

Chapter 2 Conditions

2.1 Introduction

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

conditions may be altered – but not consumed

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

For some conditions we can recognize an optimum concentration or level at which an organism performs best, with its activity tailing off at both lower and higher levels (Figure 2.1a). But we need to define what we mean by 'performs best'. From an evolutionary point of view, 'optimal' conditions are those under which individuals leave most descendants (are fittest), but these are often impossible to determine in practice because measures of fitness should be made over several generations. Instead, we more often measure the effect of conditions on some key property like the activity of an enzyme, the respiration rate of a tissue, the growth rate of individuals or their rate of reproduction. However, the effect of variation in conditions on these various properties will often not be the same; organisms can usually survive over a wider range of conditions than permit them to grow or reproduce (Figure 2.1a).

The precise shape of a species' response will vary from condition to condition. The generalized form of response, shown in Figure 2.1a, is appropriate for conditions like temperature and pH

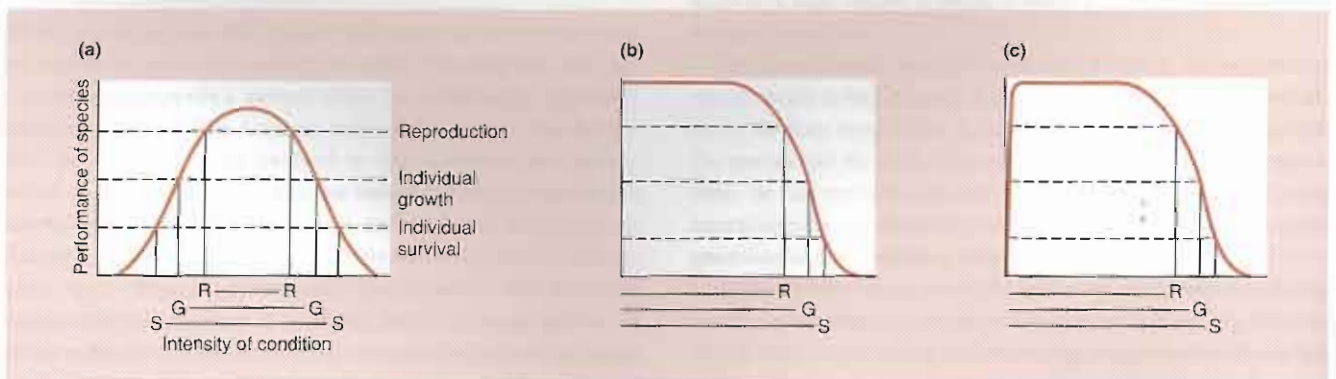


Figure 2.1 Response curves illustrating the effects of a range of environmental conditions on individual survival (S), growth (G) and reproduction (R). (a) Extreme conditions are lethal; less extreme conditions prevent growth; only optimal conditions allow reproduction. (b) The condition is lethal only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

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

In this chapter, we consider responses to temperature in much more detail than other conditions, because it is the single most important condition that affects the lives of organisms, and many of the generalizations that we make have widespread relevance. We move on to consider a range of other conditions, before returning, full circle, to temperature because of the effects of other conditions, notably pollutants, on global warming. We begin, though, by explaining the framework within which each of these conditions should be understood here: the ecological niche.

2.2 Ecological niches

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

The modern concept of the niche was proposed by Hutchinson in 1957 to address the ways in which tolerances and requirements interact to define the conditions (this chapter) and resources (Chapter 3) needed by an individual or a species in order

to practice its way of life. Temperature, for instance, limits the growth and reproduction of all organisms, but different organisms tolerate different ranges of temperature. This range is one *dimension* of an organism's ecological niche. Figure 2.2a shows how species of plants vary in this dimension of their niche: how they vary in the range of temperatures at which they can survive. But there are many such dimensions of a species' niche – its tolerance of various other conditions (relative humidity, pH, wind speed, water flow and so on) and its need for various resources. Clearly the real niche of a species must be *multidimensional*.

It is easy to visualize the early stages of building such a multidimensional niche. Figure 2.2b illustrates the way in which two niche dimensions (temperature and salinity) together define a two-dimensional area that is part of the niche of a sand shrimp. Three dimensions, such as temperature, pH and the availability of a particular food, may define a three-dimensional niche volume (Figure 2.2c). In fact, we consider a niche to be an *n-dimensional hypervolume*, where *n* is the number of dimensions that make up the niche. It is hard to imagine (and impossible to draw) this more realistic picture. None the less, the simplified three-dimensional version captures the idea of the ecological niche of a species. It is defined by the boundaries that limit where it can live, grow and reproduce, and it is very clearly a concept rather than a place. The concept has become a cornerstone of ecological thought.

Provided that a location is characterized by conditions within acceptable limits for a given species, and provided also that it contains all the necessary resources, then the species can, potentially, occur and persist there. Whether or not it does so depends on two further factors. First, it must be able to reach the location, and this depends in turn on its powers of colonization and the remoteness of the site. Second, its occurrence may be precluded by the action of individuals of other species that compete with it or prey on it.

Usually, a species has a larger ecological niche in the absence of competitors and predators than it has in their presence. In other words, there are certain combinations of conditions and resources that can allow a species to maintain a viable population, but only if it is not being adversely affected by enemies. This led Hutchinson to distinguish between the *fundamental* and the *realized* niche. The former describes the overall potentialities of a species; the latter describes the more limited spectrum of conditions and resources that allow it to persist, even in the presence of competitors and predators. Fundamental and realized niches will receive more attention in Chapter 8, when we look at interspecific competition.

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

the *n*-dimensional hypervolume

fundamental and realized niches

niche dimensions

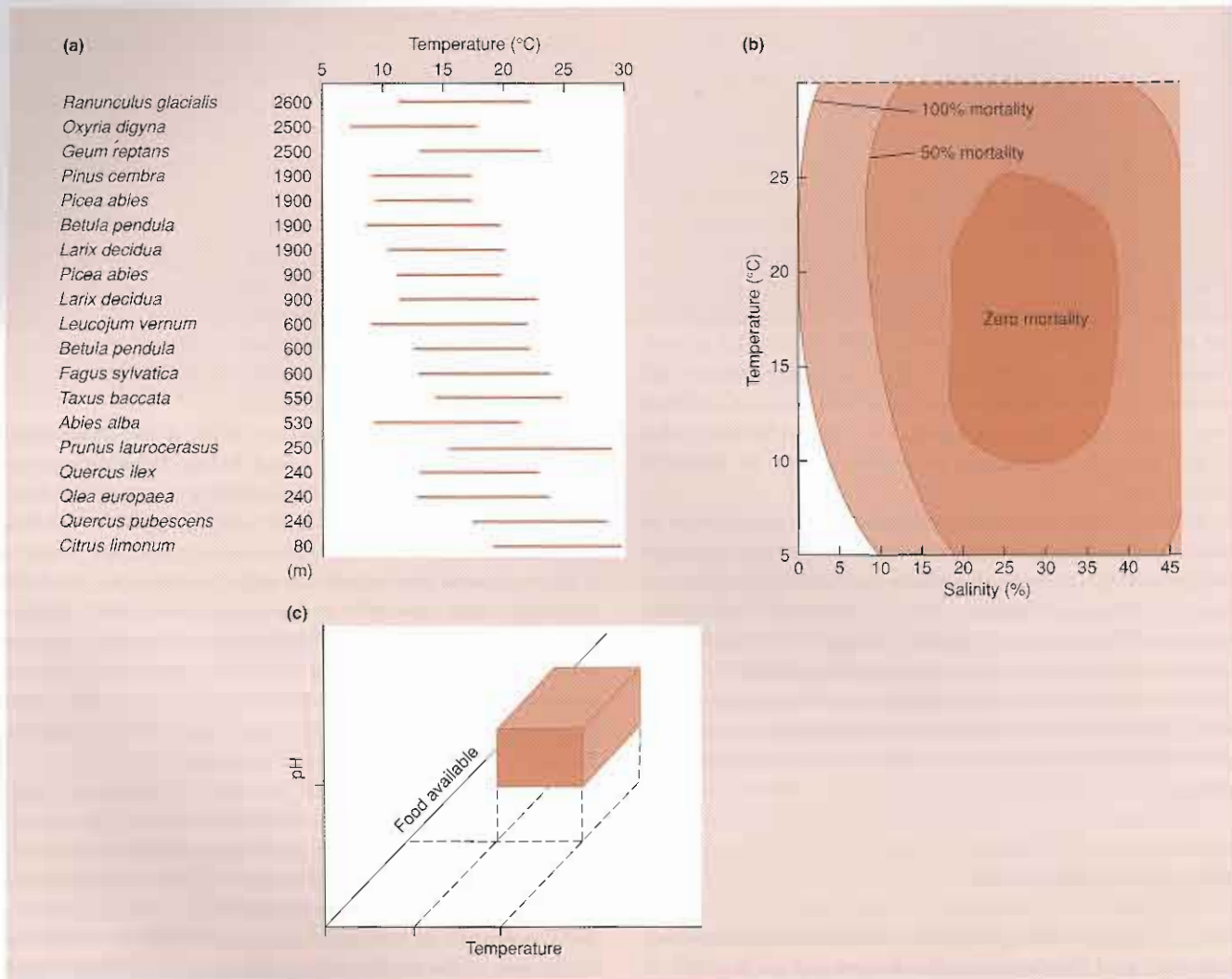


Figure 2.2 (a) A niche in one dimension. The range of temperatures at which a variety of plant species from the European Alps can achieve net photosynthesis of low intensities of radiation (70 W m^{-2}). (After Pisek *et al.*, 1973.) (b) A niche in two dimensions for the sand shrimp (*Crangon septemspinosa*) showing the fate of egg-bearing females in aerated water at a range of temperatures and salinities. (After Haefner, 1970.) (c) A diagrammatic niche in three dimensions for an aquatic organism showing a volume defined by the temperature, pH and availability of food.

2.3 Responses of individuals to temperature

2.3.1 What do we mean by 'extreme'?

It seems natural to describe certain environmental conditions as 'extreme', 'harsh', 'benign' or 'stressful'. It may seem obvious when conditions are 'extreme': the midday heat of a desert, the cold of an Antarctic winter, the salinity of the Great Salt Lake. But this only means that these conditions are extreme *for us*, given our particular physiological characteristics and tolerances.

To a cactus there is nothing extreme about the desert conditions in which cacti have evolved; nor are the icy fastnesses of Antarctica an extreme environment for penguins (Wharton, 2002). It is too easy and dangerous for the ecologist to assume that all other organisms sense the environment in the way we do. Rather, the ecologist should try to gain a worm's-eye or plaut's-eye view of the environment: to see the world as others see it. Emotive words like harsh and benign, even relativities such as hot and cold, should be used by ecologists only with care.

aposematism

Whilst crypsis may be a defense strategy for a palatable organism, noxious or dangerous animals often seem to advertize the fact by bright, conspicuous colors and patterns. This phenomenon is referred to as *aposematism*. The monarch butterfly, discussed above, is aposematically colored, as is its caterpillar, which actually sequesters the defensive cardiac glucosinolates from its food. The usual evolutionary argument for this runs as follows: conspicuous coloration will be favored because noxious prey will be recognized (memorized) as such by experienced predators, and thus will be protected, whereas the costs of 'educating' the predator will have been shared amongst the whole population of conspicuous prey. This argument, however, leaves unanswered the question of how conspicuous, noxious prey arose in the first place, since when initially rare, they seem likely to be repeatedly eliminated by naive (i.e. 'uneducated') predators (Speed & Ruxton, 2002). One possible answer is that predators and prey have coevolved: in each generation – from an original mixture of conspicuous and inconspicuous, noxious and edible prey – conspicuous edible prey are eliminated, and, with conspicuous prey therefore becoming disproportionately noxious, predators evolve an increased wariness for conspicuous prey (Sherratt, 2002).

Batesian and Mullerian mimicry

The adoption of memorable body patterns by distasteful prey also immediately opens the door for deceit by other species, because there will be a clear evolutionary advantage to a palatable prey, 'the mimic', if it looks like an unpalatable species, 'the model' (Batesian mimicry). Developing the story of the monarch butterfly a little further, the adult of the palatable viceroy butterfly mimics the distasteful monarch, and a blue jay that has learned to avoid monarchs will also avoid viceroys. There will also be an advantage to aposematically colored, distasteful prey in looking like one another (Müllerian mimicry), though many unanswered questions remain as to where exactly Batesian mimicry ends and Müllerian mimicry begins, in part because there are more theoretical viewpoints than impeccable data sets that might distinguish between them (Speed, 1999).

By living in holes (e.g. millipedes and moles) animals may avoid stimulating the sensory receptors of predators, and by 'playing dead' (e.g. the opossum *Didelphis virginiana* and African ground squirrels) animals may fail to stimulate a killing response. Animals that withdraw to a prepared retreat (e.g. rabbits and prairie dogs to their burrows, snails to their shells), or which roll up and protect their vulnerable parts by a tough exterior (e.g. armadillos and pill millipedes), reduce their chance of capture but stake their lives on the chance that the attacker will not be able to breach their defenses. Other animals seem to try to bluff themselves out of trouble by threat displays. The startle response of moths and butterflies that suddenly expose eye-spots on their wings is one example. No doubt the most common behavioral response of an animal in danger of being preyed upon is to flee.

3.8 A classification of resources, and the ecological niche

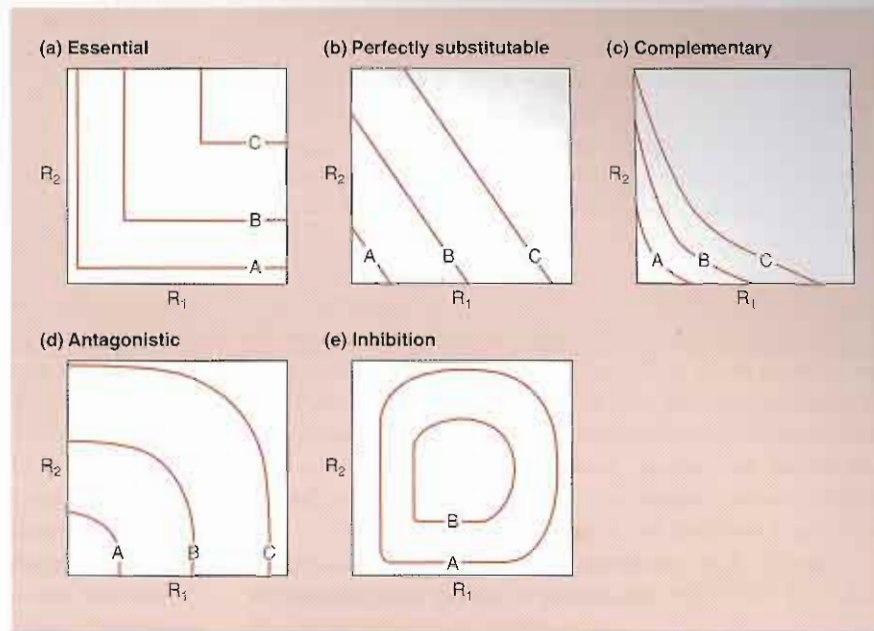
We have seen that every plant requires many distinct resources to complete its life cycle, and most plants require the same set of resources, although in subtly different proportions. Each of the resources has to be obtained independently of the others, and often by quite different uptake mechanisms – some as ions (potassium), some as molecules (CO₂), some in solution, some as gases. Carbon cannot be substituted by nitrogen, nor phosphorus by potassium. Nitrogen can be taken up by most plants as either nitrate or ammonium ions, but there is no substitute for nitrogen itself. In complete contrast, for many carnivores, most prey of about the same size are wholly interchangeable as articles of diet. This contrast between resources that are individually *essential* for an organism, and those that are *substitutable*, can be extended into a classification of resources taken in pairs (Figure 3.27).

In this classification, the concentration or quantity of one resource is plotted on the *x*-axis, and that of the other resource on the *y*-axis. We know that different combinations of the two resources will support different growth rates for the organism in question (this can be individual growth or population growth). Thus, we can join together points (i.e. combinations of resources) with the same growth rates, and these are therefore contours or 'isoclines' of equal growth. In Figure 3.27, line B in each case is an isocline of *zero net growth*: each of the resource combinations on these lines allows the organism just to maintain itself, neither increasing nor decreasing. The A isoclines, then, with less resources than B, join combinations giving the same *negative* growth rate; whilst the C isoclines, with more resources than B, join combinations giving the same *positive* growth rate. As we shall see, the shapes of the isoclines vary with the nature of the resources.

zero net growth isoclines**3.8.1 Essential resources**

Two resources are said to be *essential* when neither can substitute for the other. Thus, the growth that can be supported on resource 1 is absolutely dependent on the amount available of resource 2 and vice versa. This is denoted in Figure 3.27a by the isoclines running parallel to both axes. They do so because the amount available of one resource defines a maximum possible growth rate, irrespective of the amount of the other resource. This growth rate is achieved unless the amount available of the other resource defines an even lower growth rate. It will be true for nitrogen and potassium as resources in the growth of green plants, and for two obligate hosts in the life of a parasite or pathogen that are required to alternate in its life cycle (see Chapter 12).

Figure 3.27 Resource-dependent growth isoclines. Each of the growth isoclines represents the amounts of two resources (R_1 and R_2) that would have to exist in a habitat for a population to have a given growth rate. Because this rate increases with resource availability, isoclines further from the origin represent higher population growth rates – isocline A has a negative growth rate, isocline B a zero growth rate and isocline C a positive growth rate. (a) Essential resources; (b) perfectly substitutable; (c) complementary; (d) antagonistic; and (e) inhibition. (After Tilman, 1982.)



3.8.2 Other categories of resource

Two resources are said to be *perfectly substitutable* when either can wholly replace the other. This will be true for seeds of wheat or barley in the diet of a farmyard chicken, or for zebra and gazelle in the diet of a lion. Note that we do not imply that the two resources are as good as each other. This feature (perfectly substitutable but not necessarily as good as each other) is included in Figure 3.27b by the isoclines having slopes that do not cut both axes at the same distance from the origin. Thus, in Figure 3.27b, in the absence of resource 2, the organism needs relatively little of resource 1, but in the absence of resource 1 it needs a relatively large amount of resource 2.

Substitutable resources are defined as *complementary* if the isoclines bow inwards towards the origin (Figure 3.27c). This shape means that a species requires less of two resources when taken together than when consumed separately. A good example is human vegetarians combining beans and rice in their diet. The beans are rich in lysine, an essential amino acid poorly represented in rice, whilst rice is rich in sulfur-containing amino acids that are present only in low abundance in beans.

A pair of substitutable resources with isoclines that bow away from the origin are defined as *antagonistic* (Figure 3.27d). The shape indicates that a species requires proportionately more resource to maintain a given rate of increase when two resources are consumed together than when consumed separately. This could arise, for

example, if the resources contain different toxic compounds that act synergistically (more than just additively) on their consumer. For example, D, L-pipecolic acid and djenkolic acid (two defensive chemicals found in certain seeds) had no significant effect on the growth of the seed-eating larva of a bruchid beetle if consumed separately, but they had a pronounced effect if taken together (Janzen *et al.*, 1977).

Finally, Figure 3.27e illustrates the phenomenon of *inhibition* at high resource levels for a pair of essential resources: resources that are essential but become damaging when in excess. CO₂, water and mineral nutrients such as iron are all required for photosynthesis, but each is lethal in excess. Similarly, light leads to increased growth rates in plants through a broad range of intensities, but can inhibit growth at very high intensities. In such cases, the isoclines form closed curves because growth decreases with an increase in resources at very high levels.

3.8.3 Resource dimensions of the ecological niche

In Chapter 2 we developed the concept of the ecological niche as an n -dimensional hypervolume. This defines the limits within which a given species can survive and reproduce, for a number (n) of environmental factors, including both conditions and resources. Note, therefore, that the zero growth isoclines in Figure 3.27 define niche boundaries in two dimensions. Resource combinations to one side of line B allow the organisms to thrive – but to the other side of the line the organisms decline.

The resource dimensions of a species' niche can sometimes be represented in a manner similar to that adopted for conditions, with lower and upper limits within which a species can thrive. Thus, a predator may only be able to detect and handle prey between lower and upper limits of size. For other resources, such as mineral nutrients for plants, there may be a lower limit below which individuals cannot grow and reproduce but an upper limit may not exist (Figure 3.27a–d). However, many resources must be viewed as discrete entities rather than continuous variables. Larvae of butterflies in the genus *Heliconius* require *Passiflora* leaves to eat; those of the monarch butterfly specialize on plants in the milkweed family; and various species of animals require nest sites with particular specifications. These resource requirements cannot be arranged along a continuous graph axis labeled, for example, 'food plant species'. Instead, the food plant or nest-site dimension of their niches needs to be defined simply by a restricted list of the appropriate resources.

Together, then, conditions and resources define a species' niche. We turn in the next chapter to look in more detail at the most fundamental responses of organisms to those conditions and resources: their patterns of growth, survival and reproduction.

Summary

Resources are entities required by an organism, the quantities of which can be reduced by the activity of the organism. Hence, organisms may compete with each other to capture a share of a limited resource.

Autotrophic organisms (green plants and certain bacteria) assimilate inorganic resources into packages of organic molecules (proteins, carbohydrates, etc.). These become the resources for heterotrophic organisms, which take part in a chain of events in which each consumer of a resource becomes, in turn, a resource for another consumer.

Solar radiation is the only source of energy that can be used in metabolic activities by green plants. Radiant energy is converted during photosynthesis into energy-rich chemical compounds of carbon, which will subsequently be broken down in respiration. But the photosynthetic apparatus is able to gain access to energy only in the waveband of 'photosynthetically active radiation'. We examine variations in the intensity and quality of radiation, and the responses of plants to such variations. We examine, too, the strategic and tactical solutions adopted by plants to resolve the conflicts between photosynthesis and water conservation.

Carbon dioxide is also essential for photosynthesis. We examine variations in its concentration, and their consequences,

including global rises over time and those at the smallest spatial scales. There are three pathways to carbon fixation in photosynthesis: C_3 , C_4 and CAM. The differences between the different pathways and the ecological consequences of them are explained.

Water is a critical resource for all organisms. For plants, we examine how roots 'forage' for water, and the dynamics of resource depletion zones around roots, for water and for mineral nutrients. Mineral nutrients, broadly divisible into macronutrients and trace elements, each enter a plant independently as an ion or a molecule, and have their own characteristic properties of absorption in the soil and of diffusion, which affect their accessibility to a plant.

Oxygen is a resource for both animals and plants. It becomes limiting most quickly in aquatic and waterlogged environments, and when organic matter decomposes in an aquatic environment, microbial respiration may so deplete oxygen as to constrain the types of higher animal that can persist.

Amongst heterotrophs, we explain the distinctions between saprotrophs, predators, grazers and parasites, and between specialists and generalists.

The carbon:nitrogen ratio of plant tissues commonly exceeds greatly that in bacteria, fungi and animals. The main waste products of organisms that consume plants are therefore carbon-rich compounds. By contrast, the main excretory products of carnivores are nitrogenous. The various parts of a plant have very different compositions. Hence, most small herbivores are specialists. The composition of the bodies of different herbivores is remarkably similar.

Most of the energy sources potentially available to herbivores comprise cellulose and lignins, but most animals lack cellulases – an evolutionary puzzle. We explain how, in herbivorous vertebrates, the rate of energy gain from different dietary resources is determined by the structure of the gut.

Living resources are typically defended: physically, by chemicals, or by crypsis, aposematism or mimicry. This may lead to a coevolutionary arms race between the consumer and the consumed.

Apparency theory and optimal defense theory seek to make sense of the distribution of different protective chemicals, especially those that are constitutive and those that are induced, in different plant species and plant parts.

Taking resources in pairs, plots for the consumers of zero net growth isoclines allow resource pairs to be classified as essential, perfectly substitutable, complementary, antagonistic or displaying inhibition. The zero net growth isoclines themselves define a boundary of a species' ecological niche.