



Species

*'That which we call a rose
By any other name would smell as sweet.'*

William Shakespeare: *Romeo and Juliet*

CHAPTER OUTLINE

The binomial system of classification.

- Phylogeny of the major groups of organisms.
- The biological species concept.
- Defining species using morphological, biochemical, and genetic techniques.
- Ecological niche—intraspecific and interspecific competition.
- Types of speciation.
- The potential risks and benefits of genetically modified organisms.

← Mirror orchid (*Ophrys speculum*).

Classification comes naturally to us. We try to compare the unfamiliar with objects or events which are already part of our experience. Recognizing similarities allows us to place something into a category and assume it shares the properties of that group. Establishing categories and describing their characteristic properties is central to the way in which we learn.

This is a good strategy. It means that we can make predictions and perhaps anticipate situations that we have never encountered before. Indeed, pattern recognition is common to all animals with sufficient neural machinery to store the information. Identifying key patterns is so important to the behaviour of many higher animals that some plants have developed means of exploiting it. The male bee looking for a mate is readily fooled by the orchid displaying signals associated with the category ‘female’. The flower may have no wings, no legs, and no genitalia, but it does have what a male looks for in a female bee, or at least enough for him to change his behaviour.

One difference between us and the animals is that we use our language to name the categories. Names are labels that imply the properties of a category, a term that serves to summarize a complex description. The general term ‘dog’ implies all that we take to be characteristic of this category, from being hairy with a leg at each corner, to the fine detail that distinguishes dog from cat. Even then we are sometimes surprised to learn that our category ‘domestic dogs’ contains everything from a chihuahua to a great dane.

The danger, as Romeo reminds us, is to mistake the name for the category. We need to draw a distinction between the agreed term for an object, its

name, and its essential properties. Sometimes our distinctions are not a true reflection of the real world. At other times, we are not sufficiently discerning to pick out the fine detail of nature. This is certainly true of biology, where we have had to repeatedly refine our ideas about the variety and diversity of life.

All sciences begin by creating categories and classifications to help us understand the relations between their important elements. This is invariably a hierarchy, ordered into levels of increasing similarity. In biology this is termed **systematics** and it groups species according to their shared properties. In the process, biologists can pick out the evolutionary lines linking species, more formally called their **phylogenetic relationships**.

In this chapter, we introduce systematics and also the conventions used in describing, naming, and classifying organisms—**taxonomy**. The basic unit in biology is the species, defined earlier as individuals sharing a common gene pool and able to produce viable fertile offspring (Box 2). Although this is a good functional definition, the boundaries between species are often poorly defined, sometimes because we are witnessing the process of speciation in action, sometimes because we are unable to measure the distinguishing traits, or at other times because no real distinctions exist. Here we consider how new species arise and become fitted to their place in an ecosystem by their interactions with other individuals and other species, and with their abiotic environment. We finish by considering the ecological implications of our capacity to change the genotype of species and the variety of genetically modified organisms we have created.

2.1 What's in a name?

The closest we get to a universal language is in the sciences. Even if nations do not use the same names or even the same alphabet we invariably share the same symbols. Chemists speak to each other using one- or two-letter symbols as shorthand for the elements of the periodic table. Biologists have the con-

vention of referring to species with two Latin names, the **binomial system** (Box 2.1). This was developed by Linnaeus in the eighteenth century, who streamlined earlier systems that used several names.

The binomial system establishes a unique combination of two names for each species. When Europeans

BOX
2.1

From the Keys to the Kingdom to the Tree of Life

Modern classification is a hierarchical system based on Aristotle's designation of the Kingdom as the highest category in which living organisms can be grouped. This was further developed into the binomial system by the Swedish botanist Carl Linne, who latinized his own name to Carolus Linneaus (Figure 2.1). His system consisted of seven nested categories ending with the species as the fundamental unit:

- Kingdom (originally either plant or animal)
- Phylum (suffix –phyta for plants)
- Class (suffix –phyceae for plants)
- Order (suffix –ales for plants)
- Family (suffix –aceae for plants and –idae for animals)
- Genus
- Species



Figure 2.1 Carolus Linnaeus (1707–1778).

The hierarchy still works well today, but biologists have found it necessary to extend it considerably, dividing and subdividing these main categories. Nevertheless, it retains an important property—organisms grouped together at the lowest levels have more in common than those grouped further up. Plants or animals belonging to the same genus or family share more characters than others in the same order or class. In effect, the hierarchy helps us pick out the evolutionary history of a species.

By the nineteenth century problems were starting to emerge with the Two-Kingdom system of plants and animals. The development of the microscope revealed an unexpected world of micro-organisms. These clearly did not belong in either grouping and in 1866 Ernst Haeckel proposed a third kingdom, the **Protista**, to include the protozoa, primitive algae, and fungi. These groups were lumped together with the prokaryotic bacteria in what was little more than a biological dustbin for groups that did not fit anywhere else. Eventually this was divided to produce a fourth Kingdom, the **Monera**, containing the bacteria and the cyanobacteria (also known as the blue-green algae). In 1969, Robert H. Whittaker separated the Fungi from the Protista into a fifth kingdom of their own.

Even so, the Five-Kingdom System had its problems. Disparate organisms were sharing the same grouping, all kingdoms had equal status, and the fundamental differences between prokaryotes and eukaryotes (readily distinguished by the organization of their chromosomes) were ignored. Lynn Margulis attempted to address the problem by introducing the concept of **Superkingdoms**, the **Prokaryota** and **Eukaryota**. More recently, advances in genetic analysis have designated three **Domains—the Bacteria, Archaea and Eukaryota** (Figure 2.2)—to more closely represent the evolutionary links between the major groups of organisms.

There are still problems because some life forms still do not fit readily into any group. Viruses are so varied and so different from anything else that Margulis once half-joked that they were more closely related to their hosts than to each other. To this day, viruses remain outside mainstream classification as little more than replicating molecules that hijack the replication machinery of living cells.

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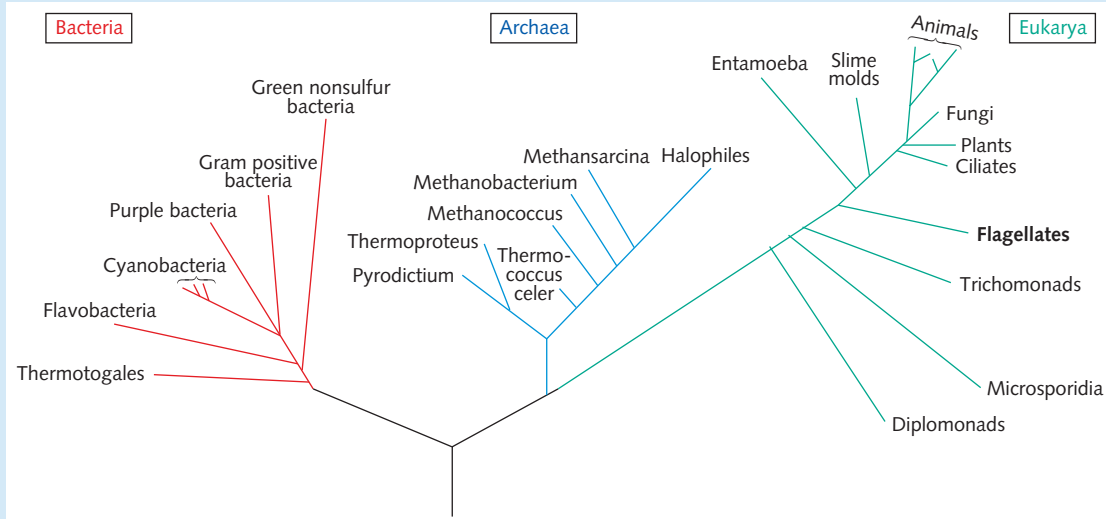


Figure 2.2 The three domains. The comparison of genetic sequences of ribosomal RNA has made it possible to cluster groups of organisms into three domains—Bacteria, Archaea, and Eukaryota—according to their degree of evolutionary relatedness.

Taxonomists have a very different problem with the lichens. Although these may look like individual organisms, they are actually a close association of algal and fungal cells. Lichens are the only true naturally occurring **chimeras**—organisms which have more than one genotype (Section 4.2).

There are relatively few algal species involved in these associations and, in some cases, several different algae occur in a single lichen. However, each ‘species’ of lichen has its own particular fungal species and so they are therefore classified on the basis of their fungal partners.

and Americans use the term ‘blackbird’ they are invariably referring to different species with different Latin names. *Turdus merula* is the European blackbird and this belongs in a different genus from North American blackbirds, such as the red-winged blackbird (*Agelaius phoeniceus*). The same is true for plants: the British bluebell is *Hyacinthoides non-scripta*, of the lily family, whilst a bluebell in California is *Phacelia tanacetifolia* (Figure 2.3), from an unrelated family, the Hydrophyllaceae.

- Notice the detail of using a Latin (or scientific) name.
- Each consists of two names (hence the **binomial** system).
- The first name is the **generic name**, the name of the genus (this always begins with a capital letter).
- The second name is the **specific name**, the name of the species (this always begins with a lower-case letter).
- A scientific name is always printed in italics or, if handwritten, underlined.
- It is the combination of the generic and specific names that is unique. So two species may belong to the same genus, and therefore share the same generic name, but will have different specific names; for example, *Mustela erminea*—the stoat—and *Mustela nivalis*—the weasel. Two species belonging to different genera may share the same specific name; for example, *Primula vulgaris*—the primrose—and *Calluna vulgaris*—heather.
- After first being cited in full, the name may subsequently be abbreviated if there is no possibility of confusion; for example, *P. vulgaris* and *C. vulgaris*.





 		Classification	 	
European Blackbird	American Blackbird	Category	European Bluebell	Californian Bluebell
Animalia (animals)	Animalia (animals)	Kingdom	Plantae (plants)	Plantae (plants)
Chordata (chordates)	Chordata (chordates)	Phylum	Trachaeophyta (vascular plants)	Trachaeophyta (vascular plants)
Aves (birds)	Aves (birds)	Class	Angiospermae (flowering plants)	Angiospermae (flowering plants)
Passeriformes (songbirds)	Passeriformes (songbirds)	Order	Liliales (lilies)	Polemoniales (Jacob's ladders)
Turdidae (thrushes)	Icteridae (icterids)	Family	Liliaceae (lily family)	Hydrophyllaceae (phacelia family)
<i>Turdus merula</i>	<i>Agelaius phoeniceus</i>	Genus Species	<i>Hyacinthoides non-scripta</i>	<i>Phacelia tanacetifolia</i>

Figure 2.3 The full hierarchical classification of European and North American blackbirds and bluebells.

- Often the name is descriptive, even for those with just a little knowledge of Latin or Greek. For example, ‘vulgaris’ means ‘common’.

Sometimes the citation also gives the name of the **authority** immediately afterwards; for example, *Cantareus aspersus* (Müller)—the garden snail. The authority is the first person to have described that species in its currently accepted classification and named it. Scientific papers usually cite the authority when the Latin name is used for the first time. There are strict rules about naming and giving authorities for species, with well-known authors having their names abbreviated. In *Homo sapiens* L., here the L refers to Linnaeus, the authority behind our own species.

These rigorous rules make the binomial system universal. Species names are agreed by an international committee which operates the International Codes of Biological Nomenclature. Animals are dealt with by the International Code of Zoological

Nomenclature (ICZN), which recognizes organisms down to sub-species level, whilst the International Code of Botanical Nomenclature (ICBN) goes further, recognizing sub-species, varieties, sub-varieties, forms and sub-forms (Box 2.1). The classification of all groups is under constant review, not only as new species are found, but also as we learn more about their evolutionary history.

Even within a well-defined species there can be considerable variation between individuals, and this can make it difficult to decide where one species ends and another begins. We can observe this simply by looking around a room of people, noting the range of sizes and shapes. For many species, much of the variation we observe will be incidental, the phenotypic variation acquired during the life of the individual and which could not be passed on to the next generation. Our problem is to decide which characters are part of the genome, characters that can be inherited, and whether this variation could be important for the species' future.

2.2 Origins of the major groups

In its original form, the binomial classification system used mainly morphological characters to classify around 10 000 plants and animals. Grouping species into this hierarchy, according to their shared characters, made it obvious which species were closely related. Darwin and other naturalists recognized that this gives us important clues to the evolutionary history or **phylogeny** of a species, helping us to pick out the ancestry of multicellular organisms. Originally, the living world was divided between two kingdoms—the plants and animals. Following the improvements in microscopy, this became the Five-Kingdom system with the addition of the bacteria, protista, and fungi (Box 2.1). The advent of the electron microscope revealed small cell organelles and membranes, but these are universal features of cells found across the major groups, so the Five Kingdoms remained the standard classification.

In the last quarter of the twentieth century, other ways of distinguishing life developed and new techniques in molecular biology allowed us to start counting differences in the sequence of genes or the structures of key proteins and nucleic acids. Carl Woese and other molecular biologists have used such differences to reformulate the whole classification of life using the single, albeit ancient, molecule of ribosomal RNA (Figure 1.11). Part of the genetic sequence of rRNA has been used to divide all organisms into just three major domains—**bacteria**, **archaea**, and **eukaryota**.

The three domains help resolve a number of problems arising from the Five-Kingdom system. Three of the original kingdoms (Animalia, Plantae, and

Fungi) are now united within the Eukaryota, joining a number of other groups including the protista (single-celled algae and fungi, amongst others). All eukaryotes have their DNA wound around proteins to form linear chromosomes that are held within a nuclear membrane (Figure 1.10). The Monerans, organisms without a distinct nucleus, are now divided between the Bacteria and Archaea, a division that recognizes the latter's shared ancestry with the eukaryotes and a physiology adapted to extreme environments (Box 6.1). However, both bacteria and **archaeobacteria** share prokaryotic features, principally a simple looped chromosome with no nuclear membrane.

A key feature of eukaryotic cells is the presence of membrane-bound organelles. In her **endosymbiont theory**, Lynn Margulis argues that organelles such as chloroplasts and mitochondria were derived from prokaryotic cells that combined symbiotically with a host cell. This would explain why both chloroplasts and mitochondria have their own DNA and are similar in size and shape to photosynthetic and chemosynthetic bacteria. However, chloroplasts and mitochondria are synthesized using the DNA of the eukaryotic nucleus, so their code had to somehow find its way into the host chromosomes. Although this is a complication, there are known mechanisms by which this could happen. The **eukaryote** cell is thought to have arisen from a series of cellular mergers between **prokaryote** cells with all the partners benefiting from this arrangement. Now, after many generations evolving together, they can only reproduce and survive in association with each other.

2.3 The species

Ideally, our classification system would accurately reflect the important differences between organisms. Then, each species would represent a unique collection of traits, the current endpoints of different evolutionary histories. However, the boundaries

may be blurred where two species have only recently diverged or if the trait which distinguishes them is not obvious.

Distinctions between orders, families, or genera are easily made. For example, it is easy to distinguish

a grasshopper from a butterfly. Though they are both insects, the differences in their anatomy (the enlarged hind legs of the grasshopper and the broad, dusty wings of the butterfly) readily place them in different orders. As we descend down the hierarchy, deciding where a family or genus begins or ends requires closer and closer observation (Figure 2.4). At the level of the species, the difficulty is deciding whether the differences observed between individuals are distinguishing traits. Are the variations in the coloration of the butterfly's wings part of the natural variation within a species, or a character that helps to define a distinct species? Often, variations in colour mark only a different race, a variety confined to a particular area, but whose members are still capable of interbreeding with the rest of the species.

Shared morphology remains the most common means of classification and the basis of most identification keys for higher plants and animals (Figure 2.4). In a key, a series of descriptions are offered at each level in the hierarchy. An unknown specimen is compared against each description and placed in the category with the closest match. This continues, running down a sequence of alternatives, each giving directions to the next stage. By choosing the most appropriate description at each step, the key arrives at an identification and provides a description that could only match the named species.

This works best, of course, with species that are well described, where we know the most reliable characters to observe. Without these, classifications based on appearances alone can be misleading. For example, morphological variation caused Edward Poulton considerable difficulty when he tried to classify the African mocker swallowtail butterfly (*Papilio dardanus*). The males were obvious enough, but there seemed to be no females of the species. Females of the genus were known, but there were at least three different types and these were so variable they neither resembled the males nor each other. Each group of females was therefore classified as a separate species. In fact, the females come in three forms, each of which mimics one of three species of an unpalatable butterfly (*Amauris* species) (Box 4.3). Despite being **polymorphic** in appearance, the different forms share the same internal anatomy. A similar scale of variation in the males would be a major

disadvantage because the females need to recognize them to allow them to mate. Equally, females that vary too far from their matching unpalatable species risk being eaten by a discerning predator. Both the males and the females represent cases of **stabilizing selection**, where variation from one or more 'normal' forms may incur greater selective pressure.

Another complication in classifying from morphology alone is that natural selection can produce very similar structures from very different starting points. This is known as **convergent evolution**. One of the most spectacular examples is the thylacine or marsupial wolf. Probably now extinct, this was, to all outward appearances, a member of a dog family, but, as a marsupial, was more closely related to possums and kangaroos (Figure 2.5).

Such structural resemblance is termed **homoplasy** and is particularly common amongst plants. Again, similar selective pressures will tend to produce similar results. Mediterranean-type plant communities are found in five distant regions of the world, but although they comprise very different plant groups, many of their species have evolved thick, tough leaves and a short shrubby stature. These are adaptations to a prolonged summer drought and periodic fires (Section 5.1; Figure 5.2). A more general example of homoplasy are tendrils. Plants with tendrils are able to raise themselves towards the light without the cost of producing substantial stems and trunks. Instead, they exploit the supporting structures of their neighbours. Various families have evolved tendrils, but as modifications of different structures (Figure 2.6) including leaves, stems, petioles (leaf stalks), and stipules (scales).

The biological species

The complications of variation and convergent evolution have led biologists to treat species defined by their morphology with a large measure of caution. Today, most use a more functional definition of a species, termed the **biological species concept**. A biological species comprises those individuals able to interbreed to produce fertile and viable offspring, forming a gene pool and sharing a common set of adaptations. This definition recognizes that species are variable and changeable but by referring to an



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Figure 2.4 A simple key for some members of the primrose family (Primulaceae).

1. Leaves in basal rosette—go to 2
- Leaves in rosette and along stem—water violet (*Hottonia palustris*)
2. Petals flat/turned forwards (*Primula* species)—go to 3
- Petals turned backwards—cyclamen (*Cyclamen purpurascens*)
3. Flowers in cluster—go to 4
- Flowers solitary—primrose (*Primula vulgaris*)
4. Flowers fragrant—cowslip (*Primula veris*)
- Flowers not fragrant—oxlip (*Primula elatior*)



Figure 2.5 The marsupial thylacine is remarkably similar to placental dogs, or perhaps a blend of dog, cat, and hyena. As one of the few major carnivores in Australia during the Pleistocene, it probably filled the role of all three, and shows how evolution can converge on similar adaptive solutions in the case of placental mammals.



Figure 2.6 Clematis uses its petioles as tendrils.



Figure 2.7 An apomictic species: dandelion (*Taraxacum officinale* agg.).

interbreeding group, it allows the possibility of change in the future. Eventually, some individuals may become excluded from the breeding population and new species may then evolve.

The biological species concept cannot be applied universally. It does not readily encompass the many species that reproduce asexually. More complicated still are groups which reproduce sexually and asexually, and which do so within defined groupings. Although it is given a single binomial, *Taraxacum officinale*, the dandelion (Figure 2.7), is more properly described as an aggregate (*Taraxacum officinale* agg.), comprising 10 sexual types and 2 000 asexual forms. These latter types are **apomictic**—they produce seed without pollination—and are consequently genetically isolated. Since the flow of genes from one individual to another has stopped, different apomictic species (also known as **micro-species**) are often found growing very close together, but remaining distinct from each other—John Richards discovered as many as 100 micro-species of dandelion within a single hectare. Micro-species are difficult to differentiate and we avoid the complication of naming them by adding the abbreviation agg. after the specific name.

A further complication is the freedom with which some organisms exchange genes across species boundaries and thus fail to conform to the definition of the biological species. Sometimes, perhaps under special circumstances (such as cultivation or captivity), the barriers between species may be breached and interbreeding occurs. Any offspring from such a union is called a **hybrid**. Interspecific hybrids are rare amongst most animal groups. Very occasionally the normally sterile mule (the hybrid from a horse and donkey) may parent its own offspring, but other hybrids are consistently sterile, so that ligers and tigons (crosses between tigers and lions sometimes produced in zoos) are invariably genetic dead ends.

Interestingly, there are examples of fertile hybrid animals which have been classified as different species. Often we have learnt about their true ancestry only after looking at their genetic signature (Box 2.2). An example was the discovery that the red wolf (*Canis rufus*) was actually a fully fertile hybrid between two distinct species, the coyote and the grey wolf (Figure 2.8).

The red wolf underwent dramatic decline after 1900 due to hunting, loss of habitat and increasing hybridization with the coyote, which had been extending



Figure 2.8 The red wolf of North America. Classified as *Canis rufus*, the red wolf is actually a hybrid of the coyote (*Canis latrans*) and the grey wolf (*Canis lupus*).

its range. Robert Wayne and Susan Jenks compared the mitochondrial DNA (mtDNA) of the few red wolves collected together for a captive breeding programme with that of coyotes and grey wolves. They also collected mtDNA from six pelts of red wolves that dated to a time before hybridization was considered to have begun on a large scale. The mtDNA and its cytochrome b sequences revealed the red wolf to be a hybrid of coyotes and grey wolves; its geographical range represents the zone of hybridization between the two parent species. Indeed, Wayne and Jenks suggest that some of the animals they sampled in the wild would have been classified morphologically as grey wolves even though their genotypes were closer to that of the red wolf.

Fertile hybrids are quite common in the plant Kingdom. Many species of orchid of the genus *Dactylorhiza* will readily cross with each other, and whilst some hybrids appear to be a perfect blend of the two parent species, others resemble one or other species. This makes them particularly difficult to identify (Figure 2.9).

The results of crosses between fertile hybrids make it even more difficult to trace phylogenies. For these groups, the idea of a species as a discrete entity is misleading and we have to accept a more fluid classification. We can now at least explore their possible ancestry with molecular biology and genetics (Box 2.2).



Figure 2.9 (a) The southern marsh orchid (*Dactylorhiza praetermissa*) and (b) the common spotted orchid (*Dactylorhiza fuchsii*). These two species naturally hybridize to produce an interspecific hybrid orchid (c).

BOX
2.2

Reading the molecular code

The genetic code, the blueprint for a species, may seem the obvious place to look for the real differences between one species and another, but it is only recently that we have been able to read gene sequences. Before that, molecular biologists had to look at the products transcribed from the code (Figure 1.11). This meant comparing the composition of proteins, especially those responsible for key functions, to reconstruct the phylogenetic relationships of a species. The greater the genetic distance between individuals, the less likely they are to share proteins with exactly the same structure.

Even in the absence of a selective pressure, genotypic differences and chance variations will change the amino acid composition or sequence, and such differences in structure are easily quantified in proteins. Immunological methods use the capacity of mammalian immune systems to detect 'non-self' proteins. Antibodies produced against the foreign protein are highly specific, and the degree of binding between an antigen (the protein under test) and its antibody can give us a gross measure of the structural similarities of proteins from different species.

Gel electrophoresis separates proteins according to their electrical charge and molecular weight. The greater the charge across a protein molecule and the smaller its size, the faster it will migrate towards one pole of an electrical field. Two protein samples migrating the same distance through a gel are likely to have the same configuration and amino acid composition. This technique is widely used because it can pick up subtle differences in structure and is particularly good at identifying hybrids that otherwise look the same.

Sequencing their amino acids using a series of enzymic scissors and assays has paved the way for more detailed analysis of proteins. One protein, cytochrome, is of particular interest because it is found in all living organisms and is therefore very ancient. Cytochrome plays an important role in the energy-generating activity of mitochondria and chloroplasts. Analysis of its 104 amino acids has allowed biologists to group species according to these sequences. All share a sequence of 33 amino acids in the same position along the protein chain, but the remainder fall into groups, creating a hierarchy that mirrors the phylogeny of the major groups. All vertebrates, for example, fall into a group of their own, as do the invertebrates, plants, and fungi. The cytochrome of human beings and chimpanzees is identical.

The most direct way of deciding the genetic differences between individuals and species is to read the genetic code itself. Part of the double strand of DNA is unzipped when the genetic code is being read (Figure 1.11). Strands can also be separated by heat treatment and will re-associate as they cool. In DNA hybridization, DNA from two sources is heat treated, mixed together and allowed to cool. Some strands from each source will associate to form hybrid strands. The hybridized DNA is then separated again by heat treatment, but the closer their match, the higher the temperature required to dissociate the strands. Using the temperature scale over which complete dissociation takes place between hybridized and non-hybridized strands, we can calculate the percentage similarity for an entire genome.

More precise information can be gained from gene sequencing. Central to the several techniques available is the polymerase chain reaction (PCR). This allows minute samples of DNA to be copied (amplified) and then sequenced by a process known as the Sanger method. The technique uses a series of dyes to tag each of the bases that make up DNA. PCR is used to build copies of the DNA fragment with the tagged bases which are then separated out using gel electrophoresis and read off using a laser scanner linked to a computer. The result is a series of bases corresponding to the gene sequences within each gene fragment. The more fragments shared between two individuals, the greater their relatedness and the longer their common evolutionary history. These techniques can be used wherever DNA or RNA occurs. Carl Woese used them to rewrite the family tree of the major groups using the sequence for small subunit rRNA (Section 2.2). PCR also allows us to amplify fragments of DNA from the remains of long-dead organisms (including Neanderthal human remains) or identify living individuals through DNA 'fingerprinting'.

It is important to distinguish the DNA of the nucleus from that of the mitochondria or the chloroplast. Mitochondrial DNA (mtDNA) is inherited from the mother with the cytoplasm supplied in the egg cell, making it particularly useful for working out relatedness within parthenogenic species, where females produce young without having to mate. It also helps us sort out the parents of hybrids—for example, Steven Carr was able to unravel the complex mating system of white tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*) in Texas. He found the mtDNA

of hybrids was the same as *O. virginianus*, indicating that crosses between the two species invariably had a mule deer male and a white tail female as their parents.

Classifying species and working out their origins by genes alone can be problematic. Changes in DNA may not accurately reflect evolutionary change and DNA molecules are more changeable in some groups than others. This makes

it difficult to construct accurately timed phylogenies on the basis of molecular evolution alone. For example, plants within the sunflower family, the Asteraceae, show little variation compared with other flowering plants. This may mean that sunflowers are a recent evolutionary development and have not yet had time to change or simply that the DNA within their chloroplasts is slow to change.

Defining species by their chemistry

We could also take Romeo's advice and identify a rose by its scent. Flowers are recognized for their ability to produce complex chemical signals used to attract insect pollinators. Some even mimic an animal's sex pheromone, the smell used to attract a potential mate.

For more than three centuries, a group of Panamanian orchids had defied all attempts at classification. Defeated, taxonomists bundled them into a single species, *Cynoches egertonianum*, and referred to them as the 'Egertonianum complex'. Unable to classify the plants by traditional means, Katherine Gregg looked at the sex lives of the bees that pollinate them. After they have attempted to mate with the orchid, male bees collect the delicate lemon scent and use it as a pheromone to mark out their mating sites. Several species of bees do this and field observations showed that each was extremely selective about its choice of plant. A chemical analysis of the scents revealed they were composed of up to 18 separate compounds, and Gregg found their differences reflected links with different pollinators. By reference to the species of bee and type of scent, she was able to make sense of the Egertonium complex, dividing it into four 'chemotypes', which are now recognized as four separate species.

Although the bees might have got there first, our use of chemistry to classify organisms also has a long history. The standard test for lichen identification was developed by Nylander back in 1866 and grouped lichens into six chemical races. The molecular classification of higher plants is also well developed because of our detailed knowledge of secondary plant metabolites (Section 4.4), the characteristic chemicals produced by some groups of plants, especially those

compounds having a medicinal or economic value. Genera such as *Eucalyptus* hybridize freely and it is not always obvious which species were the parents, more so when one of the parents was itself a hybrid. A particular group of these compounds—the terpenoids—have proved invaluable in settling such plant paternity cases and have also been used to work out the origins of hybrids in other aromatic species such as junipers (*Juniperus* spp.) and pines (*Pinus* spp.).

Even though morphological characteristics still remain the basis of most keys to multicellular plants and animals, chemical and biochemical techniques enable us to make finer distinctions. Our goal is to arrive at a classification that reflects the real phylogenetic history of a species, though this can be challenging when the demarcation between species is not clear. The picture of human speciation we painted earlier (Section 1.1) presents the very bare branches of a phylogenetic tree, whereas the current scientific literature shows a much fuller bush. The branch connecting all *Homo*, for example, might contain as many as 13 species, including a separate species for Neanderthals—*Homo neanderthalensis*. Classification is always problematic when we have to rely on an incomplete fossil record. The reduced list we use here refers to those species for which there appear to be distinct ecological differences, but passes over fine anatomical variations. These four species of *Australopithecus* and the three species of *Homo* are those which most authors agree lived in different habitats or adopted distinct ways of life. This same approach is used in microbial ecology, where many micro-organisms are known principally by their actions—by their source of food or the waste they produce. Such a classification uses the **ecological species concept**, recognizing an organism by its role in its environment—that is its ecological niche.

2.4 Variation within a population

Variation between individuals is usually fairly obvious. We use these differences to distinguish one person from another and to recall their name—at least most of the time. Under other circumstances, we might wish to know what significance these differences have for an individual's survival and reproductive success.

If we plot some measure of fitness (say growth rate or abundance) against some key environmental factor (such as temperature or water availability), we invariably find a species has an optimum range (Figure 2.10). Usually this produces a characteristic curve, termed a normal distribution. Most individuals are found close to the mean value and numbers rapidly tail off with distance away from the mean.

This tells us something about the species' adaptation to that parameter. Away from the optimum,

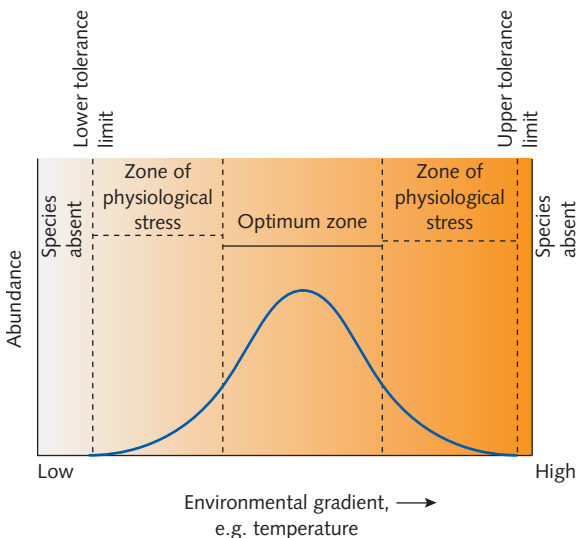


Figure 2.10 A plot of abundance of a species against some environmental parameter, in this case, temperature. This shows the range to which a species is best adapted, and the same sort of pattern will be found for any important parameter, such as water availability, nutrient level, salinity, and so on. Outside the optimum range, numbers decline rapidly because individuals have to expend energy or other resources to adapt physiologically to the poor conditions. At extreme temperatures, conditions are too harsh and the species is not found. We could create the same plot for any other measure of a species' performance, such as reproductive success or growth rate.

conditions would be less favourable and individuals will incur physiological costs to maintain themselves. For a warm-blooded animal (or endotherm), for example, this may mean using energy to keep warm or to keep cool. If the costs are high, or have to be sustained for a long time, an individual will have fewer resources to devote to growth or reproduction (Section 4.1). Those forced to live at the margins of their physiological range may thus fail to reproduce or grow.

Over time, individuals may arise which are better adapted to living outside the optimum range of the larger population. Some change in their genotype allows them to flourish where most struggle. This is the nature of variation within a species—not every individual responds in the same way to a selective pressure, and there will be some who favour conditions away from the population optimum.

A dramatic example is seen in human populations' resistance to disease. When challenged by unfamiliar diseases, those able to resist the pathogen, either through variation in their immune system or some other adaptation, have a greater chance of survival. The landing of Columbus and his successors sealed the fate of many millions in America because the native peoples had no immunity to the diseases carried by the conquistadors. It is estimated that the indigenous population of Mexico fell from 30 million to 3 million between 1519 and 1568 following their first exposure to smallpox and measles. Genetic variability within the native population meant some developed resistance and it is their descendants we see today. Isolated Amazonian tribes have more recently succumbed to the diseases of invaders, though on this occasion carried by lumbermen and miners (Box 2.3).

Much of the variation we observe between individuals does not have an adaptive significance, and individuals then differ because of the chance combination of genes they were dealt at fertilization. This is termed neutral variation (Section 1.3). Proteins have variations in structure (Box 2.2) that appear not to be adaptive and impart no selective advantage

**BOX
2.3****The shock of the new**

The native Americans arrived in the New World around 13 000 years ago when they crossed the Bering Strait between Alaska and Siberia. Their genes, and perhaps their language (Box 1.2), record the history of their walk through the continent. The early colonists had to survive the harsh and unpredictable conditions of the Arctic Circle, to pass through what has been called the 'arctic filter'. From the evidence of today's peoples the severe conditions in the north favoured particular genotypes, particularly those able to survive periods of famine.

Life must have become easier as they moved south into the temperate regions, as a thriving and expanding population quickly established itself. However, what started as a relatively rapid spread then seems to have slowed. Archaeologists and anthropologists have repeatedly found evidence that colonization was checked further south. Some new challenge must have faced those moving towards Central and South America. One suggestion is that these peoples were confronted with a range of diseases for which they had no immunity: diseases prevalent in the tropical forest and resident in the mammals of these regions. Human populations had to adapt and acquire immunity before they could move on. Again, only those genotypes able to pass through the tropical filter would enter South America.

This second genetic bottleneck is again suggested by the genetic make-up of native South American peoples. By the same token, their geographical and genetic isolation became obvious when they were exposed to the diseases of later European colonists. Many millions fell to the diseases of the conquistadors and those who followed.

Ironically, their geographical and cultural isolation saved some natives from the worst of these epidemics, at least in the first waves of European colonization. The Yanomamo Indians number 20 000 individuals spread across 150–200 villages in remote forest areas on the border between Brazil and Venezuela. They survive through a regime of hunting, gathering, and cropping, but this requires large areas of forest so their villages tend to be widely dispersed. Because there is little contact between the villages, individuals tend to marry within their own community and other

pairings occur only rarely. The small size of communities and their reproductive behaviour has had important consequences for the disease resistance of the Yanomamo.

For a viral disease like measles or influenza to remain within a population there has to be a sufficient number of individuals to maintain a reservoir of infection. Measles, for example, is only virulent within an individual for 14 days, after which it needs to move on to someone else. Epidemiologists estimate that measles will remain active within a population of more than 200 000 individuals. In smaller, isolated populations the disease is easily lost, and with time, so is the immune response of the people. When the disease returns, it can devastate such a population.

This is exactly what happened when the Yanomamo people were 'discovered' by the outside world in the latter half of the twentieth century. Their first encounters with anthropologists, explorers, and missionaries in the 1960s led to a series of epidemics amongst the natives in which the 'diseases of civilization' such as measles, mumps, and influenza swept through their villages. With our frequent exposure to such diseases, most of us take these infections in our stride—our regular contacts with others helps to build and maintain our immune response.

The Yanomamo did not have this frequency of contact with other people and were further devastated when these and other diseases arrived with later colonists. The building of the Northern Circumferential Highway in the 1970s brought construction workers and, more recently, an influx of loggers, ranchers, and miners. Now tuberculosis and HIV/AIDS are the major killers of the Indians and a whole way of life is under threat. Whilst genotypic variation is important for disease resistance, so is exposure to low levels of infection from childhood, without which the immune system cannot adapt. Globally, the human population is threatened in the same way by a new pathogen or a variation on the influenza virus at regular intervals. Today, the avian H5N1 virus could result in the next flu pandemic, should it cross the species barrier from birds to humans.

Isolation only offers protection as long as it lasts . . . thereafter, the shock of the new can prove fatal.

or cost. Even so, in a new or changing environment, such variability may equip, again by chance, some individuals to survive and reproduce with a higher frequency than their neighbours. Then the amount of

variation in some critical trait may allow a species to adapt and evolve quickly. A population lacking such variation has fewer alleles from which to select, and less chance of adapting to change in its habitat.

2.5 Ecological niche

If a species is defined in nature by its collection of adaptations, which selective pressures have been most important in shaping it? And what selective pressures have led to it becoming separated from its close relatives?

Major morphological adaptations, such as those needed for flight, have a long evolutionary history and will separate animals high up in the hierarchy, at the Class level (Class Aves, the birds) or Order level (Order Chiroptera, the bats). Smaller adaptive changes—variations in colour, for example—may not require major physiological or structural changes. They distinguish closely related species which have diverged relatively recently. Even more recent are the distinctions between varieties of plants or subspecies of animals that are perhaps only separated geographically rather than genetically.

But what about closely related species that share the same geographical range, but apparently remain distinct? Often, it is the details of their life history, or the habitat they use, which keeps them separate. For example, two micro-moths, *Lampronia rubiella* and *Lampronia praeletella*, share a similar range, and as adults, have similar markings. Their caterpillars are leaf miners, but one attacks strawberry leaves (*L. praeletella*) and the other raspberry fruit stalks (*L. rubiella*). They have evolved to use different resources and, indeed, their larvae live in different habitats. This separation at one stage in their life cycle means they are not in direct competition with each other. The larval food plant is one of a large range of factors to which each species has to adapt, any one of which might serve to distinguish them from other species in the same genus.

For any environmental factor, whether biotic or abiotic, we can define the optimum range for a

species and measure its performance over this range (Figure 2.11). The distribution of the species will reflect its adaptation to that factor and, more generally, to the other myriad factors to which it responds. This totality of factors to which a species has adapted is called its **ecological niche**.

Niche is a complex idea that tries to describe the fit between a species and its environment. An ecological niche is not a place in the normal sense of the word and is much more than a species' habitat. It represents the interaction between a species and its habitat, describing where a species lives and how it lives there. Niche is sometimes described as a species' role in its community. That role depends on its interaction with other members of the community and so can include everything from being, say, a strawberry leaf miner to a prey item for a bird, or a host to a parasite.

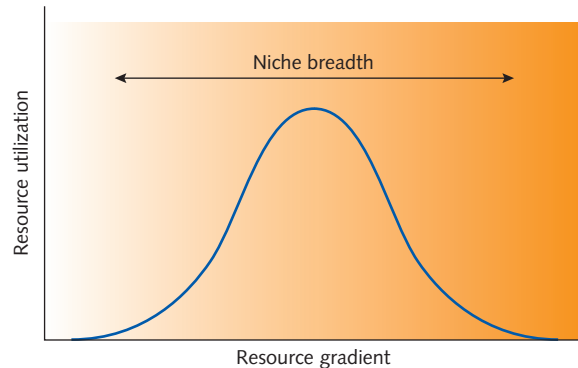


Figure 2.11 Niche, defined by one environmental gradient—in this case, the resource being used. For every environmental parameter we can define an optimum (Figure 2.10), but the full range over which a species is found is its niche breadth. For example, plants may respond to a gradient of light at different intensities; for an insectivore it might be the size of insects on which it feeds.

Although niche is difficult to define, it does have a very real ecological meaning. We can see this in convergent evolution, where species filling equivalent niches in different areas arrive at the same adaptive solution. The thylacine and the dog are one example (Figure 2.5). Another is the anteaters found on the three southern continents, all of which have elongated snouts and long probing tongues—equivalent adaptations to the same selective pressure. Like the thylacine, one of these (*Myrmecobius*) is a marsupial, another (the echidna) is an egg-laying mammal, while the pangolins of Africa or the tamandua of South America are placental mammals. These fundamental differences in reproductive physiology place their separation high up in the hierarchy (at the level of the sub-class), indicating a large phylogenetic distance between them. Yet each has evolved equivalent adaptations to collect ants and termites.

These similarities emphasize that a particular niche will apply particular selective pressures which may produce comparable adaptive solutions. But they are not perfect matches and differences between most convergent species are obvious on even the most casual inspection. A niche is defined by the organism and its fit with its living and non-living environment. Rather than simply being a role that might be played by a number of species, a full description of a niche must include the detail of the species which occupies it. So, part of the niche occupied by *L. rubiella* is defined by the raspberry stalk it uses when a caterpillar.

Clearly, there are practical difficulties in measuring every significant factor in a species' niche. Usually, studies have concentrated on those which seem to be important in separating species and which are also easily measured. **Niche breadth** is the range of a factor over which a species is found (Figure 2.11). This could be an abiotic factor like temperature, or (more often) the range of a resource the species uses. An insect that feeds on the leaves of a variety of plants is said to have a larger niche breadth than one which feeds on only a single species. A large niche breadth implies a **generalist species**, able to exploit a wide range of resources, whereas specialists are adapted to a narrow range of resources. Being a generalist is a good strategy in an unpredictable habitat, when switching to a different resource is advantageous during times

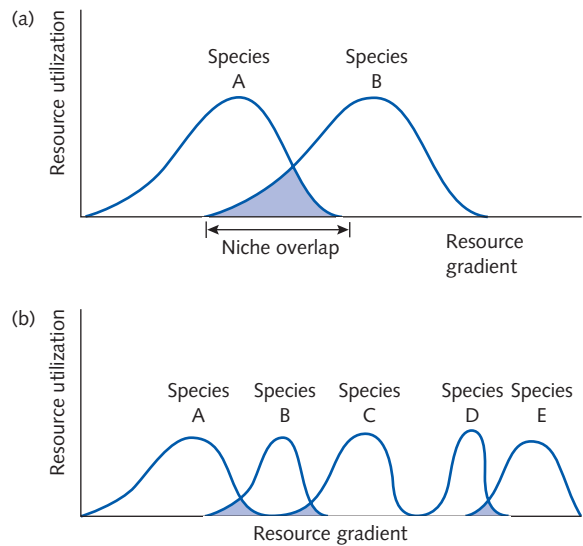


Figure 2.12 (a) Two species that exploit the same part of a resource gradient (or 'spectrum') are said to show niche overlap. In some cases, this may indicate competition between them for that resource. (b) A collection of species exploiting the same resource can only coexist if they exploit different parts of the gradient.

of shortage. Being a **specialist** is only viable when the resource supply is reliable, in constant or predictable habitats (Section 3.5). In these situations a species can become highly adapted to a resource, out-competing its neighbours by being more efficient.

Niche overlap is the part of a resource spectrum that two species occupy (Figure 2.12a). Sometimes, overlap indicates that two species are competing with each other for the resource. At other times it can mean the opposite.

Niche and competition

Different species invariably concentrate on different parts of the range of a resource—they are spread out along the resource spectrum (Figure 2.12b). A large zone of overlap may indicate where two species are competing for a resource, say the same prey or the same soil nutrients, or some other limited resource. If, however, this resource is abundant, the two species may coexist and the overlap may persist over many generations. In this case there is little competition because neither species is limited by this particular resource.

By the same token, a lack of overlap between two species only indicates there is no current competition for this particular resource. It tells us little about their past battles or their ongoing fight for other resources. We may, in fact, be observing the outcome of a competitive battle fought long ago, after each has become adapted to a different range.

Or we may be witnessing a competitive battle in progress. Where a resource checks the growth or reproduction of both species, utilization by one species depletes the supply for the other. **Interspecific competition** (competition between species—Section 4.3) means either species would perform better in the absence of its competitor. Then niche overlap does indeed denote competition.

Under these circumstances, ecologists distinguish two types of niche. The range a species could occupy in the absence of interference from other species is its **fundamental niche**. The range to which it is confined by competitors or predators is its **realized niche**. Under severe competition, a species may only use a very narrow part of a resource spectrum and have a small realized niche. Then selection will be intense, favouring those individuals able to make best use of what is available. These will be the most successful reproducers and will soon dominate the population and gene pool. In this way, a species becomes highly specialized, often showing distinct morphological or other changes that adapt it to use a resource most effectively. This is known as character displacement and becomes most obvious when two closely related species or races begin to diverge.

Competition between individuals of the same species is termed **intraspecific competition** (Section 4.3) and is one of the prime forces driving natural selection. Those most able to secure resources—food, space, or shelter—are better able to reproduce and ensure their genetic code enters the gene pool of the next generation. Ordinarily, we would expect those individuals close to their optimum range to have the greatest reproductive success. However, genetic change might adapt some individuals to a different part of this environmental gradient. Perhaps a change at one locus means a key enzyme is more effective at higher temperatures. The new genotype thrives at a different optimum and its numbers increase in the absence of competition from its neighbours.

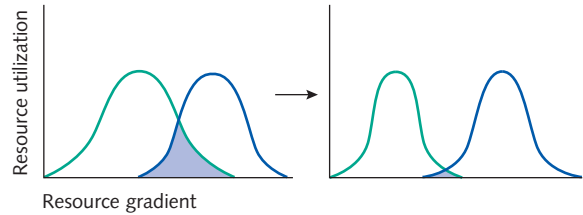


Figure 2.13 Where overlap represents a high competitive pressure on each species, one or both of them will, through natural selection, gradually change to reduce the overlap, shifting their niche. This is termed character displacement and may be represented by some change in physiology or morphology.

Mutation has produced a variety that might eventually lead to a new species, though at the moment, it can still breed with the rest of the population. Over time, the entire population may become dominated by the new genotype and its optimum range shifts (Figure 2.13).

Dolph Schluter has shown how rapidly intra-specific competition can lead to significant character displacement. Schluter and his colleague Don McPhail work on the three-spined stickleback (*Gasterosteus aculeatus* complex), a variable group of ‘species’ whose taxonomy has yet to be fully worked out. These fish have been isolated in a series of small coastal lakes in British Columbia since the retreat of the ice sheet 10 000–13 000 years ago. In some lakes, two different ‘species’ are found—a larger and rounder fish that feeds on invertebrates on the lake bottom (‘benthic species’) and a smaller slender ‘species’ that feeds on the zooplankton closer to the surface (‘limnetic species’) (Figure 2.14). In



Figure 2.14 Benthic (above) and limnetic (below) forms of the three-spined sticklebacks (*Gasterosteus aculeatus*).

lakes where there is only one 'species', an intermediate form is found that is able to exploit both food sources. Although limnetics and benthics do not readily interbreed with each other in the wild, they will breed in captivity.

This has enabled Schluter to run experiments to measure the pressure for character displacement when two forms share similar morphologies and the same diet. In one experiment he bred three intermediate

forms: one close to the limnetic form, another close to the benthic form, and the third a true intermediate form. These were then grown in experimental ponds in the presence or absence of the wholly limnetic 'species'. By measuring the performance of each form (in this case by measuring their growth rate over a season) Schluter was able to work out the response of the different intermediate forms to the presence of a limnetic (Figure 2.15).

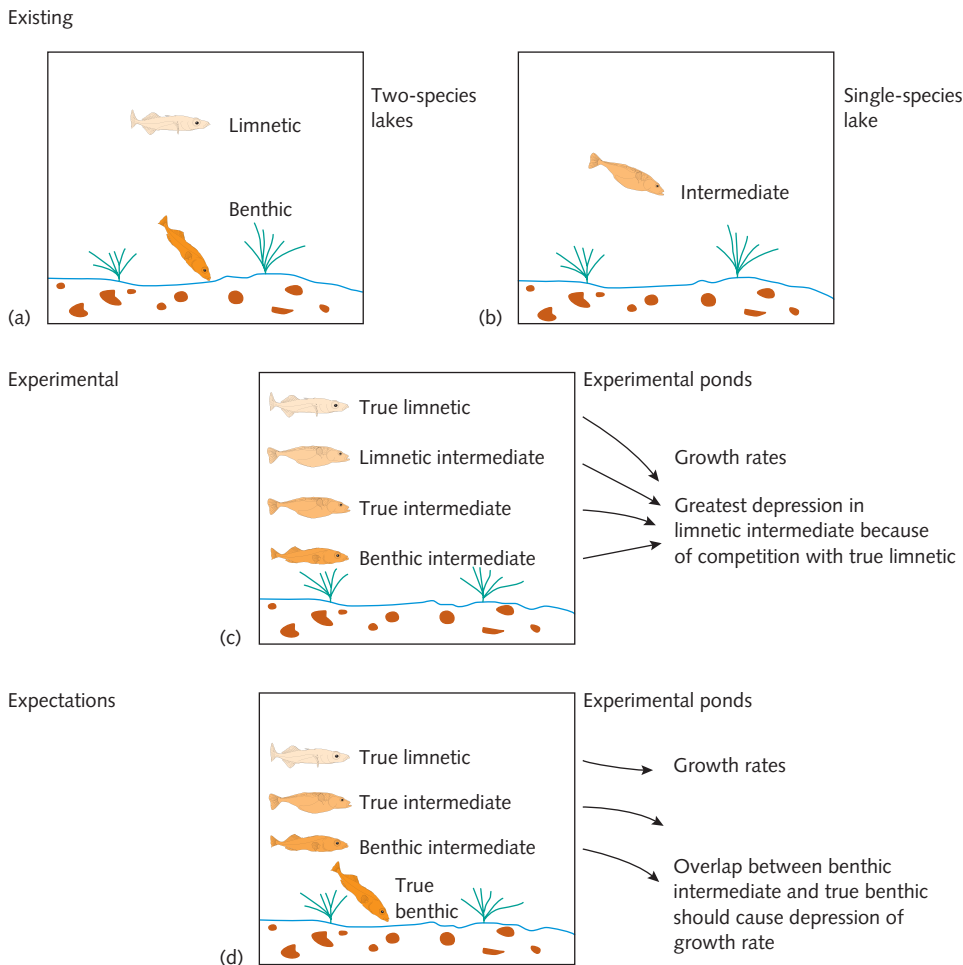


Figure 2.15 Schluter's experiments with three-spined sticklebacks (*Gasterosteus aculeatus* complex) demonstrating character displacement. Lakes in British Columbia have either two species of stickleback with different morphologies or one which is intermediate between the two. (a) One form (the benthic 'species') feeds on bottom-dwelling invertebrates and has a large mouth and rounded body; the other feeds on zooplankton in open water and has a smaller mouth and slender body (the limnetic 'species'). (b) Intermediates feed in both habitats. (c) Schluter has shown that intermediates with forms closest to the limnetic species have the greatest growth depression. (d) Similarly, we would expect benthic intermediates in closest competition with benthic species to grow less well when competing with benthics instead of intermediates.

As expected, the intermediates closest to the limnetics grew less well in the presence of limnetics. In control experiments (in the absence of a limnetic) the same intermediates showed no depression in their growth rate. Thus the greater the similarity between an intermediate form and limnetic, the greater the niche overlap and the greater the reduction in the intermediate's growth rate. Eventually this might result in the loss of intermediates since they would not compete with the efficient limnetics. Over a number of generations the intermediates would be expected to show character displacement, presumably approximating to the larger, rounder form of benthic sticklebacks, shifting to a niche not occupied by the limnetics.

It seems that the niche separations seen in some lakes today are the result of past displacements. Perhaps, with time, the intermediate forms found in single species lakes would begin to separate into two distinct types, and partition the resource spectrum. In further experiments, fish from single-population lakes (either all benthic-like or limnetic-like) were introduced to lakes where both forms occur. Given the option, females tended to select male partners that were closer to their own type—a preference known as **assortative mating**. Schluter's team suggest that lowered hybrid fitness will favour such selection, reinforcing the process of character displacement.

The alternative to moving to a different part of the resource spectrum may be oblivion. If the competition for a resource between two species is very intense, one may lose out completely. This is the

competitive exclusion principle. Simply stated, it says that two species may not occupy the same niche at the same time in the same place (Section 4.3). Competitive exclusion means there are probably limits to the number of species that can be packed along a resource spectrum, depending on how different they have to be to avoid excessive competition. This has proved very difficult to measure, partly because a separation along one gradient is often tempered by the interactions between the species on other gradients.

However, not every niche has to be filled. Sometimes an alien species manages to establish itself in a new habitat and find an unoccupied niche. Sometimes an invader may squeeze between two resident species, by being better adapted to a resource space neither fully occupies. For any newcomer to persist, it needs to be sufficiently different from its new neighbours to carve a niche for itself (Box 5.3). There are numerous examples of the alternative outcome, where an introduced species out-competes the native niche-holder, and the resident is lost (Section 4.3).

Niche theory is powerful because it links the evolution of species to their use of resources and the number of species that a community can contain (Sections 5.2 and 9.1). It also links the range of resources used by a species to the constancy of its habitat and explains why we might expect more species and more specialist species in constant or predictable habitats, a subject we explore in some detail in Chapter 9.

2.6 Speciation

Whilst Dolph Schluter's sticklebacks are in the process of becoming new species, they are not yet perfectly separated. The reproductive barriers that would define them as distinct species have not yet formed, but they are underway: hybrids produced in the wild have reduced fitness and tend to die off by the next breeding season. If two populations remain isolated for long enough, genetic differences emerge which eventually prevent them from mating at all.

Their gene pools are then separated and any changes that develop in one pool are not transmitted to the other. Schluter and his colleagues are observing the development of such reproductive isolation between benthics and limnetics through the behavioural isolation of assortative mating (Table 2.1).

Separation in its various forms is an important part of speciation. Consider the allele we described earlier, coding for an enzyme that had a different

temperature optimum. Under character displacement, individuals with different alleles flourish in different places in which the temperature regime is most suitable for each type. This means they are physically separated—perhaps in space, say by living on different sides of a hill, or perhaps in time, if they are active at different times of day. Either way, the effect may be the same: the two populations rarely meet or interbreed with each other and genes are only exchanged between individuals active at the same time or in the same place. Then differences between separated populations are never diluted by gene flow. After a long period of isolation their accumulated genetic differences may preclude mating, even if they are reunited, a process that appears to be underway with Schluter's sticklebacks.

Divergence following a separation in space is termed **allopatric speciation**. With **sympatric speciation**, populations may live together, but gene flow is initially restricted because of some genetic change.

Allopatric speciation

Spatial separation can occur when a population becomes divided into isolated fragments, perhaps as some become adapted to more marginal environments. This happens most readily in highly fragmented habitats, where very different conditions are found within short distances, selecting different traits in their resident populations. For example, adjacent valleys can differ in the amount of sunlight they receive or in their geology and soil type. This is a major cause of the rapid speciation and high plant diversity in mediterranean-type ecosystems around the world (Section 5.3).

Adaptations needed to survive in one pond may differ from a second pond perhaps only a few kilometres away. Then an individual moving to the next pond or the next valley has a lower chance of survival in its new habitat, where it is less well adapted. The same sort of separation can occur temporally, where populations become specialized for flowering or feeding at different times of the day or year.

Sometimes, a small section of a population is cut off by a major disturbance, such as a flood or a forest fire, and gene flow with the parent population is reduced. In the same way, individuals invading a new

habitat (say an island) may only breed with those present. With just a small number of breeding individuals, either as colonists or survivors, any novel code is found in most of the offspring within a few generations. Only a small number of individuals may show any adaptive change, but if this proves successful their numbers quickly build as they benefit from a lack of competition. Their separation means they mate primarily with each other, rather than with the main population. As a result, their adaptive traits soon become fixed within their sub-population.

These few individuals will have only some fraction of the genetic variation of the parent population, with two important consequences for future genetic change. First, the few individuals establishing the sub-population may be unrepresentative of the larger population, and traits that might occur at a low frequency in the main population could, by chance, be common here. Within the small breeding population this code is preserved and differences from the main population become exaggerated. This is known as the **founder effect**, and allows small gene pools to diverge rapidly from the parent population.

Second, rare alleles can easily be lost in small populations. In large populations rare code may persist because, even with a low incidence, a significant number of individuals will carry the gene. The same proportion in a small population implies very few individuals and a small chance of the code passing to the next generation. The frequencies of some alleles change rapidly because rare code has a high chance of being lost, a process called **genetic drift** (Section 3.6). Again, with no exchange with the parent population, the two gene pools quickly diverge, perhaps reaching a point when they can no longer interbreed.

Reproductive isolation and genetic divergence underpin the concept of the **evolutionary significant unit** (ESU). Ollie Ryder coined this term to describe populations considered to be on a different evolutionary trajectory from their counterparts. Conservation strategies aim to identify populations requiring particular management regimes to maintain their long-term genetic integrity, and in some cases this recognizes the distinct genetic identities of some local populations. ESUs have been used extensively to manage fishery stocks, in particular the Pacific salmon (*Oncorhynchus* spp.), where sub-species

have been given the legal protection more usually accorded to species. For example, one species, the Chinook (*O. tshawytscha*), has six ESUs, some confined to a single river system where they are reproductively isolated from other populations. Protecting such ecotypes, however, raises concerns that preserving variation may negate the evolutionary process itself, perhaps deflecting or halting the very trajectory that makes the population evolutionarily significant.

Reproductive barriers

Of course, populations that have become physically separated can be reunited again, when gene flow may be resumed. To produce a new species, their physical separation must last long enough for the two populations to diverge. Then any subsequent mating between them is either impossible or unproductive.

Reproductive barriers take one of two forms according to whether they operate before or after fertilization—pre- and post-zygotic barriers (Table 2.1). **Pre-zygotic** barriers are mechanical, physiological, or behavioural. For example, many insects have intricately sculptured genitalia, so that the male fits the female rather like a key inside a lock. This is one (mechanical) way in which the female ensures she is fertilized by the correct male.

An equivalent situation exists in the apple (*Malus × domestica*) but in this case it prevents self-fertilization using a biochemically based pre-zygotic barrier (Figure 2.16). Apple growers know that isolated trees seldom self-pollinate and that another variety is needed nearby to ensure a good harvest. This is due to an ‘anti-selfing mechanism’ known as genetic self-incompatibility (GSI)—a process controlled by a single gene at the S locus. The S gene is highly polymorphic, so each variety of apple produces a slightly different S protein. The stigma (the female part of the flower) is able to differentiate its own S proteins from those of other varieties. Fertilization proceeds only when non-self S proteins are detected.

Even when pollen is introduced to the ova or sperm are introduced to the egg, fertilization may still not happen. Often there are physiological barriers between the gametes of different species, and at

TABLE 2.1

Reproductive barriers

Pre-fertilization (pre-zygotic barriers)

Ecological isolation

Populations are separated by distance or barriers (such as mountains or water bodies)

Temporal isolation

Populations may be reproductively active at different times; they may flower at different times or have different breeding seasons

Behavioural isolation

Without the correct signals to initiate reproductive activity, males and females of different populations may never interbreed

Mechanical isolation

Reproductive organs need to complement each other for the exchange of gametes

Anatomical differences can thus prevent fertilization

Gametic isolation

Unless the sperm and the egg recognize each other, fertilization may be prevented by their failure to fuse

Post-fertilization (post-zygotic barriers)

Hybrid inviability

Embryonic development may be impaired so a hybrid never reaches the adult stage

Hybrid sterility

Offspring are produced but they are infertile, producing either dysfunctional gametes or no gametes at all

Hybrid breakdown

Although the offspring are fertile and may reproduce, their young fail to develop properly, cannot reproduce, or are poorly adapted to new habitat

the cellular level, the two cells have to recognize each other. The failure of an egg cell to recognize a sperm (or *vice versa*) prevents fertilization between species, and sometimes within species too.

Compared to the intricacies of cellular recognition, behavioural barriers to reproduction are easily observed since they frequently involve spectacular courtship rituals. In a variety of animals, females



Figure 2.16 Apple (*Malus × domestica*), in this case Kidd's Red Orange, is a mid-season variety that is not self-fertile. The stigma of the flowers distinguish between self and non-self pollen on the basis of a protein coded by a single gene.

select between males according to some indication of the quality of their genotype—the so-called **good gene hypothesis**. The males boast of their prowess by their appearance, or by their song or dance routine. Fanciful plumage or the capacity to build a complex nest is an indication of the fitness of the male—those with poor colours or offering a poorly built nest may not have genes that will confer an advantage to any offspring. The female selects between competing males, using her judgment of their fitness. This can be a potent selective pressure that helps explain the elaborate displays and behaviour of many males, particularly amongst birds, such as peacocks or the birds of paradise.

This is termed **sexual selection** because the success of the male is determined by the selectivity of the female (or *vice versa*). In some species, males select females in the same way, especially if the male makes a large contribution to the reproductive effort, perhaps by helping to feed or protect the young.

Sexual selection has been a key driver of evolutionary change. It is one reason why there are visible differences between the sexes (**sexual dimorphism**) in

some species, including ourselves. Sexual selection may also be responsible for the diversity within a population. The jumping spider *Habronattus pugillis* lives on isolated Arizona mountain tops, which limits gene flow between populations. Females choose mates according to their capacity to drum their legs and wave their palps. Damian Elias and his colleagues found the females consistently preferred males that could drum to a different beat rather than hammer out the familiar rhythms. This may be a means of ensuring outbreeding, by selecting partners with very different genes, or simply those which are adaptable and more inventive.

These displays or signals can be important in ensuring that mating does not take place between closely related species. Part of the massive variety of fruit flies (*Drosophila*) in Hawai'i is due to sexual selection. Males of some species are required to dance for the right to mate with a female. By their dance so they are known, and getting the steps right signals to the female that the male belongs to the correct species. In this way, different species have developed on different islands and have remained separate. If the signals

are not recognized by the female or the male fails to impress, he may never get to pass on his genes.

Other reproductive barriers operate after fertilization has occurred. These **post-zygotic barriers** operate at various stages in the development of the zygote. A mismatch between the number of chromosomes in the sperm and the egg means that the development of the offspring is not likely to proceed very far. Even amongst closely related species, matching (homologous) chromosomes may differ according to their gene sequence and such incompatibilities usually cause meiosis to fail.

Sterile hybrids unable to produce effective and viable gametes are often the result of interspecific crosses. Even where a hybrid develops to full maturity, there are a number of reasons it may not breed, collectively called **hybrid breakdown**. Many hybrids are poorly adapted to the habitat. One example is the intermediate forms of *Papilio dardanus*. When females are a poor match to any of the distasteful butterflies mimicked by others, they are readily taken by predators. In the same way, hybrids are likely to lose competitive battles with a parent population closely adapted to a specific niche.

Reproductive barriers preserve species differences and, for animal species at least, make them the most well-defined taxonomic unit. Whereas the rest of the hierarchy is our classificatory convenience, many species are distinct and operate as functional units. Reproductive barriers prevent closely related species from blending into each other. The faster these reproductive barriers are erected the quicker the identity of a species becomes established. The longer the barriers have been in place, the less likely it is that hybrids will form.

Sympatric speciation

With sympatric speciation, species are formed by becoming reproductively isolated through genetic change, even though they are living side by side. Gene flow is halted not by a physical barrier but by individuals becoming separated by their genetic differences.

One mechanism by which sympatric speciation can occur is through **polyploidy**. This happens when

normal diploid ($2n$) individuals produce gametes with multiple copies of their chromosomes. A gamete that fails to undergo meiosis will remain diploid. When it unites with a standard haploid gamete, a triploid ($3n$) zygote is formed. Tetraploids ($4n$) form when two diploid gametes combine. Polyploidy rarely results in viable or fertile offspring in animals and is much more common in plants. This may be because plants tend not to have sex chromosomes (save for a few exceptions such as hops (*Humulus lupulus*), cannabis (*Cannabis sativa*), and white campion (*Silene latifolia*)—Figure 2.17, most are hermaphrodite and any polyploidy offspring grow bigger and may out-compete their diploid counterparts). Polyploidy has been an important element in the speciation of several crop plants, especially cereals (Box 2.5).

Sympatric speciation may follow relatively small changes in the environment. Character displacement is seen in Schluter's sticklebacks as individuals begin to feed in one part of the resource spectrum, reinforced by the genetic isolation created by assortative mating. Other evidence that speciation can follow genetic change alone comes from other freshwater fish—the remarkable cichlids of Africa.

The ribbon of lakes within the African Rift Valley includes both fresh and saline waters. Water levels change dramatically from one year to the next, and over thousands of years the lakes have expanded and contracted considerably. Some lakes have been cut off from each other for thousands of years, during which time their fish communities have speciated into a large number of forms. Even within a single lake, differences in habitat type as well as the range of available habitats created by changing water levels have promoted speciation. Lake Victoria, for example, has over 300 species of cichlid fish that have evolved in the last 750 000 years, largely differentiated by their food source and method of feeding. For example, there are several species that feed primarily on molluscs but are differentiated by their feeding methods. The similarities in their genetic code and their mitochondrial DNA suggest the cichlids in Lake Victoria have evolved from a single ancestral species.

Outside the Rift Valley there are some lakes which have never been connected to other water courses.



Figure 2.17 White campion (*Silene latifolia*), one of the few plant species to have sex chromosomes.

Two volcanic crater lakes in Cameroon studied by Ulrich Schlieven and his co-workers also have endemic cichlids unique to each lake (11 and 9 species respectively), despite being very small and with little habitat differentiation. Again, their molecular biology suggests each group was probably derived from a single colonization event in each lake. Since the lakes are very uniform, with no effective inflow from surrounding rivers, the speciation within each was almost certainly sympatric. Indeed, the phylogenetic tree for the cichlids of each lake suggests that their divergence was prompted by niche differentiation driven again by their feeding behaviour.

Some ecologists also recognize another form of speciation termed **parapatric speciation**, which is a feature of small, isolated, and rapidly reproducing populations. This is a particular form of sympatric speciation in which gene exchange is confined to individuals occupying a small area. The resultant inbreeding leads to highly adapted local populations, found in distinct and discrete habitats. The immobility of plants with especially restricted gene flow can produce local races or **ecotypes**. A good example of this is the metal-tolerant ecotypes of various grasses (Box 2.4).

In this case, some individuals have colonized a marginal habitat poisonous to most members of the parent population. Here they grow in the absence of competition. We often find that highly adapted ecotypes are less competitive forms that would lose any intraspecific battles with the normal types. It seems that the costs of withstanding the high levels of stress (the toxic metals) put them at a disadvantage in normal soils.

However, the benefits can far outweigh the costs when growing unhindered on contaminated soil. Tom McNeilly and his colleagues studied a colony of common bent grass (*Agrostis capillaris*) growing on an abandoned copper mine in North Wales. The metal-tolerant ecotypes were surrounded by non-tolerant individuals on uncontaminated pasture but with the wind carrying pollen on and off the contaminated site. McNeilly found metal-tolerant individuals growing 1 m upwind and 180 m downwind of the mine, so tolerant genes did move off the site (Figure 2.19). Similarly pollen from non-tolerant plants arrived on the site, but, not surprisingly, seed containing non-tolerant genes failed to grow on the toxic spoil. Because of their competitive disadvantage,

BOX
2.4

The evolution of the metal tolerance in plants

Large-scale extraction of metal ores has created a series of distinctive habitats in which most plant species cannot survive. Yet some plants have colonized these sites, providing evidence of the speed of adaptive change. In Britain, sites first exploited 200 years ago now have varieties of grasses tolerant of toxic metals, several of which appear to have evolved from local populations where no tolerance is evident. These grasses have proved useful in restoring spoil heaps, where little else will grow (Section 7.3).

Tolerance seems to evolve fairly readily in some grasses. Adaptations to lead, copper, zinc, and others have arisen in different species and some varieties are tolerant to combinations of metals. Sowing normal grass seed onto a toxic spoil will usually produce one or two seedlings that are able to survive. This is an indication that the genetic information for tolerance occurs as part of the background variation in the population. Interestingly, while a range of plants are known to have such alleles, albeit at a low frequency, others never show this capacity. Locally adapted varieties are known as ecotypes. Metal-tolerant ecotypes are also found among some animal groups, especially soil-dwelling invertebrates.

The genetic change needed to create an ecotype may not be that large. Some plants produce special proteins that bind toxic metals and prevent them passing from the roots to more sensitive parts of the plant. The most important adaptive change is simply an increase in the amount of this protein produced. Others actually accumulate the metal and store it in parts of the cell where it will do the least damage. This includes vacuoles within the cell or storage in the cell wall. Several plants are so effective at accumulating metals in this way that they are being developed as a means of concentrating precious metals from wastes (Section 7.3).

Strangely, the nature of the tolerance mechanism in grasses may have been revealed by studies of non-tolerant ecotypes of Yorkshire fog (*Holcus lanatus*—Figure 2.18). These will grow on arsenic-contaminated soil provided they are supplied with additional phosphate. Mark MacNair and Quinton Cumbes found *Holcus* was unable to distinguish between the poison and the nutrient, simply because the size and shape of their two ions are so similar. By swamping the soil with excess phosphate the uptake of arsenate could be reduced to a level low enough for the plant to survive. Tolerant ecotypes of *Holcus* can make the distinction

between the nutrient and the poison. Not only does this tell us how this tolerance mechanism functions but it also shows how non-tolerant plants may become poisoned.

Very often, we find that tolerant ecotypes pay a price for their capacity to live in marginal habitats. In normal conditions—say growing in an unpolluted soil alongside normal plants—the ecotypes grow less vigorously than their non-tolerant neighbours. It seems the costs they incur in being tolerant, perhaps the costs of producing metal-binding proteins, mean they are less well adapted to this habitat. This is possibly the reason their genotype is only found at a low frequency in unpolluted habitats.



Figure 2.18 Yorkshire fog grass (*Holcus lanatus*). Varieties of this species have evolved a tolerance to toxic metals.

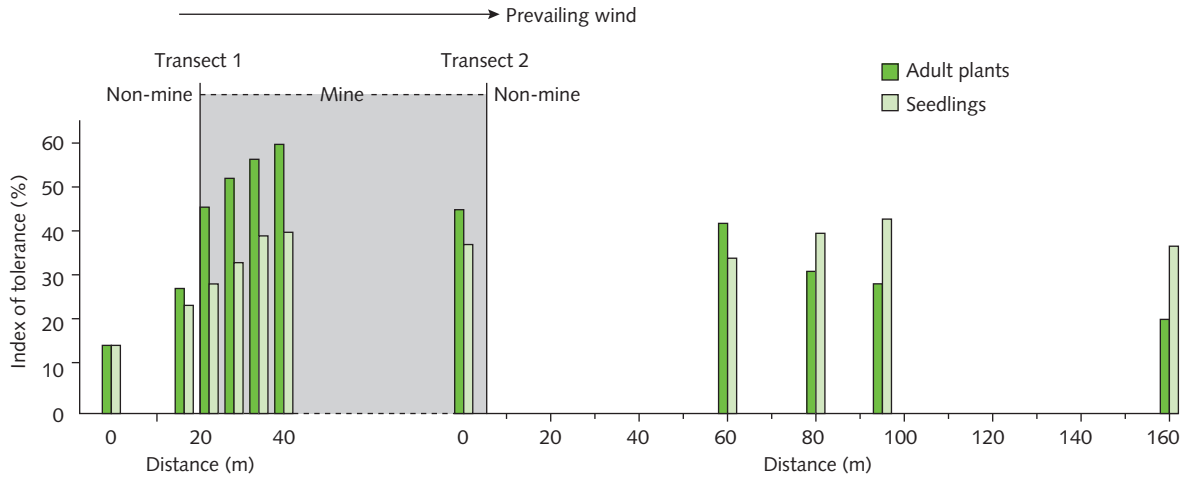


Figure 2.19 Copper tolerance in adult plants (darker coloured bars) and seedlings (lighter coloured bars) of common bent grass (*Agrostis capillaris*). Note the polarization of gene flow, where non-tolerant pollen fails to dilute the tolerant population and the plants growing on the mine spoil. Downwind of the mine, seeds containing genes for metal tolerance fail to develop into adult plants.

metal-tolerant ecotypes were, in the same way, unable to establish on uncontaminated soil.

McNeilly and Janis Antonovics found the two ecotypes had different flowering times, with metal-tolerant individuals producing their pollen much earlier than their non-tolerant counterparts. This minimized the chance of picking up non-tolerant genes and maximized the sharing of genes from other tolerant individuals. McNeilly and Antonovics were able to show that early flowering was an inherited

characteristic and that a reproductive barrier was forming between the two ecotypes.

Man-made species

Over the past 10 000 years or so, humans have been the major selective pressure in the lives of thousands of plant and animal species. By means of domestication and cultivation, we have selected those varieties most suited to our purpose (Box 2.5).

BOX 2.5

The seeds of civilization

Around 12 000 years ago, humans began the move away from hunter-gathering towards a more settled life dominated by agriculture. Wheat, as one of the first plants to be cultivated, was central to this change and remains one of the staple foods of many peoples today. Indeed, the evolution and spread of wheat and other cereals closely follow those of a number of civilizations (Box 5.1, Table 5.2).

Archaeological evidence from the Near East suggests that wheat was widely grown in the Jordan Valley, Jericho, and Damascus around 10 000 years ago, though its first use may have been a thousand years before, during a cooling in the

climate known as the Younger Dryas. Perhaps then the grain was simply collected from the wild, but eventually some seed was saved and sown to ensure the size of the harvest the following year. In so doing, human beings began its cultivation and in the process, its domestication, selecting and sowing seed from plants with the most useful characteristics.

The cultivation of wheat probably began in the 'Fertile Crescent'—an area stretching across the Near East through to Mesopotamia (the land between the rivers Tigris and Euphrates). The origins of wild wheat have been revealed (continued overleaf)

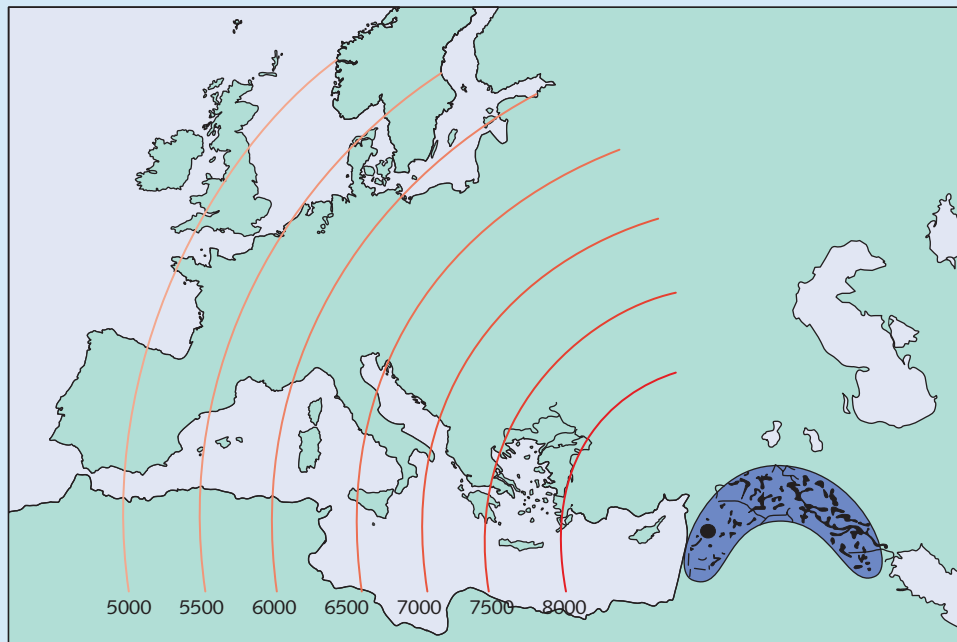


Figure 2.20 The rate of spread of modern wheat (*Triticum aestivum*) and barley (*Hordeum distichon*) from their origins in the 'Fertile Crescent' (blue area). Lines show the approximate date of arrival in years before present.

by genetic sequencing using amplified fragment length polymorphisms (AFLPs), a genome-wide measure of genetic similarity (Box 2.2). The technique identifies einkorn (*Triticum boeoticum*), a grass growing in the western foothills of the Karacadag mountains of southeastern Turkey, as the first cultivated wheat.

By 12 500 years ago, the wild form had been domesticated and was being cultivated in the Fertile Crescent as a new sub-species of cultivated einkorn (*T. monococcum*, ssp. *monococcum*). Cultivated einkorn quickly spread throughout Europe, though by the time of the Bronze Age it too had been superseded by new varieties.

Unlike the diploid einkorn, more recent wheats are polyploid and are derived from wild emmer wheat (*T. dicoccoides*). Emmer enjoys several key advantages from being a tetraploid ($4n$)—it is larger, grows more vigorously, and is also free-threshing, allowing the seeds to be readily separated from their ears. Emmer was the product of a hybridization event between another wild wheat (*T. urartu*) and goat grass (*Aegilops tauschii*). By 9 000 years ago, cultivated emmer wheat (*T. dicoccum*) had supplanted einkorn

to become the single most dominant wheat in cultivation. Within 2 000 years it had spread as far as Europe, Ethiopia, and India, and along with barley (*Hordeum distichon*), became the staple cereal of the Neolithic Period (Figure 2.20).

Around this time, another new species appeared that would eventually come to dominate world agriculture. This was bread wheat (*T. aestivum*), a hexaploid with six sets of chromosomes ($6n$). Again, there seems to have been an intergeneric hybridization with goat grass (*A. tauschii*), this time with the tetraploid cultivated emmer (*T. dicoccum*) somewhere in the Southern Caspian Basin.

Although bread wheat has become the most widely grown of all wheats, with hundreds of different cultivars adapted to different soil types and climates, other wheats are still cultivated. Chief among these is durum or 'macaroni' wheat (*T. durum*). Durum, a descendent of the tetraploid emmers, has a high protein content and is also rich in the pigment beta-carotene, and these give pasta its firm texture and golden colour. This has ensured its continued use in traditional agriculture and cookery and, along with the other cereals, it has had an important role in civilizing humanity.

There are thought to be around 70 000 cultivated plant hybrids derived from a mere 1 100 wild species, though some have an ancestry that includes as many as 35 species. Not surprisingly, this makes them particularly difficult to classify. In the case of hybrids, we simply list the most recent parents using an '×' to indicate the cross.

In the past, cultivated plants were known as varieties, but this term is now used to describe naturally occurring variation within a species. Today, plants bred and cultivated by humans are called **cultivars**. According to the International Code of Nomenclature of Cultivated Plants, a plant must be listed according to its genus and species followed by its cultivar name (usually abbreviated to cv.). For example, Red Ace, a cultivar of shrubby cinquefoil, is usually written as *Potentilla fruticosa* cv. Red Ace.

Hierarchical classification tends to break down at the level of hybrids and cultivars, primarily because we have so often blended very different genotypes to create new varieties. Even so, understanding the evolutionary history of domesticated plants can be very important. Their wild-type relatives often hold genes which make them tougher and more resilient, and we use this genetic diversity to produce more resistant cultivars. For example, potatoes are plagued by aphids and the cost of insecticides to protect them is considerable. The wild hairy potato of Central America has been used to produce aphid-resistant cultivars that impale aphid attackers on short, sharp hairs.

Unfortunately, pests evolve too and our pest-resistant cultivars often have only a limited useful life. Most strains of wheat resistant to fungal attack ('rust') last little more than 5 years before the fungi itself adapts to the change in its niche. Within a decade, the build up of pests and diseases associated with a cultivar may make it uneconomic to grow. Crop-breeding programmes continue the evolutionary battle between our domesticated plants and their pests (Section 4.5).

Genetic engineering has taken some of the guesswork out of crop and stock improvement. By incorporating selected genes from other organisms into the genome of economically-important species, we can enhance their productivity or confer protection

against pests and disease. Gene technology offers the opportunity to move genetic code across species boundaries and even between phyla. Today, we can practise evolution by intelligent design.

The first commercial applications of genetic engineering sought to extend the shelf life of tomatoes by manipulating the genes that control the ripening process. Since then, herbicide resistance genes have been incorporated into the genome of soybeans to allow the blanket application of herbicide (in this case *Roundup*) without damage to the crop. However, such techniques are highly controversial. First, it seems contrary to our increasing emphasis on sustainable and 'green' agricultural practices, relying as it does on biocides. Second, the technology is seen by some as tying farmers into buying both seed and pesticide from the same biotechnology company. Finally, there is the possibility of the introduced genes moving into less desirable species, perhaps creating resistant weed species.

The latter is a critical issue, given the ease with which most crop plants will hybridize with their wild relatives (Box 2.5). At least 13 major crop species are known to do this (Table 2.2). Plants of the cabbage family, the Brassicaceae represent a particular risk for transgene escape. Wild cabbage (*Brassica oleracea*) has been domesticated to produce varieties which include cauliflower, broccoli, spring greens, and sprouts. Rapeseed (*B. napus* ssp. *oleifera*), a major oilseed crop throughout the world, arose out of a chance hybridization between *B. oleracea* and wild turnip (*B. rapa*) in the western Mediterranean. Both remain highly inter-fertile with other species within the Brassicaceae.

The potential risks of transgene escape led Mike Wilkinson and his colleagues to measure the probability of hybridization between rapeseed and their wild relatives. In the United Kingdom, wild turnip occurs around crops and alongside watercourses. Wilkinson and his team used a series of techniques—satellite imagery, biological databases, survey work, and genetic analysis—to locate areas of overlap and to measure its rate of hybridization with rapeseed. By identifying gene sequences unique to these plants, they could distinguish hybrids from the diploid wild turnip and tetraploid rapeseed. Mixed parentage

TABLE 2.2

Plant families known to hybridize with wild relatives

Plant family	GM species of potential risk
Asteraceae (formerly Compositae)	Lettuce, sunflower
Apiaceae (formerly Umbelliferae)	Carrot
Brassicaceae	Broccoli, cabbage, rapeseed (canola)
Chenopodiaceae	Sugar beet
Ericaceae	Blueberry
Juglandaceae	Walnut
Leguminosae	Alfalfa, soybean, peanut
Malvaceae	Cotton
Poaceae (formerly Graminae)	Creeping bentgrass, maize (corn), rice, sorghum, wheat
Rosaceae	Apple, strawberry
Salicaceae	Poplar
Solanaceae	Aubergine (egg plant), potato, tobacco, tomato
Vitaceae	Grape

which included *B. rapa* was found in 1.46 per cent of the samples, one measure of their likely hybridization.

Transgene escape might be avoided by incorporating the engineered genes into chloroplast DNA rather than the nuclear genome. This would ensure that genes do not escape within the pollen, the male gamete, since chloroplast DNA, like mitochondrial DNA, is inherited only through the maternal line. Moving a gene from one species to another is an obvious genetic transformation, but how do we regard copying an existing gene and placing multiple copies in the original owner? No foreign code has been incorporated into the genome, but some form of genetic modification has taken place. Joachim

TABLE 2.3

Potential sources of foreign genes or gene products of genetically modified organisms

Organism/product	Sources
Animals	Carcasses Faeces Urine
Plants	Biomass Food chain effects Pollen Root exudates
Microbes	Fermentor malfunction Waste media Waste micro-organisms

Messing and Jinsheng Lai have modified the genome of maize to increase its content of the amino acid methionine by altering the genes controlling its production. They suggest this might be regarded as no more than a special, accelerated form of plant breeding.

In contrast, foreign genes can pose practical and ethical dilemmas to those that consume them. Engineering high-methionine soybean by incorporating a gene from the Brazil nut resulted in beans with a protein capable of triggering nut allergies in susceptible consumers. The risks to human health were considered so great that the project was eventually abandoned. A clear identification of the genetic composition of transgenic material and its consequences is therefore needed to protect those who avoid contact with a species for reasons of health, custom, or ethical concerns.

There is also the question of specificity, and whether non-target species can be affected. A gene derived from the bacteria *Bacillus thuringiensis* produces δ -endotoxin, a protein that could protect plants from insect pests. Unfortunately, plant material from transgenic maize containing the endotoxin

gene has been implicated in poisoning the larvae of the Monarch butterfly (*Danaus plexippus*). Other non-target species may be at risk because δ -endotoxin will leach out of the host plant and persist in the environment for up to 180 days. Traces have been found in earthworms, and this has raised concerns that it might pass further along the food chain.

In trying to escape the problems of conventional biocides—such as toxicity and persistence—we have created a new generation of pest control technologies with some of the faults of the old and the fears of the new (Table 2.3). Gene technology offers the potential to combat disease, hunger, and pollution but we are only just beginning to understand its ecological implications.

● SUMMARY

The binomial system for classifying and naming living organisms provides an internationally accepted convention for naming species, and its hierarchical structure is indicative of their phylogenetic relations. Most classification has traditionally been based on morphology, but we now measure genetic differences and arrange phylogenies using molecular biology. The biological species concept is useful for many higher plants and animals but is not readily applicable to those groups that hybridize freely.

A species' ecological niche is the totality of factors, biotic and abiotic, to which it has adapted. Species occupying a narrow niche are specialized for a particular part of a resource spectrum whilst generalist species have a broad niche. Two species may not occupy the same niche. Intense competition for a resource will lead to character displacement, and within a species, some individuals adapt to exploit a different part of a resource spectrum.

Speciation occurs where gene flow ceases between two populations. This can occur because the populations become physically separated (allopatric speciation) or isolated from each other by a genetic change (sympatric speciation). Barriers to gene flow can occur before or after fertilization (pre- and post-zygotic barriers). Speciation follows not only from natural selection but also occurs as a consequence of selective pressures applied by humans in their breeding of plants and animals. Genetic engineering offers new opportunities but also presents new challenges in environmental protection.

● FURTHER READING

Jeffrey, C. 1977. *Biological Nomenclature*. Edward Arnold, London. [A useful introduction to the rules of naming.](#)

Jones, S. 1999. *Almost like a Whale*. Anchor, Doubleday, London. [A highly readable review of current evidence and understanding of evolution by natural selection.](#)

Price, P. W. 1996. *Biological Evolution*. Saunders, Fort Worth. [A systematic and comprehensive introduction to current thinking on evolution.](#)

Weiner, J. 1994. *The Beak of the Finch*. Knopf, New York. [An excellent account of detailed research into the Galapagos finches originally studied by Darwin and other research, including Schluter's work on sticklebacks.](#)

Zohary, D. and Hopf, M. 2000. *Domestication of Plants in the Old World*. Oxford University Press, Oxford. [A useful reference source.](#)

● WEB PAGES

The Tree of Life site provides a wide range of information and links on phylogeny and biodiversity: <http://tolweb.org/tree/phylogeny.html>

The following is a web directory to several aspects covered here, including biological nomenclature: <http://www.biologybrowser.org>

More about Dolph Schluter and his sticklebacks can be found at: <http://www.zoology.ubc.ca/~schluter/>

The Sanger Institute is a key participant in the Human Genome Project. Its website has general resources and specific information on gene sequencing techniques: <http://www.sanger.ac.uk/>

CASE STUDY 2

How to produce a new palm

The Kentia palm (*Howea forsteriana*) is a familiar sight in homes and offices across the world, yet it is far away from its evolutionary home. It grows naturally on Lord Howe Island in the South Pacific, alongside its close relative, the curly palm (*H. belmoreana*) (Figure 2.21). How did the two species arise and did this result from their proximity on Howe?

How indeed? Plant populations on the road to sympatric speciation often reinforce the process by shifting their flowering times. Vincent Savolainen of the Royal Botanic Gardens, Kew investigated the evolutionary history of the two palms that were known to have reproductive phases approximately six weeks apart (Savolainen *et al.* 2006; Figure 2.22).

Savolainen and his team used amplified fragment length polymorphism (AFPL) to measure how much of their genome is shared by the two species. This was then compared against a DNA-based phylogenetic tree for all Indo-Pacific palms (Dransfield *et al.* 2005) to place the *Howea* species on this evolutionary time-line. *Howea* appears to have split into two species around 1.92 million years ago, having evolved from the Australian palm *Laccospadix*.

The pattern of genetic differences within their genome also indicated the time since their separation occurred. With allopatric speciation, differences caused by genetic drift tend to be spread evenly across the genome, across many different loci, and these will accumulate as the period of genetic separation increases (Via 2001). In contrast, the differences found between the *Howea* were restricted to a small part of

the genome, just four loci, indicative of a relatively recent separation.

H. belmoreana grows in acid and neutral soils whereas *H. forsteriana* tends to favour more alkaline conditions (Figure 2.23). A common ancestor would have had to colonize the nutrient-poor, acidic volcanic ash in the early days of the island. Over time more alkaline soils would have developed, especially in lowland areas where organic material accumulated and calcareous deposits blew in from the ocean (Figure 2.24). This created a new abiotic factor in relation to which the plants could adapt and differentiate themselves, a new niche associated with the new soil conditions. However, since individuals would be growing near enough to cross-pollinate, it would need a shift in flowering time, rather like in the case of the metal-tolerant grasses (Section 2.6), to produce the divergence. A recent sympatric speciation therefore seems the most likely mechanism.

Savolainen's findings are supported by other evidence, in particular the timing of the alkaline coastal deposits, which coincides with the genetic splitting of the species (Brooke *et al.* 2003). As with the grasses, the advantages of adapting to a different soil were best preserved by keeping their genes to themselves rather than swapping them with their neighbours, so a difference in flowering time may once again have been the mechanism of sympatric speciation in the palms. Molecular changes in their genotypes correspond to the changes in the soils of Howe and the opportunities for a new niche that the island offered.

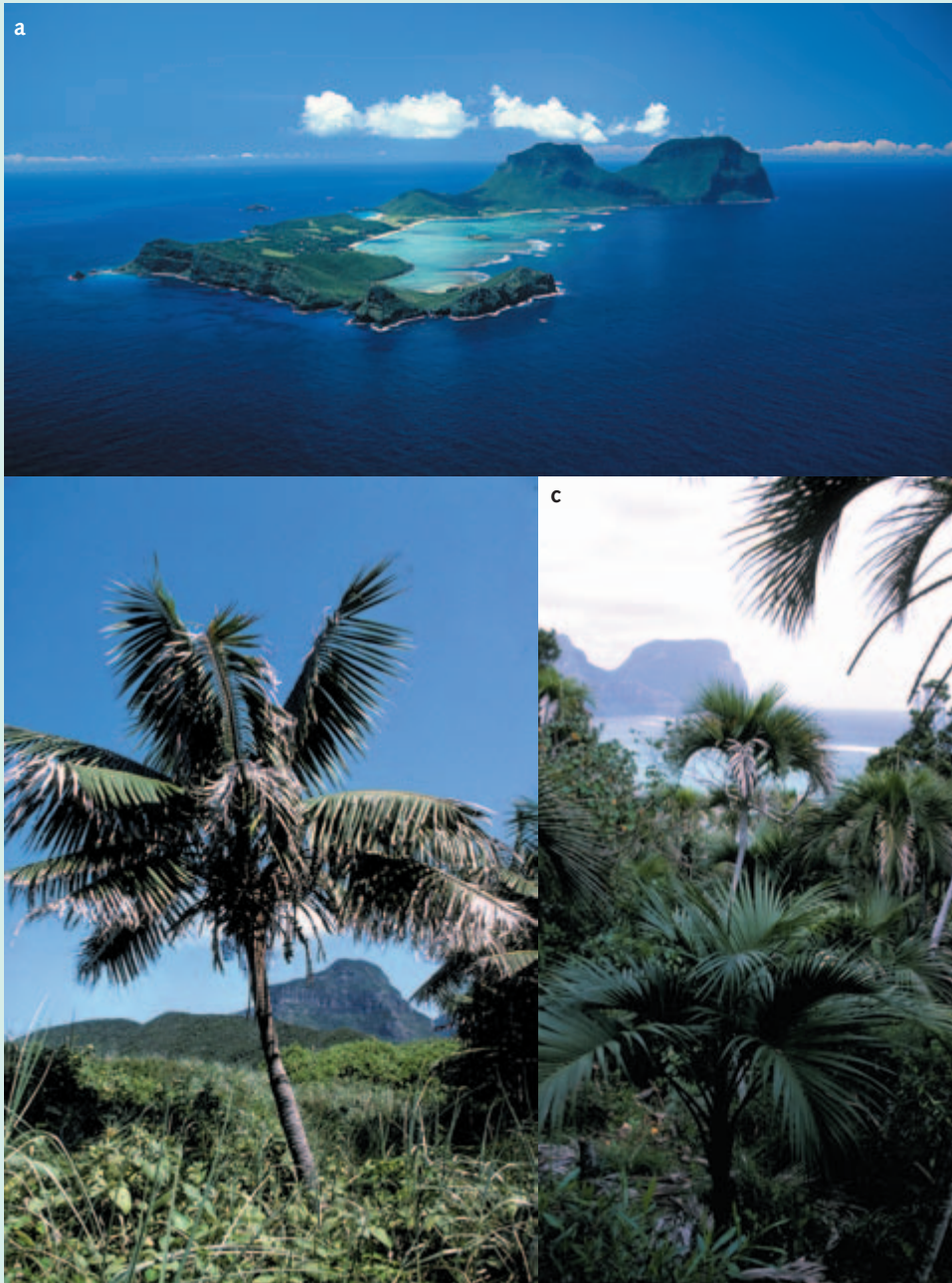


Figure 2.21 (a) Lord Howe Island, a small volcanic island less than 12 km². Australia is the closest land mass, 580 km to the west. (b) Kentia palm (*Howea forsteriana*), an endemic of Lord Howe Island but known the world over as an ornamental plant. (c) The curly palm (*H. belmoreana*) the other endemic *Howea* of the island.

(continued overleaf)

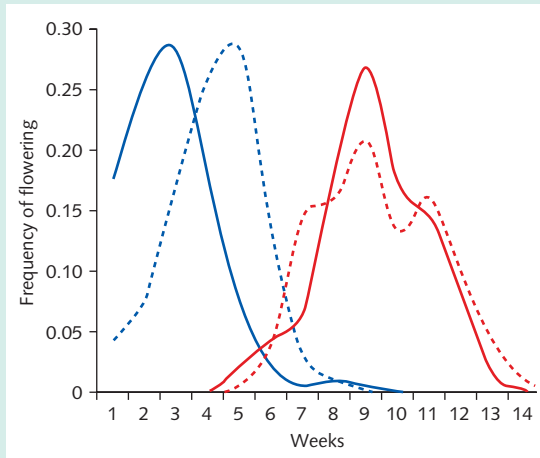


Figure 2.22 The flowering times of the two *Howea* species. *H. forsteriana* in blue and *H. belmoreana* in red (solid line male flowers, dotted line female flowers). Note the strong separation between the peak flowering period of the two species.

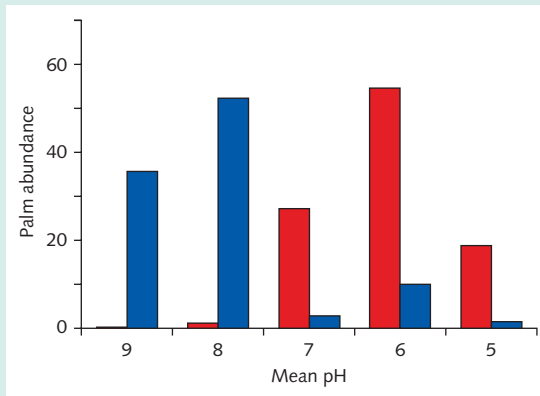


Figure 2.23 Distribution of *H. forsteriana* (blue) and *H. belmoreana* (red) according to mean pH. The two species show distinct preferences for acidic (*H. belmoreana*) or alkaline soils (*H. forsteriana*).

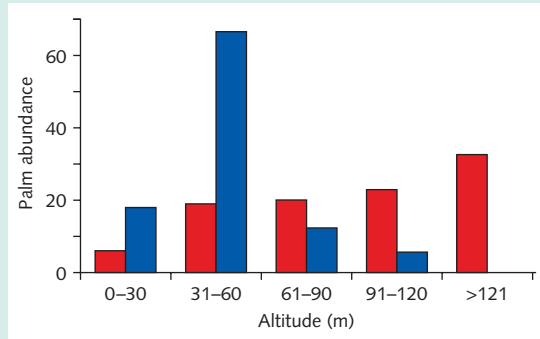


Figure 2.24 Distribution of *H. forsteriana* (black) and *H. belmoreana* (grey) according to altitude: with *H. belmoreana* tending to favour the higher ground and *H. forsteriana* lowland areas.

References

- Brooke, B. R., Woodroffe, C. D., Murray-Wallace, C. V., Hejijinis, H., and Jones, B. G. 2003. Quaternary calcarenite stratigraphy on Lord Howe Island, southern Pacific Ocean and the record of coastal carbonate deposition. *Quaternary Science Review* 22, 859–880.
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- Savolainen, V., Anstett, M.-C., Lexer, C., Huton, I., Clarkson, J., Norup, M. V., Powell, M. P., Springate, D., Salamim N., and Baker, W. J. 2006. Sympatric speciation in palms on an oceanic island. *Nature* 44, 210–213.
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EXERCISES

1. Using Figure 2.4 as an example, devise a key to classify the following insects according to the characteristics listed in the table below. Seek to use the minimum number of steps.

Characteristic	Insect type					
	Wasp	Beetle	Butterfly	Fly	Grasshopper	Ant
Wings present	Y	Y	Y	Y	Y	N
Number of wings	4	4	4	2	4	0
Hard wing case	N	Y	N	N	N	N
Large dusty wings	N	N	Y	N	N	N
Large jumping legs	N	N	N	N	Y	N

2. Match the following modes of speciation with their correct descriptions:
- Allopatric
 - Parapatric
 - Sympatric
- Divergence within populations which share the same range but become adapted to local conditions.
 - Geographical isolation within a population leading to the formation of new species.
 - Speciation arising within a population as a result of a genetic change that restricts gene flow.
3. What are the advantages of using mitochondrial DNA in genetic analysis?
4. Match the following types of reproductive barriers with their appropriate description. Then group them into either pre- or post-zygotic barriers.
- Behavioural isolation
 - Ecological isolation
 - Gametic isolation
 - Hybrid breakdown
 - Hybrid inviability
 - Hybrid sterility
 - Mechanical isolation
 - Temporal isolation
- Anatomical differences can prevent fertilization as reproductive organs need to complement each other for the exchange of gametes.
 - Although the offspring are fertile and may reproduce, their young fail to develop properly, cannot reproduce or are poorly adapted to new habitat.
 - Embryonic development may be impaired so a hybrid never reaches the adult stage.
 - Offspring are produced but they are infertile, producing either dysfunctional gametes or no gametes at all.
 - Populations are separated by distance or barriers (such as mountains or water bodies).

- (vi) Populations may be reproductively active at different times; they may flower at different breeding seasons.
- (vii) Unless the sperm and the egg recognize each other fertilization may be prevented by their failure to fuse.
- (viii) Without the correct signals to initiate reproductive activity, males and females of different populations may never interbreed.

5. The following measurements of niche breadth were made for four species along a resource gradient and its overlap with neighbouring species:

(Note—1.0 indicates maximum niche breadth across the entire resource spectrum. 1.0 also indicates complete niche overlap with other species.)

	Niche breadth	Niche overlap
Species A	0.7	0.8
Species B	0.2	0.1
Species C	0.2	0.8
Species D	0.7	0.1

Identify:

- (a) Specialist species likely to be suffering intense competition
- (b) Generalist species likely to be suffering intense competition
- (c) Specialist species likely to be little competition
- (d) Generalist species likely to be little competition

Which species may have a realized niche almost as large as its fundamental niche?

6. Explain what is meant by:
- (a) the morphological species concept
 - (b) the biological species concept
 - (c) the ecological species concept

In your answers indicate the limitations of each concept.

Tutorial/seminar questions

- 7. Does genetic variability have a conservation value? How should we measure it and would it be comparable between species we are trying to protect?
- 8. Given that we have bred domesticated plants and animals for many thousands of years, why should we not regard genetic manipulation as another form of artificial selection?