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Understanding soil processes: one of the last frontiers in biological and ecological research

Keynote Address from 6th Australian Soilborne Disease Symposium 2010

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Abstract Soils are one of the great unknown realms on earth, despite decades of extensive research. We still see soils "through a ped darkly". This opacity in milieu and understanding rewards innovative study, however, as soils are indeed "complex adaptive systems", and show very sophisticated levels of self-organization. Viewed historically, soil ecological studies have progressed from what major groups of biota are present, what is their biomass, and what major processes occur. More recent studies have delineated multi-trophic interactions, extending both above- and below-ground, as well as specifically-targeted studies of substrates and organisms that are involved in the development and function of suppressive soils. One of the great unknowns in soil ecology is a fuller understanding of the complete array of predatory biota. Soils are teeming with organisms in all three Domains, but are also rife with many viruses infecting Archaea, Bacteria and Eukarya, meaning that they need more study in soil processes. Pursuing a more holistic approach including viral biology and ecology may enable us to more capably manage our soils that have supported the biosphere so much over the millennia. Looking into the future, the opportunity to exploit soil biodiversity in the context of ecosystem development should pay considerable dividends. Using chronosequence analysis, the relationships between soil biodiversity and ecosystem function are beginning to be understood. The interplays of aboveground and belowground herbivores on plant function and feedbacks on the attraction of the herbivores' natural enemies. Finally, management of the plant-soil–microbial-faunal system via varied organic amendments shows possibilities in the study and management of suppressive soils.

Keywords Domains · detrital food webs · suppressive soils

Introduction

Soils are one of the last great unknown realms on earth, despite decades of extensive research. We still see soils "through a ped darkly" (Coleman 1985). This opacity in milieu and understanding rewards innovative study, however, as soils are indeed "complex adaptive systems" (Young and Crawford 2004; Crawford et al. 2005). Soils have sophisticated levels of self-organization, and are considered as central organizers for terrestrial ecosystems (Coleman et al. 1998).

After investigating the nature and extent of the complex adaptive systems of soil, I then address aspects of biocomplexity in soil systems. A strong case can be made for considering the activities of viruses along with the three Domains in soil: Bacteria, Archaea, and Eukarya. Some of the trophic interactions between members of the first three Domains are undoubtedly mediated by viruses, although much of our information comes from measurements in aquatic ecosystems (Kimura et al. 2008).

One of the more informative approaches to dynamics of organic detritus and nutrient cycling in soils has been via food web analyses. Some examples of these are explored in the paper. The nature of the food webs informs some current studies of the nature and extent of soil biodiversity. Further studies of biotic complexity and their impacts on key soil processes, including decomposition and plant growth rates, have benefited from the use of removal and additions of key taxa and trophic groups. Some examples of these, including conjoint measurements of aboveground and belowground interactions (Wardle 2002; van der Putten

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et al. 2009), provide some guidelines for possible future studies.

This paper considers next analyses of soil biodiversity in long-term studies, conducted across chronosequences of similar soils with differing histories in conservation and conventional tillage managements. In conclusion, some thoughts on "putting the soil to work for us" are addressed to the intriguing problems of managing suppressive soils, and soils in general.

The nature of domains in the soil

The nature and extent of biodiversity in soils is impressively large (Whitman et al. 1998; Coleman and Whitman 2005). Discoveries of new species and phyla in the archaea and bacteria are increasing rapidly (Pace 2009). Among the eukarya, discoveries of ever more diverse arrays of fungi and unicellular eukarya is proceeding apace as well (Coleman 2008; Buée et al. 2009b). Even now, perhaps as much as 70 per cent of the arthropods on earth (total number described to date: 855,000) or ca. 2.1×10^6 arthropods yet await description (Hamilton et al. 2010). To be fully comprehensive in soil ecological studies, however, a fourth major group, the viruses, need to be considered explicitly (Fierer et al. 2007). Considerable new knowledge of virus ecology is being gained in aquatic realms: limnology and oceanography. Much less is known about viruses and their ecology in soils, despite their known effects on beneficial bacteria and soil-borne plant pathogens and horizontal gene transfer (transduction) (Kimura et al. 2008). From six to 25% of the carbon fixed by primary producers is estimated to enter into the microbial loop (microbes and the micro- and meso-fauna feeding upon them) via virus-induced lysis at various trophic levels in aquatic environments (Fig. 1). Yet despite concerns about the amount of viral adsorption to soil particles, particularly clays, the greater physical and chemical diversity of soils makes it possible that viruses have an even larger potential to play roles that are similar to those in aquatic environments (Weinbauer 2004; Kimura et al. 2008; Buée et al. 2009a).

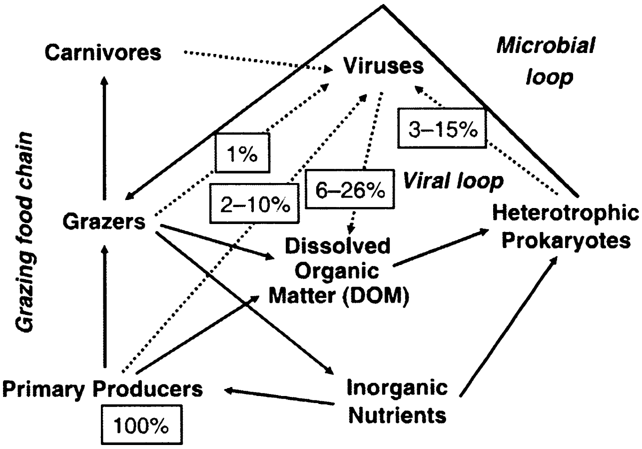


Fig. 1 Pelagic food chain model and virus-mediated carbon flow (Kimura et al. 2008; modified from Weinbauer 2004). The dotted lines show virus-mediated pathways. All values are based on the flux of carbon fixed by primary producers (100%)

Recent molecular studies of mechanisms to fend off phages and other forms of invasive DNA, including clustered regularly interspaced short palindromic repeats (CRISPRs) are increasing the ways in which we can quantify phage and prokaryotic interactions (Andersson and Banfield 2008; Tyson and Banfield 2008; Horvath and Barrangou 2010). Although the current usage of phages in soil biological control studies has focused primarily on plant-pathogenic bacteria (Jones et al. 2007), the existence of consortia in which insects, bacteria(as primary and secondary symbionts), and viruses (phage-borne toxin genes) interact in a complex multi-level mutualistic symbiosis is proof that interactive complexities exist and are worth exploring (Moran et al. 2005).

The time scale of viral evolution and the diversity of viral linkages that emerged during that extended time period would explain why viral-specific genes now seem to outnumber cellular ones in metagenomic studies, which forms a very large reservoir of molecular diversity (Forterre and Prangishvili 2009). As an example of virus-microbial-eukarya interactions, consider the giant Marseillevirus, a previously uncharacterized giant virus of amoebae. The genome repertoire of the virus is typical of nucleocytoplasmic large DNA viruses (NCLDV), core genes and genes apparently obtained from eukaryotic hosts (Boyer et al. 2009, Fig. 2). There is a distinct possibility that amoebae are "melting pots" of microbial evolution where diverse forms emerge, including giant viruses with complex genetic repertoires of various origins (Boyer et al. 2009).

The diversity of archaea and bacteria is as yet little known, but with the use of new massive parallel sequencing devices (Roche 454 and other pyrosequencing techniques; Buée et al. 2009b), we are beginning to approach an understanding of the very large biodiversity of these organisms. More than one full decade into the "genomic era," it is necessary to consider a bacterial species as described by its pan-genome, which is comprised of a "core genome" containing genes common in all strains and a "dispensable genome," containing genes present in two or more strains and genes unique to only one or two unique strains (Medini et al. 2005). In essence, the pan-genome of the bacterial domain is of nearly infinite size (Lapierre and Gogarten 2009). For example, in eight genomes representative of the serogroup diversity among group B Streptococcus (GBS) strains, the pan-genome contains 2,713 genes, of which 1,806 belong to the core genome, and 907 belong to the dispensable genome. The GBS pan-

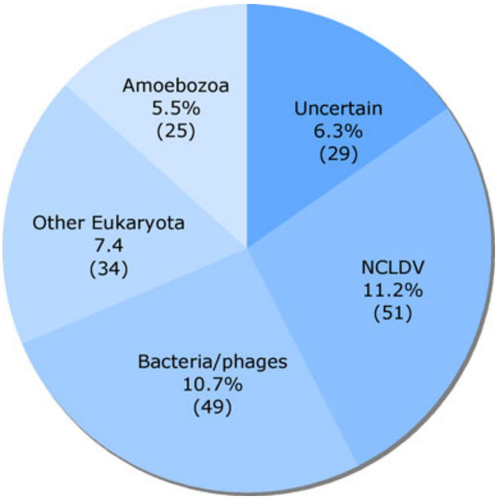


Fig. 2 Marseillevirus chromosome: The pie chart represents taxonomic breakdown of Marseillevirus genes by probable origins inferred by phylogenetic analysis (Modified from Boyer et al. 2009)

genome is predicted to grow by an average of 33 new genes every time a new strain is sequenced. This pattern does not hold for all bacterial species, however (Medini et al. 2005).

Metagenomics encompasses the full array of microorganisms present in an ecosystem at any point in time (Handelsman 2004; Van Elsas et al. 2008). Metatranscriptomics refers to the number of active microbial genes in a given community or ecosystem that are active, namely respiring or synthesizing at a given time. "At any moment, an estimated 10^{30} bacterial and archaeal genes are mediating essential ecological processes throughout the world" (Moran 2009). In a number of marine microbial ecological studies, diurnal patterns have been measured. Thus bacterioplankton communities in oligotrophic waters of the North Pacific ocean showed greater investments in energy acquisition and metabolism (photosynthesis, oxidative phosphorylation, and C1 compound metabolism) during the day and in biosynthesis (of membranes, amino acids, and vitamins) at night, according to an analysis of RNA transcripts from these periods (Poretsky et al. 2009). To my knowledge, this sort of approach has not been attempted in soil systems yet, but it seems feasible in theory.

Detrital foodwebs as an analytical tool in soil ecology

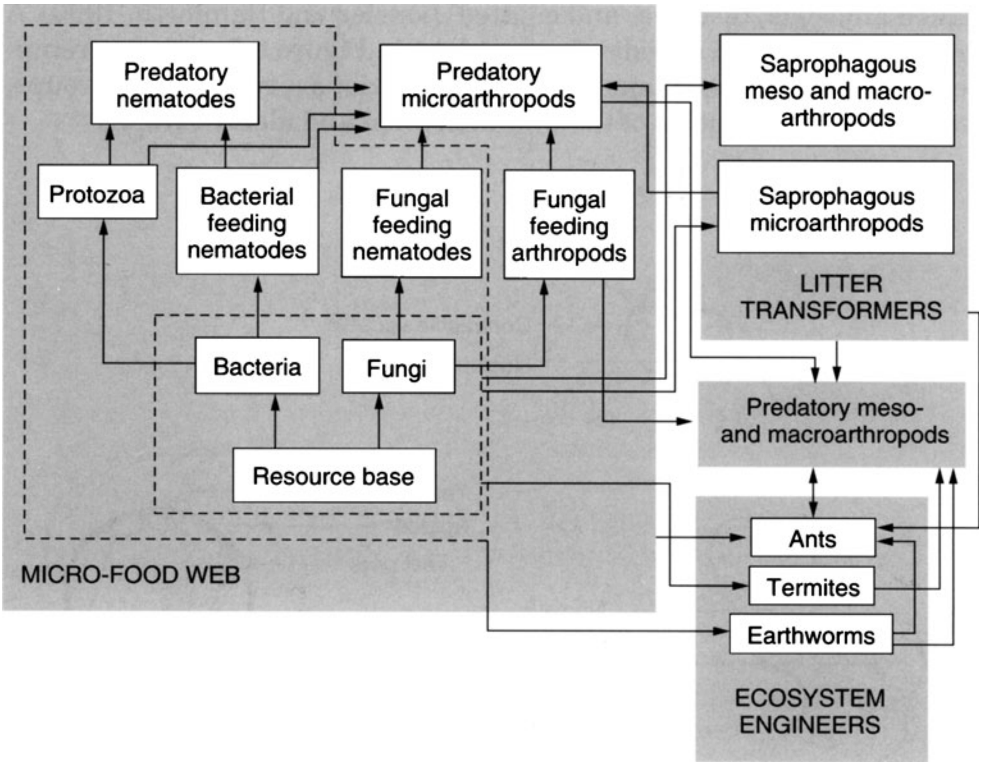
With an almost bewildering diversity of microbes and fauna present in most soils, it is essential to analyze some of their principal activities and processes in a holistic fashion, wherever possible. Examining the entire array of organisms, it is useful to consider major parts or functional groups, in the food web. They are: 1. the Micro-food web, including bacterial and fungal populations and movement of nutrients from them into microbivorous fauna and the animals feeding upon them; 2.the Litter transformers, including the saprophagous micro-, meso-, and macrofauna; and 3. the Ecosystem Engineers (Fig. 3, Coleman et al. 2004). Size-dependent interactions of the microbes and trophic groups noted above are key to an understanding the ways in which the microbes and fauna explore and utilize resources in soils, which have an amazing diversity of niches in three-dimensional space, and that evolve further into a coevolved entity during time, the essential fourth dimension (Scheu and Setälä 2002).

All of the above interactions can be most readily studied in the context of soil "hot spots": rhizosphere, detritusphere, porosphere, drilosphere, and aggregatusphere (Beare et al. 1995). An example of the interplay of above and belowground processes is the direct influence of herbivory on belowground processes, including rhizodeposition of enhanced flow of carbon to exudates and hence into the microbial-faunal food web. This is an interesting transient phenomenon for soil ecologists to be aware of (Holland et al. 1996; Fu et al. 2001; Coleman et al. 2006). Numerous studies have been carried out in aquatic and terrestrial ecosystems worldwide addressing the impacts of biodiversity on decomposition rate (Gessner et al. 2010). In a meta-analysis of 28 studies, mostly in terrestrial ecosystems, no effects were found of detrital or consumer diversity on detrital standing stock. However, reductions in detrital diversity resulted in significant reductions in decomposition rate (Srivastava et al. 2009).

Many invertebrates feed directly on plant materials and organic substrates. The fragmentation or comminution of these materials enhances their decomposition. For plant structural materials, comminution increases the surface areas of the materials and exposes cytoplasm, thereby enabling greater access by microbes. Decomposition is further accelerated as the feeding activity often results in the translocation of nitrogen from the soil to the substrate in the form of fecal material and through fungal hyphae. Grazing by invertebrates disseminates microbes from one organic source to another as many microbes adhere to invertebrate exoskeletons and cuticles and survive passage through their digestive tracts.

Historically, a variety of approaches (exclusion or gradual inclusion of biotic groups) have been used to ascertain the roles of microbes and fauna in decomposition and nutrient cycling processes. Using a series of abiotic (ultra-fine (<0.53 μm) and 1 mm mesh biotic (biocides: mercuric chloride and copper sulfate) exclusion techniques, Vossbrinck et al. (1979) demonstrated sequential effects of exclusion of all biota vs. microfauna and mesofauna or mesofauna alone exclusion on decomposition of blue grama (*Bouteloua gracilis*) litter. Ingham et al. (1985) and Gupta

Fig. 3 Organization of the soil food web into three categories: ecosystem engineers, litter transformers, and micro-food web (Coleman et al. 2004)



et al. (1999) (Fig. 4, Gupta et al. 1999), in glasshouse experiments, showed the impacts of gradually adding microbial and faunal functional groups (bacteria, fungi, nematodes, protozoa and collembola) on enhanced shoot growth in shortgrass prairie USA and Western Australian wheat systems. Microfaunal and meso-faunal contributions were calculated to be nearly 40% of the total decomposition and mineralization pathways in these ecosystems. For further information on the keystone roles of nematodes in soil food webs, see Yeates (2010).

Putting the soil to work for us—chronosequence studies

One of the ways in which progress can be made in an era of ever decreasing availability of biocides for control of soil pathogens is to “let the soil work for us” (Elliott and Coleman 1988). This quotation refers to the advantages of using conservation or no-tillage techniques in lowering fossil fuel costs and promoting soil conservation in agroecosystems. Conservation tillage also helps in promoting the production of a greater amount of fungal biomass compared with conventional tillage (Brussaard et al. 1990; Beare et al. 1992). On a wider time frame, the ratio of fungi to bacteria increases as ecosystems mature, undergoing succession (Harris 2009). One of the objectives of restoration ecology is to promote and even accelerate the switch to fungal dominance at an earlier stage in ecosystem maturity (Harris 2009). This process explicitly promotes the conditions for mycorrhizae to be more dominant. Is it possible to predict shifts in major microbial and faunal groups during agro-ecosystem management? I address that question next.

One of our agroecosystem studies in the southern coastal plain of Georgia, USA used a series of five commercial no-tillage cotton (*Gossypium hirsutum* L.) fields that followed a chronosequence of 4–25 years since conventional tillage. These sites are loamy to fine-loamy thermic, kaolinitic Kanhapludults and Paleaquults, with pH of 3.7 to 4. During the first 8 years of tillage there was some increase in organismal abundance, but only the two older fields (8–25 y) had accumulated abundance and

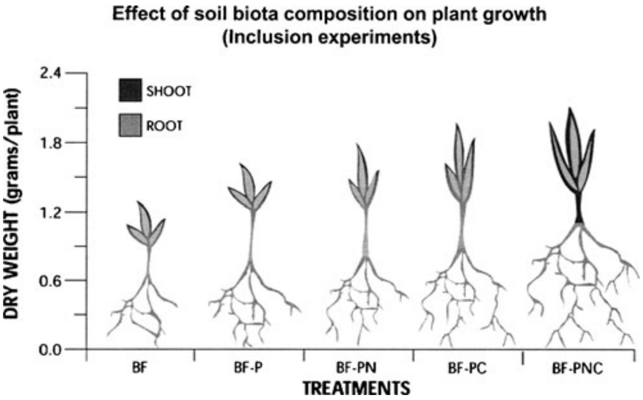


Fig. 4 Effect of soil biota composition on plant growth. *BF* bacteria and fungi; *BF-P* addition of protozoa; *BF-PN* addition of protozoa and microbivorous nematodes; *BF-PC* addition of protozoa and collembola; *BF-PNC* addition of all three faunal groups. (Gupta et al. 1999)

species richness that approached that of undisturbed sites. Total microbial biomass changed little over the years, and tended to follow the marked seasonal changes in total organic matter in spring and fall seasons (Fig. 5, Adl et al. 2006). Microbial diversity, as measured by fatty-acid methyl ester analysis (FAME) showed some shifts from bacterial to fungal dominance, with bacterial: fungal ratio being highest in site 0 and lowest in sites 1 and 5 (Fig. 6a, Simmons and Coleman 2008). Levels of 16:1ω5c, an arbuscular mycorrhizal fungal indicator, were all low, but lowest in the conventionally-tilled field (Fig. 6b, Simmons and Coleman 2008). In contrast, the changes in soil faunal species richness were more pronounced across the chronosequence. Thus there was a greater diversity of ciliates, flagellates and amoebae in the older fields (Fig. 7, Adl et al. 2006). Microarthropods were more speciose but had lower total biomass in the older fields as well (Adl et al. 2006). This amplification of species diversity effects in the detritivore fauna compared to the microbial diversity was in marked contrast to the microbial community mentioned above.

In our agroecosystem chronosequence study, the microbial biodiversity patterns did not conform to the proposed fungal: bacterial changes as proposed by Harris (2009). However, the faunal changes showed a greater response to the changes in management and organic matter levels. With the marked oscillations in SOM between spring and fall sampling seasons over the 2 years of this study, it is probably safest to consider these trends as being on the margins of significant effects. In contrast, a comparative study of microbial diversities in conventional tillage, no-tillage and forested ecosystems adjacent to the Horseshoe Bend Long-Term Research study in bottomlands near Athens, Georgia, microbial diversity, as measured by 16S rRNA genes was greater in the agricultural fields than in the

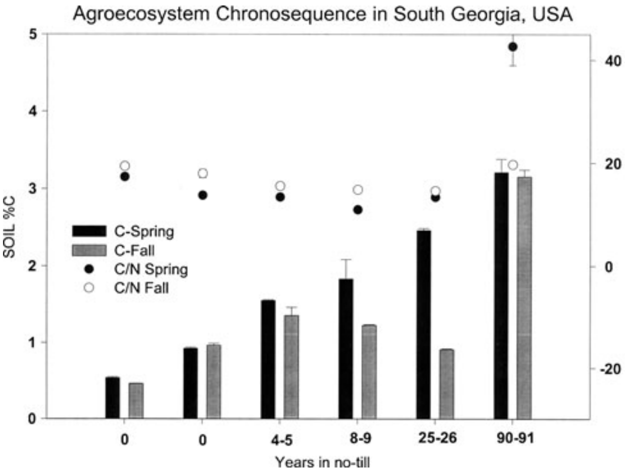


Fig. 5 Soil organic matter in a chronosequence of cotton fields (0-25-26 y.) and a nearby pine forest (90) in Coffee County, southern Georgia, USA. Note decrease in fall in 4–25 y. fields (*gray bars*) (from Adl et al. 2006)

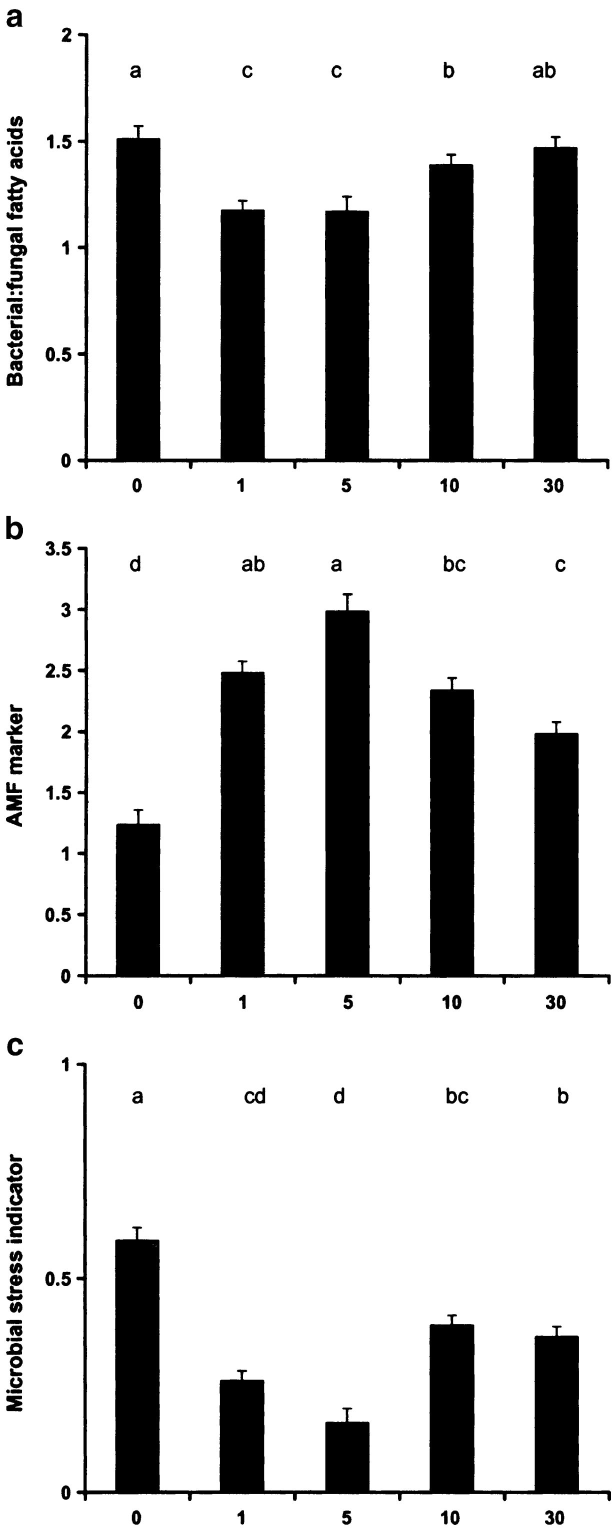


Fig. 6 The effect of age in conservation tillage in cotton fields in southern Georgia on: **a** bacterial to fungal ratios as measured by FAME biomarkers; **b** arbuscular mycorrhizal fungi (AMF) expressed as the relative% mole fraction of 16:1ω5c; and **c** an indicator of microbial stress, cy17:0: 16:1ω7c, from soils (0–5 cm depth) at five sites across a chronosequence of conservation tillage. Data shown includes standard error; different letters denote significant differences at $P<0.05$ (Tukey's) (Simmons and Coleman 2008)

nearby forest (Upchurch et al. 2008). These trends seemed to be correlated with the greater diversity of companion plants (weeds) in the agricultural plots.

Future prospects for successful management of agroecosystems

Many studies of soil pathogens are focused in one or more of the hot spots noted above. Placement of crop residues conducive to reduction of the impact of plant pathogenic nematodes is very beneficial. Thus amendments of sugarcane trash (10 tC/ha) led to more than 70% reductions in lesion nematodes (*Pratylenchus zeae*) and *Tylenchorhynchus annulatus* in a sugarcane soil (Stirling et al. 2005). Mechanisms for the suppression include increases in an unidentified predatory fungus that occurred only in the soil amended with the sugarcane trash. Westphal (2005) also noted the roles of predatory fungi in suppressing populations of key plant-parasitic nematodes.

Viewing the soil food web and suppressive phenomena in soils is very informative. Soil food web indices, based on the composition of the nematode fauna, were calculated to infer soil food web condition (Sánchez-Moreno and Ferris 2007). Long and more complex soil food webs, with more trophic links and abundant predatory nematodes in natural areas (which are approximated somewhat by zero or conservation tillage), suppressed plant-parasite populations, whereas disturbed communities in conventionally-tilled agricultural soils, did not (Sánchez-Moreno and Ferris 2007). This is demonstrated by the relationship between relative abundance and absolute suppressiveness of soils. It was positively related to the Structure Index (SI), omnivores, predatory nematodes and organic matter, and negatively related to the abundance of bacterial and fungal feeders and plant parasites (Figs. 8 and 9, Sánchez-Moreno and Ferris 2007). Thus this demonstrates a significant "top-down" impact of higher trophic level nematodes as a function of suppressiveness in these soils. For a review of the impacts of nematodes on belowground processes, see Bardgett et al. (1999).

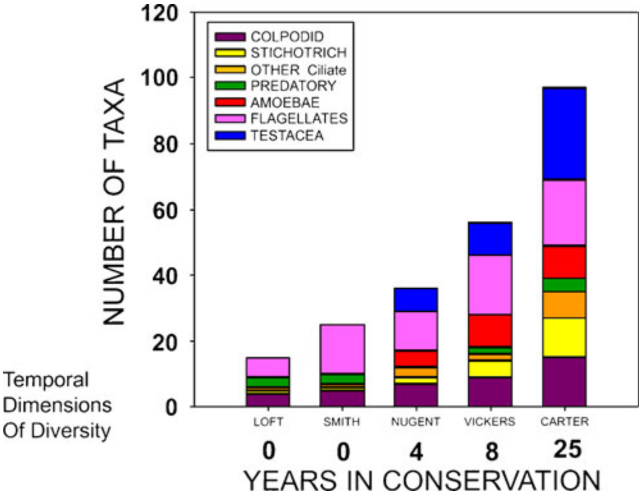


Fig. 7 The Temporal Dimensions of protozoan diversity in a southern Georgia chronosequence. Note the increasing proportions of amoebae, flagellates and testacea in the longer-term conservation tillage fields. (Adl et al. 2006)

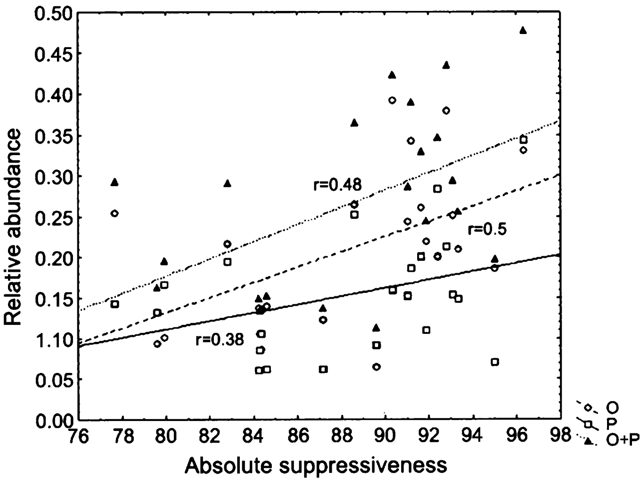


Fig. 8 Relationship between soil suppressiveness and relative abundance of predators (*P*), omnivores (*O*) and the sum of both. Correlation coefficients are $P<0.05$ (Sánchez-Moreno and Ferris 2007)

A further study of the impacts of specific fungi by Wakelin et al. (2006) found that *Penicillium radicum*, when used as an inoculant to promote the growth of wheat crops, played a significant role (along with a chemical fungicide (fluquinconazole), in controlling the pathogens involved in take-all (*Gaeumannomyces graminis* var. *tritici*, *Rhizoctonia solani, Pythium irregulare* and *Phytophthora cinnamomi*) but not the beneficial fungus *Trichoderma koningii*.

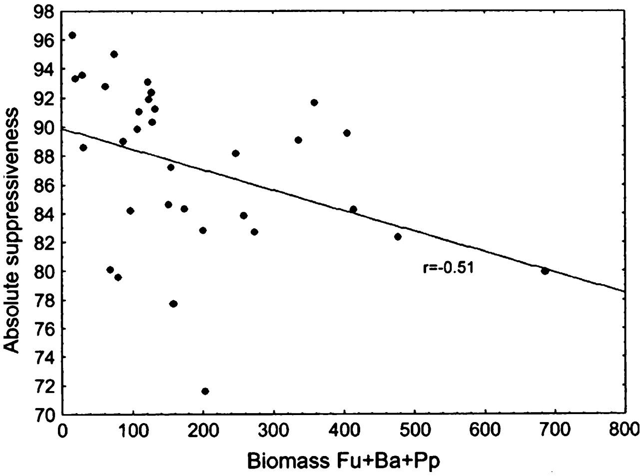


Fig. 9 Relationship between soil suppressiveness and available biomass in the soil food web. Correlation coefficient is $P<0.05$ (Sánchez-Moreno and Ferris 2007)

A more general interest in plant growth promotion (PGP) effects of fungi and bacteria (e.g., *Pseudomonas fluorescens*) is an ongoing research topic in several countries (Cook 2007). For more general aspects of soil management for sustainable crop disease control, including usage of organic amendments and use of crops in rotation to promote greater suppression of specific pathogens, see Ghorbani et al. (2008). As we move forward with problems of soil ecosystem management, we need to examine ways in which we can manage our soil food webs more effectively.

As a more general corollary to the theme of suppressive soils, it would be beneficial for us to consider the concept of "supportive soils." Most ecosystem-level phenomena that occur in soil systems are generally positive in terms of positive feedbacks on the growth of crops, either of food or forests. By harnessing the inherent richness of the biotic diversity and the interactions occurring between various biotic groups, we should be better prepared to "let the soil work for us."

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