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Cover crops to increase soil microbial diversity and mitigate decline in perennial agriculture. A review

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Abstract Commercial perennial agriculture is prone to declining productivity due to negative plant-soil feedback. An alternative to costly and environmentally harmful conventional treatment such as soil fumigation could be to manipulate soil microbial diversity through careful selection and management of cover crop mixtures. Although cover crops are already used in these systems for other reasons, their capacity to influence soil biota is unexploited. Here, we examine the role of plant diversity and identity on plant-soil feedbacks in the context of perennial agriculture. We identify key microorganisms involved in these feedbacks and explore plant-based strategies for mitigating decline of perennial crop plants. We conclude that (1) increasing plant diversity increases soil microbial diversity, minimizing the proliferation of soil-borne pathogens; (2) populations of beneficial microbes can be increased by increasing plant functional group richness, e.g., legumes, C₄ grasses, C₃ grasses, and non-leguminous forbs; (3) brassicas suppress fungal pathogens and promote disease-suppressive bacteria; (4) native plants may further promote beneficial soil microbiota; and (5) frequent tillage, herbicide use, and copper fungicides can harm populations of beneficial microbes and, in some cases, contribute to greater crop decline. Non-crop vegetation management is a viable and cost-effective means of minimizing crop decline in perennial

monocultures but is in need of more direct experimental investigation in perennial agroecosystems.

Keywords Cover crops · Perennial agriculture · Agroecology · Plant-soil feedback · Conservation biological control · Soil microbial diversity

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1 Introduction

Perennial crops often experience reduced productivity over time due to the accumulation of soil-borne pests and pathogens (Hamel et al. 2005; Mazzola and Manici 2012; Úrbez-Torres et al. 2014). This is particularly problematic in woody perennial systems where crop rotation is not possible, and ultimately, replanting is necessary to restore production levels. However, addressing this problem from an ecological perspective may lead to more sustainable solutions or avoidance of decline altogether.

An ecological concept that is useful for understanding crop decline is plant-soil feedbacks. This concept describes the reciprocal effects of plants and their associated soil microbial communities (Bever 1994). Negative soil feedback occurs when plants promote soil microorganisms that are deleterious to their own growth, contributing to the maintenance of plant coexistence in natural systems through density-dependent regulation of dominant species (Bever et al. 2015). In perennial monocultures, however, negative feedback leads to crop decline and replant problems (Hamel et al. 2005; Mazzola and Manici 2012). That is, the deleterious soil microbial community also suppresses the growth of neighboring crop plants.

The negative effect of soil microbial communities in monocultures is not altogether surprising, given the negative relationship between biodiversity and the frequency of parasitism (Civittello et al. 2015). In many systems, low levels of diversity will allow a parasite of the dominant host species to more easily find a suitable host. Increased diversity makes hosts more difficult to find and disease outbreaks less frequent and leads to the “dilution effect” associated with high species richness (Keesing et al. 2010). For plant-soil ecosystems in particular, it is well established that increased soil diversity decreases incidence of plant disease (Garbeva et al. 2004a; van Elsas et al. 2002) and improves plant productivity (van der Heijden et al. 1998, 2008).

Can growers capitalize on this dilution effect by increasing soil microbial diversity in perennial systems? While many mechanisms contribute to forming soil microbial communities, e.g., abiotic filters (Fierer and Jackson 2006; Lauber et al. 2008), there is an extensive body of literature documenting the ability of plants to “train” their associated microbial communities (Badri and Vivanco 2009; Fanin et al. 2014; Hartmann et al. 2009; Rovira 1969). While growers are limited in their ability to manipulate the diversity of crop plants in their cropping system, cover crop identity and diversity can be an efficient way to increase soil microbial diversity and suppress soil-borne pests that cause crop decline (Garbeva et al. 2004a). Cover crops are already a common feature in many perennial systems (Fig. 1), but their potential impact on the biotic component of soils is often overlooked. For the purpose of this review, we define the term “cover crop” as managed vegetation grown between crop plant rows, including annual and perennial swards.



Fig. 1 Examples of common cover cropping strategies and experimentation at the Summerland Research and Development Center, British Columbia. *Top*: a permanent cover of mixed grass species in a cherry orchard and *bottom*: a long-term cover crop experiment in wine grapes evaluating mixtures and monocultures of native and introduced grasses

Here, we incorporate ecological knowledge of plant-soil feedbacks into the context of perennial agriculture to explore the use of cover crops to increase microbial diversity and manage crop decline. The specific aims of this review are to (1) synthesize our current understanding of how plant communities influence soil microbial communities into the context of cover crops; (2) highlight key beneficial soil microbes and their role in affecting crop decline; and (3) present plant-based strategies to mitigate decline of perennial crops through soil microbial diversity.

2 Manipulating cover crops to influence soil microbial communities

2.1 Root exudates attract rhizosphere microbes

Perhaps, the most well-studied mechanism through which plants affect the soil microbial community is root exudates (Badri and Vivanco 2009; Broeckling et al. 2008; Rovira

1969). Root exudates contain C-rich compounds, including amino acids, organic acids, sugars, phenolics, secondary metabolites, and proteins that are excreted mostly from root hairs and the cells immediately behind the penetrating root tip (Badri and Vivanco 2009). Root exudates attract and sustain a variety of rhizosphere microorganisms, including arbuscular mycorrhizal (AM) fungi (Akiyama et al. 2005), entomopathogens in response to root herbivory (Rasmann et al. 2005), and N-fixing bacteria (Long 2001). However, root exudates also attract host-specific pathogens (Nicol et al. 2003; Hamel et al. 2005; Hofmann et al. 2009) and thus can lead to both positive and negative soil feedback. Since exudate composition, quantity, and seasonality depend on host plant identity (Broeckling et al. 2008; Schweitzer et al. 2008), a cover crop that includes a variety of plants should be able to maintain greater diversity of root-associated microbes with higher overall benefits to crops (Bardgett and van der Putten 2014; Garbeva et al. 2004a) (Fig. 2).

2.2 Plant litter affects decomposer community

While growers are familiar with the effect of soil organic material on disease suppression, e.g., compost addition (Hoitink and Boehm 1999), a similar effect can occur with cover crop plant litter. The identity of decomposing plant litter has been shown to affect both the activity (Bardgett and Shine 1999) and community structure of soil microbes (Fanin et al. 2014). Litter quality is largely a result of both the ratio of carbon to nutrients and the

proportions of different C chemistry, i.e., low-molecular-weight compounds (easily labile) versus more complex forms such as lignin (more recalcitrant) (Cotrufo et al. 2013).

The quality and quantity of litter differ greatly among plant species (Cornelissen and Thompson 1997) and can determine saprotrophic community composition (Fanin et al. 2014). High-quality plant litter (lower C/nutrient ratio, greater proportion of labile to recalcitrant C chemistry) is broken down more rapidly and thus favors faster-growing copiotrophic microbes, including disease-suppressive pseudomonads (Bastian et al. 2009), while oligotrophic microbes such as fungal decomposers (Holland and Coleman 1987) and *Acidobacteria* (Bastian et al. 2009) are largely responsible for the decomposition of low-quality litter. Recently, Fanin et al. (2016) compared microbial communities from soils to which litter was added that differed in C/N ratio, lignin, and total nutrients and found that litter type had a strong effect on shaping soil microbial communities, surpassed only by the influence of soil type. Other aspects of plant litter chemistry, such as glucosinolate content, can also have a dramatic and long-term effect on the soil microbial community (Mazzola et al. 2015). Stimulating soil saprotrophic communities with a diverse composition of plant litter may reduce soil-borne pathogens, either through increased competition for resources (Fontaine et al. 2003) or by increasing the abundance of beneficial, pathogen antagonistic microbes (Garbeva et al. 2004b).

Whether litter is left on the surface (as in a perennial cover crop) or incorporated into the soil via tillage will also affect the

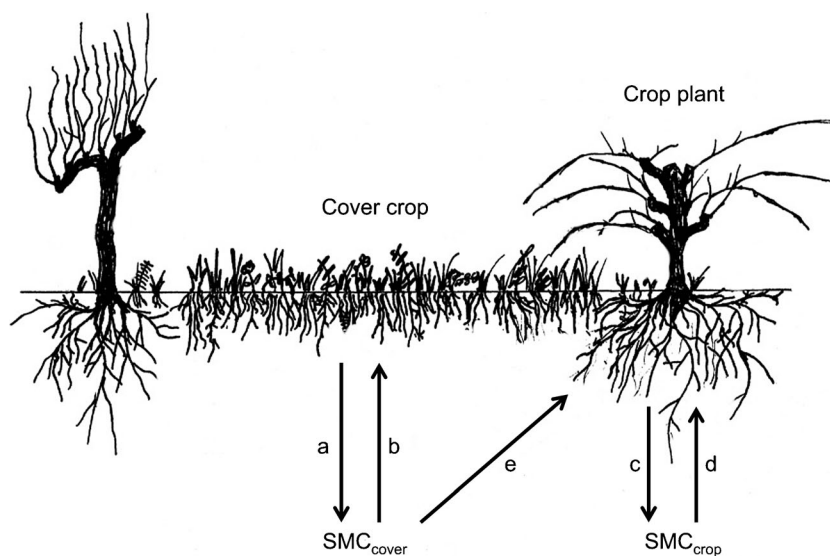


Fig. 2 Depiction of how plant-soil feedbacks might influence crop decline in the context of a highly diverse permanent vineyard cover crop (adapted from Bever et al. 2010). *a* A diverse cover crop influences the soil microbial community through deposition of root exudates and litter creating a diverse microbial community (SMC_{cover}) which provides feedback *b* to the cover crop maintaining plant diversity. *c* The vine “trains” its own soil microbial community (SMC_{crop}), which may include pest and

pathogen buildup due to a low diversity of plant-derived resources. *d* If plant diversity in the vineyard is limited to vines only, SMC_{crop} would feedback negatively on the vine leading to crop decline due to monoculture. *e* However, a highly diverse SMC_{cover} provides inoculum of microbial diversity that may interact with SMC_{crop} and the vine directly, increasing the microbial diversity available to roots of the vine and preventing decline due to negative feedback

decomposer communities and, thus, many pathogens (Govaerts et al. 2007; Holland and Coleman 1987). When litter is left on the soil surface, as in a no-till system, saprotrophic microbial communities become more structured due to the stratification of different nutrients through the soil (Holland and Coleman 1987). This heterogeneity of resources leads to increased microbial diversity found in no-till systems (Govaerts et al. 2007) and could increase the ability of soils to suppress disease (Stirling et al. 2012), but this has not been investigated specifically in a cover cropped perennial system.

2.3 Plant cover affects soil moisture

Another way in which cover crops may influence the soil microbial community is by altering soil moisture dynamics (Bezemer et al. 2006; Lange et al. 2014). In addition to differences in transpiration, plants differ in the proportion of the soil surface covered by their canopy, affecting temperature and evaporation from the soil and, therefore, soil moisture (Lange et al. 2014). In dryland ecosystems, more water from the top 15 cm of soil is typically lost to evaporation than is used by plants (Loik et al. 2004). The maintenance of soil cover, as in a no-till system, can decrease soil temperature and increase soil moisture retention at shallow depths compared to tilled soil (Pannkuk et al. 1997). Depending on the traits of the ground cover vegetation, e.g., root system architecture, photosynthetic pathway, and dormant states, differences in soil moisture from plant cover can be ecologically significant for soil microbes (Chowdhury et al. 2011; de Vries et al. 2012). Of course, this can be exacerbated by soil texture and salt content (Chowdhury et al. 2011).

Tolerance of microbes to fluctuating soil moisture levels is largely phylogenetically determined (Placella et al. 2012). Microorganisms that provide ecosystem services at shallower depths, such as entomopathogenic fungi, may benefit most from the preservation of moisture by plant cover (Pell et al. 2010). This mechanism has not been tested specifically, but there is some evidence for the persistence of natural populations of *Beauveria bassiana* when a cover is maintained (Shapiro-Ilan et al. 2012). Although plant cover and, thus, soil moisture can be an important driver of a soil microbial community (Lange et al. 2014), more work needs to be done to elucidate this effect on crop decline outcomes as some pathogens also benefit from increased soil moisture (Piecarka and Abawi 1978; Kuan and Erwin 1982).

3 The role of beneficial microbes in crop decline

While discouraging negative feedback is a critical part of managing crop decline, promoting beneficial microbes may be as important. Because generalist pathogens may not be as affected by the diversity of a plant community per se and are

common in some perennial systems, e.g., “*Cylindrocarpon*” in apple (Mazzola and Manici 2012), avocado (Vitale et al. 2012), and grape (Úrbez-Torres et al. 2014), the ability of a cover crop to encourage beneficial microbes might be paramount to avoiding crop decline if these pathogens are prevalent. Microbial antagonists such as AM fungi, disease-protective fungi, e.g., *Trichoderma* spp., and disease-suppressive bacteria, e.g., pseudomonads, are instrumental in preventing soil-borne disease whether through competition for resources or niche space (Larsen and Bodker 2001), direct antibiosis (Haas and Defago 2005), or by induction of plant systemic resistance (Pozo et al. 2002). Entomopathogenic fungi provide protection from soil-dwelling insect pests, outbreaks of which are another form of negative feedback in these systems. Here, we examine the role that beneficial microbes play in preventing crop decline and provide evidence that their populations may be regulated, in part, by plant communities.

3.1 Mycorrhizal fungi

Most perennial crops are mycorrhizal, forming a root symbiosis with fungi, e.g., apple (Gnekow and Marschner 1989), citrus (Menge et al. 1978), olive (Roldán-Fajardo and Barea 1985), raspberry (Taylor and Harrier 2000), and grape (Trouvelot et al. 2015). This mutualism confers many benefits to hosts, particularly nutritional and stress tolerance (Smith and Read 2008), but is threatened in most agricultural systems (Verbruggen et al. 2010) due to management activities that inhibit the fungi such as tillage (Brito et al. 2012), fungicide use (Graham et al. 1986), and some forms of weed control (Schreiner et al. 2001).

AM fungi (phylum *Glomeromycota*), which are the most widespread fungal mutualists, are considered pathogen antagonists in addition to nutritional symbionts (Azcón-Aguilar and Barea 1996; Cameron et al. 2013). Competition for root space is one way that AM fungi can limit root disease (Cameron et al. 2013). AM fungi may also inhibit pathogenic fungi through induced systemic resistance (ISR), by evoking an enhanced immune response in the host plant (Pozo et al. 2002). Finally, AM fungal hyphae in the soil cultivate their own diverse microbial communities (Scheublin et al. 2010) and microbes that inhabit this “hyphosphere” can include fungi and bacteria that play a role in protection from soil-borne pathogens (Filion et al. 1999).

Because some AM fungal taxa may offer more disease protection than others (Maherali and Klironomos 2007; Sikes et al. 2009), greater diversity of AM fungi could lead to broader disease suppression due to the increased probability of the presence of taxa effective in guarding against pathogens. Due to the tight link between plant diversity and AM fungal diversity (Hart et al. 2003; van der Heijden et al. 1998), using diverse cover crop mixes could increase the suite of AM fungal partners available to crop plants, with a greater chance

of symbioses forming between crop plants and multiple AM fungi that are effective in alleviating both abiotic and biotic stresses. Although nutrient transfer from a cover crop (*Bromus hordeaceus* or *Medicago polymorpha*) to neighboring grapevines has been shown to be mediated by AM fungi (Cheng and Baumgartner 2004, 2006), the effect of vegetation type and diversity on the AM fungal community and its relationship to disease outcomes has not been studied.

3.2 Disease-protective fungi

Many saprotrophic fungi opportunistically colonize roots as endophytes and aid in controlling pathogenic fungi. A notable example is *Trichoderma*, which can parasitize other fungi using cell wall-degrading enzymes and antibiotic compounds (Harman et al. 2004). Non-pathogenic strains of *Fusarium oxysporum* have been observed to function in a similar way (Benhamou et al. 2002), and there are myriad other fungi that are also known to protect roots from pathogens, e.g., *Penicillium* (Hossain et al. 2007) and *Clonostachys* (Luongo et al. 2005). Because many of these fungi can also promote increased root and plant growth (Harman et al. 2004), they may also contribute to positive feedbacks similar to those experienced by plants associating with AM fungal mutualists (Avis et al. 2008).

Some disease-protective fungi are sold commercially as biocontrol agents, e.g., *Trichoderma* spp., but they are naturally common in soil and may be affected by plant diversity as well as soil disturbance due to their additional roles as decomposers and endophytes. There is some empirical evidence for a plant host effect on populations of pathogen-antagonistic fungi. For example, Berg et al. (2005) found *Trichoderma* and other *Verticillium* antagonists such as *Penicillium* and *Monographella* to vary in diversity and abundance across sites and among host plant (strawberry and oilseed rape) rhizosphere soils. Recently, Taheri et al. (2016) reported that fungal antagonist communities differed depending on the identity of the legume in crop rotation. Unfortunately, understanding of the mechanisms by which plant communities selectively amplify disease-protective fungi does not go beyond single plant species or genotypes (Hartmann et al. 2009). Future work focusing on the role of entire communities would aid in predicting disease outcomes for agroecosystems, which are naturally complex assemblages.

3.3 Disease-suppressive bacteria

Root associated, disease-suppressive bacteria contribute another mechanism by which plants resist disease (Haas and Defago 2005; Sturz and Christie 2003). These rhizosphere bacteria, which include fluorescent pseudomonads, inhibit bacterial and fungal pathogens and even root-feeding nematodes though competition for C, N, and Fe resources as well as

through production of antimicrobial compounds such as pyrrolnitrin (PRN) and 2,4-diacetylphloroglucinol (DAPG) (Haas and Defago 2005). Although the mode of action of some of these compounds is not completely understood, both PRN and DAPG appear to interfere with fungal respiration (de Souza et al. 2003; Tripathi and Gottlieb 1969). Like AM fungi, pseudomonads can also offer indirect protection through ISR (van Loon et al. 1998; Haas and Defago 2005).

Plant genotype seems to have an effect on prevalence of DAPG-producing bacteria in rhizosphere soils (Hartmann et al. 2009; Mazzola et al. 2004), and there is evidence linking higher plant diversity with greater abundance of DAPG and PRN producers and disease suppression (Latz et al. 2012), although the specific mechanisms responsible for this effect have not yet been elucidated. Increased abundance of disease-suppressive bacteria is often associated with the onset of disease-suppressive soils after continuous monoculture of wheat (Raaijmakers and Weller 1998). Because pathogen outbreak is required for onset of soil suppressiveness and differences in the level of disease suppression seem to depend on host plant genotype (Mazzola et al. 2004), this phenomenon may involve an interaction between specific plants, fungal pathogens, and resident populations of pseudomonads (Weller et al. 2002). Although many details of bacteria-plant interactions have been studied (see review by Hartmann et al. 2009), the mechanisms by which certain plants tend to increase disease-suppressive bacteria remain in the realm of speculation. Despite this gap in knowledge, promoting disease-suppressive bacteria through the use of certain cover crops appears promising. Further assessment of commonly used cover crop species as well as the effect of plant diversity in driving populations of disease-suppressive bacteria in perennial systems is needed.

3.4 Entomopathogenic fungi

Entomopathogenic fungi (orders *Entomophthorales* and *Hypocreales*) are pathogens of many insects, including crop herbivores (Vega et al. 2009). These fungi attack insects by penetrating the exoskeleton with chitin-degrading enzymes, eventually killing them by consuming nutrients in the hemolymph or through release of toxins (Clarkson and Chamley 1996). Because they spend most of their life cycle in the soil, these fungi may be affected by cover crops and help control insect-related problems associated with crop decline. The most well-studied taxa of these entomopathogenic fungi include *Beauveria* and *Metarhizium* spp. (Meyling and Eilenberg 2007), both of which have been cultured and sold commercially as biocontrol agents. However, naturally occurring entomopathogens may be effective in reducing insect pests where the habitat encourages their persistence (Meyling and Eilenberg 2007; Pell et al. 2010).

Although their distribution was traditionally thought to be driven by the presence and movement of insect hosts, they are also found as root endophytes (Behie et al. 2015) and show rhizosphere competence (Wyrebek et al. 2011), suggesting that their distribution may depend on plant community identity. This endophytic growth strategy may be key in their additional potential role as fungal pathogen antagonists (Ownley et al. 2008). Although there has been an effort to establish a connection between habitat type and occurrence of these fungi on a landscape scale (Bidochka et al. 2002; Medo and Cagan 2011; Meyling et al. 2011), using cover crops for conservation biocontrol via entomopathogens has seen little experimentation (Meyling and Eilenberg 2007). Vegetation management strategies that encourage these beneficial fungi might also contribute to a reduction in crop decline caused by insect herbivore outbreaks, possibly even supplementing parasitism by beneficial insects.

4 Considerations for managing non-crop vegetation

Manipulating cover crops may be the simplest tool to help mitigate or reverse crop decline issues in perennial systems such as orchards and vineyards as these systems are amenable to manipulation of plant species growing between crop rows. Different parameters, including species diversity, plant identity, and whether the plants are native or exotic, need to be considered when choosing a cover crop mix. Obviously, factors other than vegetation such as soil type, climate, management of water and nutrients, etc. need also to be considered if a certain mix is to be successful. While it is unlikely that there is a one-size-fits-all solution, certain fundamental properties of the new plant community may help in guiding management. The influence of different cover crop types on soil microbes involved in plant-soil feedback is summarized in Table 1.

4.1 Plant diversity

It is well accepted that greater plant diversity leads to a suite of benefits of interest to growers including ecosystem functioning (Bardgett and van der Putten 2014). Reliability of ecosystem services also improves through functional redundancies associated with enhanced diversity (Naeem 1998; van Bruggen et al. 2006). In terms of plant-soil feedbacks specifically, research shows that negative feedback decreases with increasing plant diversity (Maron et al. 2011; Schnitzer et al. 2011) because highly diverse plant communities are less affected by soil-borne pathogens than are monocultures or low-diversity communities (Maron et al. 2011). In perennial systems, the permanent siting of crop plants and the spatial structuring of cover crops between crop rows mean that growers can most easily manipulate plant diversity between rows. Increasing the diversity of cover crop species could enhance

heterogeneity of soil microbial communities at multiple spatial scales leading to less negative feedback and decline of crop plants (Fig. 2).

While the overall species richness of cover crop vegetation may be the ultimate driver of soil microbial diversity and, thus, soil feedback (Eisenhauer et al. 2011), plant functional group diversity may also be an important consideration (Milcu et al. 2013). Common cover crop mixtures may consist of a mix of any of the four main (non-woody) functional groups (namely C_3 and C_4 grasses, legumes, and non-leguminous forbs), and plants with different functional traits often grow well together due to temporal and spatial niche differentiation (Roscher et al. 2013). Similarly, greater diversity of plant functional groups also creates heterogeneity of niches inhabitable by soil microbes. In that case, a cover crop with high plant functional group diversity should promote enhanced microbial diversity and subsequent ecosystem services such as disease suppression. Unfortunately, the effect of cover crop diversity on disease suppression has not yet been studied in perennial systems.

4.2 Considerations within plant functional groups

4.2.1 Legumes

Legumes can have significant effects on many soil microbes in addition to their nitrogen-fixing rhizobial partners. Abundance of AM fungi can be enhanced with the inclusion of legumes due to the high P cost of N_2 fixation and, thus, the need for AM symbionts at the nodulation sites of most legumes (Scheublin et al. 2004). The resulting high-quality litter may also attract copiotrophic microbes such as fluorescent pseudomonads (Bastian et al. 2009). However, disease-suppressive bacteria have been shown to decrease when legumes are present in a mix (Latz et al. 2012, 2015) possibly because of plant defense mechanisms, e.g., saponins, which are more commonly found in legumes than most grasses (Osborn 2003). Further study should focus on other plant-protective secondary metabolites produced by different legumes (Wink 2013) to better understand how they affect relationships with soil microorganisms. This knowledge could aid growers in choosing specific legumes for building beneficial microbial populations in perennial systems.

4.2.2 C_3 and C_4 grasses

Within grasses, the photosynthetic pathway can also influence plant soil feedbacks. C_4 grasses are highly dependent on AM fungi for productivity (Hetrick et al. 1988; Wilson and Hartnett 1998) as they occur primarily in arid, high-light-intensity environments (Sage et al. 2011) where efficient water and P scavenging and uptake are crucial. C_3 grasses, on the other hand, are typically adapted to cooler climates or seasons

Table 1 Influence of different cover crop types on soil microbes involved in plant-soil feedback

Cover crop type	Microbial effects	Species studied	System type	Reference
Legumes	Increases diversity of AM fungi	<i>Lotus corniculatus</i> , <i>Trifolium repens</i> , <i>Ononis repens</i>	Annual; natural	Klabi et al. (2015); Scheublin et al. (2004)
	Increases persistence of entomopathogenic fungi	<i>T. repens</i>	Perennial	Shapiro-Ilan et al. (2012)
	Decreases abundance of DAPG and PRN-producing bacteria	<i>Lathyrus pratensis</i> , <i>Lotus corniculatus</i> , <i>Medicago lupulina</i> , <i>Medicago varia</i> , <i>Onobrychis vicifolia</i> , <i>Trifolium</i> spp., <i>Vicia cracca</i>	Experimental	Latz et al. (2012)
C3 grasses	Increases abundance of DAPG and PRN-producing bacteria	<i>Lolium perenne</i>	Experimental	Latz et al. (2015)
	Cultivar-specific disease-suppressive bacterial community	<i>Triticum</i> (different cultivars)	Perennial	Mazzola et al. (2004)
	Low mycorrhizal response (less AM fungi?)	<i>Koeleria cristata</i> , <i>Bromus inermis</i> , <i>Festuca arundinacea</i> , <i>Lolium perenne</i> , <i>Agropyron smithii</i> , <i>Elymus cinereus</i>	Natural	Hetrick et al. (1988)
C4 grasses	High mycorrhizal response (more AM fungi?)	<i>Andropogon gerardi</i> , <i>Panicum virgatum</i> , <i>Sorghastrum nutans</i> , <i>Bouteloua curtipendula</i>	Natural	Hetrick et al. (1988)
Brassicas	Decreases fungal pathogens	<i>Brassica napus/mustard</i> green manure; <i>B. napus</i> seed meal	Annual; perennial	Larkin et al. (2010); Mazzola et al. (2015)
	Increases disease-suppressive bacteria	<i>B. napus</i> (living plant or seed meal)	Annual	Berg et al. (2002); Hollister et al. (2013); Mazzola et al. (2015)
	Favors <i>Trichoderma</i> and other disease-protective fungi	<i>B. juncea</i> , <i>B. napus</i> (crop rotation); seed meal	Annual	Galletti et al. (2008); Kirkegaard, et al. (2004)
	Alters microbial community	<i>B. napus</i> seed meal	Perennial	Mazzola et al. (2015)
	Inhibits AM spore germination; decreases AM fungal diversity	<i>B. kaber</i> , <i>B. nigra</i> ; <i>B. napus</i> seed meal	Experimental; perennial	Schreiner and Koide (1993); Mazzola et al. (2015)
Increased plant diversity	Increases disease-suppressive bacteria	N/A	Experimental; annual/natural	Latz et al. (2012); Garbeva et al. (2006)
	Increases AM fungal diversity	N/A	Perennial/natural	Holland et al. (2016)
	Decreases overall negative feedback	N/A	Experimental	Maron et al. (2011); Schmitzer et al. (2011)
	Increases diversity and abundance of entomopathogenic fungi	N/A	Annual/natural	Meyling et al. (2009)
Native species	Improved AM fungal diversity and plant benefit	N/A	Perennial/natural; experimental	Holland et al. (2016); Rúa et al. (2016)

with more available water. Although C_3 grasses do form associations with AM fungi, they are less reliant on them for survival due to highly fibrous root systems that are more effective at absorbing nutrients than are the coarser roots of C_4 grasses (Hetrick et al. 1988).

C_3 grasses may offer other benefits, such as increasing the abundance of disease-suppressive bacteria (Latz et al. 2015) because they may have evolved a greater need for association with protective microorganisms due to their finely branched root systems, which are more susceptible to pathogen attack (Sikes et al. 2009). Variation even at the level of genotype may influence plant soil feedback. Specific genotypes of wheat are associated with different populations of DAPG-producing bacteria in apple replant soils, leading to variation in negative feedback on newly planted trees by pathogens that had built up in the orchard soil (Gu and Mazzola 2003).

Therefore, the inclusion of C_4 or C_3 grasses in a cover crop mix is context dependent and depends heavily on climate and edaphic conditions: C_4 grasses might increase the abundance of AM fungi, while C_3 grasses could provide resources for more copiotrophic beneficial microbes such as disease-suppressive bacteria in the cooler months.

4.2.3 Brassicas

Some common cover crops are not mycorrhizal, which may suppress the mycorrhizal community associating with the crop plant (Karasawa et al. 2001; Stinson et al. 2006). For example, most of the Brassicaceae are non-mycorrhizal and inhibit AM fungal spore germination due to the antifungal volatiles (sulfur-containing isothiocyanates) produced by their roots (Schreiner and Koide 1993). Subsequently, these plants may also decrease endemic populations of entomopathogenic fungi, as seen with *Alliaria petiolata* (garlic mustard) invasion (Keesing et al. 2011). At the same time, this antifungal activity may be beneficial to crops, as brassicas may inhibit fungal pathogens (Walker et al. 1937). Indeed, brassicas are often used as “biofumigants” to kill fungal pathogens and decrease viability of their dormant spores (Smolinska and Horbowicz 1999).

The effects of brassicas are not solely antimicrobial, however, and may confer other benefits. For example, disease-suppressive bacteria have been shown to increase substantially with incorporation of brassicaceous plant material (Hollister et al. 2013) or through rhizosphere selection by living plants (Berg et al. 2005) and may help to alleviate negative feedback as seen with apple replant disease (Mazzola et al. 2015). Whether brassicas in the cover crop are as effective as *Brassica* plant litter in suppressing fungal pathogens is not clear. While decomposing *Brassica* litter can dramatically decrease fungal diversity (Hollister et al. 2013; Mazzola et al. 2015), living brassicas may not be broadly anti-fungal as they are susceptible to specific fungal pathogens, e.g., *Ophioidium*

brassicae (Bennett et al. 2014). Further, some disease-protective fungi, such as *Trichoderma*, have been shown to respond positively to both seed meal (Galletti et al. 2008) and living *Brassica* plants (Kirkegaard et al. 2004). Because much of the research surrounding brassicas has focused on their use as seed meals or green manures and thus is most relevant only to replant situations, future work should investigate their potential to shape microbial communities as living plants within a cover crop system as they are often planted as part of a mix or occur naturally as weedy species.

4.3 Native plant species in cover crops

Plant provenance may be as important as identity in cover crop selection. Native plants, as opposed to exotics or cultivars, may be better adapted to the local climate, requiring fewer inputs when employed as a cover crop (Costello 2010). For example, perennial grasses native to climates that typically experience long dry summers may be effectively dormant during those months and thus provide many ecosystem services associated with cover crops without risk of competition with the crop plant (Costello 2010). Local AM fungal populations may also associate preferentially with native plants compared to exotics (Rúa et al. 2016), leading to a more functional symbiosis and greater inoculum potential.

Whether these benefits transcend across microbial taxa is not clear, because the use of native plants in agricultural settings is not well studied. The most appropriate comparisons contrast microbial communities from neighboring natural grasslands with agronomic fields (Garbeva et al. 2006; Holland et al. 2016; Meyling et al. 2009), which offers some insight into the relationship between plant provenance and soil microbes but is conflated by too many confounding variables. Garbeva et al. (2006) found greater suppression of the generalist pathogen *Rhizoctonia solani* AG3 in soil collected from a native grassland as compared to soil from the same site that had been converted to agricultural production. Similarly, Meyling et al. (2009) saw greater diversity of the entomopathogenic fungus, *B. bassiana*, in a natural area bordering a cropping system. The increased fungal diversity and unique AM fungal community seen by Holland et al. (2016) may also have been driven by native plants in the natural sites adjacent to vineyard blocks. Agricultural habitats that more closely resemble the surrounding natural landscape may therefore benefit from the efficiency of co-evolved organisms, but it is unknown if these benefits would remain in the presence of other disturbances associated with agricultural management.

Establishment of native species can be difficult in disturbed settings, and careful management, e.g., mowing frequency and weed management prior to planting, is paramount to successful stands (Penfold and Collins 2012). Knowledge of the native species' resource requirements (water use, fertility, and soil type preference) and growth habits (germination and

flowering time, rhizome formation, etc.) is also helpful for establishment. Although native plants have not typically been used as cover crops in perennial systems, their potential to promote beneficial native soil biota while consuming few resources makes them an attractive option and warrants further investigation.

4.4 Management practices that disrupt cover crop-mediated soil feedbacks

Despite a healthy and diverse cover crop, benefits may be masked or even negated by other management practices. While any practice may alter microbial communities and, thus, ecosystem services provided by a cover crop (including irrigation, fertilization, mowing, compaction, etc.), frequent tillage, herbicide use, and fungicides may have the greatest known potential to negatively affect the soil microbial community in relation to disease outcomes.

4.4.1 Tillage

Perhaps, more than any other practice, tillage negatively affects most soil microbes and their functioning (López-Pineiro et al. 2013; Lupwayi et al. 1998). This largely results from a decrease in soil fungi, especially AM fungi (Brito et al. 2012), through the disruption of mycelial networks and reduced colonization of roots and soil (Jasper et al. 1989). Furthermore, with frequent tillage, the AM fungal community often shifts with selection for species that sporulate efficiently but may invest fewer resources in extra-radical hyphae, perhaps conferring less benefit to host plants (Verbruggen and Kiers 2010).

Bacterial functional diversity may also be greatly reduced through tillage practices (Lupwayi et al. 1998). Although much of the literature on how tillage influences the soil microbial community is based on annual vegetable or grain cropping systems, a causal link exists between maintenance of permanent cover crops and increased soil microbial biomass and diversity in perennial systems such as grape (López-Pineiro et al. 2013) and citrus (Balota and Martins Auler 2011), though implications for disease outcomes have not been explored specifically in this context.

Reduced or no-till cover crop management in perennial systems may benefit from more than just the avoidance of soil disturbance. Because the effect of a plant community on the diversity and functioning of a soil microbial community is more pronounced with time (Eisenhauer et al. 2011), a permanent cover crop may be more advantageous for promoting microbe-mediated ecosystem services to crop plants than the incorporation of annual cover crops or clean cultivation in the long term.

Of course, tillage can be necessary and beneficial in certain instances, e.g., replanting, especially if it helps distribute

disease-suppressive pseudomonads built up on the roots of cover crops (Gu and Mazzola 2003). However, the loss of diversity and heterogeneity of the soil microbial community that comes with frequent tillage may be counterproductive in preventing negative feedbacks from dominating in perennial monocultures.

4.4.2 Herbicide use

The herbicide glyphosate, which is ubiquitous in perennial agriculture, can negatively affect beneficial soil microbes. First, it can be directly toxic to microbes, including fungi, bacteria, and algae that use the shikimate pathway for production of aromatic amino acids (Steinrücken and Amrhein 1980). There is evidence that field concentrations of glyphosate have a fungicidal effect against the entomopathogenic fungi *B. bassiana* and *Metarhizium anisopliae* (Morjan et al. 2002). Perhaps, most alarming, glyphosate has been shown to affect woody perennials even when applied sparingly as a 1 % solution to bark (Levésque and Rahe 1992), weakening the plant sufficiently to enable damage by weak pathogens such as *Cylindrocarpon* spp. that were present on roots but kept in check by costly plant defense mechanisms (Levésque and Rahe 1992). This suggests that glyphosate can disrupt the delicate balance of soil feedback and may contribute to decline of crop plants.

Alternative weed management strategies in crop rows include the use of cultivation equipment, flaming, mulching, and seeding living mulches (Krohn and Ferree 2005; Hartwig and Ammon 2002). While some growers take the approach of tolerating weeds in crop rows, this strategy can either be dangerous if weeds harbor generalist pathogens that also affect crop plants (Agustí-Brisach et al. 2011) or advantageous if the weeds are a source of beneficial microbes such as disease-suppressive bacteria (Sturz et al. 2001). The local weed community likely influences these outcomes. Since weed resistance to glyphosate is becoming more common (Ghanizadeh et al. 2015; Koger et al. 2004), repeated use of materials with this mode of action often results in few dominant weed species, which may contribute to decreased soil microbial diversity.

4.4.3 Fungicides

Fungicides are used extensively in many perennial systems to control foliar pathogens such as mildews, and their non-target effects on soil microbes can be significant (Bünemann et al. 2006). Even with woody perennials such as apples or grapes where foliar fungicides are directed up into the canopy, residual material accumulates on the soil surface and has the potential to affect the soil microbial community (Mackie et al. 2012). This is especially problematic for metals such as copper and copper sulfate, which are widely used in both

conventional and organically managed systems (Mackie et al. 2012). Heavy metals like copper do not biodegrade and thus accumulate in agricultural soils with a history of copper fungicide use (Wang et al. 2009). Although some microbes can tolerate or adapt to high concentrations of heavy metals (Hassen et al. 1998; Ezzouhri et al. 2009), the reduction in microbial diversity caused by elimination of copper-intolerant species can result in decreased ecosystem functioning in the presence of additional stressors (Tobor-Kaplon et al. 2005).

Overall, copper contamination seems to have a negative effect on total soil microbial biomass and functioning (Fernandez-Calvino et al. 2010; Kandeler et al. 1996) and the potential for inhibiting specific groups of beneficial fungi, such as AM fungi, has also been demonstrated (Graham et al. 1986). Although foliar fungicide treatments are often a necessity in many perennial systems, the material used should be considered carefully as long-term effects on soil microbial functioning could be affected by accumulation of active ingredients in the soil.

5 Conclusions

The lessons learned from ecological studies have much to offer in terms of understanding and alleviating crop decline. These studies show that greater plant diversity suppresses plant disease and promotes increased overall resistance and resilience of the ecosystem. However, many of these results are from highly manipulated, artificial systems or experiments within natural systems. Consequently, these theories need rigorous testing in agricultural settings. Although there has been some success in alleviating replant disease using plant-based strategies, due to the lack of experimentation with long-term cover crop mixes in perennial systems, we can only hypothesize that crop decline could be altogether avoided with a carefully selected, diverse cover crop. Before these ideas can be adopted by growers, it will be necessary to address major gaps in knowledge, including the following: (a) How do the cover crops that we already use affect disease outcomes? (b) Does plant provenance (native vs. exotic) affect plant-soil feedback? and (c) How robust is plant-soil feedback to differences in management regimes? Improving knowledge in this area can help growers take advantage of the effect that plants have in shaping microbial communities by managing non-crop vegetation. Perennial cover crop mixtures with highly diverse, locally adapted plant communities may be best suited if the aim is preventing crop decline caused by negative soil feedback.

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