an additional fortnight to simulate 'hardening' conditions in frozen soil. Subsequently, temperature was progressively dropped to the expected lethal temperature for 50% of the plants (their  $LT_{50}$  – lethal temperature for 50% of the plants in January), using a step-wise decline of temperature. After five weeks of regrowth at 20°C, genotypes that survived the original freezing cycle were intercrossed and subject to another cycle, and so on for six cycles of recurrent selection. The experiment was repeated with a second cultivar for four cycles of selection. Figure 2.14a shows that for both cultivars, several cycles of selection for freezing tolerance led to a significant decline

in  $LT_{50}$  between the first cycle and later cycles of selection: in other words, individuals in the populations subject to selection were able to tolerate lower winter temperatures. Associated biochemical (Figure 2.14b, c) and genetic patterns (Figure 2.14d) provide good evidence that recurrent selection for superior freezing tolerance in alfalfa induces marked changes in influential traits. And if deliberate selection can change the tolerance of a domesticated plant we can certainly expect that natural selection has done the same thing for plants, animals and microorganisms in nature.

### 2.3.6 Life at high temperatures

Perhaps the most important thing about dangerously high temperatures is that, for a given organism, they usually lie only a few degrees above the metabolic optimum. This is largely an unavoidable consequence of the physicochemical properties of most enzymes (Wharton, 2002). High temperatures may be dangerous because they lead to the inactivation or even the denaturation of enzymes, but they may also have damaging indirect effects by leading to dehydration.



**Figure 2.14 Alfalfa can be selected for improved freezing tolerance.**

(a) Tolerance to freezing ( $LT_{50}$ , 5% confidence levels shown) of populations of two cultivars of alfalfa used for animal forage in eastern Canada, before selection (TF0) or after several cycles of recurrent selection for freezing tolerance (three, four, five or six cycles). (b, c) Starch and sucrose concentrations in crowns of alfalfa plants during autumn and winter (cultivar 1) before (0) and after five or six cycles of selection. (d) Relative expression of the cold-induced gene *cas15* before (0) and after five or six cycles of selection.

Source: From Castonguay *et al.* (2011).



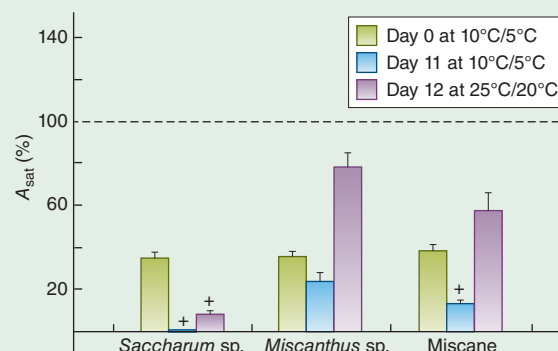
## APPLICATION 2.4 Selection for cold tolerance in crops to increase their productivity and geographic range

There have been many striking cases where the geographic range of a crop species has been extended into colder regions of the world by plant breeders. Traditional crop breeding practices have generally used crossing of closely related varieties to produce new crops with desired cold-tolerance traits.

A key challenge for plant breeders is to introgress desirable traits from wild and even quite distantly related species into important domesticated crops but at the same time retain the favourable traits of the crop. Sugar cane (*Saccharum* spp.) is a major crop whose tropical heritage makes it cold sensitive and generally restricted to latitudes between 30°N and 35°S. Another member of the Poaceae family of tall grasses, *Miscanthus* spp., on the other hand, is a temperate-adapted species with marked cold tolerance. Głowacka *et al.* (2016) have shown that the chilling tolerance of *Miscanthus* can be transferred to sugarcane (Figure 2.15) without significant loss of overall sugarcane productivity. The chilling-tolerant hybrid of sugarcane and *Miscanthus* (Miscane US87-1019) has immediate potential for increased stock food and biofuel production, and at the same time provides the basis for extending sugarcane's range as a crop into higher latitudes and altitudes, once we better understand the genes that confer the cold-tolerance advantage.

potential of genomics, transcriptomics and proteomics in crop breeding

Future crop improvements to increase production and range in colder environments are certain to involve identification of the genes responsible for cold tolerance (both chilling and sub-zero tolerance) and acclimatisation. Erath *et al.* (2017) have, for example, identified genomic regions involved in frost tolerance of winter rye (*Secale cereale*) by mapping of quantitative trait loci (QTLs). A QTL is a section of DNA that correlates with variation in the quantitative trait of the phenotype (cold tolerance in this case); the QTL can be



**Figure 2.15 The chilling tolerance of *Miscanthus* can be transferred to *Saccharum*.** Comparison of cold tolerance in a laboratory experiment involving plants of sugarcane (*Saccharum* sp. L79-1002), *Miscanthus* (Mxg 'Illinois') and a hybrid of *Saccharum* and *Miscanthus*, referred to as 'Miscane' (US87-1019). The light-saturated leaf net CO<sub>2</sub> uptake rate ( $A_{\text{sat}}$  in  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) is shown for warm conditions before chilling treatment (25°C day, 20°C night: dashed line), after transfer of plants to chilling (day 0: 10°C day, 5°C night), on day 11 of chilling treatment and one day after transfer of plants back to warm conditions (day 12: recovery) expressed as a percentage of rates observed in warm conditions before chilling (control). A plus sign indicates a significantly lower value than the control. As expected, *Miscanthus* was the most cold tolerant, sugarcane the most cold sensitive, while the hybrid did not differ significantly from *Miscanthus* after recovery. Source: From Głowacka *et al.* (2016).

expected to contain the genes that control the trait. In winter rye, a QTL on chromosome 5R harbours the Frost resistance locus 2 (Fr-R2) and the 'Puma' allele at this locus was found to significantly increase frost tolerance. Discoveries of this kind can be expected to increase selection intensity for frost tolerance by preselecting plant breeding lines based on markers from the Fr-R2 locus.

high temperature and water loss in terrestrial environments

All terrestrial organisms need to conserve water, and at high temperatures the rate of water loss by evaporation can be lethal, but they are caught between two stools because evaporation is an important means of reducing body temperature. If surfaces are protected from

evaporation (e.g. by closing stomata in plants or spiracles in insects) the organisms may be killed by too high a body temperature, but if their surfaces are not protected they may die of desiccation.

Death Valley, California, in the summer, is probably the hottest place on earth in which higher plants make active growth. Air temperatures during the daytime may approach

50°C and soil surface temperatures may be very much higher. The perennial plant, desert honeysweet (*Tidestromia oblongifolia*), grows vigorously in such an environment despite the fact that its leaves are killed if they reach the same temperature as the air. Very rapid transpiration keeps the temperature of the leaves at 40–45°C, and in this range they are capable of extremely rapid photosynthesis (Berry & Björkman, 1980).

Most of the plant species that live in very hot environments suffer severe shortage of water and are therefore unable to use the latent heat of evaporation of water to keep leaf temperatures down. This is especially the case in desert succulents in which water loss is minimised by a low surface to volume ratio and a low frequency of stomata. In such plants the risk of overheating or of damage to photosynthetic machinery may be reduced by spines (which shade the surface of a cactus) (Loik, 2008) or hairs or waxes (which reflect a high proportion of the incident radiation). Nevertheless, such species experience and tolerate temperatures in their tissues of more than 60°C when the air temperature is above 40°C.

#### fire

Fires are responsible for the highest temperatures that terrestrial organisms face on earth and, before the fire-raising activities of humans, were caused mainly by lightning strikes. The recurrent risk of fire has shaped the species composition of arid and semiarid woodlands in many parts of the world. All plants are damaged by burning but it is the remarkable powers of regrowth from protected meristems on shoots and seeds that allow a specialised subset of species to recover from damage and form characteristic fire floras (see, for example, Rundel *et al.*, 2016).

Decomposing organic matter in heaps of farmyard manure, compost heaps and damp hay may reach very high temperatures. Stacks of damp hay are heated to temperatures of 50–60°C by the metabolism of fungi such as *Aspergillus fumigatus*, carried further to approximately 65°C by other thermophilic fungi such as *Mucor pusillus* and then a little further by bacteria and archaea. Biological activity stops well short of 100°C but autocombustible products are formed that cause further heating, drive off water and may even result in fire.

#### high temperature and oxygen supply in aquatic environments

In aquatic environments there is a situation analogous to the interplay between temperature and water supply discussed earlier for terrestrial environments. But in the aquatic case the interplay is between temperature and oxygen supply. At high temperatures, oxygen supply may not be able to keep up with the organism's metabolic demand for oxygen, such that upper thermal limits occur

at temperatures lower than those that denature proteins (the oxygen and capacity-limited thermal tolerance theory of Pörtner (2001)).

#### thermal vents

An ecologically very remarkable hot aquatic environment was first described only towards the end of the last century. In 1979, a deep oceanic site was discovered in the eastern Pacific at which fluids at high temperatures ('smokers') were vented from the sea floor forming thin-walled 'chimneys' of mineral materials. Since that time many more vent sites have been discovered at mid-ocean crests in both the Atlantic and Pacific Oceans. They lie 2000–4000 m below sea level at pressures of 200–400 bars (20–40 MPa). The boiling point of water is raised to 370°C at 200 bars and to 404°C at 400 bars. The superheated fluid emerges from the chimneys at temperatures as high as 350°C, and as it cools to the temperature of seawater at about 2°C it provides a continuum of environments at intermediate temperatures.

Environments at such extreme pressures and temperatures are obviously extraordinarily difficult to study *in situ* and in most respects impossible to maintain in the laboratory. Some thermophilic bacteria collected from vents, such as *Pyrococcus furiosus*, exhibit optimal growth at 100°C (Zeldes *et al.*, 2017), but there is circumstantial evidence that some microbial activity occurs at even higher temperatures and may form the energy resource for the warm water communities outside the vents.

There is a rich eukaryotic fauna in the local neighbourhood of vents that is quite atypical of the deep oceans in general. At one vent in Middle Valley, north-east Pacific, surveyed photographically and by video, at least 55 taxa were documented of which 15 were new or probably new species (Juniper *et al.*, 1992). There can be few environments in which so complex and specialised a community depends on so localised a special condition. The closest known vents with similar conditions were 2500 km distant. Such communities add a further list to the planet's record of species richness, and more than 500 new animal species from the world's thermal vents have been described (Desbruyères *et al.*, 2006).

### 2.3.7 Temperature as a stimulus

We have seen that temperature as a condition affects the rate at which organisms develop. It may also act as a stimulus, determining whether or not the organism starts its development at all. For instance, for many species of temperate, arctic and alpine herbs, a period of chilling or freezing (or even of alternating high and low temperatures) is

necessary before germination will occur. A cold experience (physiological evidence that winter has passed) is required before the plant can start on its cycle of growth and development. Temperature may also interact with other stimuli (e.g. photoperiod) to break dormancy and so time the onset of growth. The seeds of the birch (*Betula pubescens*) require a photoperiodic stimulus (i.e. experience of a particular regime of day length) before they will germinate, but if the seed has been chilled it starts growth without a light stimulus.

## 2.4 Correlations between temperature and the distribution of plants and animals

### 2.4.1 Spatial and temporal variations in temperature

Variations in temperature on and within the surface of the earth have a variety of causes: latitudinal, altitudinal, continental, seasonal, diurnal and microclimatic effects and, in soil and water, the effects of depth.

Latitudinal and seasonal variations cannot really be separated. The angle at which the earth is tilted relative to the sun changes with the seasons, and this drives some of the main temperature differentials on the earth's surface. Superimposed on these broad geographic trends are the influences of altitude and 'continentality'. There is a drop of 1°C for every 100 m increase in altitude in dry air, and a drop of 0.6°C in moist air. This is the result of the 'adiabatic' expansion of air as atmospheric pressure falls with increasing altitude. The effects of continentality are largely attributable to the different rates of heating and cooling of the land and the sea. The land surface reflects less heat than the water, so the surface warms more quickly, but it also loses heat more quickly. The sea therefore has a moderating, 'maritime' effect on the temperatures of coastal regions and especially islands; both daily and seasonal variations in temperature are far less marked than at more inland, continental locations at the same latitude. Moreover, there are comparable effects within land-masses: dry, bare areas like deserts suffer greater daily and seasonal extremes of temperature than do wetter areas like forests. Thus, global maps of temperature zones hide a great deal of local variation.

#### microclimatic variation

On a smaller scale still there can be a great deal of microclimatic variation. For example, the sinking of dense, cold air into the bottom of a valley at night can make it as much as 30°C colder than the side of the valley only 100 m higher; the winter sun, shining on a cold day, can heat

the south-facing side of a tree (and the habitable cracks and crevices within it) to as high as 30°C; and the air temperature in a patch of vegetation can vary by 10°C over a vertical distance of 2.6 m from the soil surface to the top of the canopy. Hence, we need not confine our attention to global or geographic patterns when seeking evidence for the influence of temperature on the distribution and abundance of organisms.

Long-term temporal variations in temperature, such as those associated with the ice ages, were discussed in the previous chapter (Section 1.4.3). Between these, however, and the very obvious daily and seasonal changes that we are all aware of, a number of medium-term patterns have become increasingly apparent. Notable amongst these are the El Niño–Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO). The ENSO is an alternation between a warm (El Niño) and a cold (La Niña) state of the waters of the tropical Pacific Ocean off the coast of South America (Figure 2.16a), although it affects temperature and the climate generally in terrestrial and marine environments throughout the whole Pacific basin and beyond (Figure 2.16b). The NAO refers to a north–south alternation in atmospheric mass between the subtropical Atlantic and the Arctic (Figure 2.16c) and again affects climate in general rather than just temperature (Figure 2.16d). Positive index values (Figure 2.16c) are associated, for example, with relatively warm conditions in North America and Europe and relatively cool conditions in North Africa and the Middle East. An example of the effect of NAO variation on species abundance, that of cod, *Gadus morhua*, in the Barents Sea, is shown in Figure 2.17.

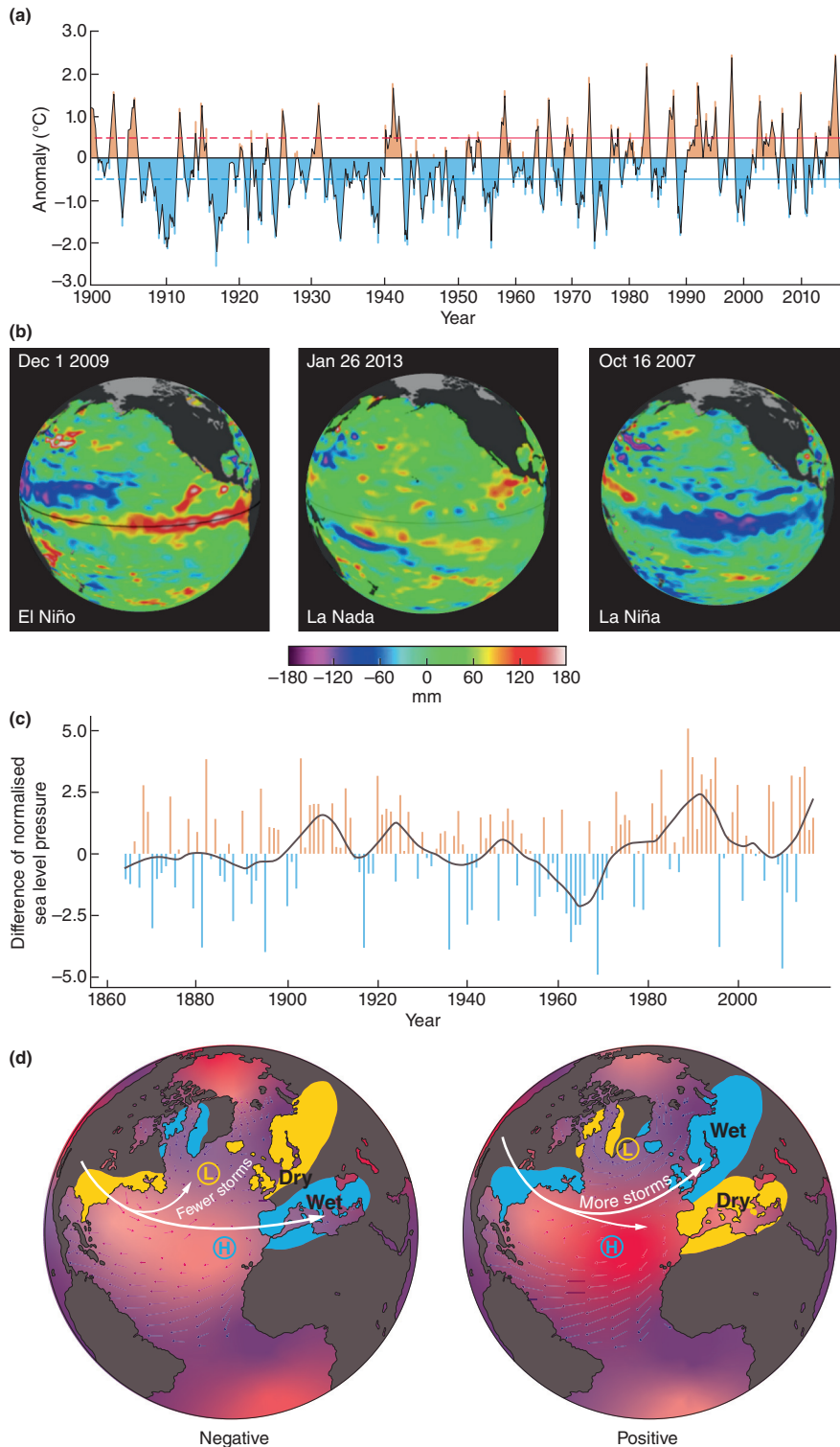
#### ENSO and NAO

### 2.4.2 Typical temperatures and distributions

There are very many examples of plant and animal distributions that are strikingly correlated with some aspect of environmental temperature (e.g. Figure 2.2a) and this kind of pattern may still hold even at gross taxonomic and systematic levels (Figure 2.18). At a finer scale, the distributions of many species closely match maps of some aspect of temperature. For example, the northern cool range boundary of wild madder plants (*Rubia peregrina*) is closely correlated with the position of the January 4.5°C isotherm (an isotherm is a line on a map joining places that experience the same temperature).

#### isotherms

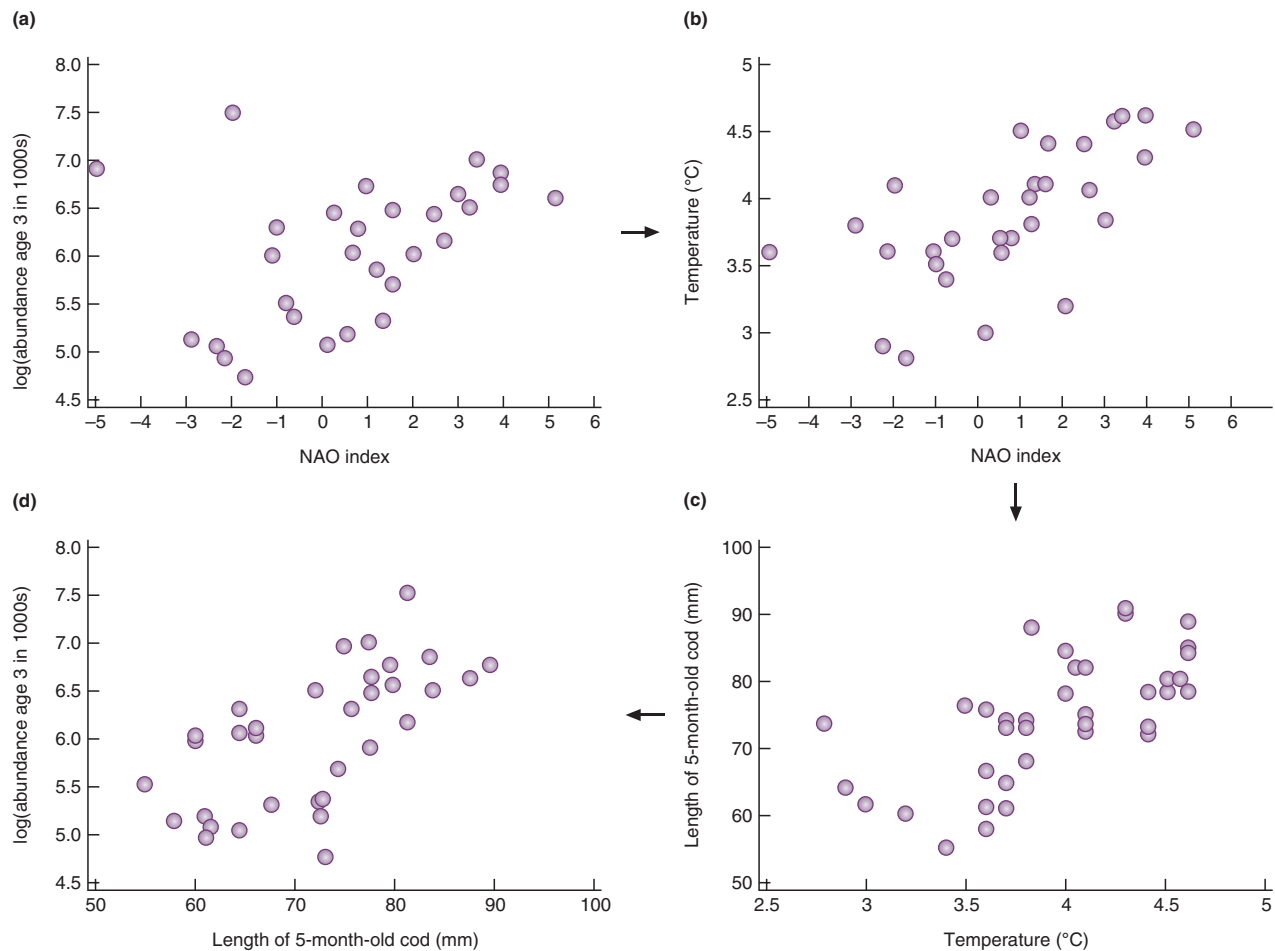
However, such relationships need to be interpreted with some caution: they can be extremely valuable in predicting where we might and might not find a particular species (e.g.



**Figure 2.16 Features of the El Niño–Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO).** (a) ENSO from 1900 to 2017 as measured by sea surface temperature (SST) anomalies (differences from the mean) in the equatorial mid-Pacific. El Niño events are defined as occurring when the SST is more than  $0.4^{\circ}\text{C}$  above the mean (red dashed line) and La Niña events when the SST is more than  $0.4^{\circ}\text{C}$  below the mean (blue dashed line). (b) Examples of El Niño (December 2009) and La Niña events (October 2007) as well as a neutral state (La Nada; January 2013) in terms of sea height above average levels. Warmer seas are higher; for example, a sea height 150–200 mm below average equates to a temperature anomaly of approximately  $2\text{--}3^{\circ}\text{C}$ . (c) NAO from 1864 to 2017 as measured by the normalised sea-level pressure difference between Lisbon in Portugal and Reykjavik in Iceland. (d) Typical winter conditions when the NAO index is positive or negative. Conditions that are more than usually warm, cold, dry or wet are indicated. The positions of the Icelandic low pressure (L) and the Azores high pressure (H) zones are shown. *Source:* (a) Compiled from the US National Ocean and Atmospheric Administration (NOAA), <https://www.ncdc.noaa.gov/teleconnections/enso/indicators/sst.php>. (b) From the US National Aeronautics and Space Administration (NASA), <https://sealevel.jpl.nasa.gov/science/elinopdo/elinino/>. (c) From <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>. (d) From <http://www.ldeo.columbia.edu/NAO/>.

Figure 2.5); they may suggest that some feature related to temperature is important in the life of the organisms; but they do not prove that temperature *causes* the limits to a species' distribution. For one thing, the temperatures measured

for constructing isotherms for a map are only rarely those that the organisms experience. In nature an organism may choose to lie in the sun or hide in the shade and, even in a single day, may experience a baking midday sun and a



**Figure 2.17** The abundance of three-year-old cod, *Gadus morhua*, in the Barents Sea is positively correlated with the value of the North Atlantic Oscillation (NAO) index. The mechanism underlying the correlation (a) is suggested in (b–d). (b) Annual mean temperature increases with the NAO index. (c) The length of five-month-old cod increases with annual mean temperature. (d) The abundance of cod at age three years increases with their length at five months. *Source:* After Ottersen *et al.* (2001).

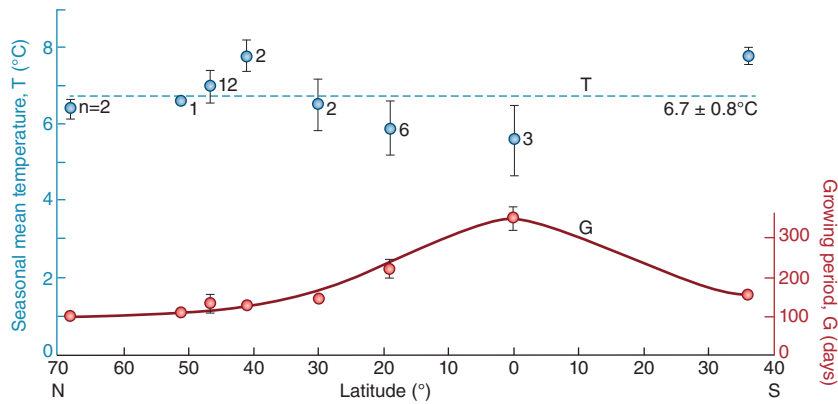
freezing night. Moreover, temperature varies from place to place on a far finer scale than will usually concern a geographer, but it is the conditions in these ‘microclimates’ that will be crucial in determining what is habitable for a particular species. For example, the prostrate shrub *Dryas octopetala* is restricted to altitudes exceeding 650 m in north Wales, UK, where it is close to its southern limit. But to the north, in Sutherland in Scotland, where it is generally colder, it is found right down to sea level.

On the other hand, Payne *et al.* (2016) were able to demonstrate a strong correlation between the warm boundary isotherms of nine well-studied fish species and their optimum temperatures for activity, somatic growth and reproductive growth (Figure 2.19): this is good evidence of a causal link.

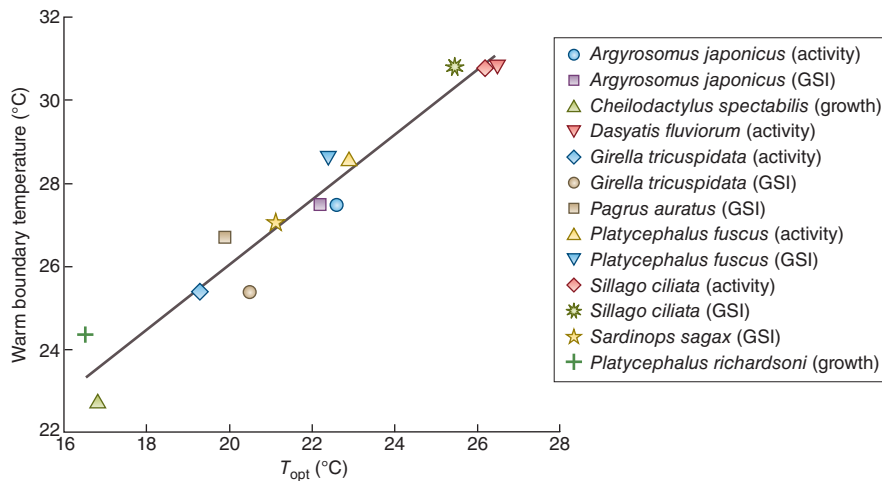
## 2.4.3 Distributions and extreme conditions

For many species, distributions are accounted for not so much by average temperatures as by occasional extremes, especially occasional lethal temperatures that preclude its existence. For instance, injury by frost is probably the single most important factor limiting plant distribution. To take one example: the saguaro cactus (*Carnegiea gigantea*) is liable to be killed when temperatures remain below freezing for 36 h, but if there is a daily thaw it is under no threat. In Arizona, the northern and eastern edges of its distribution correspond to a line joining places where on occasional days it fails to thaw. Thus, the saguaro is absent where there are occasionally lethal conditions – an individual need only be killed once.





**Figure 2.18** The treelines (high-altitude limits of forest cover) of the world's mountains seem to follow a common isotherm. This is  $6.7 \pm 0.8^\circ\text{C}$ , with very similar mean ground temperatures during the growing season across a wide range of latitudes from subarctic through equatorial areas to temperate southern hemisphere regions (the growing period differs according to latitude). The species composition of the forests is, of course, vastly different in the different regions. *Source:* From Körner & Paulsen (2004).



**Figure 2.19** Warm boundary limits of nine Australian fish species are correlated with species-specific optimum fish performance. Optimum temperature ( $T_{\text{opt}}$ ) is shown for maximum activity, somatic growth or reproductive growth (gonadosomatic index, GSI, a measure of gonad mass relative to total body mass) measured in the wild (four species provided both activity and reproductive growth data, giving 13 points in total). The species-specific warm equatorward range boundary is the average temperature of the warmest month at the range limit. *Source:* From Payne *et al.* (2016).

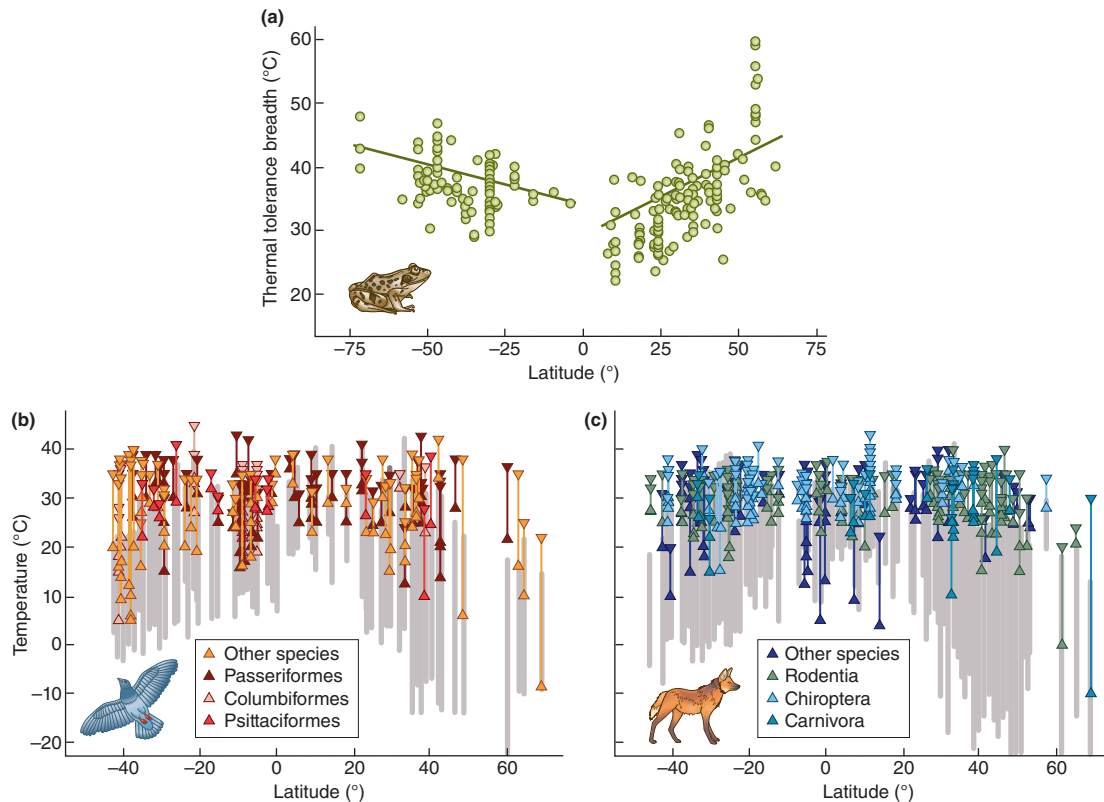
### you only die once

Similarly, there is scarcely any crop that is grown on a large commercial scale in the climatic conditions of its wild ancestors, and it is well known that crop failures are often caused by extreme events, especially frosts and drought. For instance, the climatic limit to the geographic range for the production of coffee (*Coffea arabica* and *C. robusta*) is defined by the  $13^\circ\text{C}$  isotherm for the coldest month of the year. Much of the world's crop is produced in the highland microclimates of the São Paulo and Paraná districts of Brazil. Here, the average minimum temperature is  $20^\circ\text{C}$ , but occasionally cold winds and just a few hours of temperature close to freezing are sufficient to kill or severely damage the trees (and influence world coffee prices).

Species at higher latitudes experience greater seasonal temperature variation and are expected to be able to withstand greater temperature extremes. This general pattern has been reported for ectotherms (Figure 2.20a) (Sunday *et al.*, 2011) but does it also apply to endotherms, which maintain a high and constant temperature and are thus decoupled to a degree from the influence of ambient conditions? The *climate variability hypothesis* has been tested in a meta-analysis of physiological studies that allowed the thermoneutral zones (see Section 2.3.3) to be estimated for hundreds of bird and mammal species (Khaliq *et al.*, 2014). Figure 2.20b and c plots the thermoneutral zones estimated for individual bird and mammal species in relation to both

### global variation in thermal tolerances





**Figure 2.20 Geographic variation in thermal tolerances.** (a) Terrestrial ectotherms, including arthropods, reptiles and amphibians, as estimated by the range between their upper and lower lethal or critical temperature limits, and (b) birds and (c) mammals as illustrated by the breadths of their thermoneutral zones, plotted in relation to latitude and, in the case of (b) and (c) climatic variability (grey bars) at the capture sites of the individuals used in published physiological experiments. Major bird and mammal orders are highlighted by different colours. Climatic variability is the annual range between maximum and minimum temperatures. *Source:* (a) After Sunday *et al.* (2011). (b, c) After Khaliq *et al.* (2014).

## APPLICATION 2.5 Tropical species at particular risk from climate change

Khaliq *et al.* (2014) found that most of the endotherm species in their dataset (Figure 2.20b, c) currently experience maximum ambient temperatures that are within their tolerance limits during most months of the year, and note that in a warming climate many should still be able to find suitable temperature conditions within their current range. However, vulnerability to higher future ambient temperatures increases from the poles towards tropical regions, even though increases of temperature predicted for temperate and polar regions

exceed those in the tropics. This is because species in tropical regions tend to live closer to their upper temperature limits and even small increases in ambient temperatures may challenge their survival. Moreover, projections of declining precipitation in tropical areas worsen the prospects for tropical species, because water availability is crucial for endotherms to compensate thermal stress. These results highlight the threats from global climate change in tropical zones, which harbour the greatest amount of biodiversity worldwide.

latitude and climatic variability (the latter estimated as the annual range between the monthly average of daily maximum temperatures of the warmest month and minimum temperatures of the coldest month). Note how temperature variability is generally lower in tropical regions. The climate variability hypothesis was supported in the case of birds but not mammals, a difference that may be related to their different lifestyles, with mammals often able to create their own preferred microclimates in burrows and dens.

#### 2.4.4 Distributions and the interaction of temperature with other factors

Although organisms respond to each condition in their environment, the effects of conditions may be determined largely by the responses of other community members. Temperature does not act on just one species: it also acts on its competitors, prey, parasites and so on. This, as we saw in Section 2.2, was the difference between a fundamental niche (where an organism *could* live) and a realised niche (where it *actually* lives). For example, an organism will suffer if its food is another species that cannot tolerate an environmental condition. This is illustrated by the distribution of the rush moth (*Coleophora alticolella*) in England. The moth lays its eggs on the flowers of the rush *Juncus squarrosus* and the caterpillars feed on the developing seeds. Above 600 m, the moths and their caterpillars are little affected by the low temperatures, but the rush, although it grows, fails to ripen its seeds. This, in turn, limits the distribution of the moth, because caterpillars that hatch in the colder elevations will starve as a result of insufficient food (Randall, 1982).

##### disease

The effects of conditions on disease may also be important. Conditions may favour the spread of infection (winds carrying fungal spores), or favour the growth of the parasite, or weaken the defenses of the host. For example, during an epidemic of southern corn leaf blight (*Helminthosporium maydis*) in a corn field in Connecticut, the plants closest to the trees that were shaded for the longest periods were the most heavily diseased (Harper, 1955).

##### competition

Competition between species can also be profoundly influenced by environmental conditions, especially temperature. Two stream salmonid fishes, *Salvelinus malma* and *S. leucomaenis*, coexist at intermediate altitudes (and therefore intermediate temperatures) on Hokkaido Island, Japan, whereas only the former lives at higher altitudes (lower temperatures) and only the latter at lower altitudes. A reversal,

by a change in temperature, of the outcome of competition between the species plays a key role in this pattern (discussed more fully in Section 8.2.3).

Many of the interactions between temperature and other physical conditions are so strong that it is not sensible to consider them separately. The relative humidity of the atmosphere, for example, is an important condition in the life of terrestrial organisms because it plays a major part in determining the rate at which they lose water. In practice, it is rarely possible to make a clean distinction between the effects of relative humidity and of temperature. This is simply because a rise in temperature leads to an increased rate of evaporation. A relative humidity that is acceptable to an organism at a low temperature may therefore be unacceptable at a higher temperature. Microclimatic variations in relative humidity can be even more marked than those involving temperature. For instance, it is not unusual for the relative humidity to be almost 100% at ground level amongst dense vegetation and within the soil, whilst the air immediately above, perhaps 40 cm away, has a relative humidity of only 50%. The organisms most obviously affected by humidity in their distribution are those 'terrestrial' animals that are actually, in terms of the way they control their water balance, 'aquatic'. Amphibians, terrestrial isopods, nematodes, earthworms and molluscs are all, at least in their active stages, confined to microenvironments where the relative humidity is at or very close to 100%. The major group of animals to escape such confinement are the terrestrial arthropods, especially insects. Even here though, the evaporative loss of water often confines their activities to habitats (e.g. woodlands) or times of day (e.g. dusk) when relative humidity is relatively high.

##### temperature and water availability

## 2.5 pH of soil and water

The pH of soil in terrestrial environments or of water in aquatic ones is a condition that can exert a powerful influence on the distribution and abundance of organisms. The protoplasm of the root cells of most vascular plants is damaged as a direct result of toxic concentrations of  $H^+$  or  $OH^-$  ions in soils below pH 3 or above pH 9, respectively. Further, indirect effects occur because soil pH influences the availability of nutrients and/or the concentration of toxins.

Increased acidity (low pH) may act in three ways: (i) directly, by upsetting osmoregulation, enzyme activity or gaseous exchange across respiratory surfaces; (ii) indirectly, by increasing the concentration of toxic heavy metals at higher pHs, particularly aluminium ( $Al^{3+}$ ) but also

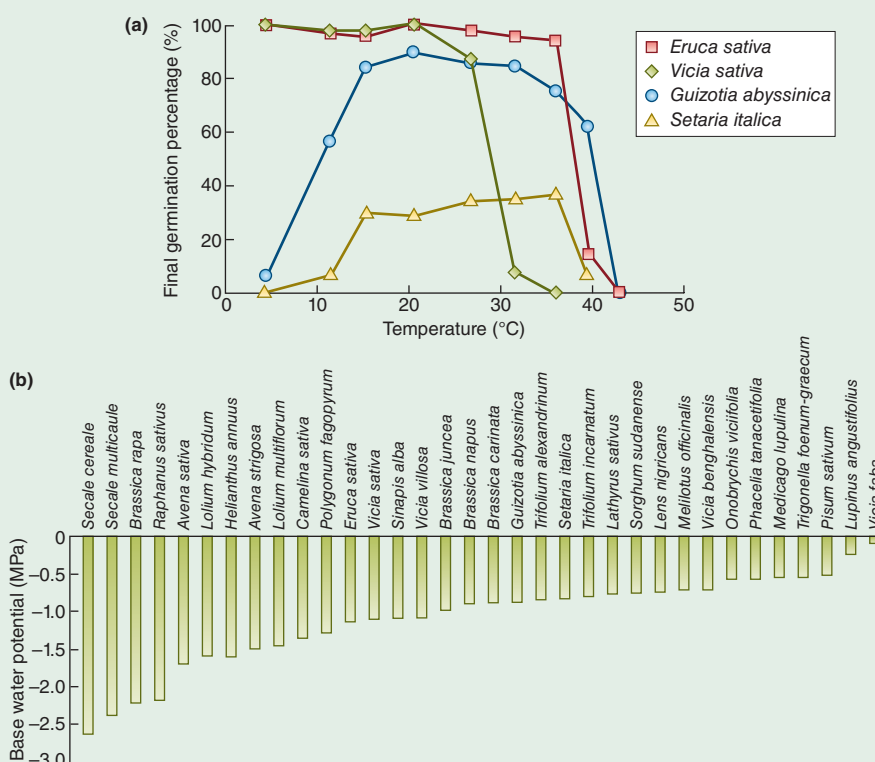
## APPLICATION 2.6 Farmers' choice of cover crops in relation to temperature and soil water potential

Farmers have a wide choice of species that can be sown as cover crops during fallow periods to improve soil quality and reduce soil erosion and runoff. But which should they choose? Seed germination is a key stage in plant establishment, particularly when sowing occurs in summer, when temperatures are high and water availability low, and germination for 34 species of potential cover crops in four families was monitored in the laboratory at temperatures ranging from 4.5 to 43°C and at four water potentials (Figure 2.21). Optimal temperatures for germination of seeds varied from 21.3 to 37.2°C; maximum temperatures at which the species could germinate varied from 27.7 to 43.0°C; and base water potentials, the lowest water potential at which a seed can germinate, varied from −0.1 to −2.6 MPa. (Note that at a potential of 0 MPa soil is in a state of saturation, while at −1.5 MPa soil is at its permanent wilting point (see Section 3.3.2).)

Most of the cover crops were adapted to summer sowing with a high mean optimal temperature for germination, but some, such as *Vicia sativa* (Figure 2.21a), were more sensitive to high temperatures. Others, such as *Secale cereale* (Figure 2.21b), were more resistant to water deficit and germinated even when water potential was very low. Tribouillois *et al.* (2016) classified the cover crops into functional groups that are of value to farmers when choosing species appropriate for their particular conditions. Thus, functional group 1, which includes *Guizotia abyssinica* and *Setaria italica*, has a minimal temperature of 10°C, a maximal temperature of 41.2°C and a base water potential of −0.9 KPa. Functional group 4, on the other hand, which includes *Brassica rapa* and *Secale cereale*, has a minimal temperature of 0.4°C, a maximal temperature of 38.6°C and a base water potential of −2.4 KPa.

**Figure 2.21** Niches of cover crops in terms of temperature and base water potential. (a) Response curves to temperature for selected species of cover crops in terms of percentage of seeds that germinate.

(b) Niches in one dimension for various species of cover crop. Base water potential is the lowest water potential at which a seed can germinate. At one extreme, *Vicia faba* is very sensitive to water potential for germination while, at the other, *Secale cereale* can germinate at very low water potentials. Source: From Tribouillois *et al.* (2016).



manganese ( $\text{Mn}^{2+}$ ) and iron ( $\text{Fe}^{3+}$ ), which are essential plant nutrients; and (iii) indirectly, by reducing the quality and range of food sources available to animals. Tolerance limits for pH vary amongst plant species, but only a minority are able to grow and reproduce at a pH below about 4.5.

In alkaline soils, iron ( $\text{Fe}^{3+}$ ) and phosphate ( $\text{PO}_4^{3-}$ ), and certain trace elements such as manganese ( $\text{Mn}^{2+}$ ), are fixed in relatively insoluble compounds, and plants may then suffer because there is too little rather than too much of them. For example, calcifuge plants (those characteristic of acid

soils) commonly show symptoms of iron deficiency when they are transplanted to more alkaline soils. In general, however, soils and waters with a pH above 7 tend to be hospitable to many more species than those that are more acid. Chalk and limestone grasslands carry a much richer flora (and associated fauna) than acid grasslands and the situation is similar for animals inhabiting streams, ponds and lakes.

Some Archaea can tolerate and even grow best in environments with a pH far outside the range tolerated by eukaryotes. Such environments are rare, but occur in volcanic lakes and geothermal springs where they are dominated by sulphur-oxidising bacteria whose pH optima lie between 2 and 4 and which cannot grow at neutrality (Stolp, 1988). *Thiobacillus ferrooxidans* occurs in the waste from industrial metal-leaching processes and tolerates pH 1; *T. thiooxidans* cannot only tolerate but can grow at pH 0. Towards the other end of the pH range are the alkaline environments of soda lakes with pH values of 9–11, which are inhabited by cyanobacteria such as *Anabaenopsis arnoldii* and *Spirulina platensis*.

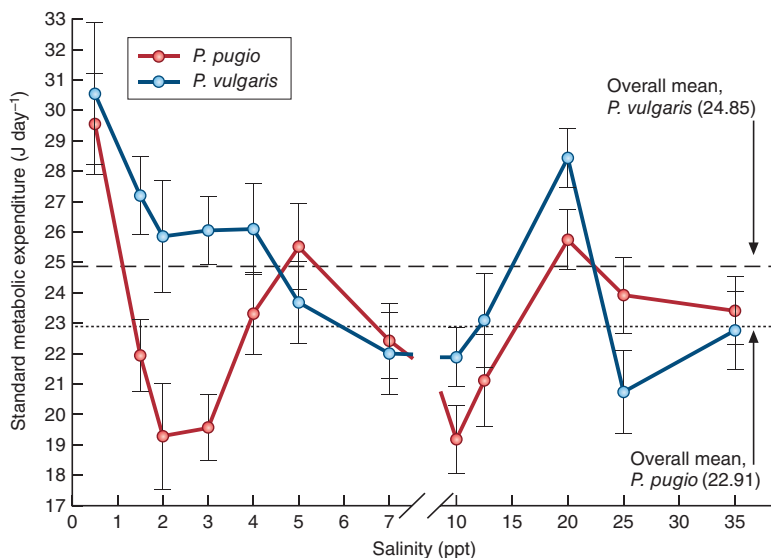
## 2.6 Salinity

For terrestrial plants, the concentration of salts in the soil water offers osmotic resistance to water uptake. The most extreme saline conditions occur in arid zones where the predominant movement of soil water is towards the surface and crystalline salt accumulates. This occurs especially when crops have been grown in arid regions under irrigation; salt pans then develop and the land is lost to agriculture. The main effect of salinity is to create the same kind of osmoregulatory problems as drought and freezing and

the problems are countered in much the same ways. For example, many of the higher plants that live in saline environments (halophytes) accumulate electrolytes in their vacuoles, but maintain a low concentration in the cytoplasm and organelles. Such plants maintain high osmotic pressures and so remain turgid, and are protected from the damaging action of the accumulated electrolytes by polyols and membrane protectants.

Freshwater environments present a set of specialised environmental conditions because water tends to move into organisms from the environment and this needs to be resisted. In marine habitats, the majority of organisms are isotonic to their environment so that there is no net flow of water, but there are many that are hypotonic so that water flows out from the organism to the environment, putting them in a similar position to terrestrial organisms. Thus, for many aquatic organisms the regulation of body fluid concentration is a vital and sometimes an energetically expensive process. The salinity of an aquatic environment can have an important influence on distribution and abundance, especially in places like estuaries where there is a particularly sharp gradient between truly marine and freshwater habitats.

The freshwater shrimps *Palaemonetes pugio* and *P. vulgaris*, for example, co-occur in estuaries on the eastern coast of the USA at a wide range of salinities, but the former seems to be more tolerant of lower salinities than the latter, occupying some habitats from which the latter is absent. Figure 2.22 shows the mechanism likely to be underlying this (Rowe, 2002). Over the low salinity range (though not at the effectively lethal lowest salinity) metabolic expenditure was significantly lower in *P. pugio*. *P. vulgaris* requires far more energy simply to maintain itself, putting



**Figure 2.22** Metabolic expenditure in relation to salinity for two shrimp species. Standard metabolic expenditure (estimated through minimum oxygen consumption) in *Palaemonetes pugio* and *P. vulgaris* at a range of salinities. Note that there was significant mortality of both species over the experimental period at 0.5 ppt (parts per thousand), especially in *P. vulgaris* (75% compared with 25%). Source: After Rowe (2002).

it at a severe disadvantage in competition with *P. pugio* even when it is able to sustain such expenditure.

### 2.6.1 Conditions at the boundary between the sea and land

Salinity has important effects on the distribution of organisms in intertidal areas but it does so through interactions with other conditions – notably exposure to the air and the nature of the substrate.

#### algae and higher plants

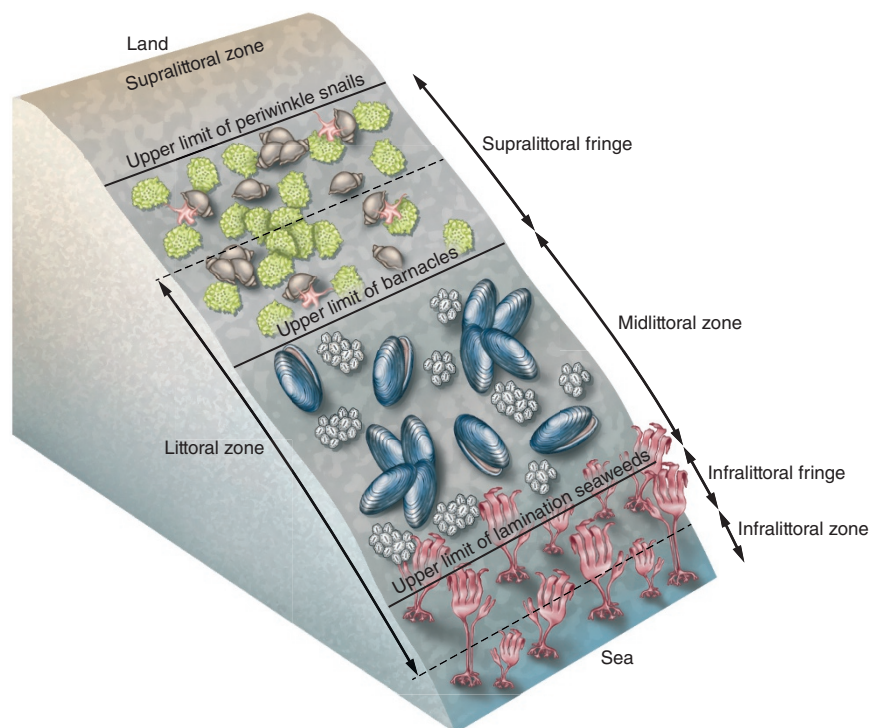
Algae of all types have found suitable habitats permanently immersed in the sea, but permanently submerged higher plants are almost completely absent. This is a striking contrast with submerged freshwater habitats where a variety of flowering plants have a conspicuous role. The main reason seems to be that higher plants require a substrate in which their roots can find anchorage. Large marine algae, which are continuously submerged except at extremely low tides, largely take their place in marine communities. These do not have roots but attach themselves to rocks by specialised 'holdfasts'. They are excluded from regions where the substrates are soft and holdfasts cannot 'hold fast'. It is in such regions that the few truly marine flowering plants, for example sea grasses such as *Zostera* and *Posidonia*, form submerged communities that support complex animal communities.

Most species of higher plants that root in seawater have leaves and shoots that are exposed to the atmosphere for a large part of the tidal cycle, such as mangroves, species of the grass genus *Spartina* and extreme halophytes such as species of *Salicornia* that have aerial shoots but whose roots are exposed to the full salinity of seawater. Where there is a stable substrate in which plants can root, communities of flowering plants may extend right through the intertidal zone in a continuum extending from those continuously immersed in full-strength seawater (like the sea grasses) through to totally non-saline conditions. Salt marshes, in particular, encompass a range of salt concentrations running from full-strength seawater down to totally non-saline conditions.

Higher plants are absent from intertidal rocky seashores except where pockets of soft substrate may have formed in crevices. Instead, such habitats are dominated by the algae, which give way to lichens at and above the high tide level where the exposure to desiccation is highest. The plants and animals that live on rocky seashores are influenced by environmental conditions in a very profound and often particularly obvious way by the extent to which they tolerate exposure to the aerial environment and the forces of waves and storms. This expresses itself in the *zonation* of the organisms, with different species at different heights up the shore (Figure 2.23).

The extent of the intertidal zone depends on the height of tides and

#### zonation



**Figure 2.23** General zonation scheme for the seashore determined by relative lengths of exposure to the air and to the action of waves. The littoral zone extends between the extreme high water and extreme low water of spring tides (upper and lower dashed lines). *Source:* After Raffaelli & Hawkins (1999).



the slope of the shore. Away from the shore, the tidal rise and fall are rarely greater than 1 m, but closer to shore, the shape of the landmass can funnel the ebb and flow of the water to produce extraordinary spring tidal ranges of, for example, nearly 20 m in the Bay of Fundy (between Nova Scotia and New Brunswick, Canada). In contrast, the shores of the Mediterranean Sea experience scarcely any tidal range. On steep shores and rocky cliffs the intertidal zone is very short and zonation is compressed.

To talk of ‘zonation as a result of exposure’, however, is to oversimplify the matter greatly (Raffaelli & Hawkins, 1999). In the first place, ‘exposure’ can mean a variety, or a combination of, many different things: desiccation, extremes of temperature, changes in salinity, excessive illumination and the sheer physical forces of pounding waves and storms (to which we turn in Section 2.7). Furthermore, ‘exposure’ only really explains the *upper* limits of these essentially marine species, and yet zonation depends on them having lower limits too. For some species there can be *too little exposure* in the lower zones. For instance, green algae would be starved of blue and especially red light if they were submerged for long periods too low down the shore. For many other species though, a lower limit to distribution is set by competition and predation. The seaweed *Fucus spiralis* will readily extend lower down the shore than usual in Great Britain whenever other competing midshore fucoid seaweeds are scarce.

## 2.7 Hazards, disasters and catastrophes: the ecology of extreme events

The wind and the tides are normal daily ‘hazards’ in the life of many organisms. The structure and behaviour of these organisms bear some witness to the frequency and intensity of such hazards in the evolutionary history of their species. Thus, most trees withstand the force of most storms without falling over or losing their living branches. Most limpets, barnacles and kelps hold fast to the rocks through the normal day-to-day forces of the waves and tides. We can also recognise a scale of more severely damaging forces (we might call them ‘disasters’) that occur occasionally, but with sufficient frequency to have contributed repeatedly to the forces of natural selection. When such a force recurs it will meet a population that still has a genetic memory of the selection that acted on its ancestors – and may therefore suffer less than they did. In the woodlands and shrub communities of arid zones, fire has this quality, and tolerance of fire damage is a clearly evolved response (see Section 2.3.6).

When disasters strike natural communities it is only rarely that they have been carefully studied before the event. One exception is cyclone ‘Hugo’ which struck the Caribbean island of Guadeloupe in 1994. Detailed accounts of the dense humid forests of the island had been published only recently before (Ducrey & Labbé, 1985, 1986). The cyclone devastated the forests with mean maximum wind

### APPLICATION 2.7 Coral reefs and mangrove forests may ameliorate the impact of tsunamis

#### ecosystem services

Ecosystems often provide valuable *ecosystem services* (see Section 15.4.1) that people use and enjoy. *Provisioning services* include wild meat and berries, medicinal herbs, fibre products, fuel and drinking water; *cultural services* include aesthetic fulfillment, education and recreation; *regulating services* include the ecosystem’s capacity to ameliorate the effects of pollutants or to moderate disasters (such as tsunamis); finally, *supporting services*, such as primary production and nutrient cycling, underlie all the others (Townsend, 2008).

The devastating tsunamis of 2004 and 2011, caused by earthquakes off Sumatra (9.3 on the Richter scale) and north-eastern Japan (9.0), took huge tolls in human lives and livelihoods and, hardly surprisingly, also greatly changed near-shore and coastal ecosystems, both aquatic and terrestrial (e.g. Urabe *et al.*, 2013). More surprising,

perhaps, has been the finding that intact coral reefs can absorb some of the wave’s power (Kunkel *et al.*, 2006). According to the American Geophysical Union, illegal coral mining off the south-west coast of Sri Lanka allowed far more destruction from the 2004 Pacific-wide tsunami than occurred in nearby areas where coral reefs were intact. It seems that exploitation of a *provisioning service* (coral crushed to create road surface) resulted in loss of a *regulating service*. Moreover, muddy shores with intact mangrove forest also seem to have moderated the devastation caused by the 2004 tsunami, both by reducing human mortality inland and by preventing the inland intrusion of saltwater that, where mangroves had been removed, ruined rice and groundnut crops (Kathiresan & Rajendran, 2005). The conservation and restoration of coral reefs and mangrove forests should help protect against these natural catastrophes.



velocities of  $270 \text{ km h}^{-1}$  and gusts of  $320 \text{ km h}^{-1}$ . Up to 300 mm of rain fell in 40 h. The early stages of regeneration after the cyclone (Labbé, 1994) typify the responses of long-established communities on both land and sea to massive forces of destruction. Even in ‘undisturbed’ communities there is a continual creation of gaps as individuals (e.g. trees in a forest, kelps on a seashore) die and the space they occupied is recolonised (see Section 18.6.1).

In contrast to conditions that we have called ‘hazards’ and ‘disasters’ there are natural occurrences that are enormously damaging, yet occur so rarely that they may have no lasting selective effect on the evolution of the species. We might call such events ‘catastrophes’, for example the devastating Japanese tsunami (tidal wave) of 2011, or the volcanic eruptions of Mt St Helens in 1980 or of the island of Krakatau in 1883. The next time that Krakatau erupts there are unlikely to be any genes persisting that were selected for volcano tolerance!

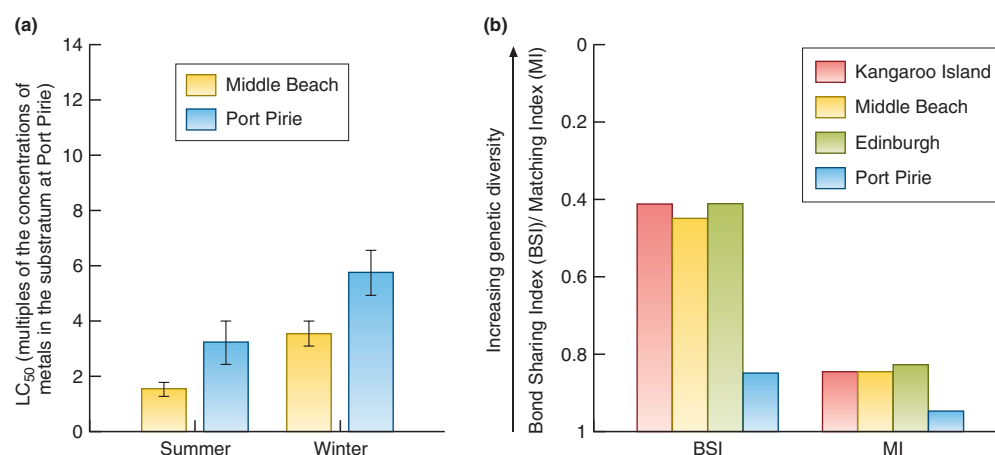
## 2.8 Environmental pollution

A number of environmental conditions that are, regrettably, becoming increasingly important are due to the accumulation of toxic byproducts of human activities. Sulphur dioxide emitted from power stations, and metals like copper, zinc and lead, dumped around mines or deposited around refineries, are just some of the pollutants that limit distributions, especially of plants. Many such pollutants are present naturally but at low concentrations, and some are indeed essential nutrients for plants. But in polluted areas their

concentrations can rise to lethal levels. The loss of species is often the first indication that pollution has occurred, and changes in the species richness of a river, lake or area of land provide bioassays of the extent of their pollution.

Yet it is rare to find even the most inhospitable polluted areas rare tolerators entirely devoid of species; there are usually at least a few individuals of a few species that can tolerate the conditions. Even natural populations from unpolluted areas often contain a low frequency of individuals that tolerate the pollutant; this is part of the genetic variability present in natural populations. Such individuals may be the only ones to survive or colonise as pollutant levels rise. They may then become the founders of a tolerant population to which they have passed on their ‘tolerance’ genes, and, because they are the descendants of just a few founders, such populations may exhibit notably low genetic diversity overall (Figure 2.24). Thus, in very simple terms, a pollutant has a two-fold effect. When it is newly arisen or is at extremely high concentrations, there will be few individuals of any species present (the exceptions being naturally tolerant variants or their immediate descendants). Subsequently, however, the polluted area is likely to support a much higher density of individuals, but these will be representatives of a much smaller range of species than would be present in the absence of the pollutant. Such novel, species-poor communities are now an established part of human environments (Bradshaw, 1987).

Pollution can, of course, have its effects far from the original source. Toxic effluents from a mine or a factory may



**Figure 2.24** Individuals of *Platynympha longicaudata* in a polluted site are more tolerant of pollution and have lower genetic diversity. (a) Tolerance of this marine isopod around Port Pirie, South Australia (the largest lead smelting operation in the world), was significantly higher ( $P < 0.05$ ) than for animals from a control (unpolluted) site, as measured by the concentration in food of a combination of metals (lead, copper, cadmium, zinc and manganese) required to kill 50% of the population ( $LC_{50}$ ). (b) Genetic diversity at Port Pirie was significantly lower than at three unpolluted sites, as measured by two indices of diversity based on RAPD (random amplified polymorphic DNA). Source: After Ross *et al.* (2002).

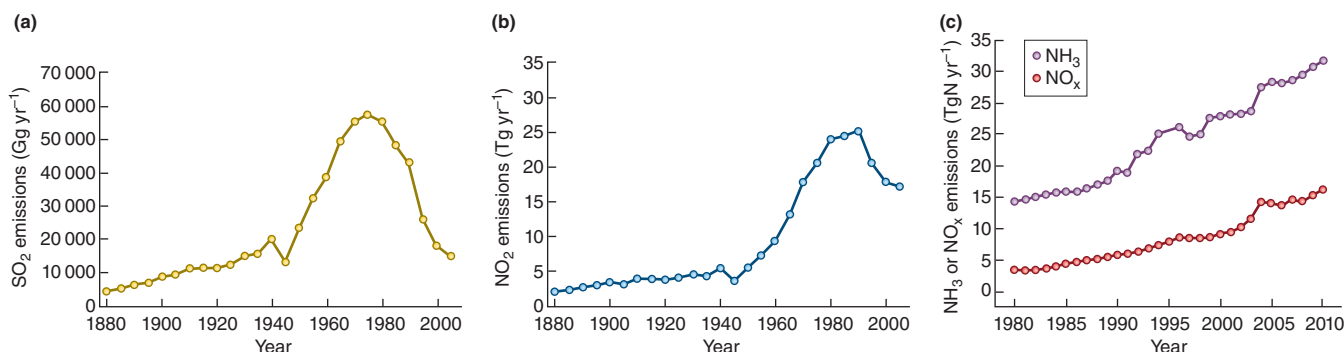
## APPLICATION 2.8 Bioremediation and phytomining

Species may differ greatly in their ability to tolerate pollutants. Some plants (often assisted by microbial symbionts in their rhizosphere) are *hyperaccumulators* of heavy metals – lead, cadmium and so on – with an ability not only to tolerate but also to accumulate much higher concentrations than the norm. As a result, species such as *Solanum nigrum* have an important role to play in bioremediation (Sun *et al.*, 2017), removing pollutants from the soil so that eventually other, less tolerant plants can grow there too.

Some may even be used for *phytomining*, where hyper-accumulator plants are used to accumulate a metal of interest from metal-rich soils and transport them to the

shoots, followed by harvesting of the shoots as a bio-ore (Thijs *et al.*, 2017). Thus, *Alyssum bertolonii* can accumulate in its aerial parts 7000–12 000  $\mu\text{g g}^{-1}$  dry weight of nickel, while *Arabidopsis halleri* and *S. nigrum* can accumulate and tolerate similarly high concentrations of zinc and cadmium, respectively.

Organisms with bioremediation potential also include fungi and bacteria (de Alencar *et al.*, 2017), and remediation can be directed not only at heavy metals but also at many other pollutants, including petroleum- and explosives-contaminated soil and polycyclic aromatic hydrocarbons.



**Figure 2.25** Acid emissions have been decreasing in Europe since 1970 while they continued to increase in China. Annual emissions of (a) sulphur dioxide and (b) nitrogen dioxide in Europe from 1880 to 2005 and of (c) ammonia and oxides of nitrogen (NO<sub>x</sub>) in China from 1980 to 2010. *Source:* (a, b) After Hildrew (2018). (c) From Liu *et al.* (2013).

enter a watercourse and affect its flora and fauna for its whole length downstream. Effluents from large industrial complexes can pollute and change the flora and fauna of many rivers and lakes in a region and cause international disputes.

### acid rain

A striking example of pollution at a distance is the creation of 'acid rain' – atmospheric deposition of acidic constituents (particularly sulphuric and nitric acid) that reach the ground as rain, snow, particulates, gases and vapour. Acid rain results predominantly from emissions of sulphur dioxide and oxides of nitrogen (Figure 2.25a, b) from the burning of fossil fuels to generate electricity, transport and industry, and increased dramatically after the Industrial Revolution in Europe and North America. Profound ecological effects, often across national boundaries at considerable distances from the polluting source, have included damage to forests and soil communities and acidification of rivers and lakes,

with associated loss of biodiversity and recreational activities such as fishing.

The only option to treat the causes of acidic deposition is to reduce emissions and the introduction of stringent air pollution regulations in Europe and North America, aimed at sulphur dioxide, oxides of nitrogen and ammonia, produced impressive results. In the UK alone, emissions of sulphur dioxide fell by 94% and nitrogen by 58% between 1970 and 2010. Emission reductions in Europe as a whole have been almost as good, while reductions in North America have been somewhat smaller. It should be stressed that the reductions are not entirely explained by government anti-pollution initiatives, but are partly due to the 'export' of emissions to China and elsewhere where many goods destined for import to the northern hemisphere are now made. Indeed, acid rain is much less of an issue now in the north while the highest rates of deposition currently occur in parts of Asia (Figure 2.25c).

As a consequence of emission reductions, chemical recovery of northern hemisphere waterways has been evident but biological recovery has generally been rather muted. This may be partly because chemical recovery is not yet complete or there may be biological constraints, such as a lack of colonists for previously impacted habitats or biotic resistance associated with changes to food webs, such that a simple reversal of acidification does not occur and the end point might not be the same community that existed before acidification (Hildrew, 2018). More encouraging has been the recent recovery of north-eastern US fish populations in lakes that were previously incapable of sustaining wild fish populations because of acid conditions (Warren *et al.*, 2017).

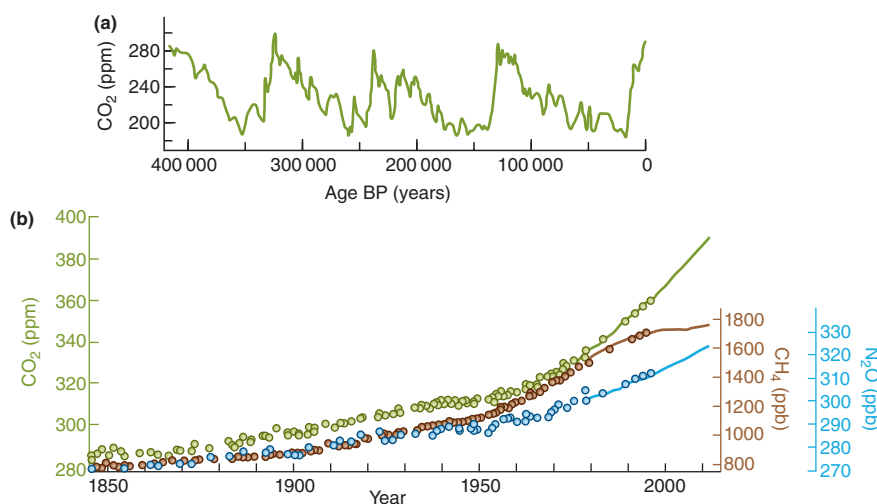
## 2.9 Global change

In Chapter 1 we discussed some of the ways in which global environments have changed over the long timescales involved in continental drift and the shorter timescales of the repeated ice ages. Over these timescales some organisms have failed to accommodate to the changes and have become extinct, others have migrated so that they continue to experience the same conditions but in a different place, and others have changed their nature (evolved) and tolerated some of the changes. We

now turn to consider global changes that are occurring in our own lifetimes – consequences of our own activities – and that are predicted to bring about profound changes in the ecology of the planet. Although part of the wider syndrome now called ‘global change’, the acid rain just discussed is not truly global but rather regional because of the restricted mean residence time of the acidic pollutants in the atmosphere (a few days) compared with carbon dioxide, whose residence time is very much longer (Hildrew, 2018). We discuss this next.

### 2.9.1 Industrial gases and the greenhouse effect

A major element of the Industrial Revolution was the switch from the use of sustainable fuels to the use of coal (and later, oil) as a source of power. Between the middle of the 19th and the middle of the 20th century the burning of fossil fuels, together with extensive deforestation, added about 90 gigatonnes (Gt) of carbon dioxide ( $\text{CO}_2$ ) to the atmosphere and more has been added since. The concentration of  $\text{CO}_2$  in the atmosphere before the Industrial Revolution (measured in gas trapped in ice cores) was about 280 ppm, a fairly typical interglacial ‘peak’ (Figure 2.26a), but this had risen to around 370 ppm by the turn of the millennium (Figure 2.26b) and in May 2013 reached 400 ppm for the first time in at least the last 800 000 years.



**Figure 2.26 Atmospheric concentrations of  $\text{CO}_2$  during the past 420 000 years and since 1850.** (a) Concentrations of  $\text{CO}_2$  in gas trapped in ice cores from Vostok, Antarctica. Transitions between glacial and warm epochs, and peaks in  $\text{CO}_2$ , occurred around 335 000, 245 000, 135 000 and 18 000 years ago. (b) Atmospheric concentrations of the greenhouse gases  $\text{CO}_2$  (green), methane ( $\text{CH}_4$ , brown) and nitrous oxide ( $\text{N}_2\text{O}$ , blue) determined from ice core data (dots) and from direct atmospheric measurements (lines) since the mid-18th century. BP, before present; ppb, parts per billion; ppm, parts per million. *Source:* (a) After Petit *et al.* (1999) and Stauffer (2000). (b) After IPCC (2014).

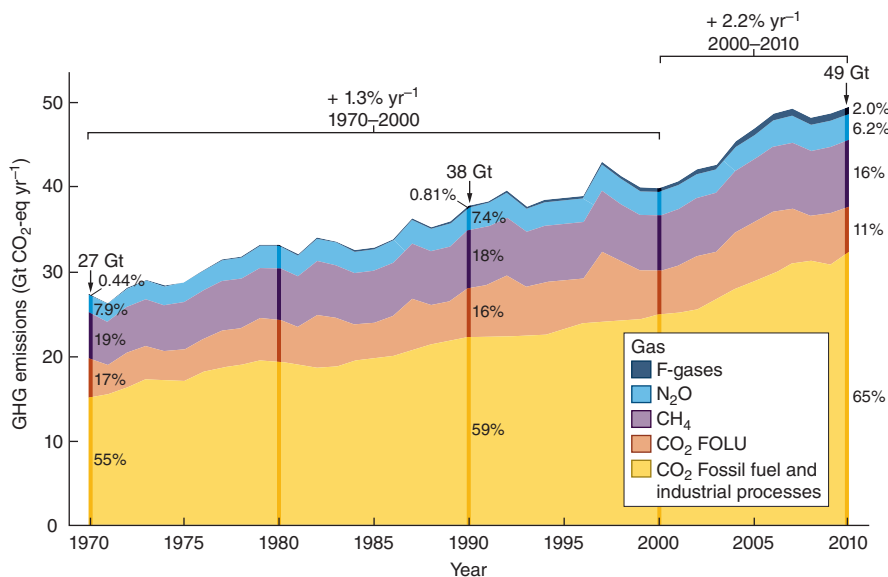
Solar radiation incident on the earth's atmosphere is in part reflected, in part absorbed, and part is transmitted through to the earth's surface, which absorbs and is warmed by it. Some of this absorbed energy is radiated back to the atmosphere where atmospheric gases, mainly water vapour and  $\text{CO}_2$ , absorb about 70% of it. It is this trapped reradiated energy that heats the atmosphere in what is called the 'greenhouse effect'. The greenhouse effect was of course part of the normal environment before the Industrial Revolution and was responsible for some of the environmental warmth before industrial activity started to enhance it. At that time, the greater proportion of the greenhouse effect was due to atmospheric water vapour.

**$\text{CO}_2$  – but not only  $\text{CO}_2$**

In addition to the enhancement of greenhouse effects by  $\text{CO}_2$  emissions, other trace gases have increased markedly in the atmosphere, particularly methane ( $\text{CH}_4$ ) and nitrous oxide ( $\text{N}_2\text{O}$ ) (Figure 2.27) and to a smaller extent the chlorofluorocarbons (CFCs, e.g. trichlorofluoromethane ( $\text{CCl}_3\text{F}$ ) and dichlorodifluoromethane ( $\text{CCl}_2\text{F}_2$ )) and some other minor contributors. Each greenhouse gas has a global warming potential (usually expressed as 'equivalents of  $\text{CO}_2$ ') that depends on how long it stays in the atmosphere and how strongly it absorbs energy. Thus,  $\text{CH}_4$  and  $\text{N}_2\text{O}$  have global warming potentials some 30 and 300 times that of  $\text{CO}_2$  over a 100-year period (they persist in the atmosphere for around 10 or 100 years, respectively, compared with thousands of years for  $\text{CO}_2$ , but absorb energy much more efficiently). Together, these gases

contribute about 35% to enhancing the greenhouse effect, compared with 65% by  $\text{CO}_2$  (Figure 2.26). The increase in  $\text{CH}_4$  is mainly of microbial origin in intensive agriculture on anaerobic soils (especially increased rice production) and in the digestive process of ruminants (a cow produces approximately 40 litres of  $\text{CH}_4$  each day).  $\text{N}_2\text{O}$  is emitted during agricultural and industrial production and the combustion of fossil fuels and solid waste. The effect of the CFCs from refrigerants, aerosol propellants and so on was potentially great (their global warming potentials are thousands or tens of thousands greater than  $\text{CO}_2$ ), but international agreements, mainly to counteract damage to the ozone layer, have strongly moderated increases in their concentrations. However, the rate of increase in annual greenhouse gas emissions has accelerated since the turn of the millennium (Figure 2.27).

It is possible to draw up a balance sheet of how the  $\text{CO}_2$  produced by human activities translates into changes in concentration in the atmosphere. Human activities have released more than 2000 Gt  $\text{CO}_2$  since 1750, but the increase in atmospheric  $\text{CO}_2$  accounts for only 40% of this (IPCC, 2014). The oceans absorb an estimated 30% of  $\text{CO}_2$  released by human activities. Furthermore, recent analyses indicate that terrestrial vegetation has been 'fertilised' by the increased atmospheric  $\text{CO}_2$ , so that a considerable amount of extra carbon has been locked up in vegetation biomass. And more is to be found as soil carbon. This softening of the blow by the oceans and terrestrial vegetation notwithstanding, however, atmospheric  $\text{CO}_2$  and the greenhouse effect are increasing.



**Figure 2.27** Total annual anthropogenic greenhouse gas (GHG) emissions from 1970 to 2010 converted to gigatonne equivalents of  $\text{CO}_2$  per year. FOLU, forestry and other land use change. Source: IPCC (2014).

The most profound effect of anthropogenic CO<sub>2</sub> emissions, global warming, is dealt with in the next section. In addition, ocean acidification is another worrying consequence.

#### ocean acidification

A large proportion of anthropogenic CO<sub>2</sub> is absorbed by the oceans, thus far reducing seawater pH by 0.1 units since the Industrial Revolution (equivalent to a 30% increase in acidity) as well as reducing carbonate ion concentrations. We have already seen that pH is a condition with significant influences on the success of organisms, but the fact that many parts of the ocean are also becoming undersaturated with calcium carbonate minerals is expected to have profound consequences for calcifying species such as corals, molluscs, sea urchins and calcareous plankton. On the other hand, photosynthetic production in the oceans is likely to benefit from higher CO<sub>2</sub> concentrations.

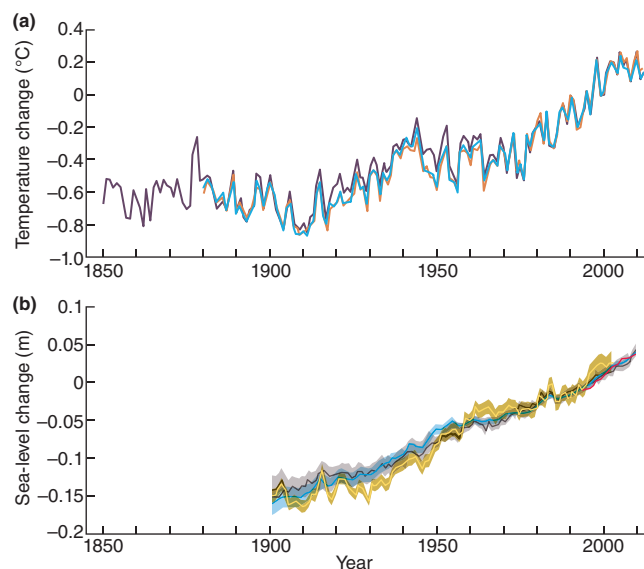
## 2.9.2 Global warming

We started this chapter discussing temperature, moved through a number of other environmental conditions to pollutants, and now return to temperature because of the effects of those pollutants on global temperatures. The globally averaged combined land and ocean surface temperature has increased by about 0.85°C from 1880 to 2012 (Figure 2.28a). We have already witnessed melting of arctic ice and rises in sea level (Figure 2.28b) (related to thermal expansion and the input of ice meltwater) and can expect further melting of the ice caps, a consequent rising of sea level and significant shifts in the pattern of global climates and changes to the distribution of species.

Predictions of the extent of global warming resulting from the enhanced greenhouse effect come from two sources: (i) trends detected in measured datasets, including the width of tree rings, sea-level records and measures of the rate of retreat of glaciers; and (ii) predictions based on sophisticated computer models that simulate the world's climate according to a variety of possible mitigation scenarios. The latter range from the best case, where there is a concerted and international political drive to minimise the temperature rise by the use and development of efficient technologies (e.g. switching to renewable energy and bioenergy, carbon capture and geological storage) to the worst case where very little is done and the expected outcome is close to the no-mitigation baseline scenario.

#### global distribution of climate change

Global warming so far has not been evenly distributed over the surface of the earth, and neither will it be in the future. Northern high latitudes are



**Figure 2.28 Annual land and ocean surface temperature anomalies and sea-level changes.** (a) Globally averaged combined annual land and ocean surface temperature anomalies from 1850 relative to the average over the period 1986–2005. Colours indicate different datasets. (b) Globally averaged annual sea-level changes from 1900 relative to the average over the period 1986–2005. Colours indicate different datasets that have been aligned to have the same value in 1993. Uncertainties are indicated by shading. *Source:* IPCC (2014).

expected to change more rapidly than the tropics, land areas will change more rapidly than the oceans, and small islands and coastal regions will be particularly prone to associated rises in sea level.

We have emphasised how the distributions of species are strongly influenced by temperature and water availability, and how many organisms are impacted by occasional extremes rather than by average conditions. Computer modelled projections imply that global climatic change will also bring greater variance in temperature, rainfall, hurricanes and so on. Hence, not only the predicted average climate changes, but also the increased frequency and severity of extremes, are certain to be accompanied by marked responses in the distribution of species and biomes.

Global temperatures have changed naturally in the past, as we have seen. We are currently approaching the end of one of the warming periods that started around 20 000 years ago, during which global temperatures have risen by about 8°C. The greenhouse effect adds to global warming at a time when temperatures are

can the biota keep up with the pace?

already higher than they have been for 400 000 years. Buried pollen provides evidence that North American forest boundaries have migrated north at rates of 100–500 m year<sup>-1</sup> since the last ice age. However, this rate of advance has not been fast enough to keep pace with postglacial warming. The rate of warming forecast to result from the greenhouse effect is 50–100 times faster than postglacial warming. Thus, of all the types of environmental pollution caused by human activities, none may have such profound effects as global warming. We must expect latitudinal and altitudinal changes to species' distributions and widespread extinctions as floras and faunas fail

to track and keep up with the rate of change in global temperatures. What is more, large tracts of land over which vegetation might advance and retreat have been fragmented in the process of civilisation, putting major barriers in the way of vegetational advance. It will be very surprising if many species do not get lost on the journey.

The ecological implications of greenhouse gas emissions are profound indeed for the spread of pest species, for future conservation and restoration management, and for the production of wild fisheries, agriculture and aquaculture. These topics will crop up throughout the book, but especially in its final chapter.





## Chapter 3

# Resources

### 3.1 Introduction

According to Tilman (1982), all things consumed by an organism are resources for it. But consumed does not simply mean 'eaten'. Bees and squirrels do not eat holes, but a hole that is occupied is no longer available to another bee or squirrel. Similarly, females that have already mated may be unavailable to other mates. All these things have been consumed in the sense that their stock or supply can be reduced by the activities of the organisms concerned.

#### autotrophs and heterotrophs

There is a fundamental distinction between *autotrophic* and *heterotrophic* organisms. Autotrophs assimilate simple inorganic resources into packages of organic molecules (proteins, carbohydrates, etc.). These become the resources for the heterotrophs (decomposers, parasites, predators and grazers), which take part in a chain of events in which each consumer of a resource becomes, in turn, a resource for another consumer. At each link in this food chain, the most obvious distinction is between *saprotrophs* and *predators*. Saprotrophs – bacteria, fungi and detritivorous animals (see Chapter 11) – use other organisms as food but only after they have died, or they consume another organism's waste or secretory products. Predators, defined broadly, feed on other living organisms, or parts of other living organisms (see Section 3.7).

#### photoautotrophs and chemoautotrophs

Autotrophs may themselves be divided into *photoautotrophs* and *chemoautotrophs*. The photoautotrophs – green plants and algae, and

photosynthetic protists and bacteria – utilise solar radiation, carbon dioxide ( $\text{CO}_2$ ), water and mineral nutrients as resources. Through photosynthesis, they use the radiation as a source of energy to reduce  $\text{CO}_2$  to obtain the organic compounds and energy that they need for growth and reproduction. Directly or indirectly, photosynthesis is the source of all energy in terrestrial and most aquatic ecosystems. Its evolution has led to the current 21% levels of oxygen in the atmosphere, driving down the levels of  $\text{CO}_2$ . By contrast, chemoautotrophs – certain bacteria and archaea – use chemical energy from the oxidation of inorganic substances such as hydrogen sulphide, elemental sulphur, ferrous iron or ammonia to reduce  $\text{CO}_2$  and so obtain the organic compounds and energy that they need. They typically live in 'extreme' environments such as hot springs and deep-sea vents.

For both autotrophs and heterotrophs, resources, once consumed, are no longer available to another consumer. This has the important consequence that organisms may *compete* with each other to capture a share of a limited resource – a topic to which we turn in Chapter 5.

In this chapter we start (Sections 3.2–3.6) with the resources that fuel the growth of individual plants, and so, collectively, determine the primary productivity of whole areas of land or volumes of water: the rate, per unit area or volume, at which plants produce biomass. Broad-scale patterns of primary productivity are examined in Chapter 20. Relatively little space in this chapter (Section 3.7) is given to food as a resource for animals, simply because a series of later chapters (Chapters 9–13) is

devoted to the ecology of predators, grazers, parasites and saprotrophs (the consumers and decomposers of dead organisms). This chapter then closes with sections on two important topics, drawing on material from the present chapter and the last – one (Section 3.8) on the ecological niche and resource classification, and a second (Section 3.9) on a so-called metabolic theory of ecology.

### 3.2 Radiation

Solar radiation is the only source of energy that can be used in metabolic activities by green plants and algae. It comes to the plant as a flux of radiation from the sun, either directly, or having been diffused to a greater or lesser extent by the atmosphere, or after being reflected or transmitted by other objects. The direct fraction is highest at tropical latitudes north and south of the equator, since cloud cover is typically high at the equator itself (Figure 3.1). Moreover, for much of the year in temperate climates, and for the whole of the year in arid climates, the leaf canopy in terrestrial communities does not cover the land surface, so that most of the incident radiation falls on bare branches or bare ground.

#### the fate of radiation

When a plant intercepts radiant energy it may be reflected (with its wavelength unchanged), transmitted

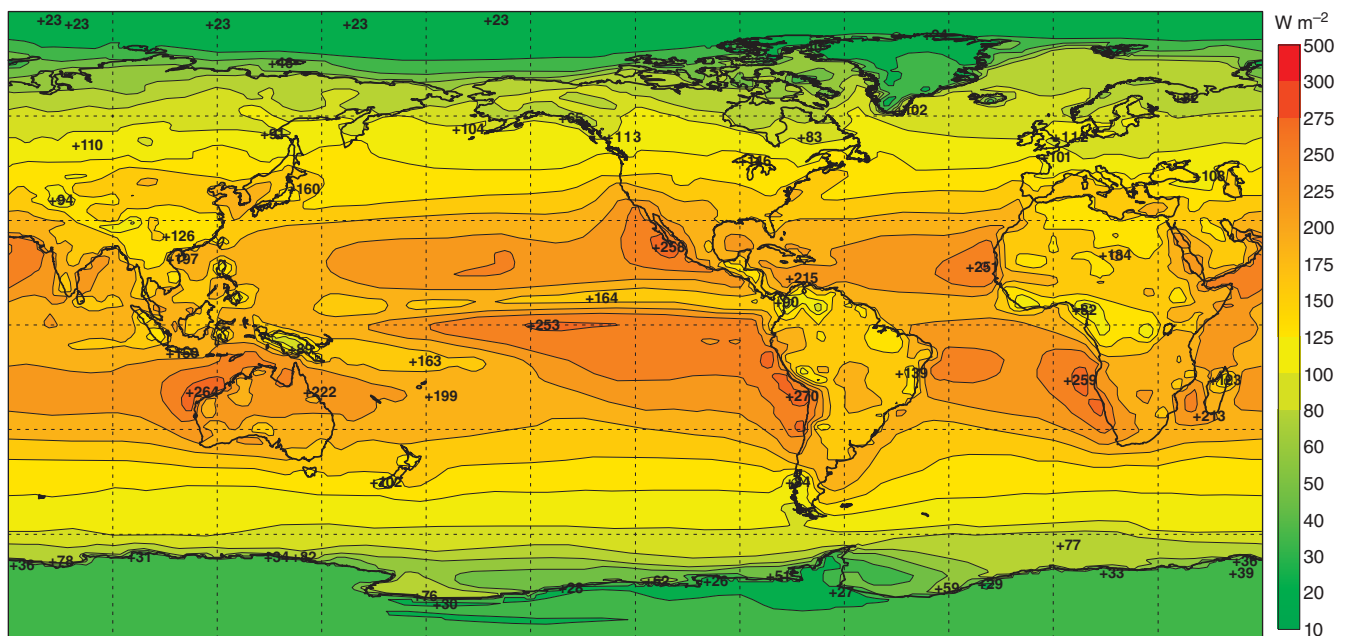
(after some wavebands have been filtered out) or absorbed. Part of the fraction that is absorbed may raise the plant's temperature and be reradiated at much longer wavelengths. In terrestrial plants, part may contribute latent heat of evaporation of water and so power the transpiration stream. Something like 80% may reach the chloroplasts and drive the process of photosynthesis, but of this, only a small proportion may end up in the plant's organic molecules, because there is insufficient capacity in carbon metabolism to use all the energy absorbed. Again, the remainder is dissipated as heat.

Radiant energy is converted during photosynthesis into energy-rich chemical compounds of carbon, which will subsequently be broken down in respiration, either by the plant itself or by organisms that consume it. But unless the radiation is captured and chemically fixed at the instant it falls on the leaf, it is irretrievably lost for photosynthesis. Radiant energy that has been fixed in photosynthesis passes just once through the world. This is in complete contrast to an atom of nitrogen or carbon or a molecule of water that may cycle repeatedly through endless generations of organisms.

Solar radiation is a resource continuum: a spectrum of different wavelengths. But the photosynthetic apparatus is able to gain access to energy in only a restricted band of this spectrum. All green plants depend on chlorophyll

radiant energy must be captured or is lost forever

photosynthetically active radiation



**Figure 3.1** Global map of the solar radiation absorbed annually in the earth–atmosphere system: from data obtained with a radiometer on the Nimbus 3 meteorological satellite. *Source:* After Laing & Evans (2011).

and other pigments for the photosynthetic fixation of carbon, and these pigments fix radiation in a waveband between roughly 400 and 700 nm. This is the band of *photosynthetically active radiation* (PAR). It corresponds broadly with the range of the spectrum visible to the human eye that we call 'light'. About 56% of the radiation incident on the earth's surface lies outside the PAR range and is thus unavailable as a resource for green plants. In other organisms, though, there are pigments, for example bacteriochlorophyll in bacteria, that operate in photosynthesis outside the PAR range of green plants. Our understanding of the breadth and importance of prokaryotic photosynthesis is increasing rapidly (Bryant & Frigaard, 2006).

Note that it is not the case simply that the rate of photosynthesis increases with the intensity of radiation. At high intensities, excess light can increase the production of potentially damaging intermediates in the photosynthetic process and *photoinhibition* of photosynthesis may occur (Li *et al.*, 2009), though what constitutes excess light varies considerably with the state of the plant. Under conditions of excess light, rapid changes in the photosynthetic membrane result in the excess absorbed light energy being harmlessly dissipated as heat, but the highest intensities of radiation may also lead to dangerous overheating. Radiation is an essential resource for plants, but they can have too much as well as too little.

Nonetheless, the highest efficiency of utilisation of radiation by green plants is 3–4.5%, obtained from cultured microalgae at low intensities of PAR. In tropical forests values fall within the range 1–3%, and in temperate forests 0.6–1.2%. The approximate efficiency of temperate crops is only about 0.6%. These can themselves be viewed in the context of a theoretical maximum efficiency of photosynthesis of 4.5–6% (Zhu *et al.*, 2010). It is on such paltry levels of efficiency that the energetics of all communities depend.

### 3.2.1 Variations in the intensity and quality of radiation

#### systematic variations in supply

One important reason why plants seldom achieve their full photosynthetic capacity is that the intensity of radiation varies continually (Figure 3.2), and the plant morphology and physiology that are optimal for photosynthesis at one intensity will be suboptimal at another. As with all resources, this supply of radiation can vary both systematically and unsystematically. Annual and diurnal rhythms are systematic variations in solar radiation (Figure 3.2a, b). The green plant experiences periods of famine and glut in its radiation resource

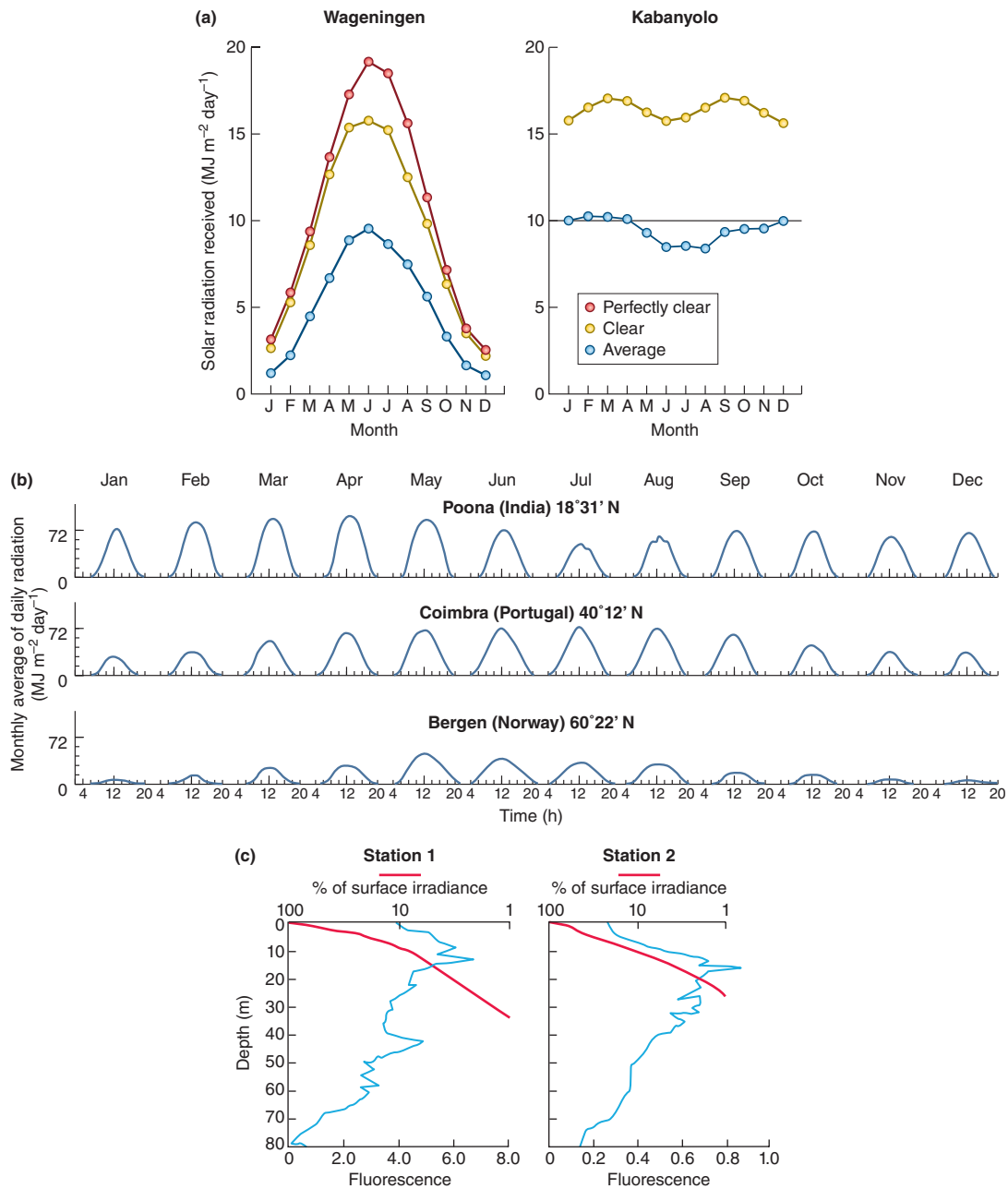
every 24 hours (except near the poles) and seasons of famine and glut every year (except in the tropics). In aquatic habitats, an additional systematic and predictable source of variation in radiation intensity is the reduction in intensity with depth in the water column, though the extent of this may vary greatly. For example, differences in water clarity mean that seagrasses may grow on solid substrates as much as 90 m below the surface in the relatively unproductive open ocean, whereas macrophytes in fresh waters rarely grow at depths below 10 m (Sorrell *et al.*, 2001), and often only at considerably shallower locations, in large part because of differences in concentrations of suspended particles and phytoplankton (Figure 3.2c).

Less systematic variations in the radiation environment of a leaf are caused by the nature and position of neighbouring leaves. Leaves in a canopy, by intercepting radiation, create a *resource-depletion zone* (RDZ) – in this case, a moving band of shadow over other leaves of the same plant, or of others. The composition of radiation that has passed through leaves in a canopy, or through a body of water, is also altered. Typically, it is depleted in the blue and (especially through water) the red parts of the spectrum – the most effective wavelengths for photosynthesis. Figure 3.3 shows an example for the variation with depth in a freshwater habitat.

#### shade: resource-depletion zones and spectral changes

The way in which organisms react to systematic, predictable patterns in the supply of a resource reflects both their present physiology and their past evolution. At a very broad scale, the seasonal shedding of leaves by deciduous trees in temperate regions in part reflects the annual rhythm in the intensity of radiation – they are shed when they are least useful. Amongst terrestrial species, plants that are characteristic of shaded habitats generally use radiation at low intensities more efficiently than sun species, but the reverse is true at high intensities (Figure 3.4). Part of the difference between them lies in the physiology of the leaves, but the morphology of the plants also influences the efficiency with which radiation is captured. The leaves of sun plants are commonly exposed at acute angles to the midday sun, spreading an incident beam of radiation over a larger leaf area and effectively reducing its intensity (Poulson & DeLucia, 1993). The leaves of sun plants are also usually superimposed into a multilayered canopy. In bright sunshine even the shaded leaves in lower layers may have positive rates of net photosynthesis. Shade plants adopt a different strategy, commonly having leaves held near to the horizontal and in a single-layered canopy.

#### sun and shade species

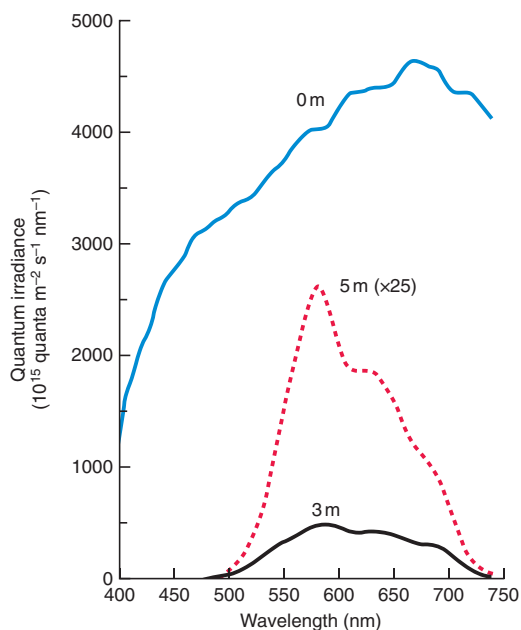


**Figure 3.2** Levels of solar radiation vary over time and space and with depth in water. (a) The daily totals of solar radiation received throughout the year at Wageningen (the Netherlands) and Kabanyolo (Uganda). (b) The monthly average of daily radiation recorded at Poona (India), Coimbra (Portugal) and Bergen (Norway). (c) The vertical distribution of algal abundance (measured as fluorescence in units of  $\text{mg chlorophyll } a \text{ m}^{-3}$ ) and of irradiance as a percentage of that at the surface, for two stations off the Arctic island of Svalbard. The decline in irradiance with water depth is apparent at both stations, but at Station 1, higher algal densities in the surface waters led to that decline being more rapid: 10% of surface irradiance at around 7 m compared with 12 m at Station 2. Source: (a, b) After de Wit (1965) and other sources. (c) After Meshram *et al.* (2017).

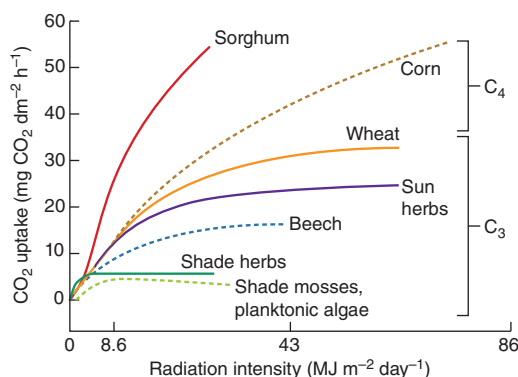
#### sun and shade leaves

Plants may also respond ‘tactically’ to the radiation environment in which they develop, producing ‘sun leaves’ and ‘shade leaves’ within the canopy of a single

plant. Sun leaves (and indeed, leaves on sun plants) are typically smaller, thicker, have more cells per unit area, denser veins, more densely packed chloroplasts and a greater dry weight per unit area of leaf. They are said to have a smaller



**Figure 3.3 The spectral distribution of radiation changes with depth** as shown here for Lake Burley Griffin, Australia. Note that photosynthetically active radiation lies broadly within the range 400–700 nm. *Source:* After Kirk (1994).



**Figure 3.4 The response of photosynthesis to radiation intensity in various plants at optimal temperatures and with a natural supply of CO<sub>2</sub>.** Note that corn and sorghum are C<sub>4</sub> plants and the remainder are C<sub>3</sub> (the terms are explained in Sections 3.3.1 and 3.3.2). *Source:* After Larcher (1980), and other sources.

*specific leaf area* (leaf area per unit leaf mass). Acclimation to shade typically involves increasing chlorophyll concentration and decreasing investment in the rest of the photosynthetic apparatus. This allows the leaf to maximise capture of light, but does not waste resource on a high photosynthetic capacity, which is not needed under shade conditions. In turn, this releases nitrogen

for use by the upper leaves. However, these tactical manoeuvres take time. It is impossible for the plant to change its form fast enough to track the changes in intensity of radiation between a cloudy and a clear day. It can, however, change its rate of photosynthesis extremely rapidly, reacting even to the passing of a fleck of sunlight.

In aquatic habitats, much of the variation between species is accounted for by differences in photosynthetic pigments, which contribute significantly to the precise wavelengths of radiation that can be utilised. Of the three types of pigment – chlorophylls, carotenoids and biliproteins – all photosynthetic plants contain the first two, but many algae also contain biliproteins; and within the chlorophylls, all higher plants have chlorophyll a and b, but many algae have only chlorophyll a and some have chlorophyll a and c. These different forms of chlorophyll all have slightly different absorption spectra, so that in combination, the plant or alga can trap more light. We see an example of variation in the nature of light with the concentration of dissolved organic matter in lake water, and the consequences of this for the photosynthetic microphytoplankton living there, in Figure 3.6. Of two lakes in north-western Patagonia, Argentina, one, Lake Morenito, had lower concentrations of dissolved organic matter, leading to ‘greener’ light (Figure 3.6a) and hence to higher densities of cryptophyte algae (Figure 3.6b). Cryptophytes have a unique combination of pigments – chlorophylls a and c, but also the carotenoid alloxanthin and one of two biliproteins – allowing them to function effectively in that range. The other, Lake Escondido, with yellower light, had a microphytoplankton community dominated by chrysophytes (‘golden algae’), which lack these biliproteins.

### 3.2.2 Net photosynthesis

Photosynthesis is measured as CO<sub>2</sub> uptake, which is roughly proportional to the amount of organic matter formed by the plant or alga, and in turn to the energy captured in that organic matter. However, it is often more important to consider, and very much easier to measure, the net gain. Net photosynthesis is the increase (or decrease) in dry matter that results from the difference between gross photosynthesis and the contemporary losses due to respiration. The *light compensation point* is the intensity of PAR at which the gain from gross photosynthesis exactly balances these respiratory losses. Hence, net photosynthesis increases with the intensity of PAR, and is negative below the

pigment variation in aquatic species

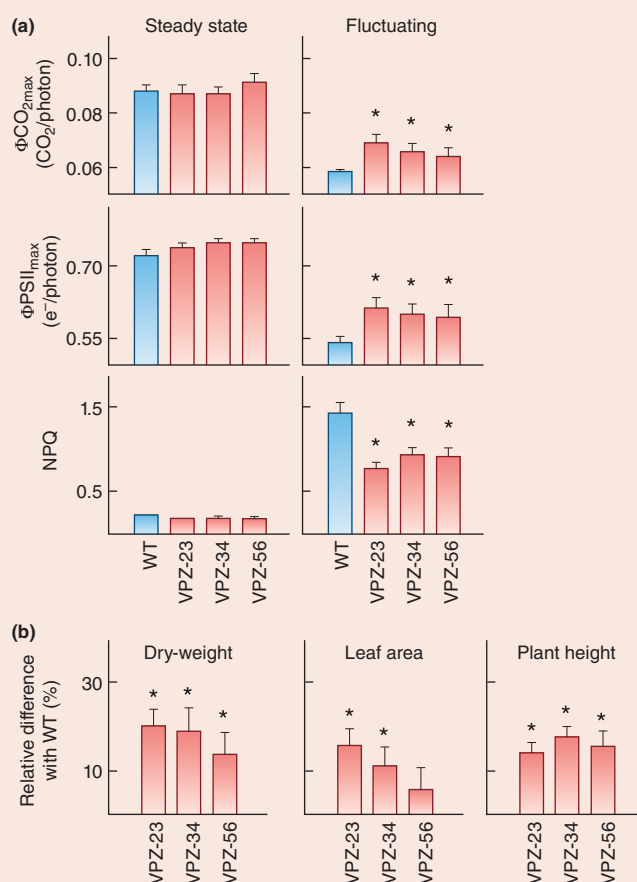
the compensation point



### APPLICATION 3.1 Bioengineering crops for accelerated recovery from photoprotection

The responses of plants to changes in the quantity of light include the induction at high light intensities of photoprotective mechanisms that prevent the photosynthetic machinery from getting ‘overexcited’ and risking the generation of damaging oxidising radicals, instead dissipating excess light as heat. However, when intensities return to harmless levels, there is typically a delay before these protective mechanisms are fully switched off, such that rates of photosynthesis at these times are lower than they might otherwise be. Some calculations suggest that this could cost field crops as much as 20% of their potential yield (Kromdijk *et al.*, 2016). It would therefore clearly be valuable if that switching off of the protective mechanisms could be speeded up. Bioengineering (the insertion of new or altered genes into a plant) offers the opportunity of applying our understanding of the physiology of photoprotection to effect such an accelerated response. Results are shown in Figure 3.5 for a study in which variants of three different genes known to be instrumental in the operation of the mechanism were selected for increased expression levels, following a screen of seedlings of the model plant *Arabidopsis thaliana*. These variants were then inserted into tobacco plants, *Nicotiana tabacum*, itself used as a model for crop plants in general, since the photoprotective mechanism being altered is common to all plants.

When the supply of light was constant, all three types of bioengineered plant behaved similarly to wild type plants in terms of photosynthetic efficiency and the harmless dissipation (‘quenching’) of excess light as heat (Figure 3.5a, left). But in the field, most leaves experience continually fluctuating light due to clouds and intermittent shading from the leaves above. It is notable, therefore, that in the fluctuating regime, photosynthetic efficiency was higher in the bioengineered plants than the wild types, and their overall level of quenching was lower, because it was compressed into a shorter period (Figure 3.5a, right). As a result, the bioengineered plants grew much better than the wild types (Figure 3.5b). Bioengineering of any sort must always be applied with caution, but these results do hold out the prospect of significant increases in yield for a wide variety of crops, since this process is common to all land plants.



**Figure 3.5 Bioengineering of photoprotection can improve crop plant performance.** (a) To the left, a comparison for two measures of photosynthetic efficiency (of CO<sub>2</sub> uptake and of electron transport) and of the rate of harmlessly dissipating excess light as heat – the rate of ‘quenching’ of chlorophyll fluorescence (NPQ) – at steady levels of light, between wild type (WT) *Arabidopsis* plants and three strains bioengineered to switch off photoprotection more rapidly. There were no differences. To the right, a similar comparison but with fluctuating light levels. The bioengineered strains were all significantly more efficient in photosynthesis than the wild type because fluorescence was dampened down more rapidly. (b) The consequences for the bioengineered plants in terms of weight, leaf area and plant height, following 22 days of growth in the field. All strains grew better. In both (a) and (b), bars are SEs and \* indicates a significant difference between bioengineered lines and the wild type ( $P < 0.05$ )

Source: After Kromdijk *et al.* (2016).