CHAPTER 1

Linking ecosystem and parasite ecology

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Parasites are rarely considered in ecosystem studies. The current interest in the relationship between biodiversity and ecosystem functioning, however, has stimulated the emergence of new synthetic approaches across the traditional divide between population and ecosystem ecology. Here we provide a brief introduction to ecosystem ecology, an overview of current trends in the field of biodiversity and ecosystem functioning, and ideas about how parasites should and could be brought into ecosystem ecology.

1.1 Introduction

Host–parasite interactions have traditionally been approached from the viewpoint of population dynamics and epidemiology. In contrast, ecosystem ecology has traditionally focused on the 'big picture' of stocks and flows of mass and energy at the whole system level, in which parasites at first sight seem irrelevant because they account for such a low biomass. Parasites are rarely considered in ecosystem studies. For example, since its launch in 1998, the journal *Ecosystems* has not published a single paper containing the words *parasite*, *parasitism*, or *parasitoid* in its title, key words or even abstract! This nearly complete separation between parasites and ecosystems in modern ecology is an expression of the broader separation between population/community and ecosystem ecological approaches. The current interest in the relationship between biodiversity and ecosystem functioning, however, has stimulated the emergence of new synthetic approaches across the traditional divide

between community and ecosystem ecology (Jones and Lawton 1995; Kinzig *et al.* 2002; Loreau *et al.* 2002). In this chapter we provide a brief introduction to ecosystem ecology, an overview of current trends in the field of biodiversity and ecosystem functioning, and ideas about how parasites should and could be brought into the 'big picture' of ecosystem ecology.

1.2 Ecosystem ecology, an integrative science in need of further integration

Because of its central role in ecological thinking, the ecosystem concept has been extensively analysed by ecologists, historians, philosophers, and linguists (e.g. Hagen 1992; Golley 1993; Dury 1999; Pickett and Cadenasso 2002). A historical overview of this concept helps to grasp the fundamentals of ecosystem science, its progress in half a century of existence and its current challenges.

1.2.1 The ecosystem concept in a historical perspective

Since it was first introduced by Tansley (1935), the ecosystem concept has designated not only the sum of the organisms and their abiotic environment, but also the 'constant interchange of the most various

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kinds within each system, not only between the organisms but between the organic and the inorganic' (Tansley 1935). Lindeman (1942) and Odum (1959, 1969) also stressed the exchange of energy and materials between the living and non-living parts in their definitions of the ecosystem. Odum (1959) recognized 'four constituents as comprising the ecosystem: (1) abiotic substances, basic inorganic and organic compounds of the environment; (2) producers, autotrophic organisms, largely green plants [. . .]; (3) consumers (or macro-consumers), heterotrophic organisms, chiefly animals [. . .]; (4) decomposers (micro-consumers, saprobes or saprophytes), heterotrophic organisms, chiefly bacteria and fungi, which [. . .] release simple substances usable by the producers.' With these constituents, an ecosystem is a 'life-support system [. . .] functioning within whatever space we chose to consider whether it be a culture vessel, a space capsule, a crop field, a pond, or the Earth's biosphere' (Odum 1964). These initial views are still prevailing among current ecosystem ecologists. Thus, for Chapin *et al.* (2002), 'ecosystem ecology addresses the interactions between organisms and their environment as an integrated system. [. . .] The flow of energy and materials through organisms and the physical environment provides a framework for understanding the diversity of form and functioning of Earth's physical and biological processes'.

Some authors, however, gave extended, more abstract definitions of the ecosystem. Evans (1956) suggested that the ecosystem concept could be used at any organizational level of life. On this view, any organism with its micro-environment could potentially constitute an ecosystem. Higashi and Burns (1991) distinguished two ecosystem concepts: 'the ecosystem as a physical entity' following Tansley (1935), and 'the ecosystem as a paradigm for science: an entity–environment unit'. With such extended definitions, a host and its parasites could be viewed as an ecosystem (as in Thomas *et al.* 1999*a*, see also Chapter 8). Pickett and Cadenasso (2002) emphasized the flexibility of the definition, the ecosystem concept being scale independent and free of narrow assumptions such as equilibrium. This general concept can then be applied to an array of models whose characteristics depend on the issue being addressed and on the nature of the system under study. Depending on the model, energy, nutrient, biodiversity, or economics can be the focus of the study (Pickett and Cadenasso 2002).

For a large majority of ecologists, and in particular for those who bridge fundamental research and applied problem solving, an ecosystem is clearly a 'spatially explicit unit of the Earth' (Likens 1992). As such it comprises abiotic substances, autotrophic and heterotrophic organisms, and their interactions. The nature and consequences of these interactions, however, has fuelled a recurrent debate: do these interactions lead to emergent properties and integration of the ecosystem into a self-regulated functional unit? A number of scientists working on subsets of ecosystems, such as physiologists Engelberg and Boyarsky (1979) and community ecologist Simberloff (1980) questioned this idea, whereas ecosystem ecologists generally supported the cybernetic nature of ecosystems (McNaughton and Coughenour 1981; Patten and Odum 1981). The strongest, and most controversial, form of this view is probably Lovelock's (1995) Gaia theory of the total Earth system as a single self-regulating unit. The debate on these issues, however, has often been led astray to one-sided positions. The theories of complex adaptive systems (Levin 1999) and multilevel natural selection (Wilson 1980), for instance, provide frameworks to understand the ecological and evolutionary emergence of properties at higher levels of organization without invoking strong top–down, integrated regulation.

Chapin *et al.* (1996, 2002) provide a useful synthetic view of what controls ecosystem structure and functioning. According to them; five external factors set the bounds for ecosystem properties: parent rock material, topography, climate, time, and potential biota. Within these bounds, actual ecosystem properties are set by a suite of interactive controls: (1) resources (soil, water, air); (2) physical and chemical modulators (such as local temperature and pH, which affect organisms without being consumed by them); (3) disturbance regime; (4) the biotic community, and; (5) human activities which affect all the other controls. The biotic community

influences ecosystem functioning through the trophic levels present, the number of species within each trophic level, their relative abundances, and their identity. Dominant species (in term of biomass) and species with particular functional attributes (like mycorrhizal fungi) are the species with *a priori* the largest role. Populations of these species are regulated by a set of negative and positive interactions among species, and parasitism is one of them. With only an indirect role on one of the five interactive controls of ecosystem processes, parasites understandably are not of first concern to most ecosystem ecologists.

1.2.2 Ecosystem science, its achievements and frontiers

Ecosystem science is characterized by the processes it addresses rather than by the type of system it deals with, although it is more often conducted at high levels of organization (several trophic levels) and large spatial scales (from a plot to the whole Earth). It is concerned mainly with the pools and the fluxes of energy and materials among ecosystem components (in contrast to population and community ecology which are concerned with the demography, diversity, and interactions of the organisms living in ecosystems). Its aim is usually to understand how these pools and fluxes are regulated by the interactive controls mentioned above, but also how they set constraints on the structure of ecosystems (community types and diversity). Temporal and spatial patterns of ecosystem processes and ecosystem management are also of primary concern. The increasing impact of humans on all these aspects and its consequences are often at the forefront of ecosystem ecology (Vitousek *et al.* 1997).

Accomplishments of ecosystem science have been numerous (Pace and Groffman 1998), and include understanding the flow of water and chemical elements and compounds in watersheds, rivers, lakes, estuaries, and oceans; analysing feedbacks between plants and animals and their biophysical environment; understanding the causes of, and remedies to, eutrophication; understanding the biophysical basis of production and its coupling to climate; assessing the importance of below-ground processes in terrestrial ecosystems; and recognizing the scale dependence of most ecosystem processes (Carpenter and Turner 1998). These accomplishments have been mainly achieved through (1) comparative studies of natural ecosystems (e.g. Matson and Vitousek 1987; Turner *et al.* 2001); (2) long-term field studies (Gosz 1996; Hobbie *et al.* 2003); (3) experimental manipulation of ecosystems from model laboratory systems to large-scale field experiments (Beyers and Odum 1993; Lawton 1995; Schindler 1998); and (4) theory and mathematical modelling (Tilman 1988; DeAngelis 1992; Ågren and Bosatta 1996; Loreau 1995, 1998*a*).

The ecosystem approach is fundamental to managing the Earth's resources. Ecosystem ecology often bridges fundamental research and applied problem solving. When environmental concerns moved from the local scale in the 1960s to the regional and now global scales, so did ecosystem science. These three scales cannot replace each other, however, and basic research is still needed at all scales. For example, the knowledge of a basic ecosystem process such as primary productivity, whose study was fostered from the 1960s by the International Biological Programme, is still developing fast, integrating new techniques, control factors, and scales (Canadell *et al.* 2000; Roy *et al.* 2001). But the main challenge ahead is getting more strongly involved in solving the ever-increasing environmental problems and working towards a more sustainable future (Lubchenco 1998; Gosz 1999). Integrating across scales is a prominent task (Levin 1992; Carpenter and Turner 2000*b*), as is integrating the various controls of ecosystem processes. Taking into account the role of biodiversity in ecosystem functioning is a critical, fast-developing area, which we develop in the next section. Integrating the socio-economic aspects of human activities from local to global scales is a novel dimension which will be crucial for achieving a sustainable management of ecosystems (Carpenter and Turner 2000*a*; Costanza 2000; Di Castri 2000). Efforts are also needed to develop stronger communication and cooperation among the research, policy and public spheres (Baron and Galvin 1990; Rykiel 1997). The Millennium Ecosystem Assessment is an example of such efforts (Ayensu *et al.* 1999; Samper 2003).

Despite its achievements in basic and applied science, ecosystem ecology has developed until recently in growing isolation from other fast-moving ecological subdisciplines such as population ecology, community ecology, and evolutionary ecology. The level of integration that it promotes has stimulated links with other scientific disciplines such as chemistry and geology, but has also tended to diminish links with other biological disciplines. Reciprocally, population ecology, commun-ity ecology, and evolutionary ecology have until recently largely ignored the higher level of integration offered by ecosystem ecology. This separation between subdisciplines that provide different per-spectives on the same ecological reality is a funda-mental limitation which needs to be overcome if we are to understand the predominantly biological basis of ecosystems, the reciprocal constraints that individual species and ecosystems exert on each other on ecological and evolutionary time-scales, the role of biodiversity in ecosystem functioning, and more particularly the role of parasites and of their diversity in ecological systems.

1.3 Biodiversity and ecosystem functioning, a new area that synthesizes population, community, and ecosystem ecology

The relationship between biodiversity and ecosys-tem functioning has emerged as a new research area at the interface between community ecology and ecosystem ecology which has expanded dra-matically during the last few years (see syntheses in Loreau *et al.* 2001, 2002; Kinzig *et al.* 2002). This new area finds its origin in a questioning that started only a decade ago on the potential con-sequences of biodiversity loss which results from the increasing human domination of natural ecosystems, a domi-nation that is likely to further develop considerably during the twenty-first century (Schulze and Mooney 1993).

Three types of reasons have been put forward to justify current concerns about threats to biodivers-ity. First, biodiversity is the source of natural resources that lead to the direct production of goods that are of economic value, such as food, wood fibre, new pharmaceuticals, genes that improve crops, or organisms that are used for bio-logical control of pests. Second, biodiversity is viewed as linked to human well-being for aesthetic, ethical, and cultural reasons. Third, biodiversity may contribute to the provision of ecosystem services that are of value to society, but are generally not given an economic value, such as primary and sec-ondary production, plant pollination, climate regu-lation, carbon sequestration, the maintenance of water quality, and the generation and maintenance of soil fertility. It is this third possibility that gave rise to the interest in biodiversity and ecosystem functioning: could biodiversity loss alter the func-tioning of ecosystems, and thereby the ecological services they provide to humans?

When this question was posed in the early 1990s, scientific ecology had a number of theories and empirical data that clearly showed the importance of 'vertical' diversity, that is, functional diversity across trophic levels along the food chain, in ecosystems. An eloquent example of the dramatic impacts that changes in vertical diversity can have is provided by the kelp–sea urchin–sea otter food chain in the Pacific. Removal of sea otters by Russian fur traders allowed a population explosion of sea urchins that overgrazed kelp (Estes and Palmisano 1974). Reduction in kelp cover in turn leads to extinction of other species living in kelp, as well as increased wave action, coastal erosion, and storm damage (Mork 1996). More intense herbivory in the absence of sea otters has also been shown to trigger evolution of chemical defences in kelp (Steinberg *et al.* 1995). Thus, removal of a single top predator generates a cascade of population dynam-ical, physical, and even evolutionary effects within ecosystems.

In contrast, little was known on the ecological significance of 'horizontal' diversity, that is, genetic, taxonomic, and functional diversity within trophic levels. Different theories of coexistence among competing species have vastly different implications for the relationship between species diversity and ecosystem processes. To take two extreme examples, neutral theory assumes that all species in a commun-ity are equivalent (Hubbell 2001). This implies functional redundancy among species, and hence an

absence of any effect of changes in diversity on aggregate community or ecosystem properties. At the other extreme, niche theory postulates that all species differ to some extent in the resources they use. This implies functional complementarity among species, and hence increased productivity and other ecosystem processes with diversity (Tilman *et al.* 1997*a*; Loreau 1998*b*).

To investigate the effects of 'horizontal' diversity on ecosystem processes, a new wave of experimental studies was developed using synthesized model ecosystems. Many of these studies were focused on effects of plant taxonomic and functional-group diversity on primary production and nutrient retention in grassland ecosystems. Because plants, as primary producers, represent the basal component of most ecosystems, they represented the logical place to begin detailed studies. Several, though not all, experiments using randomly assembled communities found that plant species and functional-group richness has a positive effect on primary production and nutrient retention (e.g. Tilman *et al.* 1996, 1997*b*; Hector *et al.* 1999; Fig. 1.1). Although the interpretation of these experiments was hotly debated (e.g. Huston 1997; Huston *et al.* 2000; Hector *et al.* 2000), this controversy has been largely resolved by a combination of a consensus agreement on a common conceptual framework (Loreau *et al.* 2001), the development of a new methodology to partition selection and complementarity effects (Loreau and Hector 2001), and new experimental data (Tilman *et al.* 2001; van Ruijven and Berendse 2003). These new studies have all shown that plant diversity influences primary production through a complementarity effect generated by niche differentiation (which enhances resource exploitation by the community as a whole) and facilitation. Thus, there is little doubt that species diversity does affect at least some ecosystem processes, even at the small spatial and temporal scales considered in recent experiments, although it is still difficult to assess how many species are important to generate functional complementarity.

Even if high diversity were not critical for maintaining ecosystem processes under constant or benign environmental conditions, it might nevertheless be important for maintaining them under changing conditions. The 'insurance' and 'portfolio' hypotheses propose that biodiversity provides a buffer against environmental fluctuations because different species respond differently to these fluctuations, leading to functional compensations
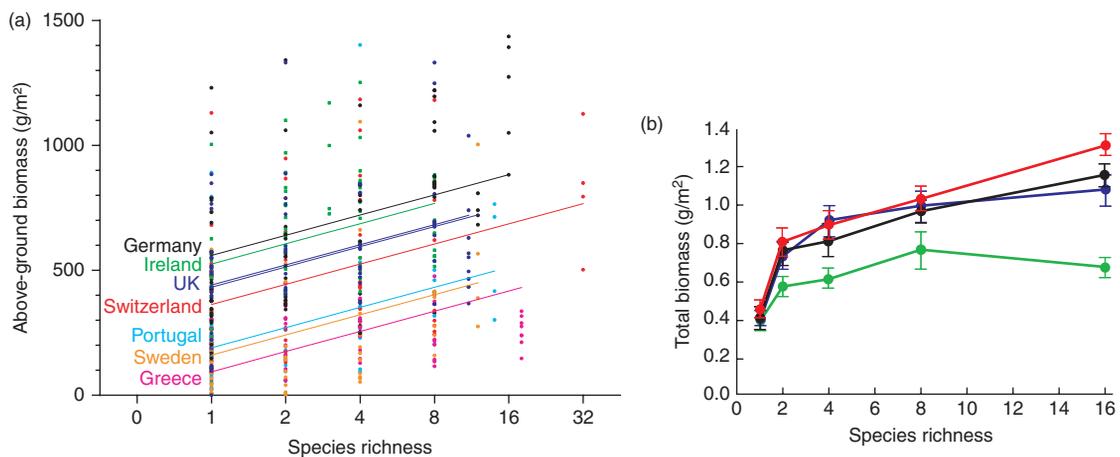
Figure 1.1 Responses of plant biomass to experimental manipulations of plant species richness in grassland ecosystems: (a) above-ground plant biomass in eight sites across Europe; (b) total plant biomass (mean ± standard error) during several years in Minnesota.

Note: Points in (a) are data for individual plots.

Sources: (a) Modified from Hector *et al.* 1999; and (b) Modified from Tilman *et al.* 2001.

between species and hence more predictable aggregate community or ecosystem properties. A number of studies have recently provided theoretical foundations for these hypotheses (e.g. McNaughton 1977; Doak *et al.* 1998; Tilman *et al.* 1998; Yachi and Loreau 1999; Lehman and Tilman 2000). Several empirical studies have found decreased variability of ecosystem processes as diversity increases, despite sometimes increased variability of individual populations, in agreement with the insurance hypothesis (e.g. Tilman 1996; McGrady–Steed *et al.* 1997). The interpretation of these patterns, however, is complicated by the correlation of additional factors with species richness in these experiments, which does not fully preclude alternative interpretations (e.g. Huston 1997).

An important limitation of virtually all recent theoretical and experimental studies on the effects on biodiversity on ecosystem functioning and stability is that they have concerned single trophic levels—primary producers for the most part. Although they have contributed to merging community and ecosystem ecology, they have unintentionally disconnected 'vertical' and 'horizontal' diversity and processes. Yet it is well known that trophic interactions can have important effects on the biomass and productivity of the various trophic levels (Abrams 1995; Oksanen and Oksanen 2000) as well as on ecosystem stability (MacArthur 1955; May 1974; Pimm 1984). An important current challenge is to understand how trophic interactions affect the relationship between biodiversity and ecosystem functioning. A few recent experiments have started to investigate biodiversity and ecosystem processes in multitrophic systems (Naeem *et al.* 2000; Downing and Leibold 2002; Duffy *et al.* 2003), and new theory now provides testable predictions on these issues (Ives *et al.* 2000; Loreau 2001; Holt and Loreau 2002; Thébault and Loreau 2003). Since parasites and diseases are cryptic higher trophic levels, this extension to multitrophic systems provides a straightforward path towards including parasites into our view of ecosystems.

1.4 Parasites in ecosystems

Parasites are typically small-sized organisms that exploit their host both as a food resource and as a habitat. They affect their host negatively either because they alter specific physiological functions or because they multiply and develop large populations within their host; individually their effect is often very small. Even collectively, their biomass and the amount of material and energy they process is often much smaller than the biomass and the material and energy flows of their host. This explains why parasites have traditionally been ignored by ecosystem ecology: they are hidden within their host, and their direct ecosystem impact is seemingly negligible.

Yet their indirect impact on ecosystem processes can be substantial through their effect on their host. Here we explore some of the ways in which they exert strong indirect influences on the biodiversity and functioning of ecosystems.

First, parasitism and disease are probably one of the most significant causes of population regulation in many species under natural conditions (see Chapter 3). By regulating populations of dominant species they can have significant effects on ecosystem processes (see Chapter 8). Massive mortality or fertility reduction in individual species, however, may be of little long-term significance for ecosystem properties under natural conditions, especially in plants. Plants compete strongly for space, light, and nutrients, so that population reduction or extinction of one species, which may have a significant effect on ecosystem productivity or other processes in the short term, is usually compensated for by population growth of another species in the long term. Compensation among otherwise functionally 'redundant' species is the very basis for the insurance effect of biodiversity on aggregated ecosystem properties (Walker 1992; Walker *et al.* 1999). A historical example is provided by the extinction of the American chestnut, once a major canopy species in Eastern US deciduous forests, following introduction of a fungal pathogen. Oaks and other species replaced the chestnut, and forest productivity and biomass returned to levels similar to previous levels in about 40 years (Whittaker and Woodwell 1972). Effects of parasites on individual animal populations might be more significant for ecosystem processes and services—at least as we perceive them from our anthropocentric perspective—because animals often have more specific roles in the complex interaction

networks of natural ecosystems. For instance, in a successful attempt to control the proliferation of the European rabbit, introduction of the myxoma virus in Australia led to decimation of rabbit populations (Fenner and Ratcliffe 1965). Rabbit mortality helped restore the vegetation which supported sheep populations utilized for wool production in range and pasture lands. Little is known on the net effect of myxomatosis on total primary and secondary production, but wool production at least was strongly influenced by the presence of the myxoma virus.

Second, by exerting top-down control on populations from lower trophic levels, parasites may substantially alter the diversity of their host species and its effects on ecosystem processes. Higher trophic levels can generate hump-shaped or other complex nonlinear relationships between species diversity and ecosystem processes (Thébault and Loreau 2003). These nonlinear relationships are critically dependent on where and how top-down or bottom-up controls occur in the food web. For instance, when all plant species are controlled from the top down by specialized herbivores, there is a monotonic increase in total plant biomass as diversity increases. By contrast, when some plant species escape top-down control or when herbivores are generalists, a unimodal relationship can emerge between total plant biomass and diversity (Fig. 1.2). Whether the agents of top-down control are herbivores or parasites is immaterial to these theoretical results. Therefore these should apply to parasites as well. Application of insecticide to a biodiversity experiment revealed major effects of insect herbivores on the relationship between plant diversity and primary productivity: there was a strong positive response of above-ground plant biomass production to plant diversity when insect herbivores were reduced, which was not apparent when herbivores were unchecked (Mulder *et al.* 1999). The reason for this difference lies again in the top-down control exerted by insects on plants, which diverts part of primary production to the herbivore trophic level. There is no reason why this should not apply to parasites too. Seed predators and pathogens are hypothesized to be one of the main factors maintaining tropical tree diversity (Janzen 1970; Connell 1971; Wright 2002, see also Chapter 8). If

this is the case, they may have a major influence on ecosystem processes in tropical forests despite their very low biomass. Similarly, viruses are arguably one of the major factors that maintain (through selective exploitation), and even create (through gene transfer), microbial diversity (Weinbauer and Rassoulzadegan 2004). Their indirect impact on microbially driven ecosystem processes, in particular nutrient cycling, should accordingly be considerable, although it is still poorly known.

Third, a well-established body of theory and empirical evidence shows that there is a gradual transition from parasitism to mutualism on both ecological and evolutionary time scales (Maynard Smith and Szathmary 1995; Johnson *et al.* 1997). In particular, the nature and intensity of symbiotic interactions can be highly variable, and change from mutualistic to parasitic, and vice versa, depending on local environmental conditions. For instance, mycorrhizal fungi are usually mutualists for their associated plant partners because they help them to better capture soil nutrients. In fertile soils with high nutrient concentrations, however, they become parasitic because plants no longer need them to gain access to soil nutrients while they still incur the cost of providing them with carbon resources (Johnson *et al.* 1997). As a consequence of this high variability in the benefits and costs derived by the two partners, mycorrhizal fungi have highly species-specific effects on plants, and may strongly affect the diversity, species composition, and relative abundances of plant communities (van der Heijden *et al.* 1998). Mycorrhizal diversity thereby contributes to maintaining plant diversity and primary productivity under nutrient-limited conditions (van der Heijden *et al.* 1998; Klironomos *et al.* 2000). Under nutrient-rich conditions, however, mycorrhizal fungi may behave as plant parasites. Their impacts on plant diversity and productivity are then expected to be more complex as discussed above. Similar shifts in impacts on plant-based ecosystem processes are likely to occur for other plant parasites as environmental conditions change and alter the physiological status of the two partners.

Lastly, nutrient cycling is a key process that determines the productivity of all trophic levels in nutrient-limited ecosystems (DeAngelis 1992;
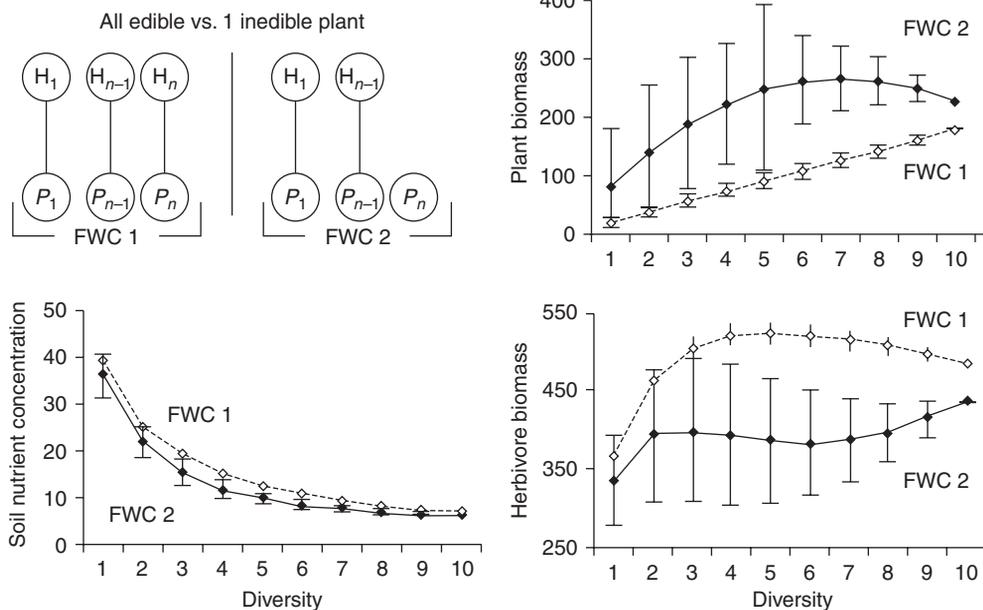
Figure 1.2 Expected soil nutrient concentration, total plant biomass and total herbivore biomass (mean $\pm$ standard deviation across all species combinations) as functions of species richness for two food web configurations: a food web in which each plant species is controlled by a specialized herbivore (dotted lines), and a food web in which one plant species is inedible and lacks a specialized herbivore (solid lines). Herbivore species richness varies parallel to plant species richness to keep the same food web configuration along the diversity gradient.

Source: Modified from Thébault and Loreau (2003).

Loreau 1995, 1998*a*; de Mazancourt *et al.* 1998). Heterotrophic consumers such as herbivores, carnivores, and parasites can substantially influence primary production through nutrient cycling. They can even increase primary production if they channel limiting nutrients towards more efficient recycling pathways, that is, to recycling pathways that keep a greater proportion of nutrients within the system (de Mazancourt *et al.* 1998). Although this theory has been mainly applied to the debated grazing optimization hypothesis, that is, the hypothesis that herbivores maximize plant production at a moderate grazing intensity, this theory should apply to parasites as well. By altering the timing and spatial location of their host's death, parasites may contribute to release nutrients locked in their host's biomass at times and places that are favourable for the conservation of these nutrients within the ecosystem or, conversely, for their loss from the ecosystem by such processes as leaching, volatilization, and sedimentation. In the former case

they will tend to enhance local productivity; in the latter case they will tend to depress local productivity. Stoichiometric constraints also come into play. For instance, bacterial decomposers often immobilize a substantial amount of limiting nutrients such as nitrogen and phosphorus because their carbon : nutrient ratio is lower than the carbon : nutrient ratio of plant dead organic matter which is their main resource (Tezuka 1989; Ågren and Bosatta 1996). Parasitic viruses are likely to enhance nutrient cycling, and hence primary production, by killing bacteria and making nutrients available again to plants.

1.5 Concluding remarks

Ecosystem ecology has provided an integrative perspective of the interactions between biological organisms and their abiotic environment, especially at relatively large spatial scales. However, it would be strengthened by better ties to, and synthesis of,

the insights and approaches of population ecology, community ecology, and evolutionary biology. After all, organisms simultaneously experience all the forces of nature, including those that are the foci of evolutionary, population, community, and ecosystem ecology. Each of these perspectives has been, and will continue to be, useful simplifications. Their synthesis, we assert, is likely to provide novel and important insights into all branches of ecology.

Recent theoretical and experimental work provides evidence that biodiversity dynamics can have profound impacts on functioning of natural and managed ecosystems and their ability to deliver ecological services to human societies. Work on simplified ecosystems in which the diversity of a single trophic level—mostly plants—is manipulated shows that taxonomic and functional diversity can enhance ecosystem processes such as primary productivity and nutrient retention. Theory also strongly suggests that biodiversity can act as biological insurance against potential disruptions caused by environmental changes. One of the major challenges, however, is to extend this new knowledge to multitrophic systems that more closely mimic complex natural ecosystems.

The role of parasites in ecosystem functioning has usually been underestimated and poorly investigated because of their low biomass, low visibility, and small direct contribution to energy and material flows in natural ecosystems. We have provided several arguments why they may nevertheless have significant indirect impacts on ecosystem properties, by controlling numerically dominant host species, by exerting top-down control and maintaining the diversity of lower trophic levels, by shifting from parasitic to mutualistic interactions with their hosts, and by channelling limiting nutrients to more or less efficient recycling pathways.

Despite recent progress towards greater convergence and dialogue between population, community, and ecosystem ecology, much remains to be done to achieve full integration of these subdisciplines. In particular, the potential importance of parasites and disease emphasize the need to take into account both direct and indirect effects in our view of ecosystems. Although indirect effects have received increasing attention in community ecology recently (Wootton 1994; Abrams 1995), their importance for ecosystem functioning has seldom been considered. Parasites, just as microbes, remind us that small causes can have large effects. Unless we better develop our understanding of the ecological significance of the whole of biodiversity, including that of parasites, we have an insufficient understanding of the functioning of natural and managed ecosystems.