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David A. Wardle: Communities and Ecosystems

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CHAPTER ONE

Introduction

All terrestrial ecosystems consist of a producer subsystem and a decomposer subsystem. These components are obligately dependent upon one another, with the producers acting as the primary source of organic carbon for the system, and the decomposers being responsible for the breakdown of organic matter and the release and cycling of nutrients. Any approach to better understanding ecosystem functioning therefore requires explicit consideration of both these subsystems. Further, both the producer and decomposer subsystems involve consumer organisms, and as a result ecosystems include both a herbivore-focused food web (located largely, though not entirely, aboveground), and a detritus-based food web. The interactions that occur within each of these food webs, as well as between these food webs, play a major role in determining how ecosystems function. Although a combined aboveground—belowground approach is necessary for the adequate understanding of community- and ecosystem-level processes, most ecological work on aboveground organisms has traditionally been conducted without much explicit consideration of belowground organisms, and most soil biology has been carried out without much acknowledgment of what interactions and mechanisms occur aboveground.

In most terrestrial ecosystems, soils contain by far the greatest diversity of organisms present. On a global basis, the majority of organisms are invertebrates, and most of these spend at least a portion of their life cycle belowground (Ghilarov 1977; Giller 1996). One gram of soil probably contains several thousand bacterial species (Torsvik et al. 1994). It has been estimated that in the Andrews Experimental Forest of Oregon, U.S.A., there are probably around 8000 species of soil arthropods in contrast to only 143 species of aboveground vertebrates (Beard 1991). On a global basis, there are likely to be over a million species of fungi (Hawkesworth 1991) and a million species of nematodes, in contrast to 6000 species of reptiles and 9000 species of birds (May 1988).

Despite the sheer diversity of belowground organisms and the functional role of soil organisms in ecosystem-level processes (both locally and globally), most of the current body of ecological theory is based on synthesizing what aboveground and aquatic ecologists have found, and soil organisms have had a negligible impact on the development of this theory. The treatment of soil organisms in most general ecological textbooks is superficial and in some cases nonexistent. Quantitative literature syntheses and meta-analyses aimed at developing general principles with regard to food web theory (e.g., Cohen et al. 1990; Pimm et al. 1991) and the role of competition and/or predation in structuring ecological communities (e.g., Connell 1983; Schoener 1983; Sih et al. 1985; Gurevitch et al. 1992, 2000; Schmitz et al. 2000) all but ignore soil organisms. A recent review of keystone organisms (Power et al. 1996) makes no mention of arguably the world's most ecologically important keystone organism group, i.e., soil-dwelling nitrogen fixing bacteria. Another recent review, on biological stoichiometery "from genes to ecosystems" (Esler et al. 2000a), makes little mention of the large soil biological literature on the role of elemental ratios as drivers of decomposition and decomposer activity. Studies on belowground organisms make up only a small proportion (characteristically less than 3%) of papers published in the major ecological journals. As a result the current body of ecological literature and main general ecological concepts are representative of only a minority of the Earth's biota (Wardle and Giller 1996). Or, as stated by Keddy (1989), "What would a body of ecological theory look like if Plantae, Fungi, Monerans, and Protistans played an appropriate role?" This remark could also be made just as strongly regarding soil invertebrates.

Further, even when the issue of the ecology of belowground organisms is acknowledged by ecologists at large, this is frequently without adequate reference to the vast soil biology literature. An extreme example of this involves a recent commentary in *Nature* titled "Ecology goes Underground" by Copley (2000), and which gives the incorrect impression that scientists are only now beginning to tackle the topic of soil biodiversity and functioning of the soil subsystem, through recently initiated projects in the U.S.A. and U.K. However, no mention is made of the significant body of work published by soil biologists over the past several decades precisely on this topic [see response to Copley (2000) by André et al. (2001), and authored by eight soil biologists from six countries].

Simultaneously, soil science, including soil biology, has tended to ignore what goes on aboveground; too often plants are seen by soil scientists merely as sources of carbon addition to the soil. As such, soil biology does not have a particularly strong theoretical framework, and few soil biologists have sought to apply concepts of ecological theory to their subdiscipline (see Wardle and Giller 1996; Ohtonen et al. 1997; Young and Ritz 1998). This is compounded by the practical problems of applying concepts developed for aboveground ecology to soil biota. First, soil organisms operate within the habitat created by the soil matrix (Coleman and Crossley 1995; Young and Ritz 1998), and there are major difficulties in studying soil organisms in situ because soil is opaque and has a very complex structure, both physically and chemically. Secondly, the extremely high diversity of soil organisms at microscopic spatial scales creates obvious problems in evaluating interactions of specific organisms with each other or with their environment. Thirdly, there are major taxonomic difficulties in identifying many components of the soil biota, especially when dealing with organisms of smaller dimensions, and probably over 90% of species of microflora and microfauna remain undescribed and unknown (Klopatek et al. 1992; Coleman and Crossley 1995).

In the last few years, there has been an increasing interest in exploring the interface of population-level and ecosystem-level ecology (see Vitousek and Walker 1989; Lawton 1994; Jones and Lawton 1995). This requires us to acknowledge the importance of both the aboveground and belowground compartments of terrestrial ecosystems as well as their interactions with each other. Despite this, there have been few attempts to bring together the widely dispersed literature on aboveground and belowground communities, or to interpret this in an ecosystem context. This is because aboveground and belowground ecology have traditionally developed largely independently of one another; the two subdisciplines usually publish in different journals and generally do not widely read each others' journals or bodies of literature. In this light it is perhaps unsurprising that often a finding that has been hailed as a breakthrough by one subdiscipline has long been common knowledge to the other.

This synthesis is aimed at both aboveground and belowground ecologists, with the aim of making both groups more aware of what goes on at the other side of the soil/surface interface. The primary goal of this book is to consider terrestrial communities and ecosystems from a combined aboveground-belowground perspective, to assess the feedbacks that exist between aboveground and belowground communities, and to interpret how these two components working in tandem govern ecosystem functioning and therefore the delivery of ecosystem services. A secondary goal is to consider aboveground-belowground linkages in the context of a changing global environment. This book is focused on concepts and issues, with examples described to illustrate these points wherever appropriate. In order to achieve this, wide use is made of both the general ecological literature and the soil biological literature.

Chapters 2–5 deal with interactions that are relevant to understanding aboveground-belowground linkages, and the consequences of these for ecosystem properties and processes. Chapter 2 considers the soil food web, including the biotic factors that regulate belowground organisms, their interactions at varying scales of resolution, and the consequences of these interactions for key belowground processes including those that regulate plant nutrient supply. Chapter 3 introduces plant communities, and evaluates how plant species effects and plant traits may be important in affecting both the soil biota and the processes that it regulates. Chapter 4 involves consideration of aboveground trophic interactions and food webs, and the consequences of these for the belowground subsystem, primarily as manifested through plants. Chapter 5 completes the circle by considering the means by which belowground organisms, their interactions, and soil food webs influence the growth and community composition of aboveground organisms. These four chapters in combination are intended to provide the basic tools for understanding how terrestrial communities and ecosystems function through explicit consideration of biotic interactions and aboveground—belowground linkages.

The next two chapters aim to apply the concepts developed in chapters 2–5 to two areas of current topical interest. Chapter 6 deals explicitly with the issue of biodiversity in an aboveground-belowground context, in terms of the factors that regulate this diversity, and with the consequences of diversity for the functioning of terrestrial ecosystems. Chapter 7 is focused on utilizing a combined aboveground-belowground approach to better understand the ecological consequences of the major drivers of anthropogenically induced global change. There is a considerable amount of research activity in the areas of both biodiversity and global change, as well as an immense production of literature on these topics. Despite this, only a minority of studies have adopted a combined aboveground-belowground strategy in investigating many of the issues relating to these topics, despite the necessity of such an approach for understanding these issues in a true ecosystem-level context. Finally, chapter 8 aims to bring together a variety of underlying conceptual threads that weave their way throughout the preceding chapters.