Chapter 1

Studying competition

"The general picture of nature which I have endeavored to delineate would be incomplete if I did not venture to trace a few of the most marked features of the human race."

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A. von Humboldt (1845) Kosmos (p. 351)

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There is some danger that a symposium on competition which begins with a section on definitions may so irritate later speakers that the whole meeting degenerates into a display of semantics.

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J. L. Harper (1961)

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We start with a word whose meaning we think we understand . . . and begin to investigate the things which it designates. We always find that it changes its meaning in the course of the investigation, and sometimes we have to invent new words for the things we discover.

<div align="right">

J. B. S. Haldane (1985)

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How every fool can play upon the word!

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W. Shakespeare, The Merchant of Venice

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Why study competition? All life forms consume resources such as water, oxygen, and nitrogen. This consumption reduces the supplies available for neighbours. In order to maintain access to resources, organisms sometimes must interfere with their neighbours. These three sentences summarize the state of affairs of both the simplest bacterium and the most self-assured twentieth century human. Without resources, organisms will die, and so the contest to find, harvest, transport, store and retain possession of resources is an essential part of the struggle for survival.

Long before scientists like Darwin concerned themselves with formal scientific study of competition, there was an intuitive appreciation of its importance in the realms of politics and agriculture. Julius Caesar, for example, well understood that competition between neighbours had two components: control of resources, and direct interference with survival (we now call these

exploitation and interference competition). In his campaigns in Gaul, Caesar describes (Handford, 1951) the siege of Uxellodonum in 51 B.C., where he not only surrounds the town by earthworks, but builds a second ring of trenches with pitfalls and sharpened stakes facing outwards to prevent any attempts at rescue by neighbouring Gauls. Learning from deserters that the town is well-supplied with grain, he decides to cut off the other essential resource: water. Roman soldiers deny access to the local river.

> "The townsmen however still resisted obstinately and held out even when numbers had died of thirst, until in the end our mines tapped the rivulets which supplied the spring and diverted them. The sudden drying up of this supply, which had never failed them before, reduced the Gauls to such despair that they ... surrendered." (p. 257)

Recognizing that military power might still interfere with the control of resources, Caesar further records "All who had borne arms had their hands cut off and were then let go, so that everyone might see what punishment was meted out to evildoers." (p. 257)

Agriculture also required an inherent understanding of competition, whether in choosing sowing densities or dealing with weeds. Says the Bible (Matt 13:3-7) "Behold a sower went forth to sow; And when he sowed ... some [seeds] fell among thorns; and the thorns sprung up and choked them."As we shall also see, the Bible also provided clear instructions on how to subdue neighbouring tribes.

1.1   THE IMPORTANCE OF COMPETITION

More than a century ago, Malthus and Darwin both appreciated the intrinsic nature of organisms to multiply exponentially towards limits set by resources. Thomas Malthus (1766–1834) was an English economist and clergyman; Charles Darwin (1809–1882) was, of course, the English naturalist who along with Alfred Wallace, discovered the theory of evolution through natural selection. This capacity for exponential growth means that both houseflies and elephants, given sufficient time, could multiply rapidly enough to entirely cover the land areas of Earth. Given a few more generations, a ball of flies or elephants would then expand outward from the Earth's surface, eventually reaching light speed; the flies, being more fecund than the elephants would, of course, have a head start. Darwin used a human example in *The Descent of Man and Selection in Relation to Sex* (1871):

> "Civilized populations have been known under favourable conditions, as in the United States, to double their numbers in twenty-five years; ... the present population of the United States (thirty millions), would in 657 years cover the whole terraqueous globe so thickly, that four men would have to

stand on each square yard of surface. The primary or fundamental check to the continued increase of man is the difficulty of gaining subsistence [resources] ..." (pp. 275–276)

Malthus and Darwin both understood that population sizes were limited because some other factor, usually a shortage of resources, prevented most young from surviving. Although each elm tree in a forest may produce millions of seeds, only one need reach adulthood for each tree to be replaced and the forest to remain intact. The other millions of young must perish. Darwin reported that he saw "on reading Malthus *On Population* that natural selection was the inevitable result of the rapid increase of all organic beings ..."; Malthus first published his *Essay on the Principle of Population* in 1798. Even in the early 1800s, then, ecological similarities between humans and other 'organic beings' were appreciated.

In his treatise *The Wealth of Nations*, Adam Smith (1776) argued, like Malthus, that humans had a propensity to reproduce exponentially, noting in particular that the poor tended to have high reproductive rates, but that poverty (that is lack of resources) generally resulted in the majority of their young dying before reaching adulthood. "A half starved Highland woman frequently bears more than twenty children ..." but it is not uncommon for "...a mother who has borne twenty children not to have two alive .... Every species of animals naturally multiplies in proportion to the means of their subsistence [resources], and no species can multiply beyond it" (pp. 38–39). The rate of reproduction of the poor, he concluded, was determined by their access to resources, as measured by the wages they received for their labour; "...the reward of labour must necessarily encourage in such a manner the marriage and multiplication of labourers ...." (p. 39)

The past century of research in ecology reveals that competition is one of the three fundamental forces (competition, predation, mutualism) that connects organisms in living systems. Competition may therefore have the same importance in ecosystems as gravity has in planetary systems and the cosmos. At this point, the study of ecosystems is not unlike the study of the solar system in pre-Copernican times. There exists a wealth of detailed observations on the natural history of selected living organisms, but the general principles (we no longer call them laws) remain elusive. There is at present no unified body of theories or laws for competition, although useful fragments are emerging. Instead, there is a rich mixture of observation, fact, experimentation, notion, concept, theory, belief, prejudice and models; the very diversity and volume of material presents a challenge to comprehension and synthesis. If these can be organized and sorted, such that evidence is separated from notion, and fact separated from belief, then we will have that least the beginnings of a body of true science. One of the added features that makes the science of ecology so exciting is the period of rapid development. The founders of physical theory, such as Copernicus, Galileo, Newton and Einstein are all dead, whereas as the founders of ecology may be now among us.

1.1.1   Politics and competition

In spite of its ubiquity in nature, in other circumstances there is still far too little awareness of competition; one can read a great many scholarly treatises on history and sociology without finding the word at all. Social scientists and politicians may find it convenient to assume that humans are infinitely malleable, or fundamentally evil, or for that matter basically decent, rather than accepting the more complicated view that competition for resources has shaped human civilisations in the past, determined our instincts and behaviour patterns, and will always be present so long as there is life with limited resources. This is not to say that competition is either good or bad; rather, we are identifying processes that occur, processes that describe the reality we have inherited.

The value of a concept like competition can be judged only by its contribution to our understanding of living systems. How can such value be assessed? First, if the concept is useful, it should allow our minds to organize and understand apparently chaotic displays of nature as perceived through our limited sensory apparatus. If we can organize some of this apparent chaos with the concept, then we can be said to in some way understand it, in that we can carry about an intellectual framework that appears consistent with patterns that we observe in nature. If this organization succeeds, then we should be able to predict – that is, given existing states and our knowledge, we should be able to forecast our world accurately. This is not only a goal sought by scientists: it seems to be basic human nature, since diviners, oracles, prophets, mystics and necromancers can be found throughout human history. Roget's Thesaurus (Chapman, 1977) lists 87 synonyms for divination, from aeromancy to zoomancy.

To begin studying nature we must attach names to objects and phenomena. This provides the vocabulary for exchange of ideas.

1.1.2   A definition of competition

While competition has long been important to humans, it is really only the last century when science has sought a precise definition. The right definition is like a sword that will clearly cleave nature into pieces that we can understand; the wrong definition is like a blunt instrument that only mashes the object of our inquiry into more confusion. This is why scientists seem to spend so much time arguing about definitions.

Definitions of competition present a particular challenge because it is such a widespread phenomenon, and occurs in so many conditions. It may be difficult to find a definition that is sufficiently robust to encompass the riotous display of possibilities in nature, yet precise enough to clarify every particular circumstance where it is applied. Further, we may look for a definition that emphasizes the mechanisms of competition, or its measurement by means of experiment, or its long term evolutionary consequences. Recent textbooks of ecology reveal a wide array of attempts to satisfy these conflicting objectives. Some authors even advocate that we no longer use the term. In this book I will define competition

as "The negative effects that one organism has upon another by consuming, or controlling access to, a resource that is limited in availability." Such a definition at least provides a starting point for exploring nature. This chapter begins with a brief historical account of definitions of competition, and then explores the many kinds of competition that occur in nature. This requires us to think about (1) the resources for which competition occurs, (2) the mechanisms of competition and (3) the kinds of organisms that are competing.

1.2   STRESS, STRAIN AND THE COSTS OF COMPETITION

One important feature of the above definition of competition is its emphasis upon the measurable costs of competition to the individuals experiencing it. There are, of course, many possible long-term consequences of competition, ranging from extinction to co-evolution, and such topics will be explored later. We must begin, however, with a clear understanding of the short term effects of competition upon organisms: competition has a cost.

Let us back up for a moment to begin with the common sense assumption that for every organism there are one or more environments which can be considered optimal. Many other environments can be tolerated perhaps, but metabolic costs increase in these less suitable environments. Many costs are immediate (increased fat consumption to maintain body temperature) but others have a longer term component (costs of producing feathers or fur for insulation). Other environments are so far removed from an organism's requirements that they are lethal. The degree to which any environment departs from the optimum conditions can be measured as the costs of maintaining homeostasis under these sub-optimal conditions. The most obvious currency for measuring cost is energy consumption (Peters, 1983; Hall et al., 1992). The more energy that must be diverted merely to maintain homeostasis, the less that is left for other activities such as growth and reproduction. In general, energy consumption rises with body mass, and with the shift from unicellular to multi-cellular, and poikilothermic to homeothermic metabolisms (Peters, 1983).

To introduce new terminology, we could further say that the more the environment departs from optimal conditions, the greater stress it imposes on the organism. We can usefully distinguish between the external conditions or environmental constraints – the actual stress – and its internal effects upon the tissues of the organism – which we can call strain. As a consequence of stress, the organism experiences strain, which might be measured as increased metabolic rate, or, more indirectly, as decreased relative growth rate (Levitt, 1977; Hall et al., 1992).

A simple example of strain being measured by metabolic rate can be produced by exposing homeothermic organisms to a range of temperatures (Fig. 1.1). If the ambient temperature is near the ideal temperature for the organism ($\sim 30°C$ in Fig. 1.1), the metabolic rate is also low. As the ambient temperature either
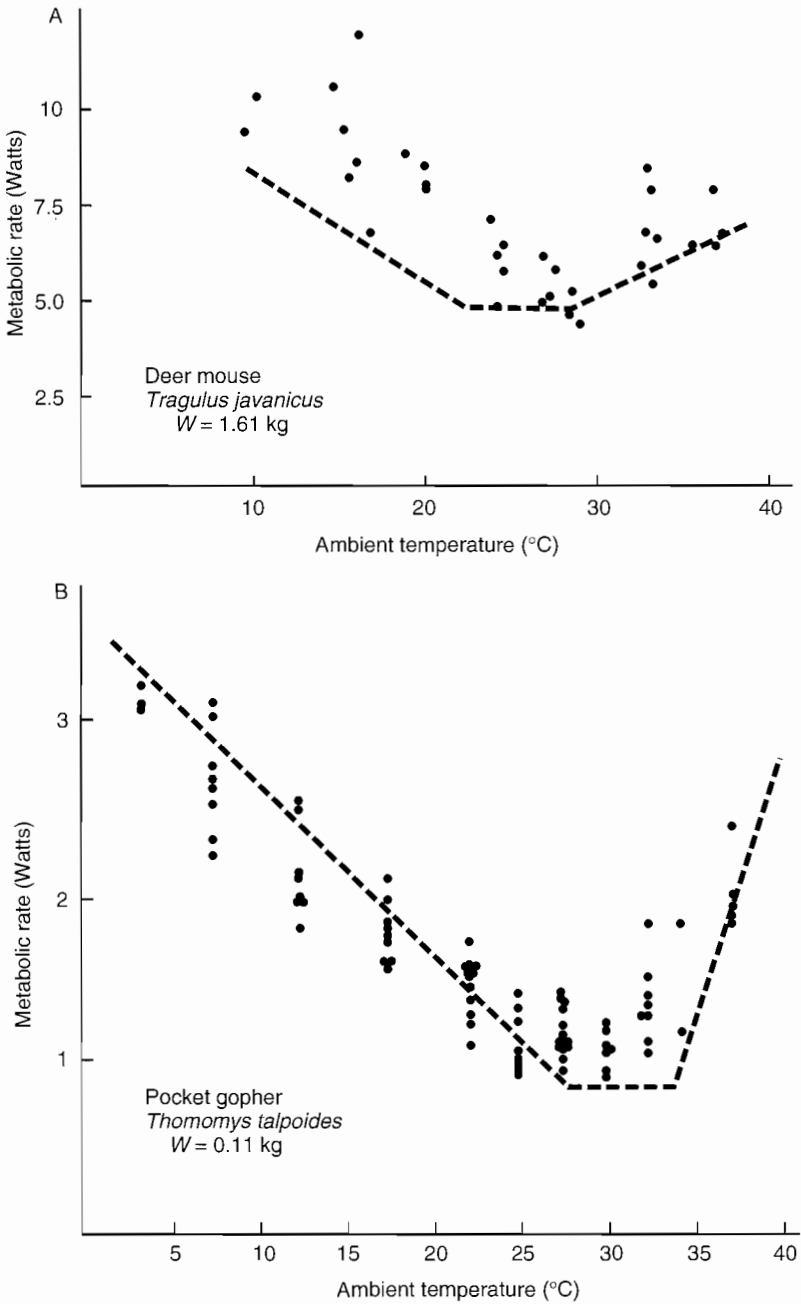
Fig. 1.1 A comparison of the predicted and observed thermal response curves for two homeotherms. (From Peters, 1983.)

decreases or increases, however, the organism must expend more energy in heating or cooling itself, in which case the metabolic rate increases. The further the environment departs from the optimum, the greater this metabolic expenditure becomes.

Now let us add in competition. We begin with a situation in which abiotic conditions themselves already impose some metabolic strain upon individuals (Fig. 1.2). If neighbours now increase the strain by further reducing resource levels, the strain of competition is superimposed upon the strain already present from abiotic circumstances (Fig. 1.3). Thus Weldon and Slauson (1986) propose that we should define competition as: "The induction of strain in one organism as a direct result of the use of resource items by another organism". While this definition places slightly greater emphasis than mine upon mechanism, by introducing the concept of strain, it is very similar in intent to the definition I have used in its emphasis upon the costs of competition. Note, though, that the costs caused by interference (e.g. territoriality, conflict, chemical interactions) do not appear to be included in competition as conceived by Welden and Slauson. As we will soon see, we must leave room in our definition for direct interference with neighbours. In practice, interference is just another cause of strain in organisms, since living in environments with aggressive neighbours, or tolerating toxin-producing neighbours, simply further increases the metabolic costs of survival. The greater these costs, the lower the performance of individuals, and the lower the probabilities of survival and reproduction.

As one illustration, consider frogs, toads or salamanders that breed in temporary ponds. Since the ponds dry out during the summer, there is an advantage associated with early metamorphosis: the sooner an amphibian leaves the pond, the lower the probability that it will be killed by desiccation when the pond
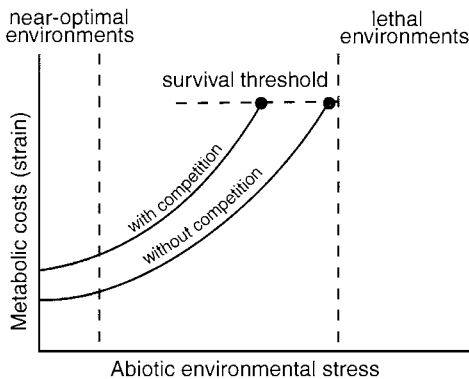

Fig. 1.2   Suboptimal environments produce strain within organisms. At some extreme combination of conditions, the organism can no longer maintain homeostasis and it dies (●). Competition increases the abiotic stress by reducing resource supplies. This can be thought of as pushing habitats to greater extremes along the stress axis.
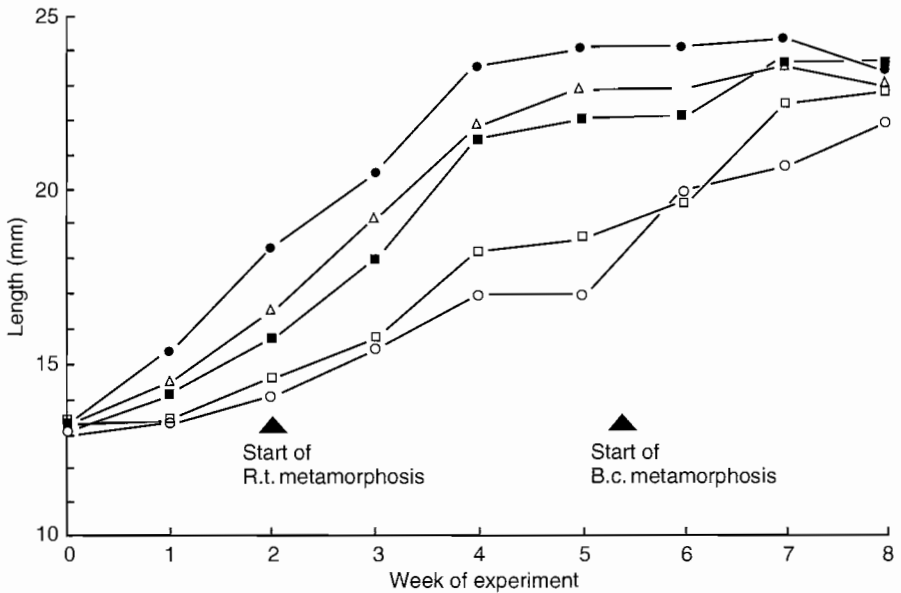
Fig. 1.3   Growth of toad tadpoles raised under different conditions: (●) control (no frogs); (△) frog-water + faeces; (■) frog faeces; (□) small frogs; (○) large frogs. Points are mean sizes based on pooled data ($n = 30$) from three replicate ponds per treatment. (Toads, *Bufo calamita*; frogs, *Rana temporaria*) (From Griffiths et al., 1991.)

dries. Further, the larger the amphibian is at metamorphosis, the greater its probability of survival as an adult. Competition from neighbouring tadpoles, however, reduces both of these measures of performance in toads (Griffiths et al., 1991): neighbours simultaneously increase the time to complete metamorphosis, reduce mean size at metamorphosis and reduce the rate of survival of tadpoles themselves. Using a series of experimental ponds, Griffiths et al. were able to tease apart some of the components of strain caused by neighbours (Fig. 1.3). In some ponds, the toad tadpoles lived with neighbours: the bottom two lines show the effects of both large and small frog tadpoles as neighbours (there were no significant differences between these two treatments). Some toad tadpoles were exposed only to indirect effects of frog tadpoles. In one set the frogs were physically separate in a wire cage, but water mixed freely, and frog faeces fell through the mesh; in another faeces from frog tadpoles were added to the toad water. After only 1 week, the toad tadpoles exposed to frog faeces (■), or frog-water and faeces (△), were significantly smaller. In conclusion, fully interacting conditions produced the greatest growth inhibition, the longest development time, and lowest rate of survival; possible causes for these effects include strain from interference with feeding, depleted food supplies, or growth inhibitors. When they were only partially exposed to neighbours, the strain on the toads was reduced, but still measurable.

These reduced effects might be caused by either reduced food supplies or growth inhibitors released by the frog tadpoles. The possible strain attributable to such growth inhibitors is still a matter of debate among herpetologists (e.g. Griffiths et al., 1991; Biesterfeldt et al., 1993; Beebee, 1996). In a remarkable convergence. the possibility that plants may poison their neighbours has also long been suspected (e.g. Molisch, 1937; Muller, 1966, 1969; Gopal and Goel, 1993). Muller (1969) noted that biochemical interactions among plants had been reviewed 13 times between 1939 and 1960, yet the role of allelopathy is still contentious (Williamson, 1990).

If we consider metabolic costs to be the currency for measuring an organism's response to any specific habitat, then we can use the inverse of cost, say the amount by which the organism is able to accumulate energy reserves per unit time, or net energy balance as a measure of habitat suitability. Hall et al. (1992) note that the range of conditions suitable for reproduction will therefore be narrower than the range of conditions permitting mere survival. Competition is superimposed upon this arrangement as an added metabolic cost associated with the effects of neighbours. The cost might be the extra energy spent searching for food, the energy consumed in defending a territory, or the costs of constructing enzymes to deal with the toxins produced by neighbours. In Figure 1.4, the costs of neighbours are assumed to be more or less the same throughout the range. This may not be the case. If competition is more intense at the limits of the range, or at one end of the gradient, then the shape and location of the net energy balance curve may be further narrowed or shifted in one direction.
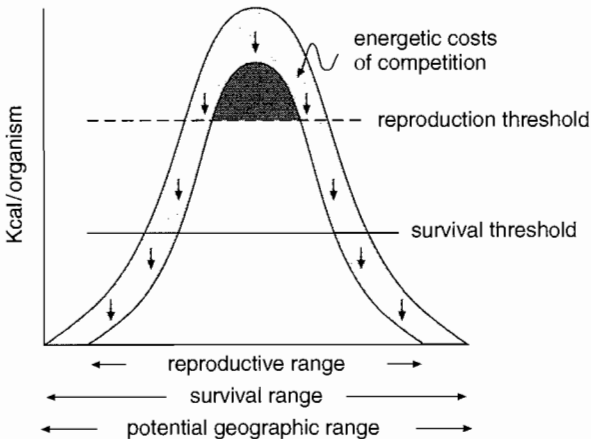

Fig. 1.4 Net energy balance of a species along a geographic gradient, showing the thresholds for reproduction and survival. Only the stippled region will support reproducing populations. By increasing the costs of survival, that is, decreasing the net energy balance, competition reduces performance and narrows distributional ranges. (Modified from Hall et al., 1992.)

1.3   OTHER VIEWS ON THE DEFINITION OF COMPETITION

A more historical perspective on competition may be helpful to some. However, the history of competition, and its definitions, is thoroughly entangled with the history of ecology and I do not intend to review that history of ecology here; two excellent books are already available (see Mayr, 1982; McIntosh, 1985). More-over, some of the past confusion may only generate further confusion; most readers may therefore wish to proceed directly to section 1.4. For those willing to descend into this realm, concern with competition was already well-established in the 1800s. "There is scarcely any biological task more attractive than that of determining the nature of the weapons by which plants oust each other from habitats" wrote Johannes Warming (1841–1924). Warming was a Danish bota-nist who is considered one of the founding fathers of ecology; his best known work was *Plantesamfund* (1895, *Oecology of Plants*) that grouped world plant communities into types that arise from similar environmental constraints.

Darwin attributed his discovery of natural selection to a passage of Malthus he happened to read in 1838 (Mayr, 1982). At that time many people thought that animals had as many offspring as they 'needed'. But Malthus had observed that every population grows until it is constrained by resources, and Darwin saw that this provided a constant struggle for existence, whereby each organism produced as many offspring as it could, only a small fraction of these surviving to adulthood. The scarcity of resources is also something he was acutely aware of: "The action of climate seems at first sight to be quite independent of the struggle for existence; but in so far as climate acts in reducing food, it brings on the most severe struggle between the individuals, whether of the same or distinct species, which subsist on the same kind of food" (p. 35). However, the term 'struggle for existence' should not be seen as synonymous with 'competition'; this has caused no small amount of confusion, because the term 'struggle for existence' is so widely appreciated as the driving force of evolution and speciation. A struggle for existence can include more than just the struggle of organisms with their neighbours for food, or more generally for resources. Certainly, competition is one component of this struggle, but in addition, struggle with other organisms can include avoiding being eaten by them, or finding them and eating them. Further, there may be situations where the struggle has little to do with neigh-bours, and is almost entirely driven by the environment. Again, Darwin says: "When we reach arctic regions, or snow capped summits, or absolute deserts, the struggle for life is almost exclusively with the elements" (p. 35).

The confusion between competition and the struggle for existence has also caused considerable difficulty for ecology. Indeed, there is still confusion between the immediate effects of competition (the cost to individuals), the short term consequences (changes in population size), and the long term effects (natural selection and evolution). Further, one still finds writers who assume that competition occurs everywhere, ignoring Darwin's suggestion that competition may be relatively unimportant in certain environments.

The first published experiment on competition appears to be the one reported by Sir Arthur Tansley to the British Ecological Society in 1917. We shall have more to say about this particular experiment later in this chapter. The first major treatise on competition was provided by Frederic Clements in 1929 (Clements et al., 1929). He reviewed earlier work including contributions by Malthus, deCandolle, Darwin, Nageli, and Warming, and then offered the following definition: "When the immediate supply of a single necessary factor falls below the combined demands of the plants, competition begins" (p. 317).

Clements, like Caesar, therefore clearly understood the connection between resources and competition. This definition is a reminder of the earlier work by the German agricultural chemist, Justus Liebig (1803–1873) whose name, at least for ecologists, is now associated with the 'law of the minimum', the assertion that any process is limited by the least or slowest factor affecting it (McIntosh, 1985). Further, Liebig rejected the old theory that humus in the soil supplied plants with food, and instead emphasized that plants took up resources such as water, nitrogen and carbon dioxide from their environment. Clements' treatise also reported on competition in forests and fields, and describes a series of experiments he carried out, the discussion of which introduces many topics resurrected in the 1960s: asymmetrical competition, competition for light as opposed to nutrients, dominance and subordinance.

Charles Elton's book, *Animal Ecology* (1927) is generally regarded as the first modern general account of ecology (Ricklefs, 1990), but interestingly Elton discussed interspecific competition only in relation to ecological succession. With respect to one species replacing another in succession, Elton asked ". . . does it drive the other one out by competition? and if so, what precisely do we meant by competition? . . . . At the present time it is well known that the American grey squirrel is replacing the native red squirrel in various parts of England, but it is entirely unknown why this is occurring, and no good explanation seems to exist. And yet more is known about squirrels than about most other animals." (Elton, 1927, p. 28).

The prominent Russian ecologist, G. F. Gause, was much concerned with natural populations of insects and in 1934 he wrote a book with the clearly Darwinian title *The Struggle For Existence*. He focused attention on competition "to such a degree that the theoretical effect of competition, the exclusion or death of one of the competitors, came to be known as Gause's principle or law" (McIntosh, 1985, p. 180). But the use of the term struggle for existence remained misleading since it confounded the effects of neighbours with those of the physical environment. We thus already seem to see the roots of an eventual dichotomy here between the clear resource-based definitions of competition among plant ecologists, and confusion among the zoologists. As we shall see in the final chapter of the book, some recent compendia in ecology have entirely forgotten about Clements and Tansley, and one cannot help but wonder whether the confusion that has therefore arisen is not entirely unnecessary.

Let us now leap ahead to the 1960s, where there was a rapid development of interest in ecology and consider three perspectives, by Milne, Harper and Jackson, respectively. Milne (1961) reviewed the historical contortions and confusion that have surrounded the use of the word competition, and concluded that we have three courses: accept ambiguous use, drop it altogether, or provide a restrictive definition: "Competition is the endeavour of two (or more) animals to gain the same particular thing, or to gain the measure each wants from the supply of a thing when that supply is not sufficient for both (or all)". He concluded with the appeal: "Clearly the need is not only for strict definition of competition but also for a discerning interpretation of the definition".

Harper (1961) observed that 'competition' is the response of plants to density-induced shortages, and examined the different definitions used by agronomists, ecologists and geneticists. The agronomist is primarily concerned with the way in which a crop exploits the resources in an environment. Usually this work follows two steps: a description of density-dependent effects and an analysis of causes. This is frequently accomplished by exploring the way in which crop yield varies with sowing density, often with a range of fertilization levels. Harper noted that the population ecologist has less control over the system being studied, and frequently is interested in processes occurring over longer time scales than those studied by agronomists. He observes that ecologists are concerned with "those hardships which are caused by the proximity of neighbours", and suggests that 'interference' is a preferable word.

Jackson (1981) has reviewed attitudes towards competition since the 1960s, finding that recent ecologists such as Hutchinson, Connell and Diamond have misrepresented the history of competition, creating 'a misguided sense of originality of ideas' and a 'revisionist history'. There is, he shows, a long lineage of studies of competition in the literature of plant ecology, with experimental work by Tansley, Clements and Watt being particularly noteworthy. A basic framework for the study of competition was established long before Volterra and Gause but ignored by zoologists associated with the development of niche theory. In summary, Jackson shows that no one trying to come to terms with current debates in ecology can afford to overlook the extent to which the recent zoological literature misrepresents both the development of ideas and accumulation of evidence in the field of competition. This problem is sufficiently emmeshed within the field of ecology that it will re-emerge several times in this book, particularly section 6 and Chapter 11.

Finally, any study of competition requires measuring the action of competition in nature, so any definition must be operational. Recall (p. 5) that competition is an interaction in which individuals (genotypes, populations): (1) have negative effects upon each other (2) by influencing access to resources. The first part, assessing negative effects upon each other, seems straightforward for measurement and testing, and some examples of this are given in Chapter 2. Whether both must be negatively affected is open to question, however, since in very asymmetrical interactions the dominant may be so little affected by the

subordinant that negative effects upon it cannot be detected; for convenience, we may regard such circumstances as a limiting case. The second part of the definition, demonstrating the mechanism causing the negative effects, is more difficult. Many animal ecologists insist that resource limitation must be demonstrated before one can conclude that competition is occurring (for example, Milne, 1961; Price, 1984a), but others have argued for a more operational approach (Wilbur, 1972; Gill, 1974). Plant ecologists in general have remained more operational (Fowler, 1981; Silander and Antonovics, 1982; Wilson and Keddy, 1986a), but Tilman (1987a) presents an opposing view (see also Thompson, 1987; Tilman, 1987b; Thompson and Grime, 1988).

Debates over definitions themselves may accomplish little, and even their entertainment value is limited, since the controversies ignited may detract from important questions rather than stimulate them. All human concepts are only limited attempts to organize complexity beyond the organizational capacity of our nervous system, so we should be realistic about why we need definitions, and proceed with the task at hand – to use the definition as an initial reference point for studying nature. We can expect our definitions to evolve as we learn more about the phenomenon itself (Haldane, 1985).

1.4   KINDS OF COMPETITION

Further investigation of competition requires us to be more specific, and to recognize that different kinds of competition may arise. In this book we shall consider four classification schemes, based upon:

(1) mechanisms of competition;
(2) the kinds of entities which are competing;
(3) the relative impacts of the competitors upon one another;
(4) the resources that are the basis of the interaction.

The fourth category, resources, will be left until Chapter 2, resources being important enough to deserve a chapter of their own.

1.4.1   Mechanism

One approach to classification is to consider mechanisms by which individuals produce the negative effects experienced by other individuals (Miller, 1967). Two basic kinds can be recognized, although these can be further subdivided into as many as six kinds (Schoener, 1983). Interference competition occurs when one individual directly affects another. Outright physical attack may occur, or subtler forms of it, such as threat behaviour, chemical poisoning or territoriality. Exploitation competition occurs when effects are indirect, and occur solely through reduction of the available pool of resources. Caesar's attack on Uxellodonoum (p. 2) has already illustrated these two components of

competition. The following four examples further illustrate these contrasting mechanisms, and show the wide array of processes by which organisms may interfere with one another.

Example 1: Exploitation and interference competition in dung beetles

The excrement of large vertebrates provides a rich source of food, exploited by many beetle species. The length of time for which dung remains usable is short, particularly in savannahs where it dries out quickly. Many beetles therefore bury the dung to maintain higher moisture levels. Their egg masses are then deposited on this dung (Crowson, 1981). Such rich patches of resource are rapidly exploited. Bartholomew and Heinrich (1978) describe putting out 1 litre of elephant dung at 10 min after sunset, and collecting 637 beetles attracted to it within the next 30 min. They cite other studies which have found as many as 7000 beetles in one pile of dung. As a consequence, these piles of dung are rapidly depleted, particularly by small beetles which eat it or bury it on site, leaving behind only a thin layer of coarse, inedible fibrous material. Consequently, beetles which require dung for making balls must arrive early, make a ball of dung and roll it away from the site quickly before it is consumed.

Bartholomew and Heinrich (1978) show that success at this exploitation competition can be predicted from body temperature. Beetles with warm bodies have a more rapid rate of dung rolling, which means that warmer beetles are, on average, more successful at exploitation competition. This may be one of the principal advantages of endothermy in these beetles.

The story does not end at exploitation competition. The vast number of individuals harvesting a rich and rapidly vanishing food supply would seem to provide an ideal environment for interference competition as well. Bartholomew and Heinrich note that "attempted theft of completed dung balls and sustained fighting over partly completed balls are commonplace". They therefore constructed an arena and explored the interactions between pairs of beetles and artificial dung balls. The winner was the individual which gained access to the dung ball and began rolling it away. They found that the winner was usually the individual with the higher body temperature (Heinrich and Bartholomew, 1979).

These studies not only illustrate the interpretation of exploitation and interference competition, but they suggest that a simple independent variable (body temperature) can be used as a predictor of success.

Example 2: Interference competition in beetles and flies

Carcasses also provide a rich supply of food for decomposers. This high quality resource is very localized, and is difficult to predict in either time or space. Both flies (Diptera) and beetles (Coleoptera) lay their eggs on such carcasses. Late arrivals are at a severe disadvantage, since not only does the quality of the cadaver decline with time, due to effects of climate and micro-organisms, but it is

increasingly likely to be occupied by potential predators and competitors (Crowson, 1981). There are thus many parallels between dung and carrion consumers.

In such situations we can postulate that there has been strong selective pressure to locate corpses early. Evolution of sensory systems and searching ability might be inferred. Invariably, however, these rich resource patches have to be shared. A most interesting example of interference competition occurs under such circumstances.

Carrion beetles (*Necrophorus* spp.) frequently arrive at carcasses already occupied by fly larvae of the genus *Calliphora*. In experimental studies, Springett (1968) showed that when fly larvae are present, the beetles are unable to reproduce successfully on the corpse (Table 1.1). However, under natural conditions these beetles usually carry up to 40 mesostigmatid mites. When the female beetle lands on a carcass, the mites disembark and seek out and kill the fly eggs. The beetles then reproduce successfully. When the larvae pupate, the female abandons the corpse and large numbers of mites depart with her. Other mites leave with the beetle larvae after they pupate. The Coleoptera thus evolved the technique of aerial search-and-destroy tactics millennia before the developed world unleashed it upon peasant villages.

This example illustrates the breadth of natural phenomena which may be included within the definition of competition. There is a resource in limited supply, and there is good experimental evidence of competitive exclusion in the absence of mites. However, the mechanism of interspecific competition which reverses the species being excluded is the effects of predation by a third party.

Example 3: Interference competition by myrmecophytes: ants and acacias
Some species of acacia are known as myrmecophytes because of their obligate mutualism with colonies of *Pseudomyrmex* ants living within their thorns. The ants feed upon nectar and solid food produced by the tree. The costs for the acacia are considerable. A 2 m acacia produces about 1 cm^3 of nectar per day, the entire sugar source of the associated ant colony. Solid food consists of Beltian bodies, constricted leaflets containing large thin walled cells apparently

Table 1.1 Interference competition for corpses. The results of experimental cultures using standard corpses (*Apodemus*) inoculated with different combinations of *Calliphora* flies, *Necrophorus* beetles and *Poecilochirus* mites. (After Springett, 1968.)

Mixture of species on corpse	Number of successful beetle cultures	Number of successful fly cultures
100 fly eggs	–	8
Pair of beetles	8	–
100 fly eggs + pair of beetles	0	8
100 fly eggs + 30 mites	–	0
100 fly eggs + pair of beetles + 30 mites	6	0

full of proteins and lipids which the ants harvest and cut up, feeding them to larvae. Further, the canopy of a 2 m acacia can bear 1 kg of swollen thorns (Janzen, 1966). This weight of thorns requires tough and resilient wood. Unlike other acacias, the stumps sprout rapidly after fire, even during the dry season; this is apparently necessary if the ant colony is not to starve waiting for new shoots to appear.

The principal benefit to the tree is protection from predation and competition (Janzen, 1966, 1969). The ants are aggressive, and will bite and sting any herbivore that attempts to feed upon the plant. Janzen (personal communication) describes ants as rushing to the ends of twigs and throwing themselves into the air to land on approaching herbivores. The ants also kill the shoots of vines or other neighbouring plants that touch the acacia. There are, therefore, bare areas around ant-occupied acacias, whereas other species are swamped by vines and over-topped by surrounding trees. Experiments have confirmed these inferences: when ant colonies were killed, the acacias were rapidly defoliated by herbivores and overgrown by vines (Janzen, 1967).

Example 4: Strategic bombing, resources and interference competition in humans

"The general picture of nature which I have endeavored to delineate would be incomplete if I did not venture to trace a few of the most marked features of the human race", says von Humboldt in his 1845 best seller *Kosmos*. In this spirit let us turn to interference competition within our own species.

Strategic bombing campaigns provide a particularly vivid illustration of the conflicting options available for interference competition with neighbours. The fundamental problem is to decide upon which target of interference with the enemy will be most effective in reducing their power. If such a target is agreed upon, there remain many tactical issues around how to destroy the target most effectively.

During the Second World War, Allied commanders faced exactly these two problems (Frankland, 1970). As early as 15 January 1941, Bomber Command was told that "the sole primary aim of your bomber offensive, until further orders, should be the destruction of the German synthetic oil plants" (p. 32). The actual ability of bombing to achieve this goal was, however, in doubt. To evaluate this option, aerial surveillance was carried out at two synthetic oil plants at Gelsenkirchen on Christmas eve 1940. These two plants had been attacked by 196 bomber sorties, and 262 tons of high explosive and an un-recorded number of incendiary bombs had been dropped, yet neither plant had apparently suffered major damage. Thus, whatever the best target in principle, there was still the thorny practical problem of finding the target, dropping the bombs accurately upon it, and escaping with acceptable casualty rates. All of these latter tactical problems had to borne in mind when considering the strategic objectives, and one by one these were solved by improvements in technology as the war progressed. Yet strategic differences of opinion remained.

Even in the last years of the war, there were still three conflicting views as to how strategic bombing should most effectively interfere with the activities of the enemy. One view was that the destruction of synthetic oil factories would still be highly desirable because it provided the fuel for the entire enemy war machine, as well as for the industrial plants which produced more war machines. Moreover, this provided a fairly specific, if well-defended, target. Lieutenant-General Carl Spaatz, Commander of the US Strategic Air Forces favoured this target, as did Sir Charles Portal, Chief of the British Air Staff. The second view was that transportation systems provided a highly visible target that would also hamper the movement of men and materials and as well as interfering with industrial production; it was so widespread that it could be attacked by many small bomber formations operating with relative independence. This approach was favoured by Air Marshall Sir Arthur Tedder. Third, there was the view that, it was necessary to destroy the enemy's morale and infrastructure, and this could only be done through area bombing of entire cities. This would have the advantageous side-effects of also destroying industrial and transportation centres. This view was taken by Air Marshall Sir Arthur Harris.

Evaluation of these positions after the war ended has tended to favour the first option; shortages of aviation fuel and diesel had become critical by August 1944, and the British and Americans were 'gravely mistaken' not to have concentrated a greater proportion of their efforts upon it after the initial successes of May and June. It is, says Frankland, virtually beyond doubt that the German economy would have been crippled if this target had been continually further attacked. This tends to reinforce Keegan's (1989) opinion that the war was primarily decided by the ability of each country to allocate industrial production to create weapons. Albert Speer, who was largely responsible for keeping the German war machine running (and was imprisoned after the Nuremberg Trials for twenty years) recalled, "As early as September 10, 1942, I had warned Hitler that the tank production of Friedrichshafen and the ball-bearing facilities in Schweinfurt were crucial to our whole effort . . . . the war could largely have been decided in 1943 if instead of vast but pointless area bombing the planes had concentrated upon the centres of armaments production." (Speer, 1970, p. 365)

This military example emphasizes two principles that may have wider application. First, interference competition will be most effective when it targets a critical limiting resource for a neighbour, or when it damages its ability to transport that resource. Second, whether in organisms or human societies, energy is often the most important resource, if only because energy reserves measure both the ability of a neighbour to forage for new resources and its potential to create structures for interference in the reverse direction.

1.4.2 Kinds of entities interacting

The most obvious way of classifying competitive interactions is to classify them as those occurring among individuals of the same species (intraspecific

competition) or those occurring among individuals belonging to different species (interspecific competition). This simple classification has dominated studies of competition. Its attractiveness may lie in the species-oriented approach of many ecologists: is competition within the favourite species being studied, or between that species and some other? This is reminiscent of early Western movies, where there are good guys in white hats and bad guys in black hats, making the plot relatively easy to follow.

Perhaps a small audience recognizes that characters are not conveniently labelled good and bad, and that characters can fill a variety of roles. The transition from simple dichotomies to multivariate classifications is not an easy one to make, as people well know if they have tried taking parents trained on early Westerns to contemporary films. So it is with classifying competition. Inter- and intraspecific is the classification which has dominated ecology to date, but nature is not a simple cowboy film. Some of the many kinds of competitive interactions we could classify are introduced below. The list is by no means exhaustive.

Intraspecific competition (Fig. 1.5) occurs between pairs of individuals within a species. It is commonly assessed in plant ecology by sowing seeds at different densities, and recording the performance of individuals (for example,
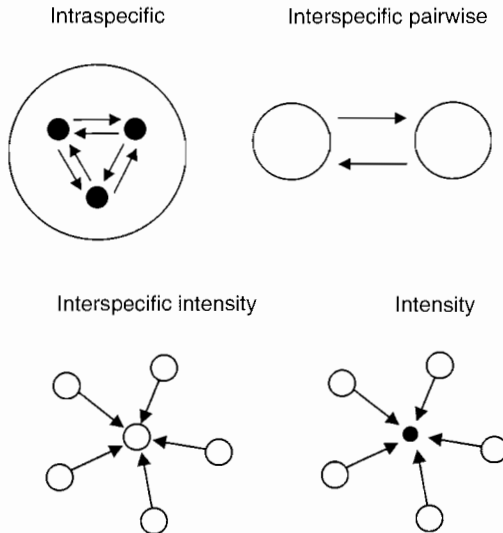

Fig. 1.5   Four kinds of competitive interactions. Each open circle represents a population; individuals, where necessary, are indicated by solid dots within these circles. The arrows indicate reduction in performance of individuals and populations, resulting from competition. A majority of examples in the literature falls into the top two categories, but communities, populations and individuals can be influenced simultaneously by all neighbours.

biomass or seed production) at a later date (for example, Harper, 1961, 1977; Watkinson, 1985a; Weiner and Thomas, 1986). It is also measured in replacement series-type experiments (for example, de Wit, 1960; Harper, 1977; Firbank and Watkinson, 1985). In animal ecology such relationships can be assessed by comparing measures of performance and population size collected over many years (Lack, 1966), although if the animals are sufficiently small, laboratory experiments (for example, Gause, 1932; Park, 1948, 1954; Longstaff, 1976; Gilpin et al., 1986) and field experiments (Connell, 1983; Schoener, 1983) can be used.

It will become apparent in this book that I am of the opinion that too much effort has been invested in assessing the relative importance of intra- and interspecific competition. It seems to have become a habit rather than a measurement being driven by important questions. However, before we are dismissive of such work, it should be noted that Mayr (1982) believes that the conceptual revolution that allowed Wallace and Darwin to discover natural selection was their shift in emphasis from the species to the individual. Up to that point, biology had been in the grip of essentialism where each species was considered to be a type. "The realisation of the uniqueness of every individual was perhaps the most revolutionary change in Darwin's thinking in 1838 . . . . It was this that made him realise that the struggle for existence due to competition, so vividly described by Malthus, was a phenomenon involving individuals not species" (p. 487). The realization that there was both intra- and interspecific competition therefore heralds the origin of populations, a concept that was virtually non-existent prior to 1800.

Example 5: Intraspecific competition in plants
Plants require basic resources such as nitrogen, phosphorus, water and carbon dioxide to construct their tissues. As the number of plants in a unit area increases, the per capita supply of resources declines; therefore as plant density increases, the mean plant size declines. This relationship has been extensively studied because agriculture requires information on the effects of sowing density upon crop yield. Even the backyard gardener thinning a patch of radishes or peas understands intuitively that reducing the density of plants will enhance the performance of remaining individuals. Ecologists have also studied the effects of density on plants because it is relatively easy to manipulate sowing density (much easier, say, than manipulating the density of bears, birds or fungi). Figure 1.6 shows that eight different plant species all decline in performance with increasing density (note the vertical scale is logarithmic). The steepness of the slope tells us how intense intraspecific competition is; the steeper the slope, the greater the effect each added individual has upon its neighbours.

The lines in Figure 1.6 are fit by an equation of the form
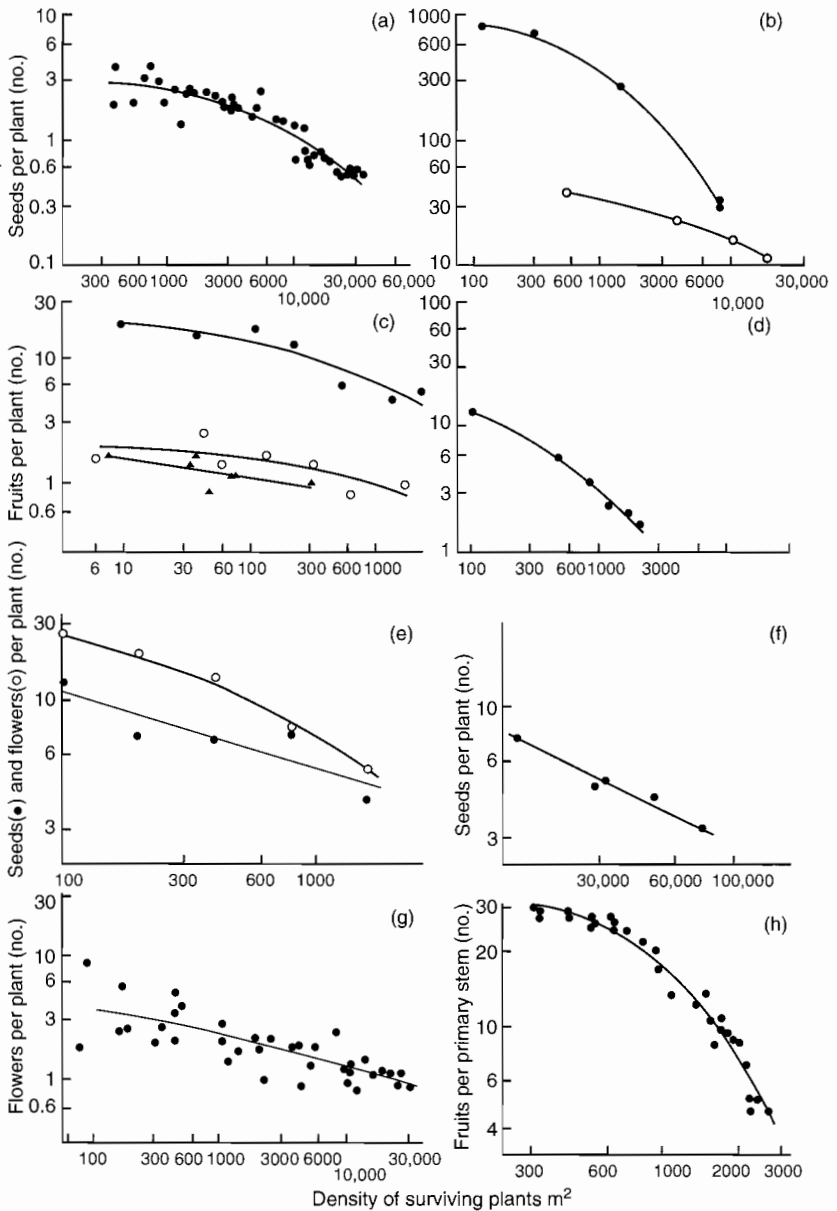
$$w = w_m(1 + aN)^{-b}$$

Fig. 1.6   The relationship between the reproductive output per plant and the density of plants at maturity. (a) *Vulpia fasciculata.* (b) *Salicornia europaea* on a high (○) and low (●) marsh. (c) *Cakile edentula* on the seaward (●), middle (○) and landward (▲) sides of a sand dune. (d) *Rhinanthus augustifolius.* (e) *Floerkea proserpinacoides.* (f) *Polygonum confertiflorum.* (g) *Diamorpha smalli.* (h) *Androsace septentrionalis.* (From Watkinson, 1985a.)

where w is the mass of an individual plant, N is density, and w_m, a and b are parameters (Watkinson, 1985a). The form of this equation is of some interest, because w_m can be interpreted as the mass a plant will attain if grown in isolation – that is, where intraspecific competition is zero. The area required to supply the resources to achieve w_m is then a. That is, a is the minimum required area, or the neighbourhood, a plant requires to find the resources necessary to achieve maximum growth. Finally, b can be considered a measure of the effectiveness with which resources are extracted from an area. Therefore, the actual mass of an individual plant, w, will decrease as N (density) increases, as a (minimum required area) increases, or as b (effectiveness of resource extraction) decreases.

This basic relationship can be regarded as one of the inescapable laws of competition: as population density increases, the resources available per capita must decrease. Some organisms, such as humans, may be able to temporarily escape this relationship, perhaps by increasing the amount of farmland per capita by clearing forests, or by increasing fertilization of the existing land to increase yields per unit area, but ultimately, as Ehrlich (1968) has so effectively described in *The Population Bomb*, human populations are unlikely to escape from the harsh imperatives set by Figure 1.6: as population density increases, the resources available per capita seem bound to diminish. Some technological optimists argue that our species alone can escape these ecological laws because we can discover and exploit new resources faster than our population exhausts the old ones (e.g. Simon, 1980). That is, they believe that we can tinker with the parameters a and b to escape from the inevitable negative effects of N upon w. The relative merits of these arguments can be explored in a series of exchanges between Ehrlich (1981a,b; 1982) and Simon (1981, 1982).

Interspecific pairwise competition (Fig. 1.5) is explored when a pair of species is examined. It is often compared with a measure of intraspecific competition in field experiments (Schoener, 1983; Connell, 1983) and laboratory experiments (Gause, 1932; Park, 1948, 1954; Gill, 1972, 1974; Longstaff, 1976; Widden, 1984). A growing number of studies has measured many pairwise interactions simultaneously (Wilbur, 1972; Goldsmith, 1978; Fowler, 1981; Silander and Antonovics, 1982; del Moral, 1983; Wilson and Keddy, 1986b; Mitchley and Grubb, 1986; Gilpin et al., 1986; Keddy et al., 1997). One can then ask questions about the relative importance of competition between different populations, or the proportion of possible interactions which are significant.

Example 6: The measurement of intraspecific and
interspecific competition for two desert shrubs
The relative importance of competition intensity, as well as intra and interspecific competition, can be measured using removal experiments. Fonteyn and Mahall (1981) used two shrubs *Larrea tridentata* (the creosote bush) and *Ambrosia dumosa* (burbage) that dominate some 70% of the Mojave Desert.

An advantage to using desert plants is that the limiting resource is almost certainly water, and the water status of plants can be determined, providing a nearly instantaneous measurement of how plants are being affected by neighbours. Specifically, by clipping off a branch, and inserting it in a pressure bomb, one can measure how much of a water deficit exists in a branch. Xylem pressure potentials were thereby determined in control and removal plots (Fig. 1.7) every 2 weeks through three consecutive wetting and drying cycles. Figure 1.8 shows that there were no detectable effects of intraspecific competition, whereas interspecific competition and total competition (that is competition intensity, our very next topic) significantly reduced the water potential of the plants.

Competition intensity (Fig. 1.5) describes the effects of all neighbours upon the performance of a population (left) or individual (right). It can be measured by removing all neighbours and observing the release (if any) of the remaining population or individual relative to unmanipulated control plots (Putwain and Harper, 1970; Fowler, 1981). A possible variant on this is to use transplanted individuals of one or several species, as a 'bioassay' of the competition intensity in different plots (del Moral, 1983; Wilson and Keddy, 1981a). Competition intensity might also be measured by comparing the physiological state of organisms in plots with and without neighbours (Welden and Slauson, 1986). Whether intraspecific competition should also be manipulated (by removing neighbours of the same species) depends upon the question being asked. If, for example, the growth of a larval anuran is reduced by neighbouring larvae, then its fitness
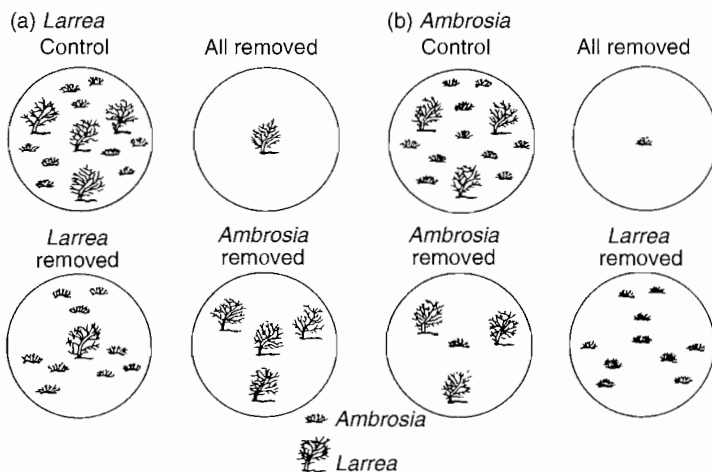

Fig. 1.7   A removal experiment in desert shrubs. Competition intensity is measured in the 'All removed' treatment, while intra- and interspecific competition are measured by removing *Larrea* or *Ambrosia*. Results are shown in Fig. 1.8. (From Fonteyn and Mahall, 1981.)
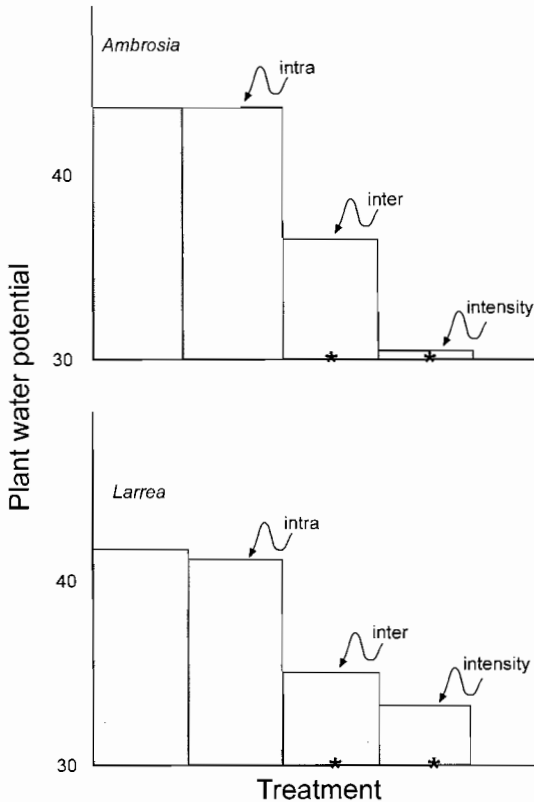
Fig. 1.8 Effects of the experimental removals in Fig. 1.7 upon the water potential of two desert plants. Asterisks denote significant differences from control plants. (Note that water potential decreases with increased competition). (From Table 2, Fonteyn and Mahall, 1978.)

declines with density regardless of whether the neighbours are conspecific or heterospecific (Wilbur, 1972). Similarly, plants will experience nutrient-depletion zones in the presence of neighbours, but the plant may have no way of detecting whether the depletion zone is caused by interspecific or intraspecific neighbours.

Example 7: Competition intensity in a riverine marsh
Many species of plants are tightly packed together in vegetation, each shoot having to forage for light, water, CO_2 and mineral nutrients while surrounded by neighbouring shoots. The neighbouring shoots may belong to the same species (or even the same clone), or to species from very different plant families. The environment can also change dramatically over a growing season as water levels rise and fall. We might begin an enquiry into competition in these

circumstances by trying to use field experiments to determine which resource is in shortest supply, or by painstakingly examining pairwise interactions between neighbouring shoots. Instead, Shipley et al. (1991) chose to assess the mean intensity of competition faced by plant shoots. They did so using individual ramets (a shoot with a short section of rhizome and roots) of three dominant plants in the marsh: a sedge (*Carex crinita*), sweet-flag (*Acorus calamus*) and cattail (*Typha angustifolia*).

Shoots of each species were planted in intact vegetation (uncleared, Table 1.2) and in clearings (cleared, Table 1.2). The clearings were maintained by weeding and by the use of plastic barriers to prevent roots or rhizomes from re-invading below ground. Further, the experiment was repeated at three elevations to test for possible changes in competition intensity along the water level gradient. After two growing seasons the transplanted shoots were harvested, dried and weighed, the difference in weight between the cleared and uncleared plots providing the measure of competition intensity. Neighbours reduced the performance of the three test species by some one-third (RCI, Table 1.2). Surprisingly, there was no evidence of a change in competition intensity with test species or elevation.

This complex vegetation type with many species and strong environmental gradients (e.g. Day et al., 1988) might be expected to have extremely intricate competitive relationships. However, in spite of the vegetation heterogeneity that meets the eye, the measured competition intensity is surprisingly uniform. Table 1.2 does suggest that larger sample sizes might uncover patchiness in competition intensity, and that further some species in some habitats (e.g. *Typha augustifolia* in site 3) might be entirely unaffected, or even assisted, by the presence of neighbours.

Diffuse competition (Fig. 1.9) is closely related to competition intensity. The cumulative effects of neighbours (competition intensity) may range along a

Table 1.2 Relative competition intensity (RCI) in a riverine wetland as measured over 2 years using three plant species at three elevations. (After Shipley et al., 1991.)

Species	Site	Cleared (g)[a]	Uncleared (g)	CI[b]	RCI[c]
Acorus calamus	1	12.81	7.46	5.35	0.42
	2	12.18	11.13	1.05	0.09
	3	7.77	2.59	5.18	0.67
Carex critina	1	21.76	11.47	10.29	0.47
	2	16.44	8.85	7.59	0.46
	3	23.34	19.89	3.45	0.15
Typha augustifolia	1	18.17	20.09	−1.92	−0.11
	2	51.42	27.66	23.76	0.46
	3	22.20	26.05	−3.85	−0.17

[a] Values are back-transformed; therefore they are model values (g)
[b] CI = Cleared − Uncleared (g)
[c] RCI = (Cleared − Uncleared)/Cleared (proportional decrease)
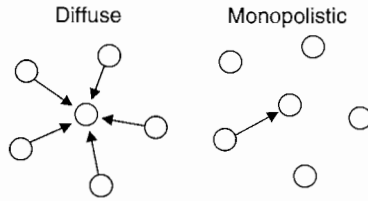
Fig. 1.9 Competition intensity can range from diffuse (all neighbour species have equal effects, left) to monopolistic (only one neighbour species has an effect, right).

continuum of possibilities; on the left, the effects of all neighbouring populations are relatively equal, in which case the competition is said to be diffuse (MacArthur, 1972). On the right, one of the neighbouring populations is the primary contributor to competition intensity, and the remaining populations have a minor effect. Rather than coining a new term ('predominant competition'), as in the first edition, we can borrow from economics (Samuelson and Nordhaus, 1992) and use the word *monopolistic* to describe the opposite of diffuse competition (Fig. 1.9).

Example 8: A hypothetical assessment of diffuse as opposed to
monopolistic competition in deciduous forest birds
To distinguish where a community lies along the diffuse/monopolistic continuum, it is necessary to perform a series of removals, and measure the change in performance of one or more test species. For example, if we wished to measure the degree of monopolism within an assemblage of six different species of wood warblers, we would choose a test species, say the black and white warbler, and then selectively remove each of the remaining species from a set of treatment plots. The response variables, in the case of birds, might be reproductive success. We would measure the effects of each removal by monitoring the change in reproductive success (if any) of black and white warblers with each removed species. Table 1.3 presents the hypothetical data set which might result, showing that the competitive effects are largely caused by species 1 and 2, whereas species 3–5 are negligible. Of course, replication and appropriate statistical procedures would be necessary for the exact interpretation of such results.

Further, a complete removal of all neighbouring species would give an estimate of competition intensity. The table shows that we might estimate intensity by summing the response of the individual removals; in practice, the situation will likely be complicated by higher order interactions. That is to say, when we remove species 1, we will likely underestimate its impact upon the test species because species 2–5 may also increase their performance/abundance, thereby using some of the resources that would have otherwise been made available to the test species.

Table 1.3 A hypothetical measure-
ment of position along the diffuse/mono-
polistic continuum by measuring the
percentage response of a species of
insectivorous bird to the removal of five
related species

Species removed	% response
1	25
2	20
3	5
4	2
5	1
Intensity (Σ)	53

These sorts of studies are rare, if not non-existent (Newton, 1992). First, there
are conceptual problems: the distinction between diffuse and monopolistic
competition has not been widely appreciated, and few scientists have therefore
been motivated to make the necessary measurements. Then there are practical
problems. Any study of this nature will require a great deal of effort, since the
minimum number of removals will be $n(s-1)$ where n is the number of repli-
cates and s is the number of potential competitors. Further, removal experi-
ments require on-going effort, since neighbouring individuals will often
rapidly move in to exploit the vacant space (Stewart and Aldrich, 1951; Newton,
1992; Marra and Holmes, 1997). This particular problem provides dramatic
evidence of the intensity of intraspecific competition; it is a major problem with
birds, but even (relatively) immobile plants and sessile marine invertebrates
generally produce large numbers of motile offspring which can rapidly
re-invade cleared treatments. There is also the potential problem that the
degree of monopolism may depend upon our test species. If we use black and
white warblers as our test species, we have no way of knowing whether the
results would be similar to those for, say, black-throated blue warblers. Perhaps
a test species that is a weak competitor will tend to reveal diffuse competition,
whereas a strong one will tend to reveal monopolism, since there may be only
one other species that affects it. The experiments have not been done, and so we
do not know. In spite of the practical problems, such experimental studies will
be needed if we are to assess the relative frequency of diffuse as opposed to
monopolistic competition.

Example 9: Competition among herbaceous plants in old fields
Many areas of eastern North America have abandoned fields that are slowly
reverting to deciduous forest. Goldenrods (*Solidago* spp.), Asters (*Aster* spp.)
and grasses predominate in this vegetation. Goldberg (1987) removed a set of
different neighbouring species to explore their effects upon a single test species,
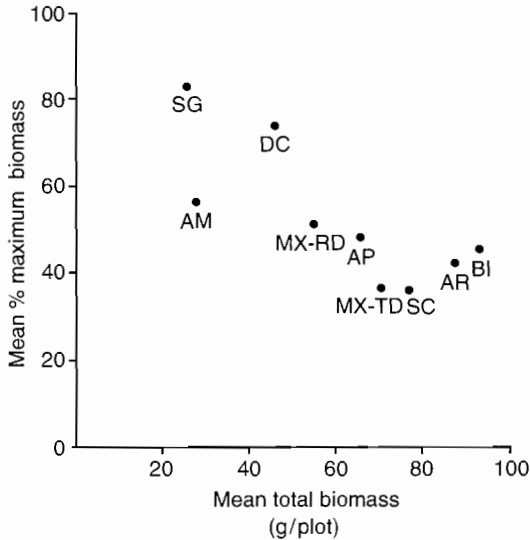the Canada goldenrod (*Solidago canadensis*). The experiment was designed to

Fig. 1.10 Mean biomass of *Solidago canadensis* transplants (target plants) in no-removal plots as a function of mean biomass of the neighbour species in those same plots. Mean target plant biomass with each species as neighbour is expressed as a percentage of target plant biomass in the complete-removal (no competition) plots for that neighbour species. SC = *Solidago canadensis*, SG = *S. graminifolia*, AP = *Aster pilosus*, DC = *Daucus corota*, AM = *Achillea millefolium*, AR = *Agropyron repens*, BI = *Bromus inermis*, MX-TD = mixture of all tall dicots, MX-RD = mixture of rosette dicots. (From Goldberg, 1991.)

allow the effects of competition to be measured either as a function of abundance (that is, per total biomass of neighbours) or as a function of biomass (that is, per gram of neighbours). Figure 1.10 shows that the performance of *S. canadensis* depended in part upon the abundance of each neighbour with the relatively abundant *S. canadensis*, *Agropyron repens* and *Bromus inermis* (lower right) causing much more depression of performance than the less common species such as *S. graminifolia*, *Achillea millefolium* or *Daucus carota* (upper left). This plant community is therefore neither monopolistic nor diffuse, but somewhat intermediate. When, however, the effects of different relative abundance were removed by expressing competitive effects on a per gram basis, all species had similar competitive abilities. On a per gram basis, then there was true diffuse competition. More recent studies (e.g. Goldberg and Landa, 1991) have found the same equivalence on a per gram basis. We shall return to this kind of experiment in Chapter 4.

1.4.3   The relative impacts of competitors

In most sports, games, battles and competitive interactions there are winners and losers, but when we (carelessly) refer to the 'intensity of competition'
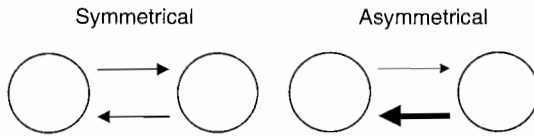
Symmetrical   Asymmetrical

Fig. 1.11   Two species may compete in a symmetrical way (with equivalent negative effects) or in an asymmetrical way (with a clear winner and loser).

between two organisms, we obscure the important – even critical – possibility that the organisms involved are being affected quite differently by the interaction. In the rare case that the two competitors are equally matched, there is true symmetric competition (Fig. 1.11, left). At the other extreme, with a clear winner and loser, there is asymmetrical competition (Fig. 1.11, right). These extremes represent two ends of a continuum along which we may plot species interactions. (We shall see that while symmetrical competition is far less common than asymmetrical competition, ecologists have tended to emphasize them in exactly the opposite degree to their occurrence in nature). At one end of the continuum are interactions in which the two competing populations are equivalent and are producing equal effects upon each other. At the other end of the continuum, one of the populations is so dominant over the other that the effects of the subordinant upon the dominant cannot be detected. The current terminology is confusing. Plant ecologists have used competitive equivalence (left) as their reference point, and adopted the term 'reciprocal' to describe these conditions (Fowler, 1981; Silander and Antonovics, 1982). In contrast, animal ecologists have used dominance as their reference point (right), and adopted the term asymmetrical to describe the latter set of conditions (Lawton and Hassel, 1981; Persson, 1985). The terms are therefore both equivalent and opposite. This distinction is illustrated in Figure 1.11; in the first case, the interaction is symmetrical (reciprocal), whereas in the second case the interaction is asymmetrical (non-reciprocal).

Example 10: Asymmetrical interference competition among nations
The competition among nations for access to global resources such as food, oil or metal ores is similar to the competition among organisms for food, water or mineral nutrients. Table 1.4 summarizes a recent asymmetric interaction between two nations of the Americas. The larger of the two was little affected by the interaction, whereas the smaller was badly damaged.

1.4.4   Competitive effect and competitive response

There is yet another possible distinction in an interaction between two species. The competitive ability of a species growing in mixture describes a situation that also has two separate components (Goldberg and Werner, 1983; Goldberg, 1990).

Table 1.4 Asymmetrical interference competition among humans for global resources (data from Matthews and Morrow, 1985; Melrose, 1985; Oxfam Canada; school category includes adult education centers).

	USA			Nicaragua
Relative size				
Gross national product (US $ *per capita*)	14 080			884
Area (km^2)	9 363 000			148 000
Population (millions)	241			3
Interference competition				
American civilians killed by Nicaragua	0		Nicaraguan civilians killed by USA	> 7500
American teachers killed or kidnapped by Nicaragua	0		Nicaraguan teachers killed or kidnapped by USA	> 300
American schools closed by Nicaragua	0		Nicaraguan schools closed by USA	> 1000
American health centres damaged by Nicaragua	0		Nicaraguan health centres damaged by USA	> 40

The first is competitive effect, that is, the damage that each species can do to its neighbours. The second is competitive response, that is, the ability of each species to withstand the effects of competition from neighbours. (In general usage, it appears that the term competitive ability is frequently used as a synonym for competitive effect; more precision is needed.)

The distinction between these components may be important in two ways (Goldberg and Werner, 1983). First, competitive effects may be relatively similar among species whereas responses may not. For example, a seedling growing in the shade is inhibited by lack of light, and may be relatively insensitive to which species is actually intercepting the light. The competitive effects of all neighbours, then, may be similar. In contrast, each species of seedling might have different means to tolerate lack of light, so perhaps competitive response could be quite different. Recent experimental work, however, fails to support this suggestion – hierarchies of competitive response appear similar regardless of neighbour species (Goldberg and Landa, 1991; Keddy et al., 1994).

Example 11: Effect and response in old field plants

Returning to vegetation of old fields, Goldberg and Landa (1991) grew seven species including the grass *Lolium perenne* and two legumes (*Trifolium pratense* and *T. repens*) in all possible pairwise combinations across an array of densities. Such results can be presented in a matrix where the rows give the relative competitive effects and the columns relative competitive response. The rows compare the effects of different neighbours upon one selected target species and the columns compare the response of one target species to different neighbours (Fig. 1.12).
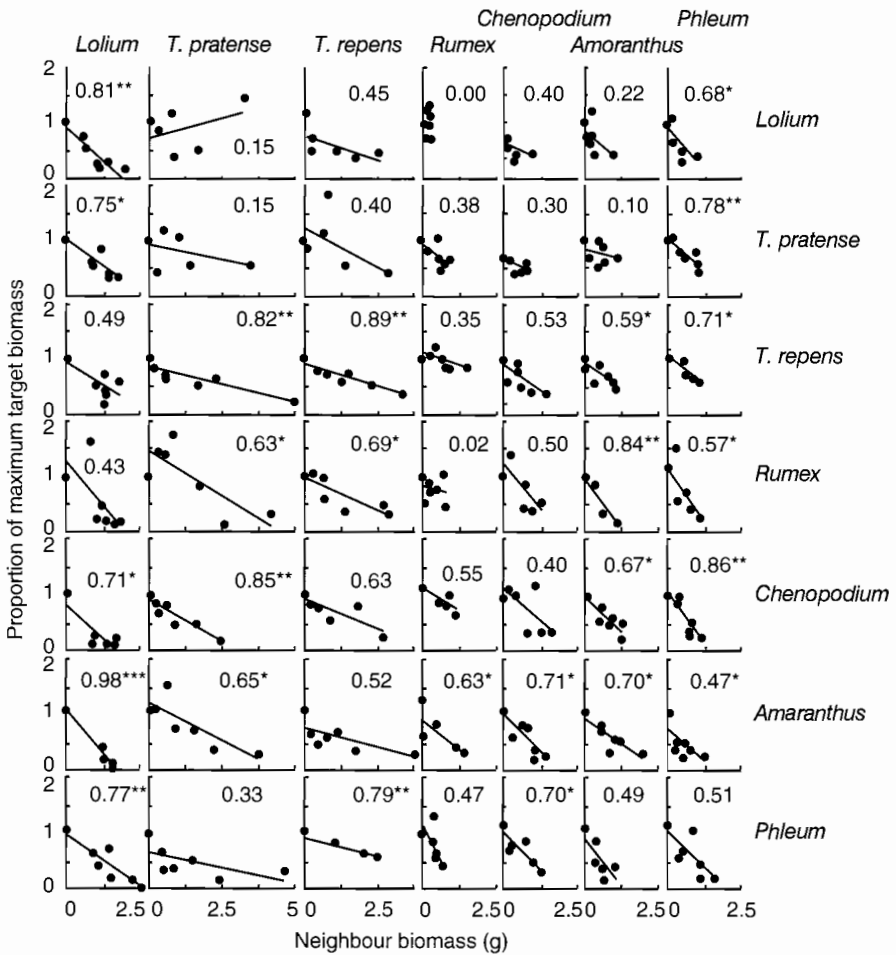
Fig. 1.12 Proportion of maximum target performance as a function of neighbour bio-mass for all forty-nine combinations of sevens species as neighbours (columns) and target (rows). The values on each graph are the R^2 and significance level ($n = 7$) from linear regressions on untransformed data. Note that all graphs are on the same scale so that slopes can be visually compared. Negative slopes indicate competitive relationships. $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. (From Goldberg and Landa, 1991.)

1.4.5 Apparent competition

Many of the examples introduced so far address interactions among small numbers of individuals or species, but the difficulties in interpreting such experiments are multiplied by their being connected to large numbers of other species through webs of competition and predation. "When multiple victim

species (e.g. prey, host) are attacked by one or more shared enemy species (e.g. predator, pathogen), the potential exists for apparent competition between victim populations" (Holt and Lawton, 1994). A parable may clarify this point.

Darwin's observations of bumblebees and red clover led him to extrapolate that since field mice, who prey on bumblebee nests, were relatively scarce near villages, they could account for the prevalence of red clover there. The mice are presumably scarce there because of predation by domestic cats. A German scientist then continued to extrapolate that since cats were responsible for the prevalence of red clover, and since red clover was a staple food of cattle and since British sailors thrived on bully beef, one could conclude that Britian's dominant world position as a naval power was ultimately determined by the presence of cats. Thomas Huxley, tongue planted firmly in cheek, went on to note that old maids were the main protectors of cats, thus showing that the British empire owed its existence to the spinsters of England (Vandermeer et al., 1985, p. 326). That is to say, interpreting the actual cause of a change in abundance of one species is devilishly difficult because it is connected indirectly to so many other species. The careful design of experiments can help minimize such indirect effects, but the problem remains that when a species is removed from a community, a host of other possible effects may accompany its removal. A test species may increase after the removal of a neighbour, for example, not because it was competing with the neighbour for resources, but because in the control plots the neighbour attracted a species of grazing insect. All such possible interactions which could produce the appearance of competition have been called 'apparent competition' (Connell, 1990; Holt and Lawton, 1993).

Figure 1.13 illustrates four possible kinds of interactions among species. In this case Connell uses plants, but exactly the same principle applies to any trophic level. In the first case, there is interference competition between the two individuals, and in the second, they have negative impacts upon each other owing to both reducing the levels of a shared resource pool. In the third case, they have negative impacts upon each other by supporting and increasing the population size of a shared enemy. In the fourth case, the apparent competition between P1 and P3 is created by their mutual interaction with P2; P1 increases the abundance of P2 which then suppresses P3. The table could be extended by creating increasingly complex feedback loops to expand the possibilities for apparent competition (Lane, 1985), a topic to which we will return in Chapter 9. Many ecologists would consider only the first two cases to be 'real competition', although Connell notes that if competition is simply defined as the negative effect of one species upon another in the same trophic level, then all four cases present true competition. Certainly, we have already seen two examples that suggest the dichotomy is not this clear: the case of beetles carrying a predator, and the case of ants protecting acacias. Both of these could be called cases of apparent competition, yet it seems likely that they are in fact intricately evolved mechanisms of interference competition. Both of these involve insects; Holt and Lawton (1993) are of the opinion that apparent interaction may be particularly
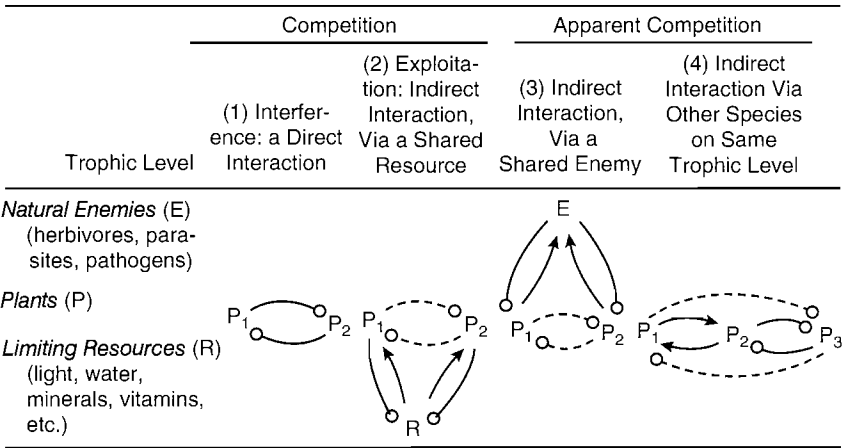
Trophic Level	Competition		Apparent Competition	
	(1) Interference: a Direct Interaction	(2) Exploitation: Indirect Interaction, Via a Shared Resource	(3) Indirect Interaction, Via a Shared Enemy	(4) Indirect Interaction Via Other Species on Same Trophic Level
Natural Enemies (E) (herbivores, parasites, pathogens)				
Plants (P)				
Limiting Resources (R) (light, water, minerals, vitamins, etc.)				

Fig. 1.13   Four types of interactions among organisms. Solid lines are direct interactions, dashed lines are indirect ones, and an arrowhead indicates a positive effect and a circle indicates a negative one. (From Connell, 1990.)

likely in insect assemblages because parasitoids can limit their hosts to levels at which resource competition is unimportant.

In another case involving insects and, in particular, plant–ant interactions, Vandermeer et al. (1985) discussed the effects of ants tending homopteran pararsites on plants. If these three players are considered alone, the ants have a negative effect on the plant since they protect the homopterans which in turn eat the plant. But if we consider more species it then appears that the ants are also excluding other insect herbivores, with the overall consequence that the plants benefit from the ants. "In other words, the incorrect conclusion that the ant must have a negative effect upon the plant derives from having conceived of a four dimensional system (ant–homopteran–plant–herbivores) as a three-dimensional one (p. 332)." The situation may become complex still more; in the case of ants on black locust trees (*Robinia* spp.), the protection the tree gains from other herbivores is apparently balanced by the protection the herbivore also gains from its enemies! The actual effect of the ants upon the plants, then, becomes dependent on the relative intensity of these different interactions.

Drawing the line between 'apparent' and 'real' competition would thus appear to depend largely if not entirely upon whether the interaction is simply fortuitous, or whether it is an outcome of an evolutionary strategy to interfere with neighbours. Making this judgement call is by no means easy, and may not even be possible except in very clear cases like ants and acacias. Hence, one needs to read the scientific literature with care, because the tendency to refer to apparent competition can create the smug impression that competition is not involved, or that one has cleverly avoided being duped into seeing competition when none

really exists. The term is useful because it reminds us of the large number of indirect interactions in nature, but it does not set a clear limit upon competitive interactions in spite of the number of times this is implied.

The above categories do not exhaust the possibilities for recognising different kinds of competition. We shall examine some more unusual and far-reaching examples sections 1.6 and 1.7.

1.5 HISTORICAL FOUNDATIONS: THE FIRST COMPETITION EXPERIMENT

According to Ricklefs (1990), the earliest published competition experiment appeared in 1917 in the *Journal of Ecology* by Professor A. G. Tansley (1871–1955) of Cambridge University. Since this paper is now primarily of historical interest, and since this first chapter is a broad introduction to competition, it may be appropriate to spend a little more time than is customary on its historical context. Tansley reported on a series of experiments carried out in the Botanic Garden at Cambridge using two small herbaceous plants that grow on rocky hillsides and pastures, species of bedstraw called *Galium saxatile* and *G. sylvestre*. This experiment was inspired, Tansley tells us, by observations published by Karl Wilhelm Nägeli in 1865. Nägeli, he says, "brought into prominence an ecological problem of considerable interest and importance, namely the relation of competition between species, particularly closely related species, to their soil preferences."

Nägeli's treatise included a description of the distribution of two closely related species of yarrow (*Achillea*) in high alpine valleys of the Bernina region in Switzerland, a region of glaciers and mountains in the Alps near the Swiss–Italian border. When both occur together, each species of *Achillea* is restricted to a favoured soil type, siliceous or calcareous. When either one is absent from a region, however, the remaining species grows on both soil types. In contemporary terms, it would appear to be a probable case of competitive release. Many pairs of closely related species appear to show such patterns of distribution with respect to soil preference, a situation which Nägeli termed 'bodenstet' where both occur and 'bodenvag' where the congener is absent.

To back up further in time, Karl Wilhelm von Nägeli (1817–1891) was a Swiss botanist best known for his work on plant cells. He observed cell division, discovered spermatozoids of ferns, described the meristems of plants (and also, alas, rejected a paper on the laws of inheritance sent to him by a certain Gregor Mendel, a paper that then languished in obscurity for some 40 years). Mayr (1982) has a good deal more to say about Nägeli, none of it very complimentary. In his history of evolutionary thought, Mayr notes that Nägeli speculated about every conceivable aspect of inheritance and development, and for the next 20 years in the field, one does not find a paper in the field that does not quote him extensively, and usually with "considerable reverence . . . . Nevertheless, almost

every detail of his theory was radically wrong and almost none of it was based on any known fact" (p. 671). Mendel, in contrast, was not a prolific writer, but he did correspond with Nägeli, and described some of his results of crossing experiments. "Instead of encouraging Mendel, he [Nägeli] apparently did just the opposite, nor did he invite Mendel to publish his results in one of the prestigious botanical journals where they could have come to the attention of others". Nägeli did, however, give a further disastrous piece of advice – to test the theories of inheritance in the genus *Hieracium*, now known to be a genus where apomixis is widespread, a genus which was bound to be intractable to Mendel's analyses. Further, "[w]hen Nägeli in 1884 published his great book on evolution and inheritance, he entirely failed to mention Mendel even a single time in a long chapter dealing with hybridisation experiments, this is almost unbelievable since everything else in the chapter is of far less significance than Mendel's work" (p. 723). Finally, one last observation by Mayr on Nägeli. There is a tendency, Mayr says for scholars to wrap themselves in the 'right words' for the times. The emphasis upon mechanism is one example. Regarding Nägeli's treatise on inheritance "All that Nägeli was actually able to present was pure speculation (and all that was new in it turned out to be wrong!) and yet Nägeli boasted of having proposed a strictly mechanistic theory. Mechanistic meant scientific . . . . a historian, looking at such statements from the outside, might fail to realise that such claims were purely psychological weapons (pp. 851–852).What has all this got to do with competition? Nägeli may have stimulated Tansley to experiment, but if we are to believe Mayr, this is small compensation for the damage he caused elsewhere. Further, it may provide an historical context for recent claims, almost exactly 100 years after Nägeli's treatise, regarding the over-riding significance of mechanistic theories of competition (e.g. Tilman, 1982, 1987a).

Let us end this historical regression with one further digression. Nägeli had been a student of the botanist Augustin Pyrame de Candolle at the University of Geneva. Augustin de Candolle (1778–1841) undertook a descriptive classification of all known seed plants, *Prodromus Systematis Naturalis Regni Vegetabilis* (17 volumes, 1824–1873). He also pioneered the study of phytogeography, carrying out botanical explorations in Brazil (1827), East India (1829) and China (1834). This work was then taken up by his son Alphonse Pyrame de Candolle (1806–1893) who edited the last 10 volumes of the aforementioned 17 volumes prodromus, and wrote his own two volume treatise on phytogeography, *Géographie Botanique Raisonée* (1855). His son, Anne-Casimar de Candolle (1836–1918) also helped him complete a series of monographs on seed plants.

Tansley, then, set out to experimentally explore the patterns of distribution of these closely related plants that Nägeli, de Candolles's student, had described. He set up four soil treatments (we shall only discuss two here) and grew each species alone and in mixture on each of the two soil types, siliceous (acid) and limestone (calcareous). "The idea was to trace the course of competition between the two species on soils which each 'prefers' in nature, and also on soil which neither naturally inhabits". Although bedevilled by problems with

getting the plants to germinate, grow and survive, he started the experiment in 1911 and grew them together for 6 years. His assistant, a Miss E. M. Hume, left in 1913 and is not heard from again.

The experiment was then taken up by "the late Captain A.S. Marsh until he joined the army in the autumn of 1914". We may assume from this short phrase in Tansley's publication that Marsh was one of the lost generation of some 9 million soldiers who perished in the First World War, perhaps in the intense period of trench warfare of 1915 or 1916; certainly he was already the late Captain Marsh by the time this paper appeared in 1917, a year before the end of the conflict. If we look further, we find reports that Marsh's scholastic and university career had been an unbroken success (Price, 1916), but he enlisted, was sent to Europe, and was shot through the heart by a sniper's bullet in the trenches of Armentieres in 1916 (Tansley, 1916; Sheail, 1987). Writes a historian of those times (Winter, 1990) "It is likely that by 1918, every household in most combatant countries had lost a relative or a friend" (p. 206).

Poignantly, near the same time, the German scientists Hauri and Schröter (1914) completed a monograph on cushion plants (338 species, 78 genera, 34 families, half of which grow in South America, especially the Andes) and Schmid (1912) completed a review on insectivorous plants (covering topics such as the insects they feed upon, the structure of roots systems and leaves, and rates of water loss). Agricultural botany had been revolutionized only a few years earlier, when a Prussian chemist named Fritz Haber developed a method for synthesizing ammonia from nitrogen and oxygen. This relieved the world from agricultural dependence upon reserves of Chilean nitrates. His incentive, however, was to relieve Germany from foreign dependence upon nitrates for the manufacture of the very munitions that were being used to kill young foreign soldiers. During the war he also played a major role in developing poison gases for use in trench warfare. (Haber received the Nobel Prize in 1918 and his work on poison gas did not stop Cambridge University from later offering him a position.)

The work of brilliantly promising poets like Wilfrid Owen was tragically cut short in the same war (Abrams, 1962), leaving us to ask how the twentieth century might have progressed without such waste of human talent. Owen, in his *Anthem for Doomed Youth* (published posthumously in 1920) wrote "What passing-bells for those who die as cattle? Only the monstrous anger of the guns, ..." (Abrams, 1962, p. 2294). Similarly, we have no way of knowing what contributions to ecology might have been made had he lived. Marsh had also set up a series of prescient experiments to separate the effects of root and shoot competition, but one gains the impression from Tansley's paper that after Marsh left, these experiments were not tended with the care they required.

Enough context: now to the actual experiment. Tansley (1917) reports that when growing alone each *Galium* species survived on both soils, but when grown in mixture, each was restricted to the soil type on which it was specialized (Fig. 1.14). "In the case investigated, the calcifuge species (*Galium saxatile*) was heavily handicapped as a result of growing on calcareous soil, and thus
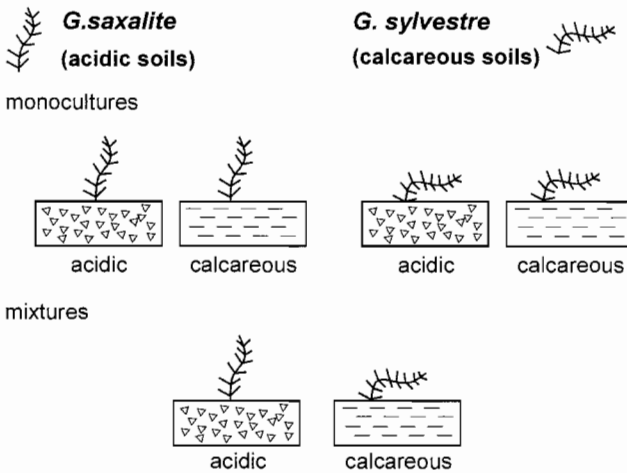
Fig. 1.14 An early competition experiment (Tansley, 1916) examined two species of bedstraw (*Galium* spp.) and asked whether performance varied among soil types or differed between monocultures (top) and mixtures (bottom). Note that only the winner in each condition is illustrated in the bottom row.

unable to compete effectively with its calcicole congener, *Galium sylvestre*. The calcicole species is handicapped as a result of growing on acid peat and is therefore reduced to a subordinate position in competition with its calcifuge rival, which is less handicapped. Both species can establish and maintain themselves – at least for some years – on either soil".

In this experiment we can see the origins of many of today's current inquiries, debates and even habits. The possible role of competition in controlling the distribution of species. The tendency to study competition between closely related species. The idea that the outcome of competition is contingent upon environment. The issue of whether species have separate or inclusive fundamental niches. The relationship between niche overlap and competition. Competitive release. Dominant and subordinate species. And note that this work is in turn enmeshed in field observations that go back nearly 100 years. Where would we be today if Marsh had lived, or if others had followed up promptly on Tansley's work? Such questions are pointless, except that they remind us that many apparently new questions have solid historical antecedents (Jackson, 1981; Booth and Larson, 1999).

The above categories do not exhaust the possibilities for recognizing different kinds of competition and competitive interactions. Two others deserve consideration. First, Arthur (1982, 1987) has emphasized competition between different genotypes within populations, and the evolutionary consequences of such interactions. This presents competition within the conceptual framework of evolutionary ecology. Secondly, Buss (1988) has explored competition among

different cell lines within individuals, and the implications of this for the evolution of development. Although investigations of intra- and interspecific competition dominate the current literature, future progress may lie along research paths exploring higher levels of organization (e.g. competition intensity gradients) and lower levels of organization (e.g. intra-organismal competition).

1.6 COMPETITIVE DOMINANCE

Competitive dominance is an outcome of interactions where one species suppresses another through exploitation and/or interference competition. It starts with asymmetric (non-reciprocal) competition between individuals, genotypes, or species. The effects of the dominant upon the subordinant are steadily enhanced through two positive feedback loops (Fig. 1.15). First, there is exploitation competition. The dominant lowers the resource levels for the subordinant, but is simultaneously better able to forage for additional resources itself by reinvesting newly captured resources in further growth. This lowers further the resource levels for the subordinant. Second, there is interference competition. The more successful the dominant is at interfering with neighbours, the greater the resources available for supporting further growth of the dominant. This increases further its ability to monopolise resources, increasing
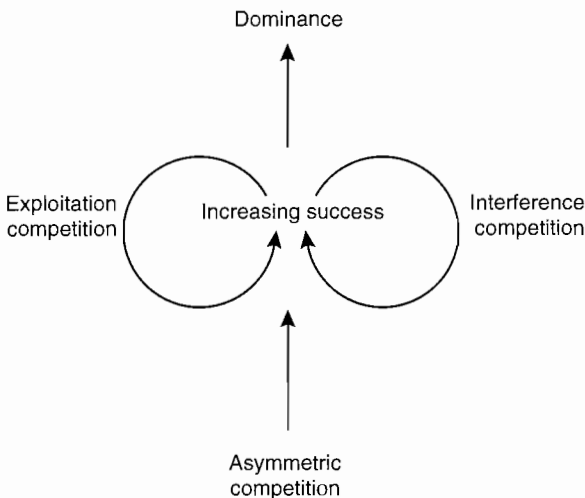
Fig. 1.15 The positive-feedback loops which generate dominance. Success at exploitation competition increases the resources available to forage for new resources, and simultaneously reduces the resource supply for neighbours. Increased availability of resources allows some to be channelled to interference competition, damaging neighbours and leaving more resources available for exploitation by the dominant.

both rates of resource acquisition and damage to potential competitors. The relative importance of the two loops is likely to vary from situation to situation, and in some cases effects may be separated into exploitation and interference only with difficulty. However, the end-result is one species suppressing another or excluding it from a given community.

One of the difficulties with discussing dominance arises from the tendency to assume that competitive interactions are symmetrical and talk loosely about 'competition' between two species. As soon as there is asymmetrical competition, the experience of the dominants and subordinants diverges. It becomes essential to specify whether competition is being viewed from the perspective of the dominant or the subordinant. The analysis of such interactions is clarified by considering that in any competitive interactions there are both effects and responses (section 1.4.4). The response of a subordinant may be to tolerate the impact of the dominant, in which case it remains present, albeit at a low level. Alternatively, it may escape from the competition by dispersing in space or time to another site (a ruderal or fugitive species). The analysis of asymmetrical interactions requires explicit consideration of the effects of the dominant and responses of the subordinant.

These issues are discussed further in Chapter 5, which looks at hierarchically structured communities. It is important here to clarify the distinctions between competitive dominance and dominance. The word dominant is sometimes used to describe any organism which is abundant in a community. This usage is misleading; abundance need not be the result of competitive dominance. Competitive dominance is abundance achieved as a consequence of exploitation and interference competition for resources – that is, there is an active process of suppressing neighbours (Fig. 1.16, bottom). Grime (1979) describes dominance as a process whereby one species achieves numerical dominance and suppresses others. His use of dominance is not equivalent to the term competitive dominance used here, since Grime includes a second group of effects – a species may become dominant because of inherently better abilities to withstand environmental effects such as fire, infertility or grazing. This added group of effects is shown by the upper portion of Figure 1.16. It seems useful to distinguish between situations where a species is dominant simply because of inherent traits for tolerating the environment and situations where a species is dominant because it has traits for suppressing neighbours. The former type of dominance could occur in the absence of any competition. Only in experiments in which possible dominants are removed and the responses of subordinants observed would it be possible to separate the effects of the two causal agents. In Figure 1.16 the environmental effects are reinforcing the competitive effects, but it is possible to imagine the opposite situation where the environment weakens the effects of the dominant. In this book competitive dominance is emphasized, but it is important to recognize that both occur in nature and that competitive dominance is a subset of dominance as used by Grime (1979).
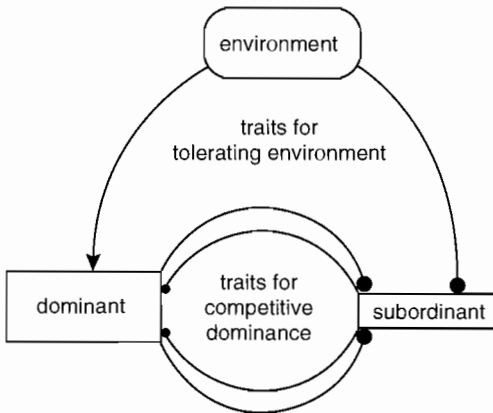
Fig. 1.16 The possible interactions between the dominant, the subordinant and the environment. Arrows are positive effects, solid circles are negative effects. Competitive dominance refers solely to the direct links between the dominant and the subordinant (bottom). The environment (top) may independently determine which species dominates a site. In this example the environment is enhancing the effects produced by asymmetric competition, so dominance is only partly attributable to competition.

Examples of competitive dominance in different plant and animal communities can be found in Chapters 2 and 6. The relationship between dominance and territoriality has been of particular interest to behavioural ecologists (Brown, 1975; Small, 1993). Kaufmann (1983) emphasizes the behavioural basis of dominance in intraspecific competition, noting that 'dominance/subordinance is a relationship between two individuals in which one (the subordinant) defers to the other (the dominant) in contest situations'. It is usually assumed, although rarely shown, that such relationships represent an adaptive compromise for each individual in which benefits and costs of giving in or not giving in are compared. Dominance provides priority of access to resources, and is therefore a behavioural aspect of asymmetrical interference competition (Dyson-Hudson, 1983; Diamond, 1992; Miele, 1996). Wilson (1975, 1978) has reminded us that ecological and evolutionary principles apply to humans as well as any other organism. Dominance has been explored in human interactions (for example, Maccoby and Jacklin, 1974; Boone, 1983; Diamond, 1992). The mechanisms of dominance are often easiest to observe in human interactions. Some of the most dramatic examples of dominance are found where human societies compete for access to global resources. These include socioeconomic positive-feedback loops and military interference competition. Examples could come from China in Tibet or France in Algeria, but Table 1.4 illustrated the USA in Latin America. The USA has a dominant economy dependent upon the acquisition of resources from Third World countries (Lappe and Collins, 1982; Myers, 1985). As success at acquiring resources increases,

large corporations have the wealth to buy more land and build more mines in developing countries, further increasing rates of resource flow into the dominant economy. This further reduces resource supplies to the local economies (Lappe and Collins, 1982), increasing economic dominance and inequities further. Resource depletion can produce hunger in countries that have more than sufficient agricultural land to feed their own populations. This is straightforward exploitation competition. The resource surplus of the dominant can then be used for interference competition, where military dictatorships that are favourable to resource extraction are installed and maintained by military and economic aid (Chomsky and Herman, 1979; Klare and Arnson, 1981; Blum, 1998). Assassinations by death squads and the destruction of hospitals, co-operative farms and day-care centres are part of the interference feedback loop.

1.7   COMPETITION AND THE ORGANIZATION OF LIVING SYSTEMS

There are many different kinds of competition at many different scales of organization. Competition among species is the most widely-appreciated and thoroughly studied, as we have seen from the examples in section 1.4. At smaller scales, however, we can recognize many of the same processes. These include competition among enzymes for reaction substrates, competition among genes for control of organisms, and competition among meristems for control over plant growth. At the larger scale, one can find competition among tribes of humans for agricultural land, competition among nation states for raw materials, and even competition among religious belief systems for access to human minds. While this book focuses upon competition among individual organisms and groups of organisms, we should appreciate that many of these same principles may apply to these other areas of scientific activity. Let us therefore look at an array of different living systems in which competition occurs: evolution and selfish genes, the origin of life, catalysis, neurotransmission, and meristems within plants. We will then look (section 1.8) at examples involving human societies, genocide, the origin of nation states, asymmetric competition between masters and works, memes and finally kleptocracies.

1.7.1   Darwin's theory and selfish genes

Ernst Mayr argues that the theory of evolution required a fundamental shift in human understanding of species, the shift from a species representing a type of creature to a population of genetically different creatures. The variation within a population provides the raw material upon which natural selection can work. Once this recognition of intra-population variation has been appreciated, the

process of evolution is a natural consequence. There are four basic principles that underlie the theory of evolution by natural selection:

(1) Production of young: Every organism on earth has the potential to produce vastly more young than can survive.
(2) Variation: These young differ in their traits, largely as a result of sexual recombination, but also as a consequence of chance mutations.
(3) Selection: The individuals with traits that most closely fit the environment tend to survive and reproduce themselves.
(4) Inheritance: The next generation of young tends to have the same traits as their parents. If the environment changes, so do the traits of the species.

Competition plays a role in this process of selection because those organisms with traits that provide the best fit to the local conditions are able to out-compete their neighbours through intense resource competition or inter-ference competition. Thus, the stronger competitors tend to replace the weaker, so long as the benefits of the competitive traits do not outweigh their costs. Another way of expressing this is to say that the presence of neighbours, both of the same and different species, becomes part of the environmental template which organisms must fit in order to survive.

One commonly hears the view that evolution cannot work because 'mere chance' cannot produce life. The diversity of life forms and their close fit to their environments cannot, the argument goes, have arisen by 'mere chance' muta-tion (and therefore, the line of argument usually continues, evolution cannot occur.) The chance event of mutation is nearly irrelevant to the process of nat-ural selection. The 'chance' element in the process is actually generated largely by sexual mixing of pre-existing genes. The order is created not by mere chance but by selection. Selection is a consequence of the mismatch between the re-shuffled genetic materials and the environment that they come to occupy. When only one out of a million offspring can survive, there is a great deal of raw material for selection to act upon. The extremely close fit between organ-isms and their habitats, is, therefore, not a matter of chance at all. Selection occurs because the environment has served as a template to which all organ-isms are forced to conform or die. When Darwin talked about survival of the fittest, this is what he meant. The fittest are those whose genetic predisposi-tion provides the best short term fit to the environment, that is, the closest fit to the habitat template. This is an entirely passive process: if an individual does not fit, it dies; if it does, it lives, and gains the opportunity to reproduce.

A twentieth century student of Darwin, Richard Dawkins, has explained that we may better understand the process of evolution by considering the scale of genes rather than organisms. Organisms, Dawkins (1976) argues are just a gene's way of producing more copies of itself. Each organism is a gene factory, and the genes that survive and multiply do so because they have made gene factories that are likely to persist and efficiently construct many more copies of

those genes that built it. Survival of the fittest then, really means survival of the factories that are most successful, factories which are busy producing copies of the genes that serve as their blueprints. From the perspective of the gene, the organism itself is relatively unimportant, so long as it produces more copies of the genes. Recalling Mayr's comment about a shift in perspective from types to populations, Dawkins may have achieved a similar important shift, the shift from individuals to genes. From this perspective, the fundamental level at which competition occurs is the competition among genes, and individuals are merely temporary factories for producing these different genes. When reproduction occurs, genes shuffle and they mix with genes from other factories. The resulting mixtures start to build new gene factories. The environment destroys all but a few factories. The remaining factories making many more copies of the genes in their blueprints. This process has taken the Earth from one-celled prokaryotic life to complex multicellular organisms that are conscious of themselves. It is not a random or chance process; rather it is a process which is inevitable given the way the environment ruthlessly eradicates any gene factory that is unsuited to conditions.

From this perspective, genes have also found it advantageous to subcontract certain of their activities. Complex behaviour, for example provides a rapid means of adjusting to different environments. It requires, however, that genes delegate their work to a nervous system. "Genes work by controlling protein synthesis. This is a powerful way of manipulating the world, but it is slow. It takes months of patiently pulling protein strings to build an embryo. The whole point of behaviour, on the other hand, is that it is fast. It works on a time scale not of months but of seconds and fractions of seconds" (Dawkins, 1976, p. 58). Complex nervous systems also allow genes to delegate the ability to gamble on the future state of the environment. Those that have gambled correctly, that is, those that are able to predict better than others, have tended to survive at the expense of their neighbours. "One way for genes to solve the problem of making predictions in rather unpredictable environments is to build in a capacity for learning" (p. 60). This is analogous to building a computer with the capacity to learn from experience and change its behaviour. If it makes the wrong decision, it is destroyed.

In summary, Dawkins argues "The genes are master programmers, and they are programming for their lives. They are judged according to the success of their programs in coping with all the hazards which life throws at their survival machines, and the judge is the ruthless judge of the court of survival. We shall come later to ways in which gene survival can be fostered by what appears to be altruistic behaviour. But the obvious first priorities of a survival machine, and of the brain that takes decisions for it, are individual survival and reproduction (pp. 66–67)".

Given the origins of neurological activities, it may come as no surprise to find later in this section that cells communicate using the process of competition among chemical compounds, that learning involves competition among

different neurological pathways, and that there is competition among ideas ('memes') for access to memory space.

1.7.2   Thermodynamics and the origin of life

The laws of thermodynamics apply without reservation to all life forms. Morowitz (1968) explores biological and ecological processes assuming that biology is a manifestation of the laws of physics and chemistry operating in the appropriate system under the appropriate constraints. Here I explore only a small fraction of his ideas, primarily those providing a context within which we can view competition. These ideas have been extended and presented in more reliable form by Margulis and Sapan (1986) and de Duve (1991). Morowitz notes that living systems are at a high potential energy level; i.e. the living state has a very unlikely distribution of covalent bonds compared with the equivalent equilibrium state at either the same total energy or the same temperature. Living systems, he shows, are not at thermodynamic equilibrium, nor could they have spontaneously originated from a chance reaction near thermodynamic equilibrium. The earth, however, is not an equilibrium system, but a steady-state system with a steady flow of energy as sunlight flows from a source (the sun) to a sink (space). Morowitz shows that this energy flow organizes matter and produces systems with high potential energy.

The origin of life is, therefore, an inevitable consequence of physical laws, and not a chance event. "The tendency to organize is a very general property of a certain class of physical systems and is not specifically dependent on living processes. Molecular organization and material cycles need not be viewed as uniquely biological characteristics; they are general features of all energy flow systems. Rather than being properties of biological systems, they are properties of the environmental matrix in which biological systems live and flourish".

Living systems on Earth are primarily water; water is an important metabolite as well as a solvent. Within this aqueous system, the major atomic components are carbon, hydrogen, nitrogen, oxygen, phosphorus and sulphur, with a variety of minor and microconstituents. Imagine a simple mixture of CHNOPS molecules (e.g. H_2O, CO_2, N_2, NH_3 and CH_4). If energy flows through this system so as to raise the average potential energy, what will be the distribution of chemical species? Compounds in higher energy states will increase at the expense of the abundant low-energy compounds. There is no alternative; if the energy is supplied in a form such that it goes into chemical bond energy, then rearrangements must occur, leading to different bonds and different molecules. This process is observed in experiments which explore the kinds of biological molecules produced in environments simulating the prebiotic period on Earth (Orgel, 1973).

Once a pool of molecules of slightly higher potential energy is created by energy flow, interactions occur within this pool, leading to the creation of

slightly larger molecules with still-higher potential energy. As long as energy flow is maintained, one can envisage a pyramid, with pools at different potential energy levels, each pool serving as raw material for the pool above it, and each similarly using the pool below it as a source of raw material (Fig. 1.17). If the energy flow is turned off, the system naturally gradually collapses to states with lower potential energy, but this possibility need not be pursued here.

Using this foundation, consider one potential energy level in Figure 1.17. At this level are molecules with similar potential energy, constantly formed from a pool of lower energy molecules (a resource pool) and occasionally converted into molecules of higher potential energy.

Within such potential energy pools a primitive form of natural selection is taking place. Those molecular forms which are 'unstable' by definition break apart into lower-energy molecules which then are returned to the resource pool. Thus, certain kinds of molecules proliferate at the expense of others.
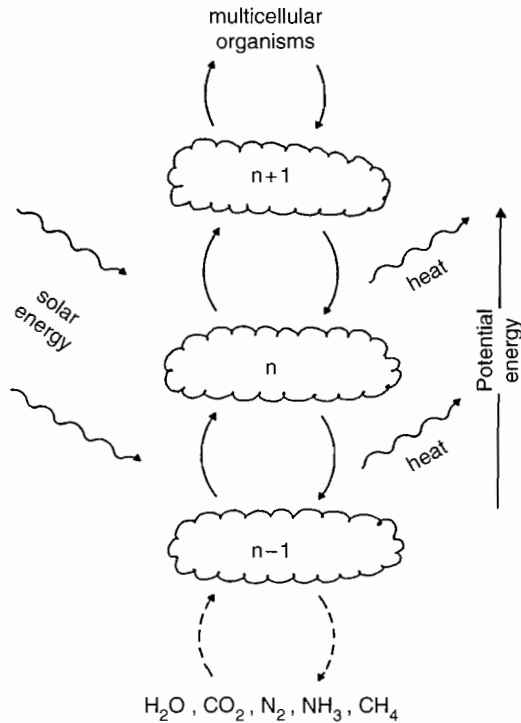

Fig. 1.17   Solar energy creates high-energy molecules out of simpler low-energy molecules. Complex molecules and multicellular organisms are inevitable thermodynamic consequences of energy flow in the biosphere (Morowitz, 1968). For any arbitrary level of potential energy there is a restricted pool of substrate molecules at the next-lower level, so that even in a simple molecular system a form of resource competition can be observed.

Their abundances are determined by three factors: (1) the rate at which molecules from the lower resource pool are converted to higher energy molecules; (2) the rate of decay of the higher energy molecules to the lower energy ones (their 'stability'); and (3) the rate at which these higher energy molecules react to produce ones of even higher potential energy.

It is clear that those molecular forms which proliferate will have three properties. First, they will be rapidly formed from lower energy molecules; if they catalyse such interactions, this process will be enhanced. Thus, one can draw the analogy of consumer molecules, each dependent upon the conversion of molecules from low to high potential energy. Secondly, the proliferating molecules will have traits which increase persistence through time. Molecular stability is an initial prerequisite, but cell walls can be seen as one relatively simple method of further enhancing stability. Third, they will be formed from common, rather than scarce precursors.

Consider cellulose, for example, which is the most abundant molecule in the biosphere, with an estimated biomass of 9.2×10^{11} tons (Duschesne and Larson, 1989). Cellulose is simply a polymer composed of repeating molecules of glucose, $C_6H_{12}O_6$. Morowitz notes that single, double and triple carbon–carbon bonds and carbon–oxygen bonds are more stable than, say, carbon–nitrogen bonds. Further, these stable bonds favour the formation of polymers. "Therefore, the accumulation of cellulose in the biosphere may be the result of a sunlight driven ... cycle of positive feedback operating on the available molecular diversity and leading to the accumulation of long-chain molecules as a natural and perhaps inevitable consequence of selection for chemical stability" (Duchesne and Larson, 1989).

At this molecular level it is already possible to discern the essential processes with which ecologists are concerned. Resource pools are consumed and converted into more-organized (higher potential energy) systems. The abundance of the higher potential energy systems like protein is limited by the abundance of the resources like NO_3, and the rate at which they can be 'harvested'. There is, therefore, a form of intermolecular competition for the resource pool. With sufficient imagination, predator–prey interactions can also be seen, with the higher-energy molecules preying upon the lower-energy ones.

Such thermodynamic processes do not prove that competition is universal. In fact, the seeds of two major counter-arrangements are hidden within that same molecular model. If the energy flow fluctuates, then the amount of a particular compound may be less dependent upon the resource pool than upon the time since the last perturbation. Thus, we have the argument that competition is not important if systems are repeatedly disturbed (that is, in Morowitz's terms, if there is variation in the energy flow producing the steady state). If molecules are continually converted to other forms by enzymes ('preyed upon'), then their abundance may be set as much by the rate of removal from the pool than by their rate of production. Thus, we have the argument that predation reduces competition.

The fact that we all share common chemical origins and are constrained by the same physical laws give good thermodynamic reasons for expecting competition in nature. The accumulation of more complex molecules is limited by, among other factors, the pool of resources. Organisms or molecules must have such resources in order to reproduce. The variety of life-forms on Earth is staggering, and it is so easy to get caught up on fascinating details of form, function and natural history. However, if the systems were stripped of all detail, they would look very much like the thermodynamic model that Morowitz presented for the behaviour of simple chemical systems.

Photosynthesis can be viewed as a process resulting from the gradual improvement of the steps in Figure 1.17. These improvements include the use of pigments to increase the efficiency of energy capture, and the use of membranes to control the concentration of raw materials. These improvements increase the rate at which complex molecules are formed. It is therefore evident that competition among photosynthetic organisms will be for the raw materials limiting this process, and that both the efficiency of use and rate of formation of photosynthate will be key traits of these organisms.

In the same context, the ubiquitous citric acid cycle (or Krebs cycle) shown in Figure 1.18 can be viewed as the steps in Figure 1.17 run in reverse, beginning at the top with complex molecules such as proteins, carbohydrates and fats. At each stage, simpler molecules are formed and the potential energy is extracted and stored in ATP molecules (Dickerson, 1969). One could imagine an interaction in which one step would liberate 203 kcal and form 12 ATP molecules, but in practice living systems carry this out step by step (Fig. 1.19). The terminal oxidation chain further provides 'a series of descending free energy steps' using iron-containing cytochrome proteins to control the 'free energy staircase' (Dickerson, 1969; pp. 404–405). It is also noteworthy that a majority of the ATP molecules is produced by oxidation, a process which would only have become possible once oxygen released by photosynthesis accumulated in sufficient concentrations. Prior to this, fermentation would presumably have been the primary source of ATP molecules, thereby greatly reducing the potential energy which could be extracted from large molecules (Fig. 1.18). The thermodynamic processes within living systems are therefore important to us in at least two ways. First, they reveal a good deal about the process of energy transformation that may have been present early in the prehistory of life. Second, they illustrate how the growth of primary producers and consumers will each be limited by the availability of the respective raw materials, thereby that ensuring competition for these resources will be a basic factor regulating energy flow in living systems.

1.7.3   Competition and catalysis

Life is based upon chemical reactions, many if not most of which are aided by catalysts (Figs. 1.18 and 1.19). A catalyst speeds up the rate of chemical reactions
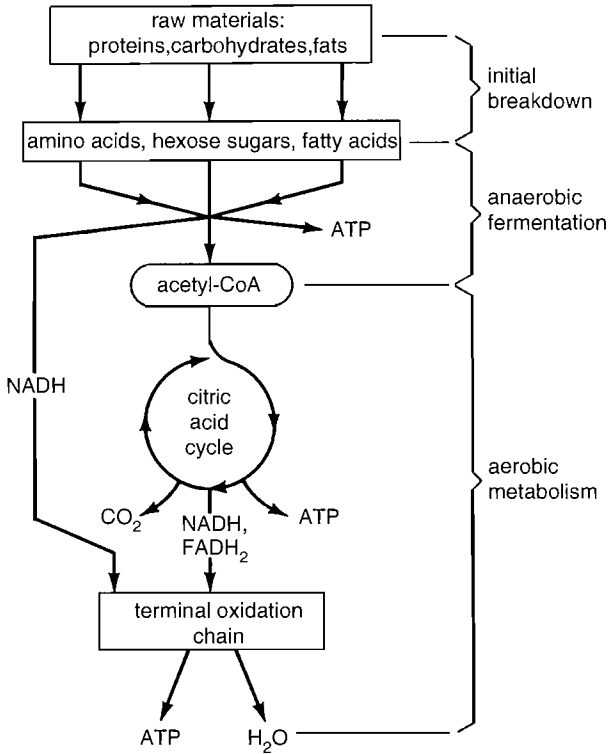
Fig. 1.18 A schematic outline of the metabolic machinery that extracts chemical free energy and stores it as ATP. (From Dickerson, 1969.)

in part by providing "a new reaction pathway in which … the rate-determining (slowest) step has a lower free energy of activation" (Bender and Brubacher, 1973). While catalysts increase rates of production of certain compounds, still other compounds can reduce rates of reaction, by interfering with the catalyst. These compounds, called inhibitors, may be used by organisms to control biochemical pathways.

One of the most basic kinds of inhibition in chemical interactions using enzymes is competitive inhibition which "occurs when a substance competes with the normal substrate at the active site of an enzyme" (Bender and Brubacher, 1973, p. 32). In a reaction mixture, some of the enzyme will be locked into an enzyme–inhibitor complex, thereby preventing the enzyme from catalyzing other reactions between the substrates. Competitive inhibition is a basic principle explored in studies of catalysis (Ashmore, 1963; Bender and Brubacher, 1973; van Santen and Niemantsverdriet, 1975). For those who are interested, this process is explored in more detail below; other readers may wish to move directly to section 1.7.4.
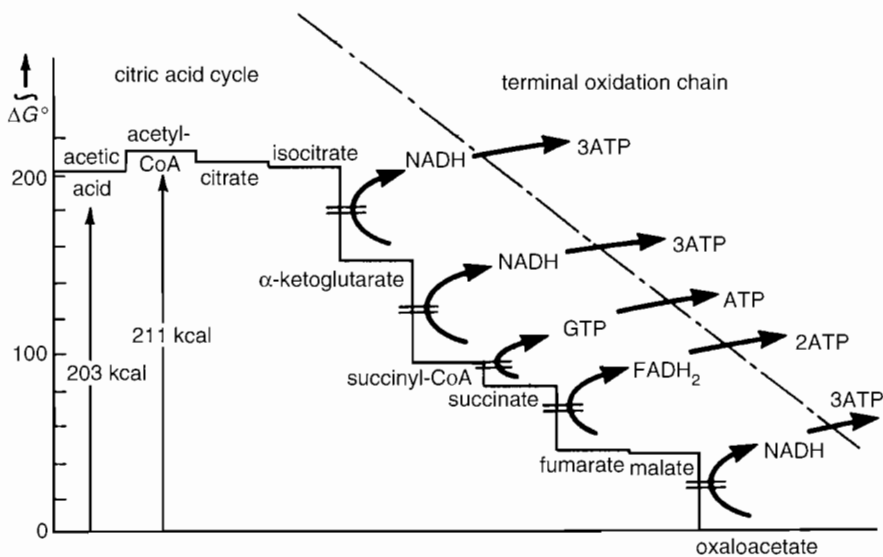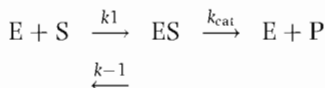
Fig. 1.19 The step by step fall in free energy as high energy molecules are disassembled in one turn of the citric acid cycle. (From Dickerson, 1969.)

Following, Bender and Brubacher (1973), a simple enzyme catalyzed reaction can be represented as

$$E + S \xrightarrow[\underset{k-1}{\longleftarrow}]{k1} ES \xrightarrow{k_{cat}} E + P$$

where S is the substrate, E is the enzyme, P is the product and the constants $k1$, $k-1$ and k_{cat} are rate constants for the reactions in the direction indicated by the arrows.

In this case, the equilibrium concentration of the intermediate, ES, is given by

$$[ES] = \frac{k1 \, [E] \, [S]}{k - 1 + k_{cat}} = \frac{[E] \, [S]}{K_m}$$

whence $K_m = [E] \, [S]/[ES]$.

K_m designates the relative concentrations at which no further changes in chemical composition occur because forward and reverse reactions are proceeding at equal rates (Brackenridge and Rosenberg, 1970). Now if an inhibitor, I, is added to the mixture it will also have an equilibrium binding constant. K_i defined as
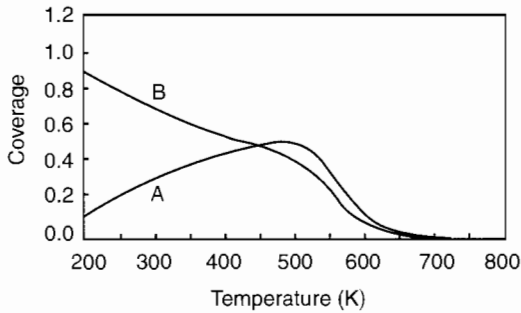
$$K_i = \frac{[E] \, [I]}{[EI]}$$

Fig. 1.20 A simulation of competition between atoms A and B for absorption sites on a metal surface (assuming the product AB desorbs instantaneously without readsorption). (From van Santen and Niemantsverdreit. 1975.)

In this case, the equation for the rate of reaction when the inhibitor is present becomes

$$v = \frac{k_{cat}[Eo][S]}{[S] + K_m(1 + [I]/K_i)}$$

where $[Eo] = [E] + [ES]$. If, for example, $[S] = K_m$ and $[I] = K_i$, then the reaction rate is reduced to $v/3$.

Such processes are not restricted to living organisms. During industrial processes where metal surfaces are used to catalyze chemical reactions, inert atoms can bond to the metal surface, thereby competing with other atoms requiring the same sites. Where two molecules are competing for absorption sites on a surface, one or the other may dominate the surface depending upon factors such as absorption bond strength, concentration and temperature. In the case of hydrocarbon conversion reactions being catalyzed by metals such as platinum 'the rate of reaction is largely controlled by competitive absorption of hydrogen and the reacting hydrocarbon' (van Santen and Niemantsverdriet, 1975, p. 256). Along a temperature gradient, the relative coverages of molecules can shift from dominance by one to dominance by the other; at very high temperatures, neither molecule may be present (Fig. 1.20).

1.7.4   Competition and neurotransmission

Competition also occurs at the molecular level of organization within the bodies of living organisms. Consider the process of neurotransmission. The brain has in the order of 10^{11} neurons and each neuron can have from a thousand to ten thousand synapses (Stevens, 1979). Stimuli cross a synapse when a neurotransmitter is released; it diffuses across the synaptic gap to act upon specific receptor sites on the membrane of the adjoining neuron. For example,

acetylcholine is released from vesicles into the synaptic cleft and the acetylcholine molecules bind to receptors in the next neuron, thereby transmitting an electrical impulse across the synapse. Some 30 different substances are now suspected of being neurotransmitters (Bloom, 1981). Receptors appear to be large protein molecules embedded in the cell membrane. Other compounds can, however, compete for access to these receptors and bind to them, thereby reducing the effectiveness of neurotransmission. Anti-schizophrenic drugs, for example, bind tightly to the dopamine receptors, thereby preventing the natural neuro-transmitters from activating them (Iverson, 1979). Opiate drugs similarly appear to bind to enkephalin receptors, mimicking the effects of enkephalins produced by the brain itself. The widely used anti-depressant, lithium competes for both the sodium and potassium sites in the sodium–potassium pump (Tosteson, 1981). In such cases, a mixed pool of transmitters (or neurologically important ions) is in competition for a limited number of receptor sites. Nerve gases such as diisopropylphosphorofluoridate inhibit the enzyme acetylcholisterase by forming a stable covalent bond. Acetylcholine then accumulates in the synapses and interferes with the transmission of nerve impulses; the brain then loses control over bodily functions including breathing (Bender and Brubacher, 1973).

These situations are analogous in many ways to the competition among different molecules earlier in the history of life, although the details of the process have obviously been considerably modified. The presence of membranes, for example allows certain substrates to concentrate out of reach of predatory enzymes. New kinds of chemical interactions become possible, along with newer styles of competition, competition for the receptors sites and ion pumps. The simple chemical process of competition, has still, however, been harnessed to control some of the most complicated control processes in living organisms.

Such use of 'competition' requires a slightly expanded definition from the one used in section 1.1.2 because the entities involved are no longer individual organisms. Rather, it is a particular process (communication by one group of neurotransmitters) that is being negatively affected by the presence of competitors. The idea of costs still applies, in that there are costs incurred by producing a neurotransmitter that cannot act upon a receptor, but the costs are born by individual neurons, or even subsystems within them.

Let us consider one more example, one in which resource uptake appears to be regulated by competition among molecules in the diet. The relative consumption of dietary carbohydrates and proteins may be regulated by the amount of tryptophan in the blood stream (Wurtman, 1982). The way in which tryptophan controls behaviour is thought to be based upon the process of competition among six comparatively large amino acids (tryptophan, tyrosine, phenylalanine, leucine, isoleucine and valine): "A single species of carrier molecule transports all six of the large, neutral amino acids across the blood-brain barrier; the amino acids compete with one another for attachment to the carrier and hence for uptake from the blood-stream into the brain" (p. 55). A high protein

meal will reduce the plasma ratio of tryptophan to the 'competing amino acids'; less tryptophan is carried across the barrier and less serotonin is synthesized. In experimental rats, tryptophan/serotonin levels appear to control carbohydrate intake. Eating a meal rich in carbohydrate increases serotonin synthesis that causes an animal to reduce its intake of carbohydrate but not of protein.

1.7.5   Competition among meristems within individual plants

Plants can be considered to be populations of shoots, each producing a single meristem of actively dividing cells. These meristems communicate with one another using plant hormones such as auxin (King, 1997). From this perspective, plants and corals are both colonial organisms. The earliest land plants had dichotomous branching, like many algae (Stewart and Rothwell, 1993). In dichotomous branching, each meristem occasionally divides in half to produce a new pair of shoots, so that the number of meristems increases geometrically with height above the ground. So long as there is little competition for light, this sort of top-heavy growth form seen in extant species such as *Psilotum nudum* would appear to offer a perfectly satisfactory light gathering apparatus. As the density of shoots increases, however, there is an advantage to being higher than neighbouring shoots (and neighbouring plants) in order to intercept light. There was a steady increase in plant height through the early fossil record (Niklas, 1994). Most plants, therefore, now have a type of ramification called lateral branching (Foster and Gifford, 1974) in which one meristem becomes dominant and is largely responsible for increases in height, while subordinate meristems provide short side branches. Most of the meristems in an individual tree are therefore progeny of this apical meristem.

This phenomenon of apical dominance arises out of interference competition. The apical meristem produces auxin, a substance closely resembling the amino acid tryptophan, which diffuses downward through tissues and inhibits the growth of lateral meristems (Raven et al., 1992; King, 1997). If the apical meristem is damaged, the diffusion of auxin declines, and the lateral meristems begin to grow.

In summary, during dichotomous branching, the apical meristems of a plant compete with one another for resources (light, water, N and P) not unlike individual plants involved in exploitation competition. The competition among individual cell lines within organisms (Buss, 1988) may be a more general example of this phenomenon.

1.8   COMPETITION AND HUMAN SOCIETIES

1.8.1   Agriculture and genocide

Long before ecologists conceived of experiments on competition, the process was appreciated in an informal way. The origin of agriculture some 5000 years

BP (before the present) would presumably have required some appreciation of the benefits associated with the removal of neighbouring plants (either weeding or thinning – note that we have the two words in our language for non-crop or crop density manipulations, respectively). Before agriculture arose, there would have been competition within and among tribes for mates and food (Leakey and Lewin, 1992; Diamond, 1997).

Land would always have been important for the food gathering, but it is likely that the discovery of agriculture intensified competition for land. Let us turn to a specific written example – the Bible's ancient, but explicit, instructions for eradicating neighbours. The ancient Hebrews were in constant conflict as they tried to wrest land away from the Canaanites who already occupied the area, and as they encountered the Philistines, who were already settling along the Gaza coast (Wells, 1931). God gives specific instructions for competition with these peoples in Deuteronomy 20:13 and 14. Talking about besieged cities, He commands "And when the Lord thy God hath delivered it into thine hands, thou shall smite every male there of with the edge of the sword: But the women, and the little ones, and all that is in the city ... shalt thou take unto thyself." In addition, in those nearer cities which God has given the Israelites " . . . thou shalt save alive nothing that breatheth: but thou shall utterly destroy them;" (Deut. 20:16-17). In summary, God advises, extirpate your nearest competitors and enslave the females of the slightly more distant neighbours.

The Koran is somewhat less specific about the treatment of neighbouring tribes, although Mohammed revealed Allah's view that " . . .only those who make war upon Allah and His messenger . . . will be . . . killed or crucified, or have their hands and feet on alternate sides cut off, or will be expelled out of the land" (Sûrah V: 33; Pickthall, 1953). Such actions would be likely to reduce the reproductive rates of competing individuals.

Recent examples from Germany, Turkey, Argentina and Cambodia have been summarized by Staub (1989) and suggest that the capacity for this behaviour remains. The prevalence of such behaviour in the past is illustrated by the proportion of ancient cities with walls for protection.

1.8.2   The origin of nation states

Nation states arose during the Neolithic in eight independent centres: Mesopotamia, Egypt, Africa: outside of Egypt, China, the Indus Valley, Europe, Mesoamerica and Peru. This world wide parallelism is, says Sanderson (1995), the single most important thing that must be explained by any theory of the origin of the state. The use of the word state requires clarification, since definitions of the word may be as diverse as definitions of competition. Definitions may stress the power of a centralized government to wage war and enforce laws, or the existence of social classes, the rulers and the ruled. Sanderson defines a state as a form of sociopolitical organization that has achieved a monopoly over the means of violence within specified territory and argues that the state is the next
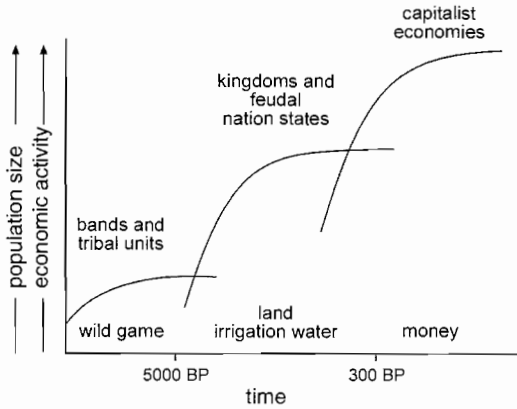
Fig. 1.21 Three main phases in the organization of human societies in relationship to resources, population size and time (after Sanderson, 1995). Two transitional periods (5000 and 300 BP) involve a shift in the essential resources of the society, and a shift in the nature of intraspecific competition for those resources.

logical step in human organization going in a sequence from bands to tribes to chiefdoms (Fig. 1.21).

Bands are small egalitarian groups ordinarily containing a few dozen people who move continuously in the search for food. Bands have informal leaders who may give advice, but who have no authority or power over others. Tribes according to Sanderson, are similar in many respects to bands, "and no person acquires real power or authority over anyone else" (p. 54). He contrasts these forms of social organization with the chiefdom, which has a centralized government and hereditary hierarchical status arrangements. Based upon our knowledge of dominance hierarchies in other mammalian and particularly other primate species, one cannot help but suspect that Sanderson over-emphasizes the egalitarian nature of bands and tribes. Perhaps this illustrates the difference in perspective between evolutionary biologists and anthropologists, or else Sanderson's effort to emphasize the degree of centralization and hierarchical authority in states.

1.8.3 Asymmetrical competition between masters and workers

From plants in fields to global conflicts, we can see a similar tendency for dominance and asymmetrical competition. Economists have long been interested in competition, and it may therefore be helpful to digress to two familiar examples in economics viewed from the perspective established in ecological communities.

Adam Smith (1776) began his classic treatise on economics with an enquiry into labour and wages paid for it. It is clear that he regarded wages as the basic

and essential human resource, since the value of all commodities is set by the rate at which they are exchanged for labour. The energetic model for competition (section 1.2) meshes well with Smith, who asserts "A man must always live by his work, and his wages must at least be sufficient to maintain him" (p. 33). Smith then considers the role of wages in determining reproductive success, noting that if a wife is dependent upon the man, and half the children die before adulthood, a man's labour must support a minimum of six people. Below this, the population of labourers will decline.

The allocation of resources within a society (to use my words not Smith's) depends upon the level of wages for workers, and this depends upon a contract between a labourer and a factory owner. Their interests are "by no means the same. The workmen desire to get as much, the masters to give as little as possible." It is not difficult to see, he says, where the advantage lies. "The masters, being fewer in number, can combine much more easily; and the law, beside, authorises or at least does not prohibit their combinations, while it prohibits those of the workmen" (p. 32). In short, in terms of section 1.4.3, competition for wealth between workers and masters is inherently asymmetric. Finally, Smith adds when conflict arises, the greater wealth of the masters allows them to hold out longer, for most workers could subsist for only a matter of weeks without work. "Masters are always and everywhere in a sort of tacit, but constant and uniform combination, not to raise the wages of labour . . .".

In spite of Smith's observations on this asymmetry, one still one often hears that competition is inherently beneficial. Let us consider the consequences of this asymmetry with an example, the conditions that workers encountered in the industrial revolution. Smout (1969) for example, describes circumstances in Scotland. Masters had "ferocious powers of corporal punishment" (p. 404). Children not only worked in the mines and factories, but were actually signed into servitude by 'arling' at their christening; in one example from 1733 a William Kennedy and his heirs "duly and thankfully" agreed "to serve the said Sir James Wemyss, heirs and assigneys whatsomever in the station of coallier all the days of our lives" (p. 405). In the mills, a government report on child labour in 1833 observed that "poor, neglected, ragged, duty children, they are seldom taught anything, and they work as long as the weavers, that is, as long as they can see; standing on the same spot, always barefooted, on an earthen, cold, damp floor, in a close damp cellar, for thirteen or fourteen hours a day" (p. 399). Similarly, in the mines, it was customary for the collier's wife or daughter to drag the coal from the face where her husband or father worked up to the distant surface. In 1812 Robert Bald wrote *A General View of the Coal Trade of Scotland*, in which he describes the fate of subordinates in these asymmetric interactions among humans: "The mother . . . descends the pit with her older daughters, when each, having a basket of suitable form, lays it down, and into it the large coals are rolled: and such is the weight that it frequently takes two men to lift the burden upon their backs: the girls are loaded according to their strength. The mother sets out first, carrying a lighted

candle in her teeth; the girls follow, and in this manner they proceed to the pit bottom and with weary steps and slow, ascend the stairs, halting occasionally to draw breath, till they arrive at the hill or pit top, where the coals are laid down for sale; and in this manner they go for eight or ten hours almost without resting. It is not an uncommon thing to see them when ascending the pit weeping most bitterly from the excessive severity of the labour" (Smout, 1969, p. 408).

1.8.4   Competition among memes to infect human minds

If, as seems likely, the conscious experiences of humans are related to the activities of different neurological pathways within the brain, then aspects of human consciousness will also have a foundation in competition. What is choice, or free will, after all, but psychological/neurophysiological competition between two or more potential alternative actions? Choice is most difficult when the alternatives appear equally weighted, that is, when there is symmetrical competition between possibilities. Speculating further, we frequently see within human beings conflict between emotions and thoughts, as for example when rationality attempts to restrain lust or anger (Neumann, 1970; Blakemore, 1977). Consciousness has temporarily achieved dominance over less conscious processes such as animal instincts and what is it that consciousness fears more than loss of control, that is, the competitive displacement of rational thought by irrational emotion?

Conflict within individual humans may therefore be studied from the perspective of competition. Dawkins (1976) further suggests that major ideas, such as style of fashion or religious belief, called 'memes' (to stress the analogy with genes) compete with one another for space within the human consciousness. A successful meme is one that achieves dominance within a specific mind, and which transmits itself effectively to other minds (see also Blackmore, 1997). Memes, then, compete with each other for the limited space available in the collectivity of human minds.

Memes which protect themselves and transmit themselves will be relatively more successful in the competition for mental space. Religion might be a particularly successful meme. Many religions discourage rational examination of belief, a process which would, of course, tend to damage the meme, since many religious memes have no rational foundation. Further, practices such as having many children, raising them within the faith and deliberately spreading the meme to uninfected minds through missionary work would all tend to increase the frequency of a specific meme. From this perspective, the presence of a non-reproductive priest class might even be advantageous if this class remained numerically small but spread the meme more effectively through teaching than reproduction. Priests, then, might be seen as meme protectors and meme replicators. Similarly, the spread of styles of clothing or music or even politics could be studied in the same detached manner. Radio, television and the internet

could all, then, be viewed primarily as tools by which memes tend to replicate themselves.

From this perspective, it is even possible to understand the persecution of heretics. Those memes which included practices that enhance rates of damage to other memes by killing their containers may enhance their own rate of spread, and will tend to proliferate within human minds.

As Blackmore concludes her essay, "Many important questions about memes are still unanswered, yet they may be some of the most challenging parts of Darwin's legacy, particularly in an age which prides itself on the generation and rapid transmission of information. Imagine a world full of brains, and far more memes than can possibly find homes. Which memes are most likely to find a safe home and get passed on again?" An effective author is one who maximizes the infection rate of memes, not unlike an information age Typhoid Mary. This book, by the way, is a collection of memes, and by reading only this far, you are already infected by some of them.

1.8.5   Energy flow and competition: from evapotranspiration to kleptocracy

The process of competition can be superimposed on Morowitz's view (p. 43–46) as a series of interactions that determine which structure will enrich itself from the pool at the expense of other similar ones. The structure could be a plant, an animal, a nation, or a dictator. From the perspective of plants, in particular, we can treat competition as an entirely passive process driven by the evaporation of water from the soil into the atmosphere, a process that occurred long before there was life at all. Plants occupy the precise interface where this evaporation occurs, increasing its efficiency, so much so that biologists now describe this step in the hydrological cycle as evapotranspiration. Water is pulled from the stomata in leaves by evaporation, and this draws water upwards through the tissues of the plant; as the upper tissues of the plant dry out, osmotic differentials draw water out of the roots (Canny, 1998). As the roots dry out, water from the soil is drawn in. Plants therefore occupy the site of phase transition from liquid water to water vapour. As the sun withdraws water vapour, mineral nutrients are pulled out of the soil, conducted through the xylem of the plant, and used in the manufacture of carbohydrates and proteins. Smaller amounts of water are actually consumed in the process of photosynthesis, releasing the waste product oxygen back into the atmosphere. This is a difficult perspective to retain, in part because biologists have been trained to think of populations and individuals as the natural units of the living world, and humans in general tend to view the world as a composite of individuals. But if we maintain this anonymous perspective of plants as largely passive conductors of water to the atmosphere, we gain a fresh perspective upon the process of competition. From this perspective, some structures, by virtue of their size or location or internal resistance, passively transport more water to the atmosphere. Others, because

they are exposed to less sunlight, or in drier soils, or depletion zones created by neighbours, or because they inherited higher resistance to water flow, transport less water to the atmosphere. The physical processes of diffusion ensure that, in general, the larger individuals conduct a greater flow of water, and so they withdraw from the soil more nitrogen and phosphorous, and consequently, during photosynthesis, more proteins and carbohydrates are constructed. These in turn increase the evaporative area of the plant, which increases rates of transpiration, which increases the rate of passive evapotranspiration. A little more biology must be spliced in here to ensure that the plants with the larger rates of evapotranspiration construct roots to provide the necessary resources, but one can even image some simple feedback loop whereby those roots which conduct the greatest flow of water and nutrients upwards are provided with the most return flow from the branches. Indeed, in many plants individual roots can be associated with individual branch systems in just this way, so a tree may be regarded a set of weakly interconnected shoots, a community of branches, each somewhat isolated from the other, and each competing within the tree for access to light and water. Those shoots that lie, for example, low on the tree where they are shaded, die, and these weakened branches fall to the ground, whereas other shoots that are exposed to conditions where they can grow rapidly, attract more water from within the plant, thereby growing larger. Thus trees passively respond to light and moisture gradients created by the sun and surface of the planet, and there is natural and largely passive response whereby some shoots and meristems multiply at the expense of others. A plant can be viewed as a mechanical evaporative structure that enhances the flow of water from the soil to the atmosphere. Competition is a word we apply when we see that some of these units, which we call individuals, and which we assume to be genetically distinct, increase by diverting resources from their neighbours.

The same passive perspective can be applied to human nation states. Consider the region of Africa which humans have temporarily designated the Republic of Zaire; formerly, perhaps just as temporarily, it was the Democratic Republic of the Congo. Resources here range from tropical forests to copper mines. For the past few decades, the leader and dictator, a former sergeant major in the Belgian Congolese army, Mobutu Sese Seko, has distinguished himself with a form of rule that has come to be called a kleptocracy. In a kleptocracy, a leader systematically loots his own country. Resources have flowed from the mines and forests through Mobutu and into foreign bank accounts, allegedly making him one of the world's richest men. Meanwhile, the infrastructure of Zaire has decayed; forests have even reclaimed major roads. This dismal history can be viewed as just another illustration of the passive flow of resources from a source (forests and mines) to a sink (bank accounts and villas), a financial flow that is in many ways as natural and passive as the flow of water from the soil to the atmosphere. Adjoining branches, that is political allies in the Mouvement Populaire de la Révolution, have benefited as the resources flowed past them towards Mobutu.

Rival political groups who would direct the resources to another branch have been ruthlessly suppressed. A guerrilla army which arose in the east of the country near the Rwanda border in 1996 has slowly cut into Mobutu's resource base; wealth that once flowed into Mobutu's depletion zone now flows eastward into the rebel army's depletion zone. Several months pass, and now Kabila is in power, and as reviled as Mobutu. One branch replaces another on the tree trunk, or one ruler replaces another in a country; in either case, the winner is distinguished by having the resources trickle through its own tissues rather than those of a neighbour.

Superimposed upon these fundamentals are all the other details of biology and chance events of history. Perhaps some plants have genetically superior foraging abilities, or genetically more efficient photosynthetic systems, or differences in the numbers of stomata per square centimetre, or larger diameter cells in the xylem, and these are part of the details involved in tipping the balance from one neighbour to another. Similarly, Kabila may be smarter than Mobutu Sese Seko, he may have a better grade of weapon, or he may have a more efficient command and control system. Such are the details that ecologists and political scientists study in an attempt to explain outcomes, but in focusing upon the outcomes and details, we may fail to discern the identities in process.

Resources flow in response to energy gradients. As they flow, they enrich some structures at the expense of others. The enriched structures withdraw resources from the pool and thereby expand at the cost of their neighbours. Perhaps if ecologists and economists both paid more homage to Lavoisier and von Humboldt, and less to Charles Darwin and Adam Smith, respectively, we might see these similarities more widely appreciated. From Lepidodendron trees to Magnolias, from Mobutu Sese Seko to Mr. Kabila, the melodies may differ but, in the words of Led Zeppelin, the song remains the same.

1.9   CONCLUSION

Fundamental progress is likely to come from re-evaluating fundamental assumptions and looking for common patterns and processes in apparently different classes of events. The overview in this chapter illustrated the many kinds of competition that can exist in nature. Important generalizations about the nature of competition may emerge when we find a classification of competitive interactions which has high explanatory and predictive power. To succeed, there will have to be objective (measurable) criteria for assigning situations to the different categories (or sections of a continuum).

Important progress is possible here if innovative approaches are tried more often. That pairwise interspecific and intraspecific competition has received such attention is remarkable, given the range of possibilities that can be postulated to exist. That humans are so rarely included in such studies is also illuminating.

Chapters 2–4 explore how the conceptual foundation in Chapter 1 has been used to explore nature. Chapters 5–7 present some avenues where rapid progress appears possible. Chapters 8–10 return to the search for general principles about how competition manifests in our world. Finally Chapter 11 returns to basics and asks why ecologists do science in the way in which they do, and what this has to do with progress in the study of competition.

QUESTIONS FOR DISCUSSION

1. What are the strengths and weaknesses of the classifications of competition presented? Can you devise an alternative classification?
2. How do we make such classifications operational? That is, how would we actually measure them in order to make ecological predictions?
3. How would you design an experiment to measure each of the kinds of competition described?
4. Are there other kinds of competition you believe should be recognized? Why? How would you measure them?
5. Are there any reasons for expecting the biosphere to be structured primarily by a subset of the above possibilities?
6. Why are studies of inter- and intraspecific competition so abundant in the ecological literature?
7. What would be the ecological and evolutionary consequences of asymmetrical competitive interactions between pairs of populations?
8. Can you find other examples of each kind of competition?
9. Can you argue from first principles which kinds of competition should predominate in each of the five kingdoms of living organisms?
10. Why are symmetrical interactions more widely studied than asymmetrical interaction?