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Role of soil in the regulation of human and plant pathogens: soils' contributions to people

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Soil and soil biodiversity play critical roles in Nature's Contributions to People (NCP) # 10, defined as Nature's ability to regulate direct detrimental effects on humans, and on human-important plants and animals, through the control or regulation of particular organisms considered to be harmful. We provide an overview of pathogens in soil, focusing on human and crop pathogens, and discuss general strategies, and examples, of how soils' extraordinarily diverse microbial communities regulate soil-borne pathogens. We review the ecological principles underpinning the regulation of soil pathogens, as well as relationships between pathogen suppression and soil health. Mechanisms and specific examples are presented of how soil and soil biota are involved in regulating pathogens of humans and plants. We evaluate how specific agricultural management practices can either promote or interfere with soil's ability to regulate pathogens. Finally, we conclude with how integrating soil, plant, animal and human health through a 'One Health' framework could lead to more integrated, efficient and multifunctional strategies for regulating detrimental organisms and processes.

This article is part of the theme issue 'The role of soils in delivering Nature's Contributions to People'.

1. Introduction

(a) Overview

Soil's vast biodiversity is crucial in regulating the impacts of pathogens and pests on microorganisms, plants and animals, including humans [1,2]. The complexity of soils' diverse communities and micro-environments provide a myriad of mechanisms, and potential solutions, for regulating detrimental organisms. Many of these biological processes are indirect, not visible, involve the actions of complex consortia of organisms, and are intimately linked to their physical environment and its management. Nonetheless, over the past few decades, the growing availability of new tools, both molecular and imaging, has expanded our ability to investigate and elucidate these complex soil phenomena.

The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) introduced the framework of Nature's Contributions to People (NCP) defined as 'all the positive contributions, losses or detriments, that people obtain from nature' to capture both beneficial and harmful effects of nature on people's quality of life [3–5]. NCP include both positive and negative contributions of all of living nature (e.g. diversity of organisms, ecosystems and processes) to people's quality of life [6]. Here, we specifically explore how soil contributes to NCP #10, defined as nature's ability to regulate direct detrimental effects on humans, and on human-important plants and animals, through the control or stimulation of particular organisms considered to be harmful [6].

Though NCP #10 encompasses the regulation of a variety of categories of detrimental organisms, including pests, predators, competitors, parasites and other potentially harmful organisms, we focus specifically on microbial pathogens, with an emphasis on humans and crops. Considering both biological and abiotic processes and properties, we first review the ecological principles underpinning regulation of pathogens, as well as relationships between pathogen suppression and soil health. We provide specific examples of ways in which soil can control the potential for pathogens to infect humans and crops. Agricultural management practices used to control pathogens are discussed with respect to how they may promote or interfere with soils' ability to regulate detrimental organisms. Though our focus here is on agroecosystems, many concepts and examples are relevant to less disturbed ecosystems.

(b) How soil biota regulates detrimental organisms and processes

Soil hosts arguably the most diverse biological communities on Earth [7,8]. Soil's heterogeneity, created by complex arrangements of minerals and organic matter of different structure and composition, organized into aggregates of different sizes, provides a vast variety of ecological niches [1]. Many of soil's inhabitants are either directly or indirectly involved in regulating organisms that may have detrimental effects on humans. At the same time, soil is also a reservoir of a variety of bacterial, fungal and viral pathogens capable of causing diseases in plants, animals or humans [9–15].

Pathogens are common members of soil communities who may be transient inhabitants, consistently present for parts of their life cycle, or permanent fixtures within the community [16]. Whether or not potential pathogens have negative impacts on humans and other biota depends on if they successfully colonize and establish themselves in soil (if they are not resident species) and come in contact with a susceptible host. Some pathogens require transfer via vectors or carriers who live in the soil. Other important factors include whether pathogen populations reach high enough levels to cause infections (inoculum potential) and whether they are metabolically capable of causing infection [17–19].

The survival of any organism in soil, pathogenic or not, depends on its interactions with other members of their biological communities (biotic factors). In soil, a diversity of interspecific interactions—mutualism, antagonism (including parasitism and predation), competition and commensalism—determine the presence and impacts of soil organisms, including those who become pathogenic. Some relationships are indirect, with pathogen invasion, establishment and survival depending on relatively general changes in soil communities, such as an increased population density or biomass. For example, diffuse competition with a broad swathe of the microbial community could regulate pathogens in soils by limiting their access to resources [20,21]. However, in other cases, more direct antagonistic or competitive interactions can prove critical. Kinkel *et al*. [22], for example, present a coevolutionary framework for investigating and managing soil communities capable of suppressing plant diseases. Drawing on the importance of antagonistic coevolutionary relationships in disease suppression, they demonstrate the importance of direct interactions between pathogens and non-pathogenic indigenous soil microbes for promoting and sustaining disease suppression in soils [22].

The remarkable diversity of soil microbial communities is crucial in deterring pathogen establishment and growth. Soil communities with greater diversity may be more likely to include antagonists or competitors that are particularly effective at suppressing invasive pathogens (i.e. the 'sampling effect') [23–25]. They may also contain more competitors or antagonists that act in concert to suppress pathogens (i.e. niche complementarity). Strong relationships between diversity and invasibility are observed in many ecological systems [25]; for example, non-native plants are more likely to invade grasslands as native plant diversity is lost [26]. Similarly, reduction of bacterial or fungal diversity in soil, demonstrated experimentally, increases vulnerability to invasion by pathogens [20,27].

Another consequence of high levels of biodiversity is greater ecological resilience; that is, 'the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks' [28,29]. Soil microbiomes have a high degree of functional redundancy whereby multiple actors play similar roles in the soil ecosystem [30]. The resilience of complex biological systems is defined not just by the number of different species that respond to a specific disturbance, but more importantly by response diversity, i.e. the range of responses to the disturbance [31,32]. Diverse soil communities also have the capacity to bounce back more quickly from perturbations (such as invasion of a pathogen) and not bounce as far in subsequent exposures [33]. However, repeated disturbances that reduce the diversity of soil microbial communities, as is common in large-scale, intensive agricultural management, can reduce the response diversity, and, therefore, reduce the resistance and resilience of agroecosystems, creating opportunities for invasion by non-native organisms [32,34]. Fortunately, targeted management practices that increase soil microbial diversity and biomass can strengthen direct and indirect antagonistic interactions and consequently help regulate deleterious organisms.

Changes in soil abiotic factors are interdependent and exert substantial impacts on soil function and biodiversity [35]. For example, disturbing soil aggregates, key components of soil structure, homogenize the soil environment, expose protected organic matter to degradation, reduce niche complexity and lead to biodiversity losses [36]. Intensive agricultural practices, land-use changes and global climate change are recognized as major threats that modify the soil environment and reduce soil biodiversity [7,37]. Even so, none of these factors can be considered in isolation to test their effects on biodiversity as they interact and influence one another. Better understanding of mechanisms underlying management practices that focus on soil environment can facilitate the conservation of soil biomass and biodiversity [7,38].

(c) Relationship between the concept of soil health and the regulation of detrimental organisms

The concept of soil health has reemerged over the last few decades and grown in importance in sustainable agriculture and climate resilience [39]. Healthy soils are broadly defined as those being 'capable of supporting the production of food and fiber, to a level and with a quality sufficient to meet human requirements, together with continued delivery of other ecosystem services that are essential for maintenance of the quality of life for humans and the conservation of biodiversity' [40]. Much of the emphasis in soil health assessments has been placed on soil organic carbon, nutrient cycling, soil structure and water relations, and general microbial activities. Most existing conceptual frameworks or tools for soil health do not directly consider suppression of detrimental organisms to plants and humans [41], despite the fact that suppressiveness is often an additional benefit of practices targeting other soil health indicators.

Two decades ago, van Bruggen & Semenov [42] proposed considering incidences of plant and animal disease as symptoms of an ecosystem in poor health. They argued that the ability of the biological community to suppress or reduce populations of pathogens (e.g. 'disease suppression') is an important indicator of a stable and healthy soil ecosystem. Several years later, Janvier *et al*. [43] proposed including suppressiveness as an indicator of soil health. More recently, Lehmann *et al*. [44] proposed a 'new generation' of soil health indicators and recommended the inclusion of biological assessments of ability of soil to suppress disease. Thus, an emerging consensus is disease suppressiveness is an integral component of soil health. A challenge is the difficulty in assessing disease potential in soils and thus in identifying appropriate and feasible indicators, as well as methodologies for measuring them [11,43,45].

2. Role of soil and soil biota in regulation of human and animal pathogens

(a) Pathogens of humans and other animals in soil

Soil is a reservoir for a variety of microorganisms—including bacteria, fungi, protozoa and viruses—that can be pathogenic to humans and animals. Human and animal pathogens in soil can be categorized into four broad groups that reflect their degree of residency in soil: permanent, periodic, transient and incidental [46]. Permanent pathogens are soil inhabitants which spend their entire life cycle in soil and sometimes become infectious for humans and animals. Examples include organisms like *Clostridium botulinum* or *Clostridium tetani* that produce neurotoxins when contaminated food is ingested or through contaminated wounds, respectively. Many zoonotic pathogens also either live in soil or their vectors live or spend part of their life cycle in soil [15]. Periodic pathogens are soil organisms which require the soil environment to complete part of their life cycle. For example, *Bacillus anthracis*, the causative agent for anthrax in humans or livestock, is often found in soils and can survive for long periods as endospores [47]. Transient organisms are those which naturally occur in soil, often due to their hosts being in contact with soil, but do not require soil to complete their life cycle. For example, the protozoan parasite *Giardia lamblia* can be introduced into soil via urine and faeces of rodents but does not need soil to survive. Finally, incidental pathogens may be introduced to soil via anthropogenic sources, human and animal activities, or other pathways but only survive in soils for relatively short periods. For

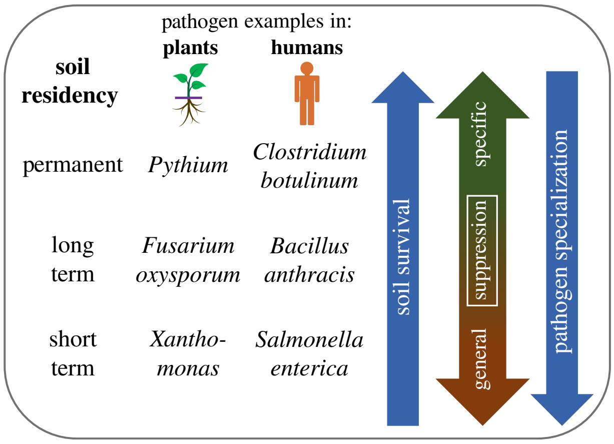

Figure 1. Pathogen ability to survive and grow in soil is typically inversely proportional to its specialization for a specific plant or animal (human) host. Long-term presence is necessary for pathogen–antagonist interactions that generate specific suppression; by contrast, pathogen presence is not required for antagonist–antagonist interactions that contribute to general suppression [41]. Permanent members of microbial communities are, therefore, likely controlled by specific suppression, while short-term survivors are likely regulated by general suppression. (Online version in colour.)

example, pathogens enter soil via application of improperly treated raw manure, contaminated irrigation water or via runoff, especially when croplands are in close proximity to livestock grazing areas or feedlots [48–51]. Examples include enteric pathogens (e.g. *Salmonella enterica* subsp. *enterica* and shiga toxin-producing *Escherichia coli* (STEC)) who are introduced into soil via raw or untreated manure or sewage [52,53]. Pathogen residency in soil is important as it determines the potential mechanisms for suppression (figure 1). The impacts of soil microbial pathogens on vertebrates have been reviewed extensively elsewhere [54,55].

(b) How soils regulate the establishment and suppression of human/animal pathogens

The soil environment and its indigenous communities strongly influence whether or not a pathogen can colonize and establish itself in soil, as well as whether it ultimately can infect a potential host [41,56,57]. Mechanisms can include diffuse competitive and antagonistic interactions between the pathogen and the entire microbial community, akin to 'general suppression' in the plant pathogen literature (see below). For example, larger and more diverse microbial communities, such as those associated with organically managed soils, may be more effective than communities under conventional management at suppressing pathogenic *E. coli* [58]. Similar trends have also been observed with *Salmonella*: soils with higher microbial diversity were more effective at decreasing *Salmonella* abundance and survival time [14]. Conversely, pathogen survival often increases dramatically when inoculated into soils that have been sterilized [59,60]. Introduced human enteric bacteria had lower rates of survival in microbially diverse soils [61], supporting the concept that invasion may be transient and limited [62]. Finally, it is important to note that soil microbes constitute only a part of the biological community in soils: arthropods, protists and other taxa can also play key roles in soil suppressiveness [58,63]. For example, dung beetles have been shown to reduce pathogenic *E. coli* on fresh produce farms by ingesting faeces contaminated with pathogenic *E. coli* and burying them, thereby further exposing the pathogens to competitors and antagonists within the soil microbial community [58].

Soil physical properties are also important in regulating establishment and survival of pathogens in soil. First, soil texture (i.e. the relative proportions of sand, silt and clay particles) helps determine the persistence and establishment of many pathogens, e.g. fine-textured clay soil may be more conducive to survival of pathogens [46,64]. Second, pH has also shown to be important for pathogen survival; for example, *Listeria monocytogenes* survived best at soil pH values greater than 7 [60]. Third, soil moisture can also determine the ability of a pathogen to persist and survive in soil. For example, one study found that pathogenic *E. coli* populations often peak following rainfall events [65] and another reported that rainfall and soil moisture were key factors influencing pathogenic *E. coli* survival [66]. Conversely, microbial growth decreases when soil becomes drier, as dry soils can impede microbial mobility, limit nutrient availability and slow nutrient diffusion through membranes [46]. Fourth, organic matter content, which often varies according to soil types and inputs, can also govern the survival of pathogens in soil. One study showed that *Salmonella* sp. survived longer in soils with higher organic matter content [51]; however, others show the opposite trend with higher organic matter supporting greater biologically induced suppression [67,68]. And fifth, concentrations of macro and micronutrients in soil influence pathogen survival; for example, the pool of exchangeable soil cations best explained survival of *L. monocytogenes* in different soils [60]. Critically, many factors listed above are strongly associated; for example, increasing organic matter in soils also improves moisture and nutrient retention, which can make the environment more conducive for pathogen proliferation.

Many human and animal pathogens are closely interrelated. Soil can play a role as an intermediary reservoir (e.g. pathogens from soil-applied animal manure infecting humans) or represent an integral part of pathogen life cycles [15]. Approximately 75% of new and emerging infectious diseases of humans are thought to originate from animals [69] and such diseases are defined as zoonotic diseases or zoonoses [70]. Some viruses find hosts in both humans and soil animals; for example, rodents living in soil burrows can be vectors for hantavirus [71]. How we manage agricultural soil can influence the prevalence of zoonotic diseases such as those caused by enteropathogenic bacteria such as *Salmonella* or pathogenic *E. coli* [72,73]. Potential sources and routes of faecal contamination of soil and produce include contaminated irrigation water, manure applications, proximity to livestock, wildlife or domesticated animal intrusion [48]. Moreover, husbandry and management practices (e.g. diet, health status, age, location) may affect the shedding of food-borne pathogens and increase persistence and risk of faecal contamination when animal manure is applied [48,74]. Manure application may also contribute to the propagation and dissemination of antibiotic residues, antibiotic-resistant bacteria and antibiotic-resistant resistance genes in the soil–water system and pose a public health issue [75]. The One Health approach to zoonotic disease transmission investigation involves multidisciplinary teams of biologists, ecologists, epidemiologists and physicians [76]. Growing evidence suggests that the prevention of livestock-associated zoonoses must start with developing animal health management routines and welfare programmes (such as vaccinations, prebiotic and probiotic feed additives) at the farm level and this will lead to improve overall animal and ecosystem health [77].

(c) Soil health and human health

The capacity of soil biota to regulate organisms detrimental to human health can extend even beyond the soil itself and into the human body. First, the rich biodiversity of soils has been the source of most of the antibiotics and other antimicrobial agents currently used for human and animal health [16,78]. Waksman discovered streptomycin produced by soil actinomycetes using bacterial isolation techniques still employed by pharmaceutical industries today [79,80]. As antibiotic resistance rises among human pathogens, interest has renewed in identifying microorganisms that are capable of producing antimicrobial compounds in soil, building on our increasing understanding of soil community ecology and emergence of powerful new technologies (e.g. omics) [80,81].

Second, the relationship between human and soil microbiomes is a topic of rapidly growing interest for reasons of human health and nutrition [82,83]. Soils and humans have shared a long and intimate relationship [82,84]. Yet, humans have increasingly moved from rural to urban settings, leaving behind many opportunities for exposure to the soil microbiome. Recent evidence suggests that declines in human immunity and health may result from this disconnection from the natural environment. The 'biodiversity hypothesis' states that 'contact with natural environments enriches the human microbiome, promotes immune balance and protects from allergy and inflammatory disorders' [85]. For example, early childhood exposure to environmental microorganisms appears to be associated with development of the body's immune system and certain positive health benefits [83,86]. Emerging research is suggesting that gut microbial diversities of healthy adults from rural communities throughout the world (e.g. Papua New Guinea, Malawi, Tanzania and Amazon) are higher than in urban populations in Italy and the USA [83]; however, soil's specific role in promoting these differences is yet to be isolated from contributions associated with diet and genetics.

Exploring relationships between the microbiomes of animals and surrounding soil is a new and evolving area of research. The composition of gut microbiomes of foraging baboons was better explained by the baboons' environment than by genetic factors, and in particular dependent on the soil's geologic history and exchangeable sodium [87]. Comparable research on human–soil relations is rare, speculative or does not yet exist but is underway with the expansion and ease of sequencing microbiomes in humans and of different environments [88,89]. A deeper understanding of the complex interrelationships and feedback between soil and humans will not only help reduce risks of soil-borne and food-borne disease but may also improve the general health of humans.

3. Role of soil and soil biota in regulation of plant pathogens

(a) Pathogens of plants in soil

Plants face different challenges than do animals from the perspective of soil-borne diseases. Humans and most terrestrial animals are primarily in contact with the soil's surface and exposed to small amounts via ingestion, inhalation and dermal contact. Plants, on the other hand, are literally rooted in soils. To access the diffusely distributed nutrients and water in soil, their roots are in intimate contact with soil throughout their lifespans. A draw-back is that the plant has no 'down time' nor can it escape from the soil, and thus strategies are needed to deal with continuous assaults from soil pathogens. A benefit of this intimacy, however, is there is time (including evolutionary time) for the plant to develop collaborations with rhizosphere organisms to regulate impact of pathogens.

What are termed 'disease suppressive soils'—soils whose indigenous microorganisms reduce establishment, persistence or impacts of pathogen—are excellent examples of soil's potential to regulate detrimental organisms [41]. Research differentiates between general and specific suppression of pathogens, yet recognizes there is a continuum from general to specific, 'with the former underlying and potentially give rise to the latter over time' [41,90] (figure 1).

For a disease to emerge in a crop requires a susceptible host plant, a pathogen that is virulent and an environment conducive to infection. Both abiotic and biotic processes in soil regulate the potential for and severity of a pathogen's impact on plants [43]. Soil-borne plant pathogens are taxonomically quite diverse and include bacteria, archaea, fungi, viruses and protozoa [41,57,91]. A number of classification schemes have been employed for plant pathogens, ranging from plan nutritional habit, plant physiology, parasitism to ecological perspectives (see Vega *et al*. [92] for an overview). Here, we focus on soil–pathogen rather than host–pathogen interaction, and, therefore, pathogen soil residency is a primary consideration (figure 1). Whether pathogens are (i) part of the soil microbial community, (ii) survive in soil for an extended period, or (iii) are transient entities that can only briefly exist outside of a suitable plant host determines the dynamics of their interaction with soil communities and abiotic factors and, therefore, determines the mechanisms by which soils may suppress them [41]. More extensive overviews of relationships between the plant rhizosphere, pathogens and beneficial organisms can be found elsewhere [93].

(b) Mechanisms of suppressiveness of plant pathogens

What is termed 'general suppressiveness' results from the activities of consortia or communities of microorganisms, via competition for resources or antagonistic activities, and is often effective against a variety of plant diseases [23,57,94,95]. Antagonistic interactions are influenced by the nutrient and energy supply available for growth in soil of both the pathogen and to its host [42]. Properties of general suppression are (i) not transferable from a suppressive soil to another soil, (ii) can be reduced or removed by sterilization of soil, (iii) often enhanced by inputs of organic amendments and tied to increases in abundance and activity/diversity of the microbial community [90,96]. Stimulation of indigenous microbial communities is thought to deplete limiting resources for pathogen growth and infection; suppression of *Phytophthora* root rot is an example [97]. Sometimes the impact is linked to major subgroups of the community. Specific amendments, like debris of wild rocket or rice bran, can enrich *Streptomycetes* spp. and help suppress the pathogen *Fusarium oxysporum* and potato scab diseases [98,99]. Secondary metabolites, both volatile and soluble, produced by many bacterial species in response to interspecies interactions and competition is also considered to play a role in general suppression [100].

Specific suppressiveness results from individual taxa of microorganisms and, unlike for general suppression, the benefit is often transferable from one soil to another (e.g. via inoculating with suppressive soil). Antibiosis is involved in specific suppression of take-all disease of cereals and often emerges after long periods of monocropping [57]. The specific suppression of the disease take-all, caused by *Gaeumannomyces graminis*, has been directly linked to antibiotic production by fluorescent *Pseudomonas* spp. [101,102]. An example of a parasitic antagonistic interaction is the suppression of the nematode *Heterodera schachtii* via the fungi *Dactylella oviparasitica* and *F. oxysporum* infecting nematode cysts and eggs [103]. Many plant growth-promoting rhizobacteria (PGPR) release antimicrobial or antifungal compounds that deter plant pathogens [23,57]. For example, fluorescent pseudomonads produce the antibiotic 2,4-DAPG which has been extensively studied as a protectant against soil-borne diseases [104,105].

Far from the view of plants as passive factories that transform sunlight into organic molecules, it is now recognized that plants actively respond to a complex assortment of physical and chemical environmental cues and precisely regulate their immediate soil environment. Recent advances in omics and visualization techniques have revealed complex and dynamic (i.e. responsive) relationships between plants and their rhizosphere microbial communities, and that plants recruit specific taxa and functional groups to help them uptake nutrients, promote growth, increase stress tolerance and avoid or fight off disease [106]. Responses include the recruitment of beneficial rhizosphere microbes [107]. When the plant cell membrane perceives a stressor, it releases a 'cry for help' [108] transmitted by downstream signalling networks which trigger an immune response [109] in the plant. For example, kinases are produced leading to accumulation of plant hormones like abscisic acid, salicylic acid (SA), jasmonic acid (JA) and ethylene. They stimulate changes in the plant root's exudates which target and recruit selective groups of microbes to colonize its rhizosphere. These recruitments essentially create a 'suppressive soil memory' [107,110] which protects successive plants of the same type growing in the same location from infection by those pathogens.

Elucidating who, and what mechanisms, are involved in the consortia of microbes conferring general soil suppressiveness is increasingly possible through coupling culture-dependent and culture-independent methods. In studies of soils suppressive of *Rhizoctonia solani*, Mendes *et al*. [95] could link higher relative abundance of key bacterial groups like Proteobacteria, Firmicutes and Actinobacteria, and genes coding for non-ribosomal peptide synthetases, to pathogen suppression. Similarly, in a study of soils that suppress *Ralstonia solanacearum*, specific rhizosphere taxa associated with whether or not plants developed disease symptoms included members of *Pseudomonas* and *Bacillus*, along with high abundance of genes encoding antimicrobial compounds [111]. This growing knowledge provides the foundation to design strategies to better select for beneficial native organisms, identify viable microbial inoculants or engineer plant rhizosphere microbiomes to reduce disease incidence in plants.

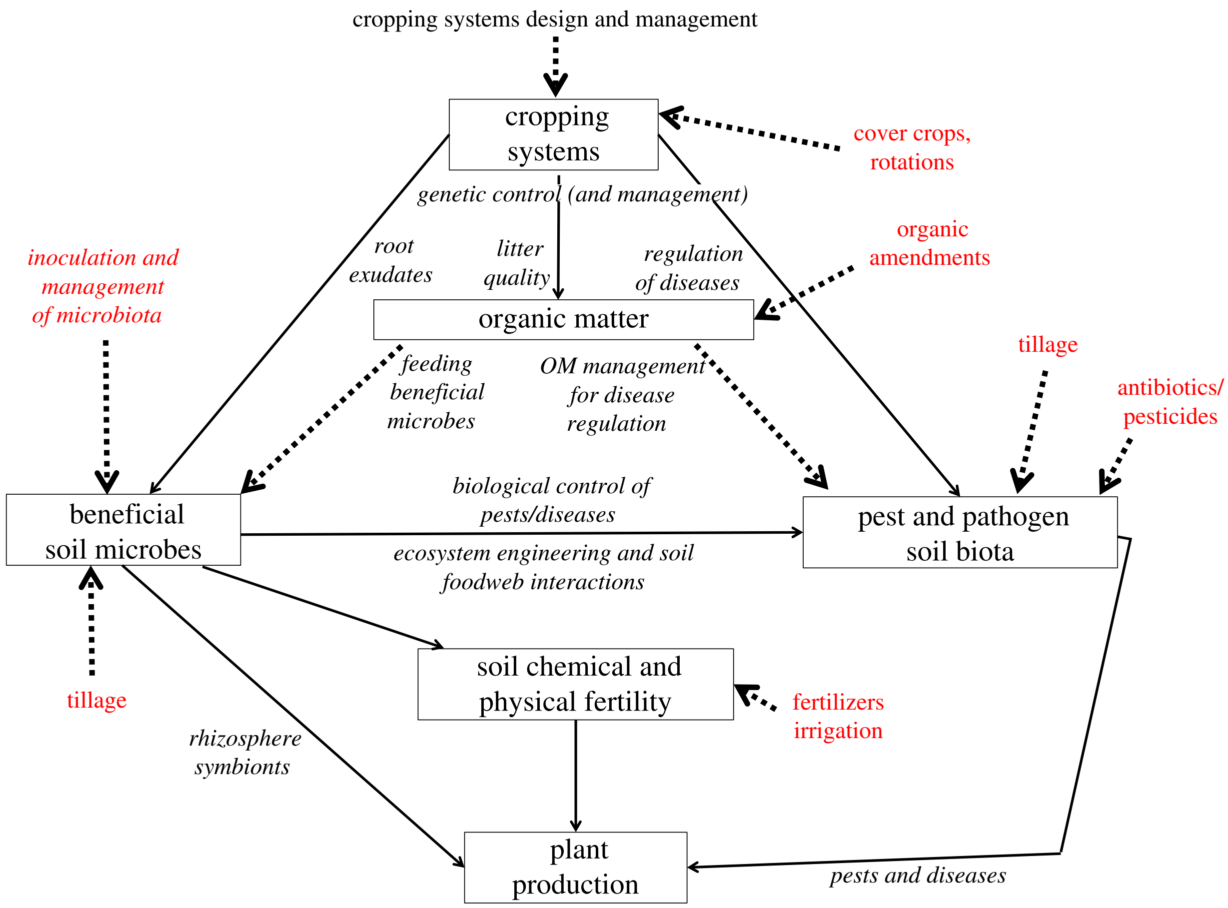

Figure 2. The entry points for beneficial and pathogenic soil microbes, and impacts of cropping practices, on plant production. Modified from Brussaard *et al.* [2]. The boxes refer to major relevant components of the agroecosystem. The text in red and the dotted arrows refer to management practices. (Online version in colour.)

Abiotic properties of soil also play many roles in regulating plant disease, both directly and through their interactions with soil biota. Higher available nitrogen can increase disease susceptibility by favouring pathogen growth [112]; for example, increasing colonization by *Pseudomonas syringae* on winter wheat [113] and higher soil moisture content can increase impacts of pathogenic *Ra. solanacearum* on ginger [114]. These interactions are reviewed in greater detail elsewhere [115–117].

4. Effect of agricultural management practices on role of soil and soil biota in regulating detrimental organisms and biological processes

We have long known that environmental conditions, and consequently how we manipulate the environment to manage soil, profoundly affect soil biota and soil health [118]. Traditional and indigenous farming typically include practices of using organic inputs and diversified rotations, at least in part to reduce crop losses from detrimental organisms [119,120]. Many of these same practices are used today in organic farming, in some cases being re-integrated into conventional farming systems to both sustain and increase resiliency of agroecosystems.

There are co-benefits and trade-offs associated with many management practices. Some implemented with the goal of improving fertility or soil structure also impact, either negatively or positively, soil's ability to regulate detrimental organisms [23]. Figure 2 depicts the major components of agricultural systems (boxes) and how biological processes mediate their interactions (arrows). Also shown are the impacts of different management practices on the biological underpinnings of the agroecosystem [2]. Whether intentional or not, farm managers choose practices that work with (or against) the ecological principles underpinning soil suppressiveness discussed earlier. Below, we briefly consider how selected management practices affect the ability of soil to regulate detrimental organisms and processes. More detailed reviews of this topic can be found in the following [11,118,121].

(a) Organic amendments

Soil organic amendments are among the most frequently used practices to reduce deleterious impacts of soil pathogens. Amendments include composts made from a variety of sources—animal manure, food waste, green wastes—and non-composted materials such as green waste, biodigestates, biochar and biosolids from sewage treatment plants [122,123]. Organic amendments can have positive or negative effects on soil's ability to regulate detrimental organisms resulting from the introduction of nutrients or toxins, and beneficial organisms or pathogens.

Of all soil amendments, compost has received the most attention because it is widely available and less associated with negative impacts (e.g. risk of adding food-borne pathogens) than, for example, untreated animal manures. Compost increases soil micro- and macronutrients, alters physical

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properties like soil structure and increases microbial biomass, activity and diversity [43,96,124]. Mechanisms of disease suppression include competition among microbial populations, antagonism via antibiosis, hyperparasitism involving direct attacks on pathogens and systemic-induced resistance (SAR) of the plant [96]. The provision of a variety of carbon and nutrient inputs also modifies the interactions and equilibrium among members of the soil community and may help the plant in recruiting beneficial organisms [125,126].

Nonetheless, improperly processed composts, as well as untreated animal manures, can introduce pathogens to soil. For example, greater concentrations of *Salmonella* spp. were detected in soils amended with poultry-based organic amendments than synthetic fertilizer [51,127]. Factors determining the efficacy of compost inputs are type of manure, method of application, type of soil, storage, composting protocols, nutrient ratios, microbial diversity of the amended soils, as well as geographical and environmental factors [124]. Concerns that animal-based composts may contribute to soil pathogens in leafy greens and other vegetables have led to changes in compost processing and application to minimize pathogen risks [128]. Compost prepared following established guidelines [129,130] greatly reduces the potential for introducing pathogens.

Recent meta-analyses showed soil-borne fungal plant pathogen suppression in more than half of studies that used traditional organic amendments; however, in 20% of cases disease incidence increased [131,132]. Specific inputs can be designed based on understanding of soil microbial interactions. For example, adding biopolymers such as chitin and chitosan can stimulate the prevalence and activity of taxa that specifically break down cell walls of pathogenic fungi [133,134]. Organic inputs can also be combined with flooding of soils in anaerobic soil disinfestation (ASD) to select for anaerobic communities that generate pathogen-suppressing fermentation products [41].

Recently, biochar has received increasing attention for its potential benefits for soil health, water relations and disease suppression [135,136]. Biochar amendments have been shown to be effective in suppressing a wide range of pathogens including bacteria, fungi, virus and nematodes [136,137]. Some of the mechanisms involved may be similar to those of compost as discussed above; however, biochar's strong sorptive properties may also play a role. Biochar sorption and inactivation of pathogen-derived toxins and enzymes are potential mechanisms in disease suppression [138,139]. Broad generalizations about the efficacy of biochar in regulating deleterious organisms are difficult to make at this time however, given how dependent results are on biochar feedstock, synthesis conditions, application rate, as well as soil and crop properties [136,140].

(b) Cover crops

Cover crops are typically included in rotations to improve soil parameters such as aggregation, water infiltration and water-holding capacity, and provide nitrogen if legumes are used. However, general suppressive activity can also result from using cover crops due to their stimulation of microbial biomass, diversity and activity [11,141]. Incorporated grasses (sorghum, millet, oats, rye), brassicas (rapeseed, mustard), legumes (alfalfa) and vines (kudzu) [142,143] as cover crops have been shown to decrease specific plant pathogen populations. Mixtures of cover crops, especially increasing plant functional group richness [144], may increase the resistance to pathogens in the following crop [144]; however, single cover crop species can also be effective [145]. There are instances, however, where cover crops increase enteric pathogen survival [146] so choosing the right cover crops is vitally important [147].

(c) Diversifying crop rotations

Recognition of host–pathogen cycles have influenced development of diversified cropping systems because they reduce the build up of soil-borne plant pathogens that results when a crop is grown continuously [148,149]. A recent meta-analysis showed crop diversification can boost soil biodiversity and fertility while also regulating disease incidence [150]. Rotations regulate pathogen populations by disrupting the host–pathogen cycles [43,151]; altering the soil's physico-chemical traits, or biological communities [152] that make the environment less conducive to pathogen development or survival (general suppression); or through direct inhibition of pathogens via production of toxic chemicals or stimulating specific antagonists (specific suppression) [148]. The specific choice of crops in rotation is important to ensure planted crops are not compatible with pathogens selected for by the previous crop. Examples of successful rotations include red clover mitigating tuber disease in a potato [149] and using brassicas to combat *Verticillium dahliae* infestation in strawberry production [153]. The integration of animal and cropping systems is another strategy. For example, to reduce parasitic loads in cattle, grazing management using pasture diversification or rotation are recognized approaches to improve livestock husbandry [154,155].

(d) Tillage

Reducing tillage of soils decreases erosion and loss of soil organic matter; however, its impacts on detrimental soil organisms are more complex and sometimes contradictory. Reduced or conservation tillage which leaves crop residues on the soil surface, or partially buried in soil, can create a competitive environment which facilitates competition and antagonistic interactions between microbes. This can result in disease suppression [156] and lead to niche differentiation and increased microbial diversity deeper in the soil profile [157]. In other cases, however, retention of crop residues can facilitate survival of pathogens by protecting them from microbial attack [158]. Some pathogens, even in the absence of their host plants, can survive as saprophytes or as spores until the host returns [159,160]. Conventional deep tillage may translocate the pathogens deeper into soil where the environment is less conducive to survival [161]. Other studies found no impact of tillage management on *E. coli* and *Salmonella* numbers [162,163].

(e) Use of antibiotics and agrichemicals

Numerous agrichemicals including herbicides, insecticides and fungicides are routinely used in intensive, large-scale agricultural management, often with negative consequences for soil communities, particularly fungi and soil fauna [164–166]. Pesticides use has increased over the past decades [167]. Of what is applied to soil, only a small portion of the pesticide reaches the target organism [168] and the remainder stays in the soil where it may be biodegraded but may also expose soil communities [165]. Seed dressing with insecticides and fungicides can reduce activities of earthworms, mycorrhizal fungi and other microbial populations and processes [169]. Many processes governing nutrient cycling, e.g. nitrification, are sensitive to pesticides and other organic chemicals [164]. The available concentrations and bioavailability of pesticide on soil microbes depend on soil properties as well, but a common impact is the disruption of specific soil functions and reduced diversity [164,170]. Although the impacts of agrichemicals on soil communities have been well documented, there is little direct information about how these chemicals impact the soil's ability to regulate pathogens. However, in aquatic ecosystems, the use of herbicides and fungicides was associated with increases in populations of pathogens by reducing densities of protozoan predators and by altering competition with indigenous microbes [171], highlighting need for performing similar studies in soil.

Similarly, antibiotics have been widely used in the suppression or management of diseases in livestock [172] and some crops [173,174]. However, overuse of such antibiotics has increased potential threats to the soil microbial community and also elevated antibiotic resistance in the soil environment [175,176]. Impacts of high concentrations of antibiotics can, but not always, cause changes in enzyme activity and carbon use, reduction in microbial biomass and shifts in the community composition [175]. Low, sublethal concentrations of antibiotics are problematic because they exert a selective pressure for antibiotic resistance in microbial populations [177] and may promote persistence of certain human and other animal pathogens in soil [178,179]. Although much effort has gone into reducing antibiotic use in livestock production worldwide, the spread and dissemination of antimicrobial resistant bacteria and genes are still a global health concern [180,181]. Efforts to improve antimicrobial stewardship worldwide need to continue and expand to reduce impacts on human and environmental health [182].

5. Conclusion

There is broad consensus on the perilous state of the environment. In December 2020, the United Nations Secretary-General António Guterres called out humanity's suicidal 'war on nature' during his State of the Planet address at Columbia University [183]. The issues facing us are complex, multifaceted and profoundly interconnected, and will require similarly interdisciplinary, integrated approaches to solve.

Soil is an important part of the solution. With respect to impacts of deleterious organisms and processes, soil has tremendous capacity both to host human, animal and plant pathogens and also to suppress establishment and survival of these pathogens. Understanding the complex interactions and ecological phenomena that govern suppressiveness in a particular place and time will provide a foundation for new tools and indicators to predict potential outbreaks and develop preventative solutions [41,184]. Better knowledge of which tools to use, and when to stay out of the way of soil's native ability to regulate detrimental organisms, will come from ecological insights gained from studies of soil biodiversity [185].

Health is a concept that bridges across and links the microbiomes of humans, animals, plants, and soil and other living members of ecosystems [45,186]. Soil health has proven to be a powerful conceptual framework that helps integrate across multiple functions, processes and solutions at play [39,40] and could increasingly play a role in how we think about regulating deleterious organisms in soil. When one considers, however, the vast set of interactions among pathogens, vectors, hosts, antagonists, abiotic environment and other players [187–191], it is evident our perspective needs to be broader than soil to transcend the silos of specific disciplines and taxa. By focusing on the connections among human, other animal, plant, microbiome and environmental health, the evolving concept of One Health [45,186,192,193] brings together disciplinary areas that rarely interact, with the goal of transdisciplinary research and new solutions. For example, finding commonalities across plants and animals with regard to taxa and mechanisms involved in regulating detrimental organisms [193] could not only cross-fertilize approaches and conceptual models, but also identify root causes and find cross-cutting solutions [194,195]. A One Health perspective on soils' role in pathogen suppression will bring new ideas and synergism, and catalyse solution-based research, to help achieve the goals of NCP [6] and particularly of NCP #10, the regulation of detrimental effects on humans, human-important plants and animals.

Data accessibility. This article has no additional data.

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