MICHAEL BEGON

COLIN R. TOWNSEND

ECOLOGY

FROM INDIVIDUALS TO ECOSYSTEMS

FIFTH EDITION

WILEY Blackwell

ECOLOGY

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From Individuals to Ecosystems

MICHAEL BEGON
University of Liverpool
Liverpool, UK

COLIN R. TOWNSEND
University of Otago
Dunedin, New Zealand

FIFTH EDITION

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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 twosome 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.

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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

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 '*ad*aptation' 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.

evolution by natural selection

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.

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.

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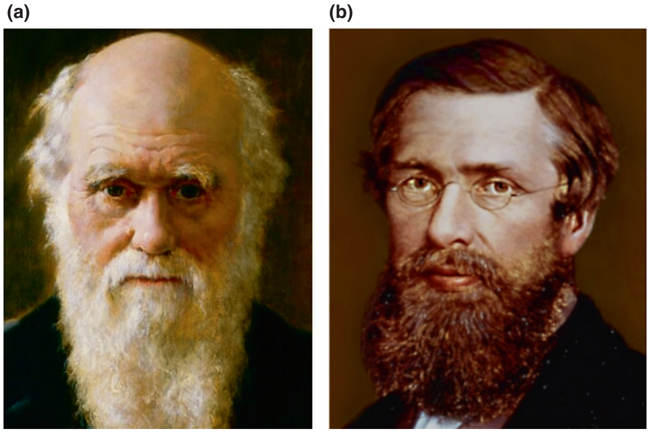


Figure 1.1 The fathers of evolution. (a) Charles Darwin. Detail from painting by John Collier 1883 (National Portrait Gallery RPG 1024). (b) Alfred Russell Wallace. Detail from photograph by Thomas Sims 1869, colourised by Paul Edwards, copyright G. W. Beccaloni.

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.

evolved perfection? no

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.

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.

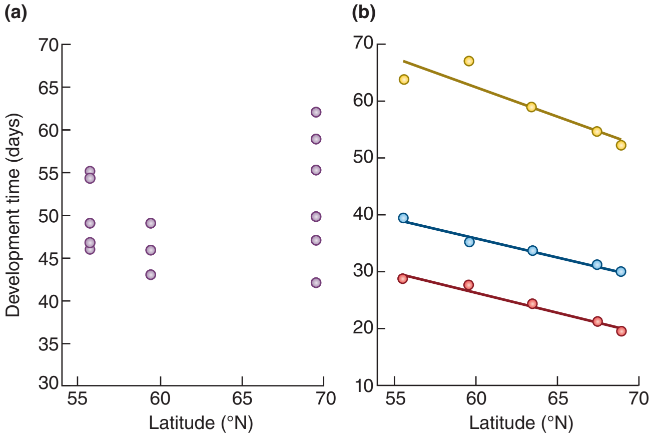


Figure 1.2 At a given temperature, tadpoles from higher latitudes developed faster than those from lower latitudes. (a) Tadpoles from ponds in two areas of Sweden, in the south, and from Finland, in the north, showed variation in development times but no consistent trend with latitude. (b) When tadpoles 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).

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 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.

the balance between local adaptation and hybridisation

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 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).

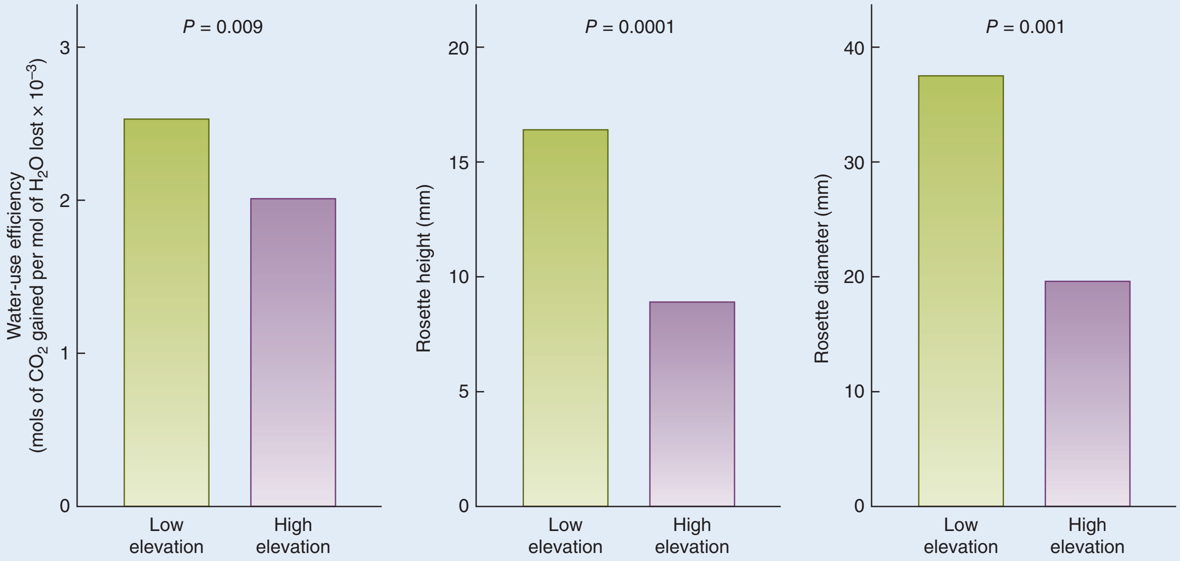


Figure 1.3 Local adaptation of rare sapphire rockcress plants. When plants of the rare sapphire rockcress from low-elevation (drought-prone) and high-elevation sites were grown together in a common garden, there was local adaptation: those from the low-elevation site had significantly better water-use 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

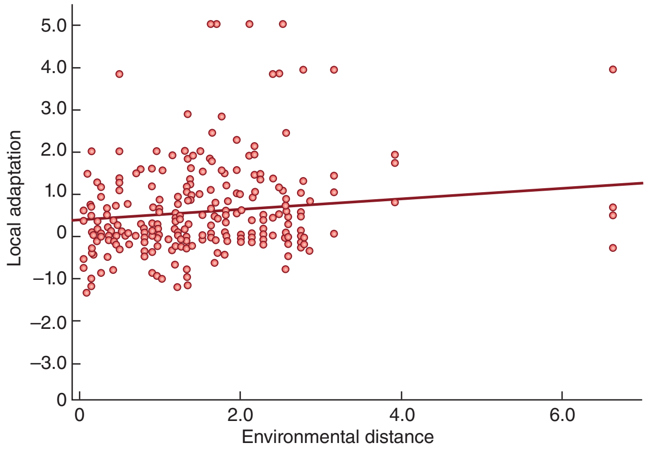


Figure 1.4 Meta-analyses reveal generalities about local adaptation. Regression of local adaptation on environmental distance between sites in a meta-analysis of reciprocal transplant experiments ($P = 0.003$). Local adaptation is the difference in relative fitness between a native population and a non-native 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.

the maintenance of polymorphisms

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

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

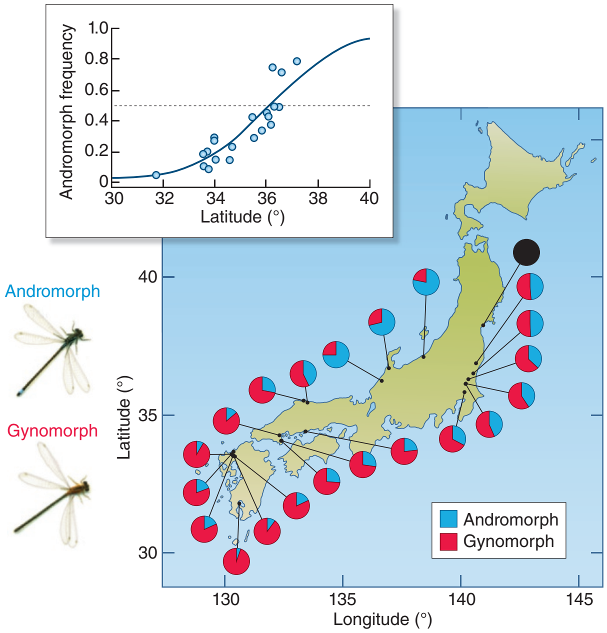


Figure 1.5 The frequency of andromorphs of local damselfly populations in Japan increases with latitude. The inset shows the logistic regression with latitude ($t = 8.15$, df = 21, $P < 0.001$), excluding the northernmost population (solid black plot). This population had been recently established in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

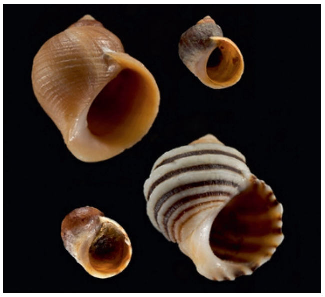


Figure 1.6 Contrasting ecotypes of the periwinkle *Littorina saxatilis* from Sweden and Spain. Swedish crab ecotype (top left) and wave ecotype (top right), and Spanish wave ecotype (bottom left) and crab ecotype (bottom right). *Source*: From Johannesson (2015).

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 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.

no clear distinction between local ecotypes and a polymorphism

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*. 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.

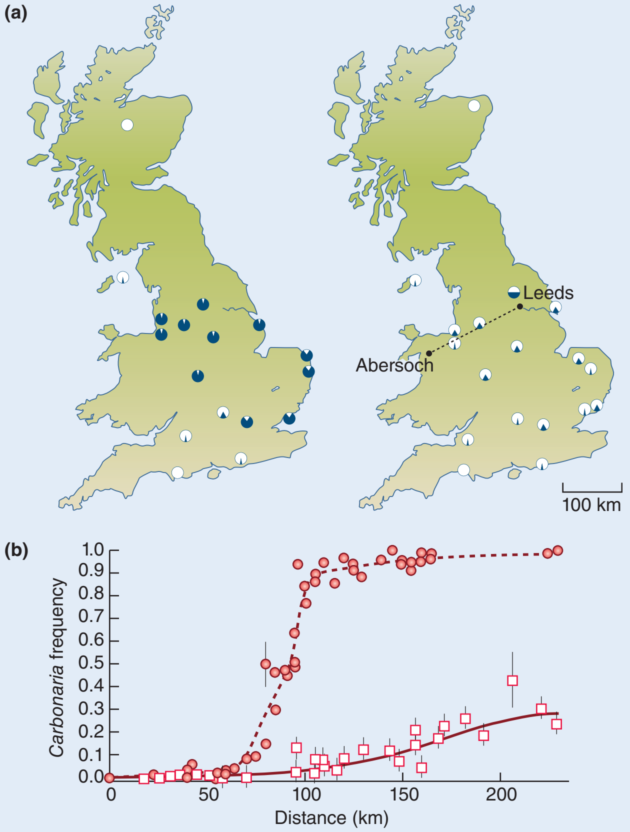


Figure 1.7 The frequency of melanic forms of the peppered moth in western Britain was high during the height of pollution from the burning of coal, but that frequency declined after the passing of smoke-free legislation. (a) The distribution of melanic (*carbonaria*) and pale forms (blue and white portions 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).

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 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).

reversing man-made selection pressures

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.

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

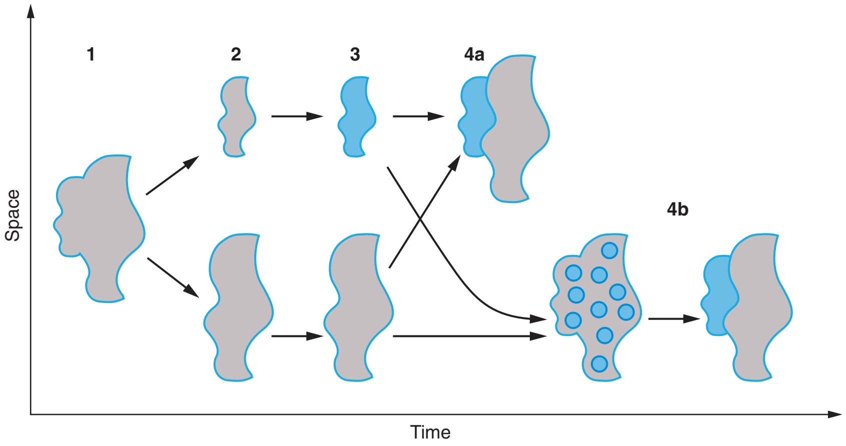
Cynics have said, with some truth, that a species is what a competent taxonomist regards as a species. On the other hand, back in the 1930s two American biologists, Mayr and Dobzhansky, proposed an empirical test that could be used to decide whether two populations were part of the same species or of 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

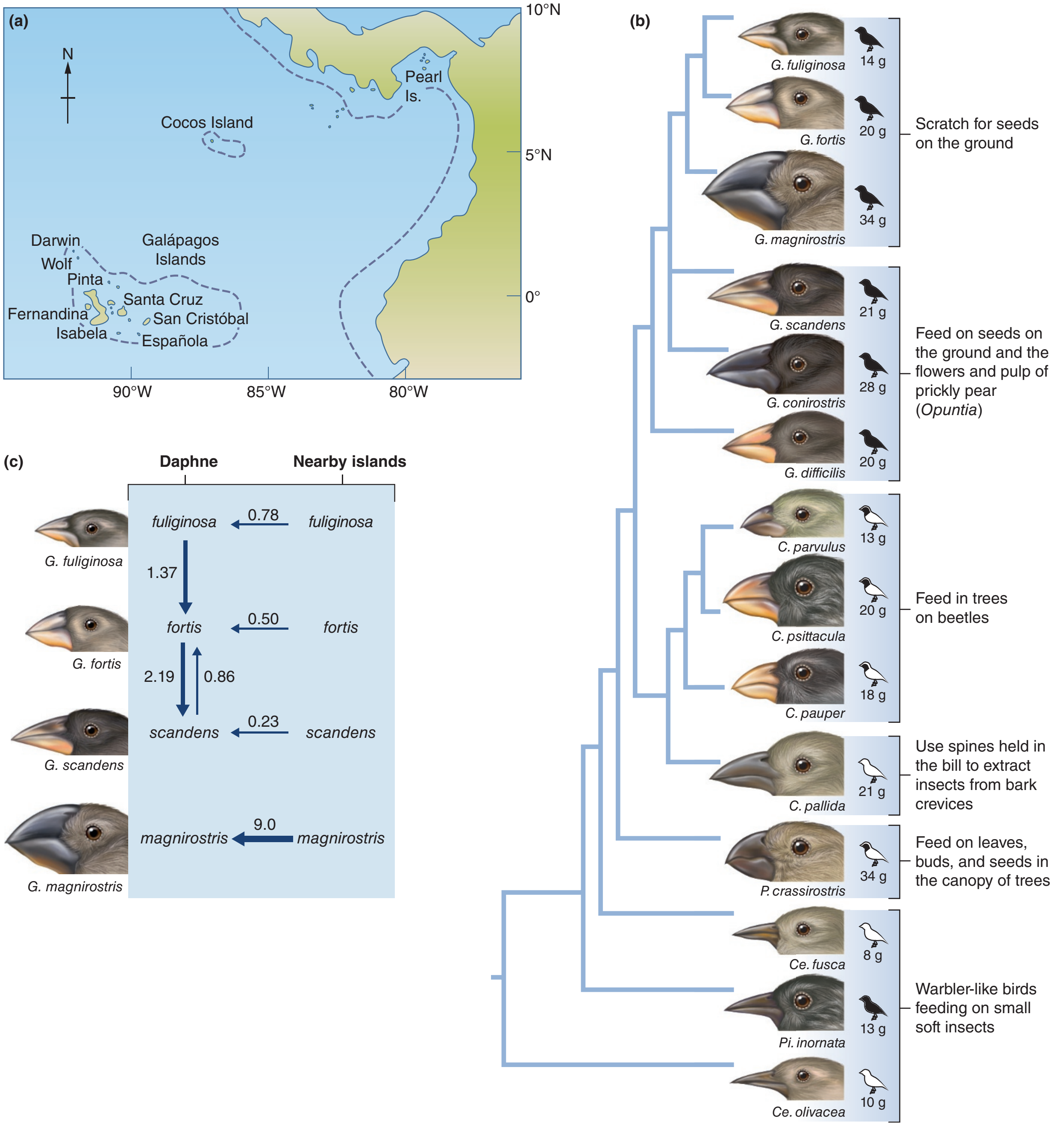

(a)
N
10°N
5°N
0°
Cocos Island
Pearl Is.
Darwin
Wolf
Galápagos Islands
Pinta
Santa Cruz
Fernandina
San Cristóbal
Isabela
Española
90°W
85°W
80°W
(b)
G. fuliginosa
14 g
G. fortis
20 g
G. magnirostris
34 g
Scratch for seeds on the ground
G. scandens
21 g
G. conirostris
28 g
G. difficilis
20 g
Feed on seeds on the ground and the flowers and pulp of prickly pear (Opuntia)
C. parvulus
13 g
C. psittacula
20 g
C. pauper
18 g
Feed in trees on beetles
C. pallida
21 g
Use spines held in the bill to extract insects from bark crevices
P. crassirostris
34 g
Feed on leaves, buds, and seeds in the canopy of trees
Ce. fusca
8 g
Pi. inornata
13 g
Ce. olivacea
10 g
Warbler-like birds feeding on small soft insects
(c)
Daphne
Nearby islands
G. fuliginosa
fuliginosa
0.78
fuliginosa
1.37
G. fortis
fortis
0.50
fortis
2.19
0.86
G. scandens
scandens
0.23
scandens
G. magnirostris
magnirostris
9.0
magnirostris

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. fulginosa* 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.

allopatric speciation without secondary contact

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

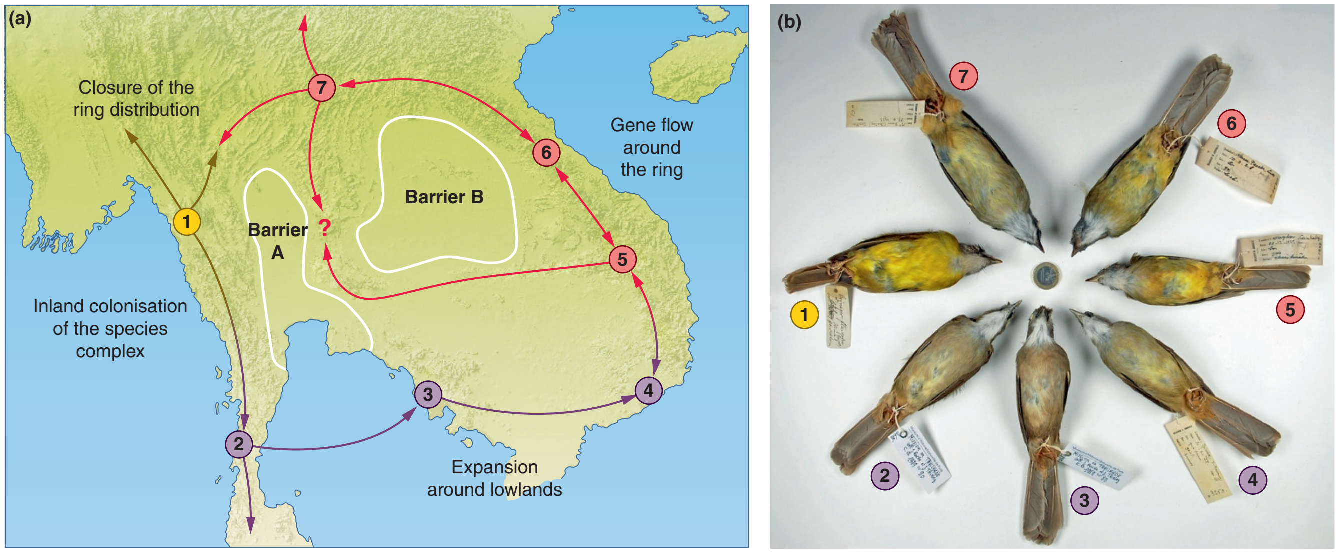

(a)
Closure of the ring distribution
Gene flow around the ring
Barrier A
Barrier B
?
Inland colonisation of the species complex
Expansion around lowlands
1
2
3
4
5
6
7
(b)
7
6
1
5
2
3
4

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

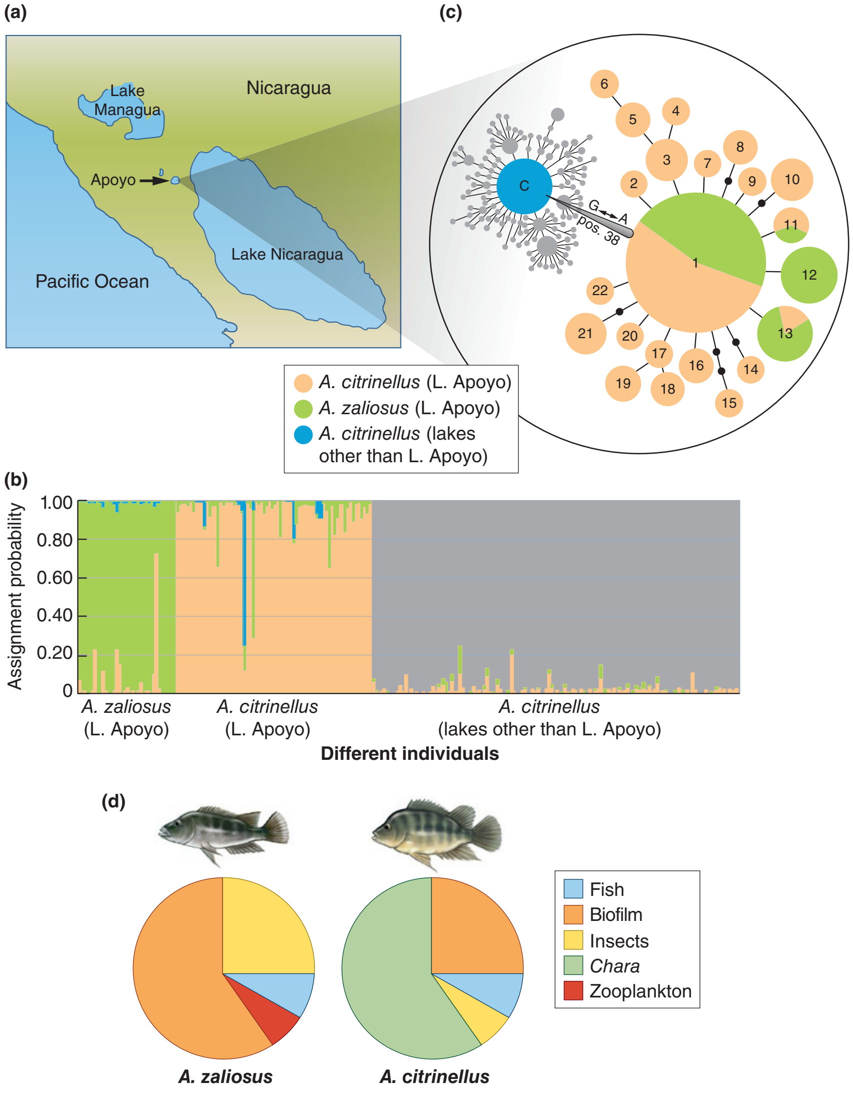


Figure 1.11 Sympatric speciation in the cichlid fish *Amphilophus citrinellus* and *A. zaliosus*. (a) The location of Lake Apoyo in Nicaragua. (b) The assignment of individuals to populations based on variation at 10 microsatellite DNA loci: *A. zaliosus* (green) and *A. citrinellus* (orange) from Lake 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.

sympatric speciation – divergence with gene flow or microallopatric speciation?

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 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). Papadopulos *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.

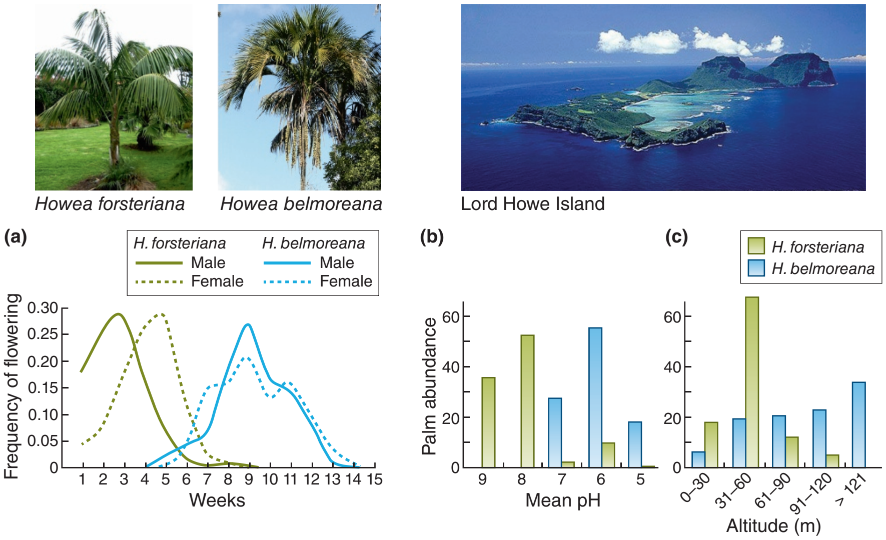


Figure 1.12 Sympatric speciation in *Howea* palms. Two species of *Howea* palm on the tiny and isolated Lord Howe Island off the coast of Australia. *Howea forsteriana* has straight leaves with drooping leaflets, while *H. belmoreana* has recurved leaves with ascending leaflets. (*H. forsteriana* is 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).