Chapter 1

Ecology and how to do it

Chapter contents

CHAPTER CONTENTS

1.1 Introduction
1.2 Scales, diversity and rigor
1.3 Ecology in practice

Key concepts

KEY CONCEPTS

In this chapter you will:

- learn how to define ecology and appreciate its development as both an applied and a pure science
- recognize that ecologists seek to describe and understand, and on the basis of their understanding, to predict, manage and control
- appreciate that ecological phenomena occur on a variety of spatial and temporal scales, and that patterns may be evident only at particular scales
- recognize that ecological evidence and understanding can be obtained by means of observations, field and laboratory experiments, and mathematical models
- understand that ecology relies on truly scientific evidence (and the application of statistics)

Nowadays, ecology is a subject about which almost everyone has heard and most people consider to be important – even when they are unsure about the exact meaning of the term. There can be no doubt that it is important; but this makes it all the more critical that we understand what it is and how to do it.

1.1 Introduction

the earliest ecologists

The question 'What is ecology?' could be translated into 'How do we define ecology?' and answered by examining various definitions of ecology that have been proposed and choosing one of them as the best (Box 1.1). But while definitions have conciseness and precision, and they are good at preparing you for an examination, they

1.1 Historical landmarks

1.1 HISTORICAL LANDMARKS

Definitions of ecology

Ecology (originally in German, *Öekologie*) was first defined in 1866 by Ernst Haeckel, an enthusiastic and influential disciple of Charles Darwin. To him, ecology was 'the comprehensive science of the relationship of the organism to the environment'. The spirit of this definition is very clear in an early discussion of biological subdisciplines by Burdon-Sanderson (1893), in which ecology is 'the science which concerns itself with the external relations of plants and animals to each other and to the past and present conditions of their existence', to be contrasted with physiology (internal relations) and morphology (structure). For many, such definitions have stood the test of time. Thus, Ricklefs (1973) in his textbook defined ecology as 'the study of the natural environment, particularly the interrelationships between organisms and their surroundings'.

In the years after Haeckel, plant ecology and animal ecology drifted apart. Influential works defined ecology as 'those relations of *plants*, with their surroundings and with one another, which depend directly upon differences of habitat among plants' (Tansley, 1904), or as the science 'chiefly concerned with what may be called the sociology and economics of *animals*, rather than with the structural and other adaptations possessed by them' (Elton, 1927). The botanists and zoologists, though, have long since agreed that they belong together and that their differences must be reconciled.

There is, nonetheless, something disturbingly vague about the many definitions of ecology that seem to suggest that it consists of all those aspects of biology that are neither physiology nor morphology. In search of more focus, therefore, Andrewartha (1961) defined ecology as 'the scientific study of the distribution and abundance of organisms', and Krebs (1972), regretting that the central role of 'relationships' had been lost, modified it to 'the scientific study of the *interactions* that determine the distribution and abundance of organisms', explaining that ecology was concerned with '*where* organisms are found, *how many* occur there, and *why*'. This being so, it might be better still to define ecology as:

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

are not so good at capturing the flavor, the interest or the excitement of ecology. There is a lot to be gained by replacing that single question about definition with a series of more provoking ones: 'What do ecologists *do*?', 'What are ecologists *interested* in?' and 'Where did ecology emerge from in the first place?'

Ecology can lay claim to be the oldest science. If, as our preferred definition has it, 'Ecology is the scientific study of the distribution and abundance of organisms and the interactions that determine distribution and abundance' (Box 1.1), then the most primitive humans must have been ecologists of sorts – driven by the need to understand where and when their food and their (non-human) enemies were to be found – and the earliest agriculturalists needed to be even more sophisticated: having to know how to manage their living but domesticated sources of food. These early ecologists, then, were *applied* ecologists, seeking to understand the distribution and abundance of organisms in order to apply that knowledge for their own collective benefit. They were interested in many of the sorts of things that applied ecologists are still interested in: how to maximize the rate at which food is collected from natural environments, and how this can be done repeatedly over time; how domesticated plants and animals can best be planted or stocked so as to maximize rates of return; how food organisms can be protected from their own natural enemies; and how to control the populations of pathogens and parasites that live on us.

a pure and applied science

In the last century or so, however, since ecologists have been self-conscious enough to give themselves a name, ecology has consistently covered not only applied but also fundamental, 'pure' science. A.G. Tansley was one of the founding fathers of ecology. He was concerned especially to understand, for understanding's sake, the processes responsible for determining the structure and composition of different plant communities. When, in 1904, he wrote from Britain about 'The problems of ecology' he was particularly worried by a tendency for too much ecology to remain at the descriptive and unsystematic stage (i.e. accumulating descriptions of communities without knowing whether they were typical, temporary or whatever), too rarely moving on to experimental or systematically planned, or what we might call a 'scientific', analysis.

His worries were echoed in the United States by another of ecology's founders, F.E. Clements, who in 1905 in his *Research Methods in Ecology* complained:

> The bane of the recent development popularly known as ecology has been a widespread feeling that anyone can do ecological work, regardless of preparation. There is nothing . . . more erroneous than this feeling.

On the other hand, the need of *applied* ecology to be based on its *pure* counterpart was clear in the introduction to Charles Elton's (1927) *Animal Ecology* (Figure 1.1):

> Ecology is destined for a great future . . . The tropical entomologist or mycologist or weed-controller will only be fulfilling his functions properly if he is first and foremost an ecologist.

In the intervening years, the coexistence of these pure and applied threads has been maintained and built upon. Many applied areas have contributed to the development of ecology and have seen their own development enhanced by ecological ideas and approaches. All aspects of food and fiber gathering, production and protection have been involved: plant ecophysiology, soil maintenance, forestry, grassland composition and management, food storage, fisheries, and control of pests and pathogens. Each of these classic areas is still at the forefront of

Figure 1.1

One of the great founders of ecology: Charles Elton (1900–1991). *Animal Ecology* (1927) was his first book but *The Ecology of Invasions by Animals and Plants* (1958) was equally influential.

lots of good ecology and they have been joined by others. The biological control of pests (the use of pests' natural enemies to control them) has a history going back at least to the Ancient Chinese but has seen a resurgence of ecological interest since the shortcomings of chemical pesticides began to be widely apparent in the 1950s. The ecology of pollution has been a growing concern from around the same time and expanded further in the 1980s and 1990s from local to global issues. The closing decades of the last millennium also saw expansions both in public interest and ecological input into the conservation of endangered species and the biodiversity of whole areas, in the control of disease in humans as well as many other species, and in the potential consequences of profound human-caused changes to the global environment.

unanswered questions

And yet, at the same time, many fundamental problems of ecology remain unanswered. To what extent does competition for food determine which species can coexist in a habitat? What role does disease play in the dynamics of populations? Why are there more species in the tropics than at the poles? What is the relationship between soil productivity and plant community structure? Why are some species more vulnerable to extinction than others? And so on. Of course, unanswered questions – if they are *focused* questions – are a symptom of the health not the weakness of any science. But ecology is not an easy science, and it has particular subtlety and complexity, in part because ecology is peculiarly confronted by 'uniqueness': millions of different species, countless billions of genetically distinct individuals, all living and interacting in a varied and ever-changing world. The beauty of ecology is that it challenges us to develop an understanding of very basic and apparent problems – in a way that recognizes the uniqueness and complexity of all aspects of nature – but seeks patterns and predictions within this complexity rather than being swamped by it.

understanding, description, prediction and control

Summarizing this brief historical overview, it is clear that ecologists try to do a number of different things. First and foremost ecology is a science, and ecologists therefore try to *explain* and *understand*. There are two different classes of explanation in biology: 'proximate' and 'ultimate'. For example, the present distribution and abundance of a particular species of bird may be 'explained' in terms of the physical environment that the bird tolerates, the food that it eats and the parasites and predators that attack it. This is a *proximate* explanation – an explanation in terms of what is going on 'here and now'. However, we can also ask how this bird has come to have these properties that now govern its life. This question has to be answered by an explanation in evolutionary terms; the *ultimate* explanation of the present distribution and abundance of this bird lies in the ecological experiences of its ancestors (see Chapter 2).

In order to understand something, of course, we must first have a description of whatever it is we wish to understand. Ecologists must therefore *describe* before they explain. On the other hand, the most valuable descriptions are those carried out with a particular problem or 'need for understanding' in mind. Undirected description, carried out merely for its own sake, is often found afterwards to have selected the wrong things and has little place in ecology – or any other science.

Ecologists also often try to *predict* what will happen to a population of organisms under a particular set of circumstances, and on the basis of these predictions to control, exploit or conserve the population. We try to minimize the effects of locust plagues by predicting when they are likely to occur and taking appropriate action. We try to exploit crops most effectively by predicting when conditions will be favorable to the crop and unfavorable to its enemies. We try to preserve rare species by predicting the conservation policy that will enable us to do so. Some prediction and control can be carried out without deep explanation or understanding: it is not difficult to predict that the destruction of a woodland will eliminate woodland birds. But insightful predictions, precise predictions and predictions of what will happen in unusual circumstances can be made only when we can also explain and understand what is going on.

This book is therefore about:

1. How ecological understanding is achieved.
2. What we do understand (but also what we do not understand).
3. How that understanding can help us predict, manage and control.

1.2 Scales, diversity and rigor

The rest of this chapter is about the two 'hows' above: how understanding is achieved, and how that understanding can help us predict, manage and control. Later in the chapter we illustrate three fundamental points about doing ecology by examining a limited number of examples in some detail (Section 1.3). But first we elaborate on the three points, namely:

- ecological phenomena occur at a variety of scales;
- ecological evidence comes from a variety of different sources;
- ecology relies on truly scientific evidence and the application of statistics.

1.2.1 Questions of scale

Ecology operates at a range of scales: time scales, spatial scales and 'biological' scales. It is important to appreciate the breadth of these and how they relate to one another.

the 'biological' scale

The living world is often said to comprise a biological hierarchy beginning with subcellular particles and continuing through cells, tissues and organs. Ecology then deals with the next three levels:

- *individual organisms*;
- *populations* (consisting of individuals of the same species);
- *communities* (consisting of a greater or lesser number of populations).

At the level of the organism, ecology deals with how individuals are affected by (and how they affect) their environment. At the level of the population, ecology deals with the presence or absence of particular species, with their abundance or rarity, and with the trends and fluctuations in their numbers. Community ecology then deals with the composition or structure of ecological communities.

We can also focus on the pathways followed by energy and matter as these move among living and non-living elements of a fourth category of organization:

- *ecosystems* (comprising the community together with its physical environment).

With this level of organization in mind, Likens (1992) would extend our preferred definition of ecology (Box 1.1) to include 'the interactions between organisms and the transformation and flux of energy and matter'. However, we take energy/matter transformations as being subsumed in the 'interactions' of our definition.

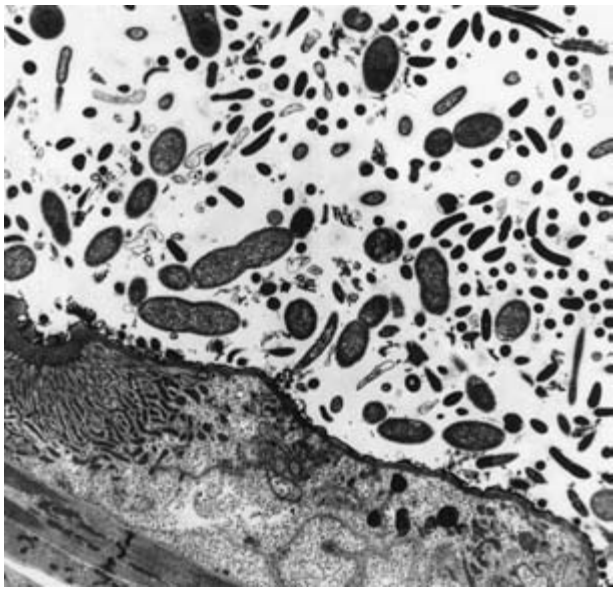
a range of spatial scales

Within the living world, there is no arena too small nor one so large that it does not have an ecology. Even the popular press talk increasingly about the 'global ecosystem' and there is no question that several ecological problems can only be examined at this very large scale. These include the relationships between ocean currents and fisheries, or between climate patterns and the distribution of deserts and tropical rain forests, or between elevated carbon dioxide in the atmosphere (from burning fossil fuels) and global climate change.

At the opposite extreme, an individual cell may be the stage on which two populations of pathogens compete with one another for the resources that the cell provides. At a slightly larger spatial scale, a termite's gut is the habitat for bacteria, protozoans and other species (Figure 1.2) – a community whose diversity is comparable to that of a tropical rain forest in terms of the richness of organisms living there, the variety of interactions in which they take part, and indeed the extent to which we remain ignorant about the species identity of many of the participants. Between these extremes, different ecologists, or the same ecologist at different times, may study the inhabitants of pools that form in small tree-holes, the temporary watering holes of the savannas, or the great lakes and oceans; others may examine the diversity of fleas on different species of birds, the diversity of birds in different sized patches of woodland, or the diversity of woodlands at different altitudes.

a range of time scales

To some extent related to this range of spatial scales, and to the levels in the biological hierarchy, ecologists also work on a variety of time scales. 'Ecological succession' – the successive and continuous colonization of a site by certain species populations, accompanied by the extinction of others – may be studied over a period from the deposition of a lump of sheep dung to its decomposition (a



AFTER BREZNAK, 1975

Figure 1.2
The diverse community of a termite's gut. Termites can break down lignin and cellulose from wood because of their mutualistic relationships (see Section 8.4.4) with a diversity of microbes that live in their guts.

matter of weeks), or from the change in climate at the end of the last ice age to the present day and beyond (around 14,000 years and still counting). Migration may be studied in butterflies over the course of days, or in the forest trees that are still (slowly) migrating into deglaciated areas following that last ice age.

the need for long-term studies

Although it is undoubtedly the case that 'appropriate' time scales vary, it is also true that many ecological studies are not as long as they might be. Longer studies cost more and require greater dedication and stamina. An impatient scientific community, and the requirement for concrete evidence of activity for career progression, both put pressure on ecologists, and all scientists, to publish their work sooner rather than later. Why are long-term studies potentially of such value? The reduction over a few years in the numbers of a particular species of wild flower, or bird, or butterfly might be a cause for conservation concern – but one or more decades of study may be needed to be sure that the decline is more than just an expression of the random ups and downs of 'normal' population dynamics. Similarly, a 2-year rise in the abundance of a wild rodent followed by a 2-year fall might be part of a regular 'cycle' in abundance, crying out for an explanation. But ecologists could not be sure until perhaps 20 years of study has allowed them to record four or five repeats of such a cycle.

This does not mean that all ecological studies need to last for 20 years – nor that every time an ecological study is extended the answer changes. But it does emphasize the great value to ecology of the small number of long-term investigations that have been carried out or are ongoing.

1.2.2 The diversity of ecological evidence

Ecological evidence comes from a variety of different sources. Ultimately, ecologists are interested in organisms in their natural environments (though for many organisms, the environment which is 'natural' for them now is itself manmade). Progress would be impossible, however, if ecological studies were limited to such

natural environments. And, even in natural habitats, unnatural acts (experimental manipulations) are often necessary in the search for sound evidence.

observations and field experiments

Many ecological studies involve careful *observation* and monitoring, in the natural environment, of the changing abundance of one or more species over time, or over space, or both. In this way, ecologists may establish patterns; for example, that red grouse (birds shot for 'sport') exhibit regular cycles in abundance peaking every 4 or 5 years, or that vegetation can be mapped into a series of zones as we move across a landscape of sand dunes. But scientists do not stop at this point – the patterns require explanation. Careful analysis of the descriptive data may suggest some plausible explanations. But establishing what causes the patterns may well require *manipulative field experiments*: ridding the red grouse of intestinal worms, hypothesized to underlie the cycles, and checking if the cycles persist (they do not: Hudson et al., 1998), or treating experimental areas on sand dunes with fertilizer to see whether the changing pattern of vegetation itself reflects a changing pattern of soil productivity.

laboratory experiments

Perhaps less obviously, ecologists also often need to turn to laboratory systems and even mathematical models. These have played a crucial role in the development of ecology, and they are certain to continue to do so. Field experiments are almost inevitably costly and difficult to carry out. Moreover, even if time and expense were not issues, natural field systems may simply be too complex to allow us to tease apart the consequences of the many different processes that may be going on. Are the intestinal worms actually capable of having an effect on reproduction or mortality of individual grouse? Which of the many species of sand dune plants are, in themselves, sensitive to changing levels of soil productivity and which are relatively insensitive? *Controlled*, *laboratory experiments* are often the best way to provide answers to specific questions that are key parts of an overall explanation of the complex situation in the field.

simple laboratory systems . . .

Of course, the complexity of natural ecological communities may simply make it inappropriate for an ecologist to dive straight into them in search of understanding. We may wish to explain the structure and dynamics of a particular community of 20 animal and plant species comprising various competitors, predators, parasites and so on (relatively speaking, a community of remarkable simplicity). But we have little hope of doing so unless we already have some basic understanding of even simpler communities of just one predator and one prey species, or two competitors, or (especially ambitious) two competitors that also share a common predator. For this, it is usually most appropriate to construct, for our own convenience, *simple laboratory systems* that can act as benchmarks or jumping-off points in our search for understanding.

. . . and mathematical models

What is more, you have only to ask anyone who has tried to rear caterpillar eggs, or take a cohort of shrub cuttings through to maturity, to discover that even the simplest ecological communities may not be easy to maintain or keep free of unwanted pathogens, predators or competitors. Nor is it necessarily possible to construct precisely the particular, simple, artificial community that interests you; nor to subject it to precisely the conditions or the perturbation of interest. In many cases, therefore, there is much to be gained from the analysis of *mathematical models* of ecological communities: constructed and manipulated according to the ecologist's design.

On the other hand, although a major aim of science is to simplify, and thereby make it easier to understand the complexity of the real world, ultimately it is the

real world that we are interested in. The worth of models and simple laboratory experiments must always be judged in terms of the light they throw on the working of more natural systems. They are a means to an end – never an end in themselves. Like all scientists, ecologists need to 'seek simplicity, but distrust it' (Whitehead, 1953).

1.2.3 Statistics and scientific rigor

For a scientist to take offence at some popular phrase or saying is to invite accusations of a lack of a sense of humor. But it is difficult to remain calm when phrases like 'There are lies, damn lies and statistics' or 'You can prove anything with statistics' are used, by those who should know better, to justify continuing to believe what they wish to believe, whatever the evidence to the contrary. There is no doubt that statistics are sometimes *mis*-used to derive dubious conclusions from sets of data that actually suggest either something quite different or perhaps nothing at all. But these are not grounds for mistrusting statistics in general – rather for ensuring that people are educated in at least the principles of scientific evidence and its statistical analysis, so as to protect them from those who may seek to manipulate their opinions.

ecology: a search for conclusions in which we can be confident

In fact, not only is it not true that you can prove anything with statistics, the contrary is the case: you cannot *prove* anything with statistics – that is not what statistics are for. Statistical analysis is essential, however, for attaching a level of confidence to conclusions that can be drawn; and ecology, like all science, is a search not for statements that have been 'proved to be true' but for conclusions in which we can be confident.

Indeed, what distinguishes science from other activities – what makes science 'rigorous' – is that it is based not on statements that are simply assertions, but that it is based (i) on conclusions that are the results of investigations (as we have seen, of a wide variety of types) carried out with the express purpose of deriving those conclusions; and (b) even more important, on conclusions to which a level of confidence can be attached, measured on an agreed scale. These points are elaborated in Boxes 1.2 and 1.3.

ecologists must think ahead

Statistical analyses are carried out after data have been collected, and they help us to interpret those data. There is no really good science, however, without forethought. Ecologists, like all scientists, must know what they are doing, and why they are doing it, *while* they are doing it. This is entirely obvious at a general level: nobody expects ecologists to be going about their work in some kind of daze. But it is perhaps not so obvious that ecologists should know how they are going to analyze their data, statistically, not only after they have collected it, not only while they are collecting it, but even before they begin to collect it. Ecologists must plan, so as to be confident that they have collected the right kind of data, and a sufficient amount of data, to address the questions they hope to answer.

ecology relies on representative samples

Ecologists typically seek to draw conclusions about groups of organisms overall: what is the birth rate of the bears in Yellowstone Park? What is the density of weeds in a wheat field? What is the rate of nitrogen uptake of tree saplings in a nursery? In doing so, we can only very rarely examine every individual in a group, or in the entire sampling area, and we must therefore rely on what we hope will be a *representative* sample from the group or habitat. Indeed, even if we examined a whole group (we might examine every fish in a small pond, say),

1.2 Quantitative aspects

1.2 QUANTITATIVE ASPECTS

Interpreting probabilities

P-values

The term that is most often used, at the end of a statistical test, to measure the strength of conclusions being drawn is a *P*-value, or probability level. It is important to understand what *P*-values are. Imagine we are interested in establishing whether high abundances of a pest insect in summer are associated with high temperatures the previous spring, and imagine that the data we have to address this question consist of summer insect abundances and mean spring temperatures for each of a number of years. We may reasonably hope that statistical analysis of our data will allow us either to conclude, with a stated degree of confidence, that there is an association, or to conclude that there are no grounds for believing there to be an association (Figure 1.3).

Null hypotheses

To carry out a statistical test we first need a *null hypothesis*, which simply means, in this case, that there is *no* association: that is, no association between insect abundance and temperature. The statistical test (stated simply) then generates a probability (a *P*-value) of getting a data set like ours if the null hypothesis is correct.

Suppose the data were like those in Figure 1.3a. The probability generated by a test of association on these data is $P = 0.5$ (equivalently 50%). This means that, if the null hypothesis really was correct (no association), then 50% of studies like ours should generate just such a data set, or one even further from the null hypothesis. So, if there was no association, there would be nothing very remarkable in this data set, and we could have no confidence in any claim that there *was* an association.

Suppose, however, that the data were like those in Figure 1.3b, where the *P*-value generated is $P = 0.001$ (0.1%). This would mean that such a data set (or one even further from the null hypothesis) could be expected in only 0.1% of similar studies if there was really no association. In other words, either something very improbable has occurred, or there *was* an association between insect abundance and spring temperature. Thus, since by definition we do not expect highly improbable events to occur, we can have a high degree of confidence in the claim that there *was* an association between abundance and temperature.

Significance testing

Both 50% and 0.01%, though, make things easy for us. Where, between the two, do we draw the line? There is no objective answer to this, and so scientists and statisticians have established a convention in *significance testing*, which says that if *P* is less than 0.05 (5%), written $P < 0.05$ (e.g. Figure 1.3d), then results are described as statistically significant and confidence can be placed in the effect being examined (in our case, the association between abundance and temperature), whereas if $P > 0.05$, then there is no statistical foundation for claiming the effect exists (e.g. Figure 1.3c). A further elaboration of the convention often describes results with $P < 0.01$ as 'highly significant'.

'Insignificant' results?

Naturally, some effects are strong (for example, there is a powerful association between people's weight and their height) and others are weak (the association between people's weight and their risk of heart disease is real but weak, since weight is only one of many important factors). More data are needed to establish support for a weak effect than for a strong one. A rather obvious but very important conclusion follows from this: a *P*-value in an ecological study of greater than 0.05 (lack of statistical significance) may mean one of two things:

1. There really is no effect of ecological importance.
2. The data are simply not good enough, or there are not enough of them, to support the effect even though it exists, possibly because the effect itself is real but weak, and extensive data are therefore needed but have not been collected.

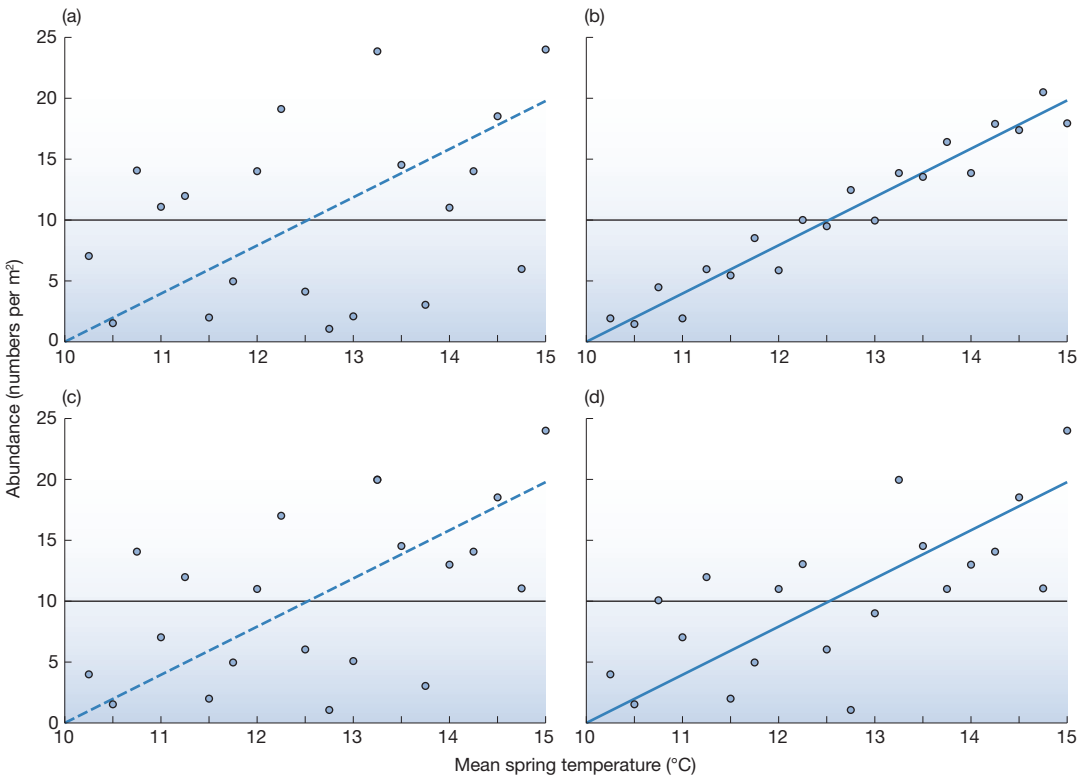


Figure 1.3

The results from four hypothetical studies of the relationship between insect pest abundance in summer and mean temperature the previous spring. In each case, the points are the data actually collected. Horizontal lines represent the *null hypothesis* – that there is no association between abundance and temperature, and thus the best estimate of expected insect abundance, irrespective of spring temperature, is the mean insect abundance overall. The second line is the *line of best fit* to the data, which in each case offers some suggestion that abundance rises as temperature rises. However, whether we can be confident in concluding that abundance does rise with temperature depends, as explained in the text, on statistical tests applied to the data sets. (a) The suggestion of a relationship is weak ($P = 0.5$). There are no good grounds for concluding that the true relationship differs from that supposed by the null hypothesis and no grounds for concluding that abundance is related to temperature. (b) The relationship is strong ($P = 0.001$) and we can be confident in concluding that abundance increases with temperature. (c) The results are suggestive ($P = 0.1$) but it would not be safe to conclude from them that abundance rises with temperature. (d) The results are not vastly different from those in (c) but are powerful enough ($P = 0.04$, i.e. $P < 0.05$) for the conclusion that abundance rises with temperature to be considered safe.

Quoting *P*-values

Furthermore, applying the convention strictly and dogmatically means that when $P = 0.06$ the conclusion should be 'no effect has been established', whereas when $P = 0.04$ the conclusion is 'there is a significant effect'. Yet very little difference in the data is required to move a *P*-value from 0.04 to 0.06. It is therefore far better to quote exact *P*-values, especially when they exceed 0.05, and think of conclusions in terms of shades of gray rather than the black and white of 'proven effect' and 'no effect'. In particular, *P*-values close to, but not less than, 0.05 suggest that something seems to be going on; they indicate, more than anything else, that more data need to be collected so that our confidence in conclusions can be more clearly established.

Throughout this book, then, studies of a wide range of types are described, and their results often

have *P*-values attached to them. Of course, as this is a textbook, the studies have been selected because their results *are* significant. Nonetheless, it is important to bear in mind that the repeated statements $P < 0.05$ and $P < 0.01$ mean that these are studies where: (i) sufficient data have been collected to establish a conclusion in which we can be confident; (ii) that confidence has been established by agreed means (statistical testing); and (iii) confidence is being measured on an agreed and interpretable scale.

1.3 Quantitative aspects

1.3 QUANTITATIVE ASPECTS

Attaching confidence to results

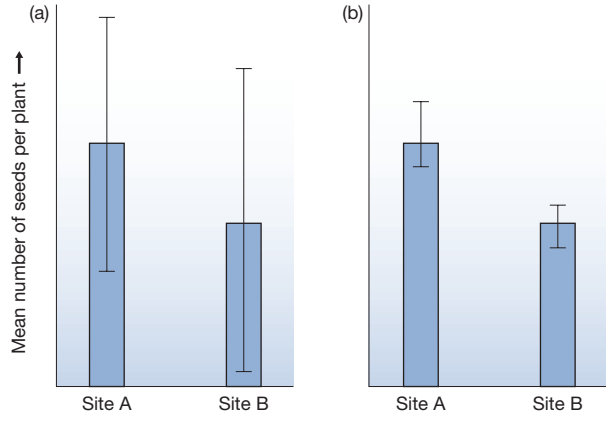
Standard errors and confidence intervals

Following Box 1.2, another way in which the significance of results, and confidence in them, is assessed is through reference to standard errors. Again, simply stated, statistical tests often allow standard errors to be attached either to mean values calculated from a set of observations or to slopes of lines like those in Figure 1.3. Such mean values or slopes can, at best, only ever be estimates of the 'true' mean value or true slope, because they are calculated from data that are only a sample of all the imaginable items of data that could be collected. The standard error, then, sets a band around the estimated mean (or slope, etc.) within which the true mean can be expected to lie with a given, stated probability. In particular, there is a 95% probability that the true mean lies within roughly two standard errors (2 SE) of the estimated mean; we call this the *95% confidence interval*.

Hence, when we have, say, two sets of observations, each with its own mean value (for instance, the number of seeds produced by plants from two sites, Figure 1.4) the standard errors allow us to assess whether the means are significantly different from one another, statistically. Roughly speaking, if each mean is more than two standard errors from the other mean, then the difference between them is statistically significant with $P < 0.05$. Thus, for the study illustrated in Figure 1.4a, it would not be safe to conclude that plants from the two sites differed in their seed production. However, for the similar study illustrated in Figure 1.4b, the means are roughly the same as they were in the first study and are roughly as far apart, but the standard errors

Figure 1.4

The results of two hypothetical studies in which the seed production of plants from two different sites was compared. In all cases, the heights of the bars represent the mean seed production of the sample of plants examined, and the lines crossing those means extend 1 SE above and below them. (a) Although the means differ, the standard errors are relatively large and it would not be safe to conclude that seed production differed between the sites ($P = 0.4$). (b) The differences between the means are very similar to those in (a), but the standard errors are much smaller, and it can be concluded with confidence that plants from the two sites differed in their seed production ($P < 0.05$).



are smaller. Hence, the difference between the means is significant ($P < 0.05$), and we can conclude with confidence that plants from the two sites differed.

When are standard errors small?

Note that the large standard errors in the first study, and hence the lack of statistical significance, could have been due to data that were, for whatever reason, more variable; but they may also have been due to sampling fewer plants in the first study than the second. Standard errors are smaller, and statistical significance is easier to achieve, *both* when data are more consistent (less variable) *and* when there are more data.

we are likely to want to draw general conclusions from it: we might hope that the fish in 'our' pond can tell us something about fish of that species in ponds of that type, generally. In short, ecology relies on obtaining *estimates* from representative samples. This is elaborated in Box 1.4.

1.4 Quantitative aspects

1.4 QUANTITATIVE ASPECTS

Estimation: sampling, accuracy and precision

The discussion in Boxes 1.2 and 1.3 about when standard errors will be small or large, or when our confidence in conclusions will be strong or weak, not only has implications for the interpretation of data after they have been collected, but also carries a general message about planning the collection of data. In undertaking a sampling program to collect data, the aim is to satisfy a number of criteria:

1. That the estimate should be accurate or unbiased: that is, neither systematically too high nor too low as a result of some flaw in the program.
2. That the estimate should have as narrow confidence limits (be as precise) as possible.
3. That the time, money and human effort invested in the program should be used as effectively as possible (because these are always limited).

Random and stratified random sampling

To understand these criteria, consider another hypothetical example. Suppose that we are interested in the density of a particular weed (say wild oat) in a wheat field. To prevent bias, it is necessary to ensure that each part of the field has an equal chance of being selected for sampling. Sampling units should therefore be selected at random. We might, for example, divide the field into a measured grid, pick points on the grid at random, and count the wild oat plants within a 50 cm radius of the selected grid point. This unbiased method can be contrasted with a plan to sample only weeds from between the rows of wheat plants, giving too high an estimate, or within the rows, giving too low an estimate (Figure 1.5a).

Remember, however, that random samples are not taken as an end in themselves, but because random sampling is a means to truly representative sampling. Thus, randomly chosen sampling units may end up being concentrated, by chance, in a particular part of the field that, unknown to us, is not representative of the field as a whole. It is often preferable, therefore, to undertake *stratified random sampling* in which, in this case, the field is divided up into a number of equal-sized parts (*strata*) and a random sample taken from each. This way, the coverage of the whole field is more even, without our having introduced bias by selecting particular spots for sampling.

Separating subgroups and directing effort

Suppose now, though, that half the field is on a slope facing southeast and the other half on a slope facing

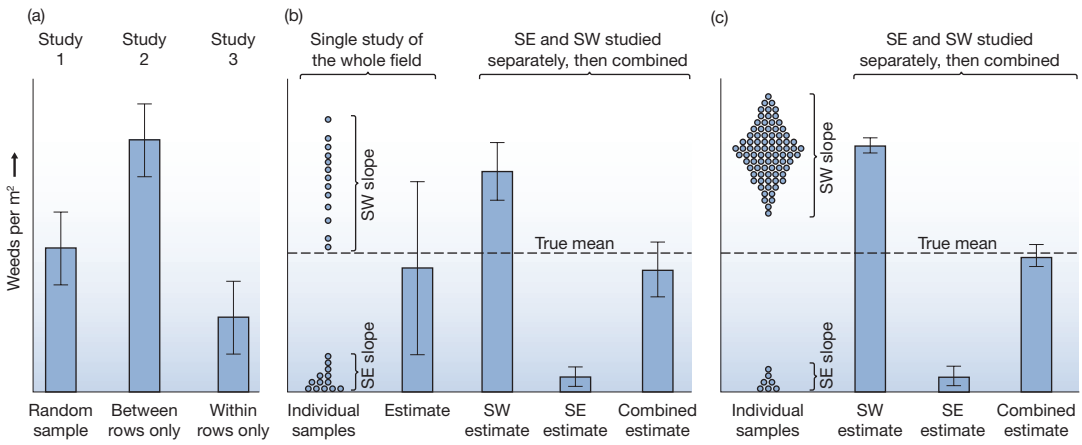


Figure 1.5

The results of hypothetical programs to estimate weed density in a wheat field. (a) The three studies have equal precision (95% confidence intervals) but only the first (from a random sample) is accurate. (b) In the first study, individual samples from different parts of the field (southeast and southwest) fall into two groups (left); thus, the estimate, although accurate, is not precise (right). In the second study, separate estimates for southeast and southwest are both accurate and precise – as is the estimate for the whole field obtained by combining them. (c) Following on from (b), most sampling effort is directed to the southwest, reducing the confidence interval there, but with little effect on the confidence interval for the southeast. The overall interval is therefore reduced: precision has been improved.

southwest, and that we know that aspect (which way the slope is facing) can affect weed density. Random sampling (or stratified random sampling) ought still to provide an unbiased estimate of density for the field as a whole, but for a given investment in effort, the confidence interval for the estimate will be unnecessarily high. To see why, consider Figure 1.5b. The individual values from samples fall into two groups a substantial distance apart on the density scale: high from the southwest slope; low (mostly zero) from the southeast slope. The estimated mean density is close to the true mean (it is accurate), but the variation among samples leads to a very large confidence interval (it is not very precise).

If, however, we acknowledge the difference between the two slopes and treat them separately from the outset, then we obtain means for each that have much smaller confidence intervals. What is more, if we average those means and combine their confidence intervals to obtain an estimate for the field as a whole, then that interval too is much smaller than previously (Figure 1.5b).

But has our effort been directed sensibly, with equal numbers of samples from the southwest slope, where there are lots of weeds, and the southeast slope, where there are virtually none? The answer is no. Remember that narrow confidence intervals arise from a combination of a large number of data points *and* little intrinsic variability (see Box 1.3). Thus, if our efforts had been directed mostly at sampling the southwest slope, the increased amount of data would have noticeably decreased the confidence interval (Figure 1.5c), whereas less sampling of the southeast slope would have made very little difference to that confidence interval because of the low intrinsic variability there. Careful direction of a sampling program can clearly increase overall precision for a given investment in effort. And generally, sampling programs should, where possible, identify biologically distinct subgroups (males and females, old and young, etc.) and treat them separately, but sample at random within subgroups.

1.3 Ecology in practice

In previous sections we have established in a general way how ecological understanding can be achieved, and how that understanding can be used to help us predict, manage and control ecological systems. However, the practice of ecology is easier said than done. To discover the real problems faced by ecologists and how they try to solve them, it is best to consider some real research programs in a little detail. While reading the following examples you should focus on how they illuminate our three main points: (i) ecological phenomena occur at a variety of scales; (ii) ecological evidence comes from a variety of different sources; and (iii) ecology relies on truly scientific evidence and the application of statistics. Every other chapter in this book will contain descriptions of similar studies, but in the context of a systematic survey of the driving forces in ecology (Chapters 2–11) or of the application of this knowledge to solve applied problems (Chapters 12–14). For now, we content ourselves with seeking an appreciation of how four research teams have gone about their business.

1.3.1 Brown trout in New Zealand: effects on individuals, populations, communities and ecosystems

It is rare for a study to encompass more than one or two of the four levels in the biological hierarchy (individuals, populations, communities, ecosystems). For most of the 20th century, physiological and behavioral ecologists (studying individuals), population dynamicists, and community and ecosystem ecologists tended to follow separate paths, asking different questions in different ways. However, there can be little doubt that, ultimately, our understanding will be enhanced considerably when the links between all these levels are made clear – a point that can be illustrated by examining the impact of the introduction of an exotic fish to streams in New Zealand.

Prized for the challenge they provide to anglers, brown trout (*Salmo trutta*) have been transported from their native Europe all around the world; they were introduced to New Zealand beginning in 1867, and self-sustaining populations are now found in many streams, rivers and lakes there. Until quite recently, few people cared about native New Zealand fish or invertebrates, so little information is available on changes in the ecology of native species after the introduction of trout. However, trout have colonized some streams but not others. We can therefore learn a lot by comparing the current ecology of streams containing trout with those occupied by non-migratory native fish in the genus *Galaxias* (Figure 1.6).

the individual level – consequences for invertebrate feeding behaviour

Mayfly nymphs of various species commonly graze microscopic algae growing on the beds of New Zealand streams, but there are some striking differences in their activity rhythms depending on whether they are in *Galaxias* or trout streams. In one experiment, nymphs collected from a trout stream and placed in small artificial laboratory channels were less active during the day than the night, whereas those collected from a *Galaxias* stream were active both day and night (Figure 1.7a). In another experiment, with another mayfly species, records were made of individuals visible in daylight on the surface of cobbles in artificial channels

COURTESY OF ANGUS MCINTOSH

Figure 1.6

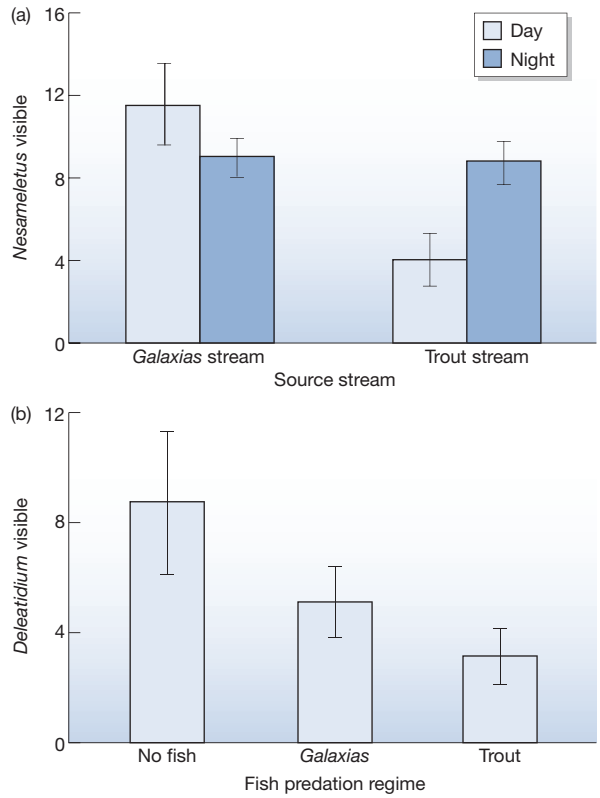
(a) A brown trout and (b) a *Galaxias* fish in a New Zealand stream – is the native *Galaxias* hiding from the introduced predator?

placed in a real stream. Three treatments were each replicated three times – no fish in the channels, trout present and *Galaxias* present. Daytime activity was significantly reduced in the presence of either fish species, but to a greater extent when trout were present (Figure 1.7b).

These differences in activity pattern reflect the fact that trout rely principally on vision to capture prey, whereas *Galaxias* rely on mechanical cues. Thus,

Figure 1.7

(a) Mean number (± SE) of *Nesameletus ornatus* mayfly nymphs collected either from a trout stream or a *Galaxias* stream that were recorded by means of video as visible on the substrate surface in laboratory stream channels during the day and night (in the absence of fish). Mayflies from the trout stream are more nocturnal than their counterparts from the *Galaxias* stream. (b) Mean number (± SE) of *Deleatidium* mayfly nymphs observed on the upper surfaces of cobbles during late afternoon in channels (placed in a real stream) containing no fish, trout or *Galaxias*. The presence of a fish discourages mayflies from emerging during the day, but trout have a much stronger effect than *Galaxias*. In all cases, the standard errors were sufficiently small for differences to be statistically significant ($P < 0.05$).



(a) AFTER MCINTOSH & TOWNSEND, 1994; (b) AFTER MCINTOSH & TOWNSEND, 1996

invertebrates in a trout stream are considerably more at risk of predation during daylight hours. And these conclusions are all the more robust because they derive both from the readily controlled conditions of a laboratory experiment and from the more realistic, but more variable, circumstances of a field experiment.

the population level – brown trout and the distribution of native fish

In the Taieri River in New Zealand, 198 sites were selected in a stratified manner by choosing streams of similar dimensions at random in each of three tributaries from each of eight subcatchments of the river. Care was taken not to succumb to the temptation of choosing sites with easy access (near roads or bridges) in case this biased the results. The sites were classified as containing: (i) no fish; (ii) *Galaxias* only; (iii) trout only; or (iv) both *Galaxias* and trout. At every site a variety of physical variables were measured (stream depth, flow velocity, phosphorus concentration in the stream water, percentage of the streambed composed of gravel, etc.). A statistical procedure called multiple discriminant functions analysis was then used to determine which physical variables, if any, distinguished one type of site from another. Means and standard errors of these key environmental variables are presented in Table 1.1.

Trout occurred almost invariably below waterfalls that were large enough to prevent their upstream migration; they tended to occur at low elevations because sites without waterfalls downstream tended to be at lower elevation. Sites containing *Galaxias* (or with no fish) were always upstream of one or several large waterfalls. The few sites that contained both trout and *Galaxias* were below waterfalls, at intermediate elevations, and in sites with cobble beds; the unstable nature of these beds may have promoted coexistence (at low densities) of the two species. This descriptive study at the population level therefore takes advantage of a 'natural' experiment (streams that happen to contain trout or *Galaxias*) to determine the effect of the introduction of trout. The most probable reason for the restriction of populations of *Galaxias* to sites upstream of waterfalls, which cannot be climbed by trout, is direct predation by trout on the native fish below the waterfalls (a single small trout in a laboratory aquarium has been recorded consuming 135 *Galaxias* fry in a day).

Table 1.1

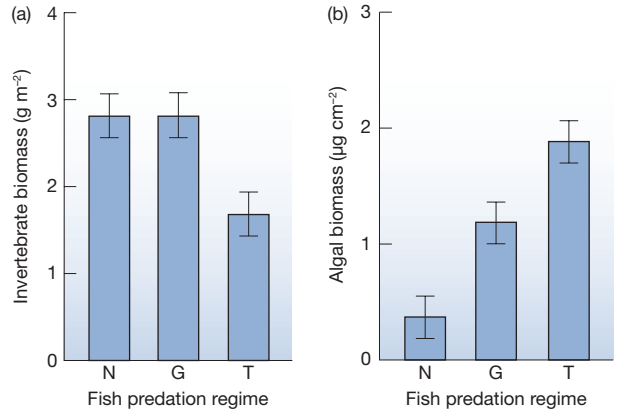
Means and, in brackets, standard errors for important discriminating variables for fish assemblage classes in 198 sites in the Taieri River. In particular, compare the '*Galaxias* only' and 'brown trout only' classes. *Galaxias* are found on their own if there are large waterfalls downstream of the site (and at relatively high elevations where the stream bed has an intermediate representation of cobbles). Brown trout, on the other hand, generally occur where there are no downstream waterfalls (at slightly lower elevations and with a bed composition similar to the *Galaxias* class).

		VARIABLES		
SITE TYPE	NUMBER OF SITES	NUMBER OF WATERFALLS DOWNSTREAM	ELEVATION (m ABOVE SEA LEVEL)	% OF THE BED COMPOSED OF COBBLES
Brown trout only	71	0.42 (0.05)	324 (28)	18.9 (2.1)
Galaxias only	64	12.3 (2.05)	567 (29)	22.1 (2.8)
No fish	54	4.37 (0.64)	339 (31)	15.8 (2.3)
Trout + *Galaxias*	9	0.0 (0)	481 (53)	46.7 (8.5)

FROM TOWNSEND & CROWL, 1991

Figure 1.8

(a) Total invertebrate biomass and (b) algal biomass (chlorophyll *a*) (± SE) for an experiment performed in summer in a small New Zealand stream. In experimental replicates where trout are present, grazing invertebrates are rarer and graze less; thus, algal biomass is highest. G, *Galaxias* present; N, no fish; T, trout present.



AFTER FLECKER & TOWNSEND, 1994

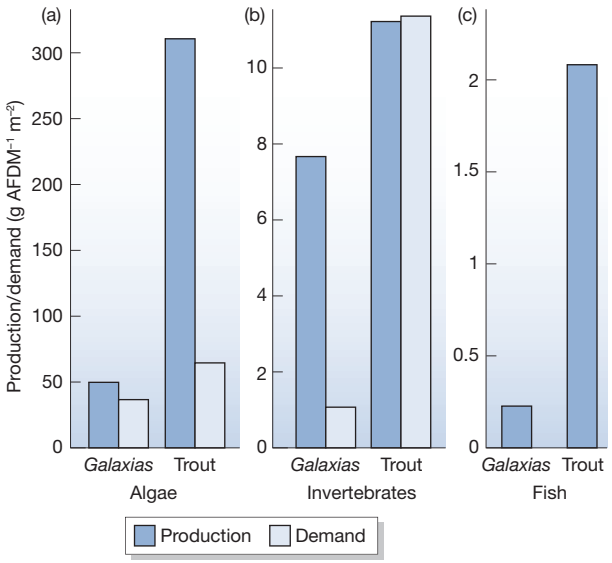
the community – brown trout cause a cascade of effects

That an exotic predator such as trout has direct effects on *Galaxias* distribution or mayfly behavior is not surprising. However, we can ask whether these changes have community consequences that cascade through to other species. In the relatively species-poor stream communities in the south of New Zealand, the plants are mainly algae that grow on the streambed. These are grazed by various insect larvae, which in turn are prey to predatory invertebrates and fish. As we have seen, trout have replaced *Galaxias* in many of these streams. An experiment involving artificial flow-through channels (several meters long, with mesh ends to prevent escape of fish but to allow invertebrates to colonize naturally) placed into a real stream was used to determine whether trout affect the stream food web differently from the displaced *Galaxias*. Three treatments were established (no fish, *Galaxias* present, and trout present, at naturally occurring densities) in each of several randomized blocks located in a stretch of a stream with each block separated by more than 50 m. Algae and invertebrates were allowed to colonize for 12 days before introducing the fish. After a further 12 days, invertebrates and algae were sampled (Figure 1.8).

A significant effect of trout reducing invertebrate biomass was evident ($P = 0.026$), but the presence of *Galaxias* did not depress invertebrate biomass from the no-fish control. Algal biomass, perhaps not surprisingly then, achieved its highest values in the trout treatment ($P = 0.02$). It is clear that trout do have a more pronounced effect than *Galaxias* on invertebrate grazers and, thus, on algal biomass. The indirect effect of trout on algae occurs partly through a reduction in invertebrate density, but also because trout restrict the grazing behavior of the invertebrates that are present (see Figure 1.7b).

the ecosystem – trout and energy flow

The sequence of studies above provided the impetus for a detailed energetics investigation of two neighboring tributaries of the Taieri River (with very similar physicochemical conditions), one being occupied by just trout and the other (because of a waterfall downstream) containing only *Galaxias*. No other fish were present in either stream. The hypothesis under examination was that the rate at which radiation energy was captured through photosynthesis by the algae would be greater in the trout stream because there would be fewer invertebrates and thus a lower rate of consumption of algae. Indeed, annual net 'primary' production (the rate of production of plant, in this case algal, biomass) was six times greater in the trout stream than in the *Galaxias* stream (Figure 1.9).



AFTER HURYN, 1998

Figure 1.9

Annual estimates for 'production' of biomass at one trophic level, and the 'demand' for that biomass (the amount consumed) at the next trophic level, for (a) primary producers (algae), (b) invertebrates (which consume algae), and (c) fish (which consume invertebrates). Estimates are for a trout stream and a *Galaxias* stream. In the former, production at all trophic levels is higher, but because the trout consume essentially all of the annual invertebrate production (b), the invertebrates consume only 21% of primary production (a). In the *Galaxias* stream, these fish consume only 18% of invertebrate production, 'allowing' the invertebrates to consume the majority (75%) of annual primary production.

Moreover, the primary consumers (invertebrates that eat algae) produced new biomass in the trout stream at about 1.5 times the rate in the *Galaxias* stream, while trout themselves produced new biomass at roughly nine times the rate that *Galaxias* do (Figure 1.9).

Thus, the algae, invertebrates and fish are all 'more productive' in the trout stream than in the *Galaxias* stream; but *Galaxias* consume only about 18% of available prey production each year (compared to virtually 100% consumption by trout); while the grazing invertebrates consume about 75% of primary production in the *Galaxias* stream (compared to only about 21% in the trout stream) (Figure 1.9). Thus, the initial hypothesis appears to be confirmed: it is strong control by trout of the invertebrates that releases algae to produce and accumulate biomass at a fast rate.

A further ecosystem consequence ensues: in the trout stream, the higher primary production is associated with a faster rate of uptake by algae of plant nutrients (nitrate, ammonium, phosphate) from the flowing stream water (Simon et al., 2004).

This series of studies, therefore, illustrates some of the variety of ways in which ecological investigations may be pursued, and both the range of levels in the biological hierarchy that ecology spans and the way in which studies at different levels may complement one another. While it is necessary to be cautious when interpreting the results of an unreplicated study (only one trout and one *Galaxias* stream in the 'ecosystem study'), the conclusion that a trophic cascade is responsible for the patterns observed at the ecosystem level can be made with some confidence because of the variety of other corroborative studies conducted at the individual, population and community levels. Although brown trout are exotic invaders in New Zealand, and they have far-reaching effects on the ecology of native ecosystems, they are now considered a valuable part of the fauna, particularly by anglers, and generate millions of dollars for the nation. Many other invaders have dramatic negative economic impacts (Box 1.5).