CrossMark

Linking ecology and plant pathology to unravel the importance of soil-borne fungal pathogens in species-rich grasslands

Eline A. Ampt · Jasper van Ruijven · Jos M. Raaijmakers · Aad J. Termorshuizen · Liesje Mommer

Abstract Soil-borne fungal diseases are a major problem in agriculture. A century ago, the Dutch plant pathologist Johanna Westerdijk recognized the importance of linking fungal biology with ecology to understand plant disease dynamics. To explore new ways to manage soil-borne fungal disease in agriculture by 'learning from nature', we follow in her footsteps: we link below ground plant-fungal pathogen interactions to ecological settings, i.e. natural grasslands. Ecological research hypothesised that the build-up of 'enemies' is reduced in species-rich vegetation compared to monocultures. To understand how plant diversity can suppress soil-borne fungal pathogens, we first need to identify fungal actors in species-rich grasslands. Next-generation sequencing revealed a first glimpse of the potential fungal actors, but their ecological functions often remain elusive. Databases are becoming available to predict the ecological fungal guild, but classic phytopathology studies that isolate and characterize – taxonomically and functionally -, remain essential. Secondly, we need to set-up experiments that reveal ecological mechanisms underlying the complex below ground interactions between plant diversity and fungal pathogens. Several studies suggested that disease incidence of (host-specific) pathogens is related to abundance of the host plant species. However, recent studies suggest that next to host species density, presence of heterospecific species additionally affects disease dynamics. We explore the direct and indirect ways of these neighboring plants diluting pathogen pressure. We argue that combining the expertise of plant pathologists and ecologists will improve our understanding of belowground plant-fungal pathogen interactions in natural grasslands and contribute to the design of sustainable and productive intercropping strategies in agriculture.

Keywords Soil-borne fungal diseases · Belowground disease dynamics · Biodiversity · Grassland ecosystems · Neighbor identity · Plant-fungal interaction

E. A. Ampt · J. van Ruijven · L. Mommer (✉)
Plant Ecology and Nature Conservation Group, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands
e-mail: Liesje.Mommer@wur.nl

J. M. Raaijmakers
Department of Microbial Ecology, Netherlands Institute for Ecology (NIOO-KNAW), PO Box 50, 6700 AB Wageningen, The Netherlands

A. J. Termorshuizen
Aad Termorshuizen Consultancy, Kabeljauwallee 11, 6865 BL Doorwerth, The Netherlands

Introduction

In her search for the causal agent of the disease that caused major die-back of Elm trees, Johanna Westerdijk did not just focus on the interaction between the pathogenic fungus and the tree alone. Rather, she and her team also studied the ecology of the European elm bark beetle *(Scolytus multistriatus)*, which acted as the vector of the fungal pathogen *Graphium ulmi* (now *Ophiostoma ulmi*) on elm trees. In essence, Westerdijk thus recognized the

important role of complex species interactions in explaining plant disease dynamics.

Managing soil-borne fungal diseases is also a matter of understanding complex species interactions. Soil-borne fungal pathogens are 'hidden' in the soil; diverse and notoriously difficult to manage in agriculture. Therefore, soil-borne fungal pathogens can cause widespread damage, reducing the yield of many economically important crops. An effective way to prevent the build-up of soil-borne pathogens is to interrupt the host-pathogen cycle via crop rotation (Krupinsky et al. 2002). In addition, various agro-chemicals have been developed to promote plant growth and to minimize the impact of pathogenic fungi on plant health and yield. However, due to the adverse environmental effects of many pesticides and the strict regulation of their use (Hillocks 2012), there is an urgent need to further reduce the use of pesticides and to identify more sustainable crop protection strategies.

When developing sustainable crop protection strategies for soil-borne fungal pathogens, we argue that 'biodiversity' is essential. Westerdijk also had a special interest in what we now refer to as 'biodiversity'. Under her supervision, the fungal collection of the Centraal Bureau voor Schimmelcultures (now Westerdijk Fungal Biodiversity Institute) expanded from about 80 fungal cultures to over 10,000 strains of fungal species. However, we will use term biodiversity in a different context as compared to the perspective of Westerdijk. The biodiversity research field in ecology has hypothesized that the build-up of natural plant 'enemies' is lower in species-rich than in species-poor (e.g. monoculture) vegetation (Bever et al. 2015; Connell 1971; Janzen 1970; Schnitzer et al. 2011). Pinpointing the actual 'enemies' (and their interactions with other 'bad' and 'good guys'), such as herbivores (e.g. insects and nematodes (Bagchi et al. 2014; de Deyn et al. 2003; Knops et al. 1999)) and pathogens (viruses, bacteria, and fungi (Maron et al. 2011; Moore and Borer 2012; Packer and Clay 2000; Petermann et al. 2008; Rottstock et al. 2014)), has proven difficult, especially belowground (Alexander 2010). There is interest in the role of fungal pathogens to explain the maintenance of biodiversity (Bever et al. 2015; Gilbert 2002), but in this review we focus on the other way around: the role of plant species diversity to reduce the build-up of soil-borne fungal disease (Latz et al. 2012; Mommer et al. 2018; Yang et al. 2015).

Similar lines of thought have been explored in agriculture, when developing mixed cropping systems (i.e.

cultivating more than one crop species on a field; Vandermeer 2011). Intercrops typically yield up to 20% more per land area than single crops grown proportionally (Yu et al. 2015). Overyielding is likely due to, at least in part, enhanced light interception and nutrient availability, but potentially also to reduced disease incidence in plant mixtures compared to monocultures. Regarding the latter, meta-analyses show that suppression of soil-borne diseases, e.g. damping-off and *Fusarium* wilt, is often reported (Boudreau 2013; Trenbath 1993). For instance, soil-borne disease incidence was reduced in 30 out of 36 mixed-cropping system studies (Hiddink et al. 2010). However, the underlying mechanisms of the soil-borne disease suppression are poorly understood (Ratnadass et al. 2012), which limits the potential to optimize intercropping systems in this respect.

Grassland ecosystems appear a good model system to study the mechanisms of soil-borne disease dynamics in vegetations that differ in plant species richness (Dignam et al. 2016). (Semi-) natural grasslands are characterized by a high plant species richness (up to 89 species per m^2 (Wilson et al. 2012)), containing both monocots and dicots. Interestingly, these plant communities are not static: many plant species show high spatiotemporal dynamics, changing positions within the grassland and fluctuating in abundance over time (Herben et al. 1993; Van der Maarel and Sykes 1993). It has been proposed that soil-borne fungal pathogens play an important role in this spatiotemporal species turnover (Olff et al. 2000). However, obvious disease foci caused by soil-borne pathogens have rarely been observed (Alexander 2010; Burdon et al. 2006; Gilbert 2002), suggesting that disease incidence is indeed low in these systems with high plant species diversity, or that other species compensate for a poorly performing plant.

Here, we review the role of plant species diversity in soil-borne fungal pathogen (including the fungal-like oomycetes) dynamics in species-rich grasslands. We first provide an overview of soil-borne pathogenic fungi reported to occur in these grasslands and their potential role in the functioning of these ecosystems. Furthermore, we explain three current hypotheses in the ecological literature about mechanisms by which plant diversity can suppress soil-borne fungal pathogens. These are: 1) host specificity-, and 2) conspecific (i.e. individuals belonging to the same species) host density dependence- of the pathogen, as well as 3) additional effects of heterospecific (i.e. individuals belonging to other species) neighbouring plants on the pathogen,

both directly and indirectly. Finally, we identify main knowledge gaps in our understanding of these complex plant-fungal interactions, and provide suggestions on how these can be tackled by combined efforts of ecologists and plant pathologists.

Soil-borne pathogenic fungi in species-rich grasslands

To date, little is known about the identity and biology of soil-borne fungal pathogens in natural species-rich grasslands. The reason for this is two-fold. The focus of most research on plant pathogens has been on: 1) above ground rather than on below ground pathogens, and 2) economically relevant pathogens in agriculture.

The greater attention for aboveground diseases in natural grasslands is because they are often easier to observe and to study experimentally (e.g. Mitchell et al. 2002; Rottstock et al. 2014). Additionally, many aboveground pathogens can induce severe epidemics, because of their fast and long-range (up to kilometers) air-borne dispersal (Fitt et al. 1989; Brown and Hovmøller 2002). In contrast, the effects of belowground soil-borne fungal pathogens are mostly obscured due to their generally short-range dispersal capacities (cm to max. Meters per year) (Termorshuizen 2016).

The focus on plant pathogens in agricultural rather than natural ecosystems has an obvious economic reason. Moreover, an area where plants perform less well is more easily spotted as a gap in a homogeneous canopy of a single crop than in a grassland with many different species. In a crop field, such gaps can be used as an indication of the presence of belowground soil-borne diseases, but if such gaps are generated in species-rich grasslands they may be effectively replaced by other, tolerant or resistant, plant species (Termorshuizen 2014). Our knowledge of the biology of soil-borne fungal plant pathogens thus largely originates from modern agriculture, where pathogens can strongly reduce crop yield. Main agricultural soil-borne fungal diseases include Fusarium wilt (*Fusarium oxysporum*), Verticillium wilt (*Verticillium dahliae*) and damping-off diseases induced by e.g. *Rhizoctonia solani* and *Pythium* spp. These are well-studied because of their widespread occurrence in many crops worldwide. For example, Fusarium wilt has been found in over 100 different hosts, including cotton, tomato, and banana (Michielse and Rep 2009). In addition, soil-borne diseases have

also been reported from the cultivation of medicinal herbs and turfgrass, which often include plant species that also occur in natural grasslands. For example, on golf courses (turfgrass), grassland species, such as *Poa pratensis* and *Festuca rubra*, are known to suffer from several of the same soil-borne pathogens found in agricultural monocot crops (e.g. brown patch disease (*R. solani*), damping-off disease (*Fusarium, Pythium*, and *Rhizoctonia* spp.), and take-all disease (*Gaeumannomyces graminis*) (Smiley et al. 2005). Similarly, the monoculture cultivation of some well-known dicot grassland species with medicinal properties has yielded some insight in their root-associated pathogens. For instance, *R. solani* and *Fusarium* spp. were found in *Plantago lanceolata* (ribwort plantain) and *Fusarium solani* in *Hypericum perforatum* (St John's Wort) commercial plantings (Gaetán et al. 2004; Zimowska 2013). Although this evidence stems from forb species, these have been cropped as monocultures and such insights may, therefore, not directly be translated to plant-pathogen associations in species-rich grasslands.

Species-rich natural systems such as grasslands may contain a larger diversity of pathogenic soil-fungi due to the large number of diverse plant species and genotypes for a given plant species (Bach et al. 2018; Dassen et al. 2017; Termorshuizen 2014; Yang et al. 2017). Plant roots in natural grasslands have indeed been shown to be colonized by a wide variety of fungi (Vandenkoornhuyse 2002), but there have been only few attempts to isolate root-associated fungi and test them for pathogenicity (e.g. performing Koch's postulates) (Table 1). Mills and Bever (1998) performed such a study and isolated five *Pythium* species from the roots of two perennial grass species (*Danthonia spicata* and *Panicum sphaerocarpon*) in a 50 year-old natural grassland. When re-introduced, four of these *Pythium* species reduced plant biomass of both grasses, while another grass (*Anthoxanthum odoratum)* and a forb (*Plantago lanceolata*) were not adversely affected. Recently, Mommer et al. (2018) isolated 27 fungal species from symptomatic roots of the grass *Anthoxanthum odoratum* and the forb *Leucanthemum vulgare* in a grassland biodiversity experiment. Two of them (*Magnaporthiopsis panicorum* and *Paraphoma chrysanthemicola)* induced adverse host-specific effects on seedling biomass, when inoculated on different plants species (Mommer et al. 2018). These studies and others (see Table 1) show that the most commonly documented fungal pathogenic effect on the host plants under controlled conditions is a reduction in (total) biomass.

Table 1 Overview of studies that have investigated fungal root pathogens (incl. oomycetes) of natural grassland plant species and confirmed pathogen-host associations in bioassays, including confirmation of Koch's postulates (re-isolation of the pathogen)

Soil-borne fungal pathogen	Host type	Host plant species	Pathogenic effect on host	Reference
Gaeumannomyces incrustans	Grasses	*Anthoxanthum odoratum* *Zoysia japonica*	Root rot Reduced growth	(Bucher and Wilkinson 2007; Hendriks et al. 2015a; Mommer et al. 2018)
Fusarium oxysporum	Grasses	*Vulpia ciliata*	Reduced fecundity	(Newsham et al. 1995b)
Pythium arrhenomanes *P. macrosporum* *P. arrhenomanes* *P. volutum*	Grasses	*Danthonica spicata* *Panicum sphaerocarpon*	Reduced growth	(Mills and Bever 1998)
P. dissotocum, *P. irregulare* *P. torulosum* *Rhizoctonia solani*	Legume	*Kummerowia stipulacea*	Seedling mortality Reduced growth	(Alexander and Mihail 2000; Mihail et al. 1998)
Paraphoma chrysanthemicola	Forbs	*Leucanthemum vulgare*	Reduced growth	(Hendriks et al. 2015a; Mommer et al. 2018)
Cylindrocarpon sp. *Fusarium sp.* *Verticillium sp.*	Forbs	*Agalinis gattingeri* *Aletris farinosa* *Gentiana alba* *Liatris spicata* *Polygala incarnata*	Reduced growth	(Klironomos 2002)

Adopting Koch's postulates is an important, and not always adopted, first step in determining the potential role of soil-borne pathogens in the spatiotemporal dynamics of plant biodiversity in grasslands.

Next-generation sequencing as a means to reveal soil-borne pathogenic fungi?

In the last decade, next-generation sequencing (NGS) techniques have allowed us to improve our knowledge of soil and root-associated fungal biodiversity in natural ecosystems (Hannula et al. 2017; Jumpponen et al. 2010; Mommer et al. 2018; Wehner et al. 2014). Such sequencing techniques provide information about the community composition of fungal operational taxonomic units (OTU) in plant roots, rhizosphere or bulk soil. It is difficult, however, to ascertain the species' ecological traits based on such sequence information alone (Peay 2014). In this context, we are facing two main challenges: (1) relating fungal OTU presence to fungal metabolic activity (as opposed to e.g. dormancy), and (2) ecological interpretation based on OTUs.

The first challenge is mainly a general problem for DNA-based sequencing, as the mere presence of DNA strands does not reveal whether a fungus is active,

inactive or not alive at all. Sequencing ribosomal RNA or messenger RNA will provide more insight into the metabolic activities of a soil-borne fungus (Anderson and Parkin 2007).

The second challenge when assigning ecological roles to fungal sequences is not as easily resolved. The fungal kingdom represents an enormous diversity estimated at 5 million species (Blackwell 2011). As a consequence, high-throughput sequencing studies of natural environments including soils and roots yield large numbers of fungal OTUs. For example, Tedersoo 2014 detected over 44,000 fungal OTUs in a total of 365 soil samples from natural ecosystems worldwide. Also within plant roots, a large fungal diversity is often found. Wehner et al. (2014) found a total of 966 unique OTUs in the roots of 25 Asteraceae species, with a maximum of 118 root-associated OTUs in a single individual of *Hieracium pilosella*. Many of the OTUs found through sequencing approaches still lack a formal description. The fraction of OTUs that matched well-described, i.e. cultured, species in the studies mentioned above ranged from only 10% (Tedersoo et al. 2014) to 39% (Mommer et al. 2018). Furthermore, when sequences from uncultured fungi are included in the matches, still 10–30% of fungal

OTUs remain unidentified at the species level (Buée et al. 2014; Hannula et al. 2017; Mommer et al. 2018; Wehner et al. 2014). This suggests that there is a large gap between our ability to detect these fungi and our knowledge regarding their identity, let alone their biological functions.

Moreover, even when an OTU has been identified as a well-described pathogenic species, this may not be sufficient to infer pathogenicity. This means that inferring pathogenicity from presence of an OTU is not as straight-forward as it may seem. For example, *Rhizoctonia solani*, often considered a generalist root pathogen of both dicot and grass crops, is a species-complex of multiple strains divided into anastomosis-groups (AG). Even subdivisions within AGs differ in host range (Termorshuizen 2016). Similarly, *Fusarium oxysporum,* known for its wide host range in dicot crops (> 100 plant species (Michielse and Rep 2009)), has a large range of individual strains that only infect a few species or are not pathogenic at all (Gordon and Martyn 1997). Some of these non-pathogenic strains can even act as antagonists of pathogenic strains (Mandeel and Baker 1991). Furthermore, it is becoming more apparent that plant-pathogenic fungi can also display an endophytic lifestyle (Brader et al. 2017), i.e. colonization without causing disease (Rodriguez et al. 2009). For example, a single genotype of *Fusarium circinatum* has been found to cause pitch canker disease in *Pinus radiata*, and to colonize several herbaceous plants growing in the same plantation without inducing disease (Hernandez-Escribano et al. 2018). Another relevant case is *Fusarium graminearum,* well-known as a pathogen of monocot crops like barley, but found to be an endophyte in other grass species (Lofgren et al. 2018). Pathogenicity can even be variable on a single host, depending on environmental and plant factors like temperature, plant age and genotype, as has been shown for *Verticillium dahliae* (Malcolm et al. 2013). Evidence is thus emerging that our knowledge on fungal pathogens obtained from agricultural ecosystems may not necessarily be predictive for their role in natural ecosystems.

Therefore, although NGS has detected well-known agricultural soil-borne fungal pathogens in natural, species-rich grasslands (Hannula et al. 2017; Mommer et al. 2018), we have to be careful in predicting the ecological fungal guild (Nguyen et al. 2016; Tedersoo 2014) in natural ecosystems. Accordingly, if we want to understand which fungi are actually acting as pathogens in natural grasslands, considerably more studies are required in which fungi are isolated, taxonomically characterized and tested for pathogenicity on the plant species present in the respective natural plant community, under various (a) biotic conditions (e.g. Hendriks et al. 2015a; Kia et al. 2018; Lofgren et al. 2018; Mommer et al. 2018).

Role of soil-borne pathogenic fungi in natural ecosystems: insights from biodiversity research

It is well established in ecology that plant species richness increases plant productivity, an important ecosystem function (Cardinale et al. 2012). Recently, soil-borne fungal pathogens have been hypothesised to play an important role in this positive biodiversity effect (Maron et al. 2011; Mommer et al. 2018; Schnitzer et al. 2011).

The biodiversity research field started in the 1990s with the question how biodiversity loss would affect ecosystem functioning (Schulze and Mooney 1994). Ecologists have investigated this question by manipulating plant species richness in experimental grasslands worldwide (Hector 1999; Tilman 1997, 2001; van Ruijven and Berendse 2005). Although there is now consensus among ecologists that in general monocultures perform less well than plant species mixtures (Cardinale et al. 2012), the main underlying mechanisms remain debated. On one hand, ecologists have focused on plant-plant interactions, with resource partitioning and facilitation between plants as the most likely explanations for the differential plant productivity (Jesch et al. 2018; Mueller et al. 2013; Ravenek et al. 2014; Wright et al. 2017). On the other hand, interactions between plants and pathogenic soil biota have emerged as an important mechanism for the positive biodiversity effect (de Kroon et al. 2012; Maron et al. 2011; Mommer et al. 2018; Schnitzer et al. 2011). The main hypothesis is that the negative effects of soil–borne pathogens, including fungi, will be particularly strong in plant monocultures (in which each plant belongs to the same species) and smaller in plant species mixtures, resulting in the positive relationship between plant species richness and productivity (Fig. 1). Thus far, ecologists have investigated this so-called 'pathogen hypothesis' with a black box approach, i.e. by comparing plant growth on soils with and without soil biota (e.g. Cortois et al. 2016; Hendriks et al. 2015b; Kos et al. 2013; McCarthy-Neumann and Ibáñez 2013; Wubs and Bezemer 2018). For example, Schnitzer et al. (2011)
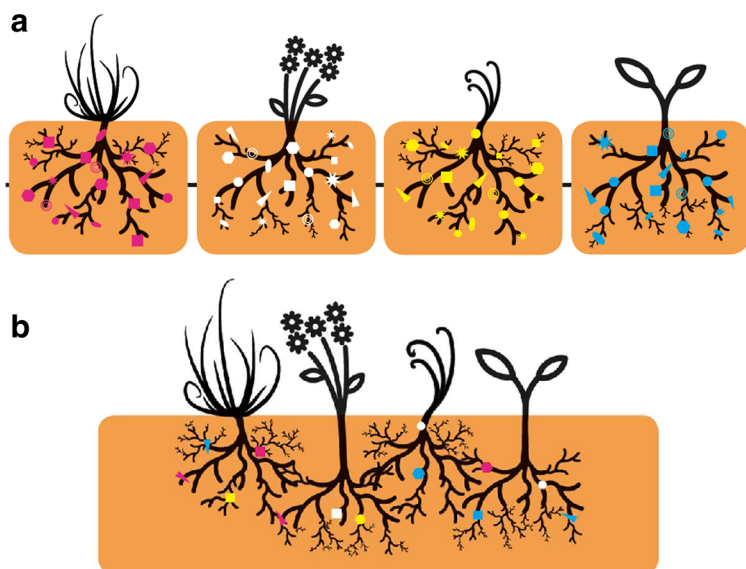
Fig. 1 Conceptual diagram of the ecological principles underlying the hypothesis that soil-borne pathogens drive the biodiversity-productivity relationship. **a** Soil-borne pathogens must be host-specific to some degree in order to result into differential negative effects among plant species. **b** Increased plant diversity is related to decreased host abundance, which may reduce the disease pressure in species-rich plant communities compared to the monocultures. In addition to the reduced host density in mixtures, the heterospecific neighbors may also affect the disease pressure. Some neighbors may also act as (asymptomatic) hosts and boost the pathogenic fungus; other neighboring species may e.g. exude antifungal compounds and further decrease the pathogen. Different colors and symbols represent different plant-pathogenic fungal species, associated to the roots

grew plant communities in field and sterilized field soil. They found that the positive effect of plant species richness on plant productivity disappeared for plants grown in sterilized soil. Specifically, sterilization enhanced plant productivity at low biodiversity, but had no effect at high plant species richness. Schnitzer et al. (2011) also included an additional treatment, in which the sterilized soil was re-inoculated with a soil wash containing soil-borne fungi. With this re-inoculation, plant productivity at low biodiversity levels was again reduced, similar to the effect observed for plants grown on non-sterilized field soil. In other words: the positive biodiversity effect, eliminated by sterilizing the soil, was 'restored' through the addition of the soil wash, suggesting an important role of soil-borne fungi in biodiversity patterns. Additional support for the role of soil-borne fungi as pathogenic actors in driving the positive biodiversity-productivity relationship comes from the study of Maron et al. (2011) who used systemic fungicides (thiophanate ethyl and mefenoxam) to suppress or kill fungi and oomycetes in the soil. Although these fungicides also adversely affect beneficial soil-borne fungi and oomycetes, they found that the positive biodiversity effect disappeared following fungicide

treatment. The work of Schnitzer et al. (2011) and Maron et al. (2011) has steered the attention of plant ecologists in the biodiversity research field toward the importance of plant-pathogen interactions. This opens up new possibilities for integrating the research from this ecological field with plant pathology and may drive the development of our knowledge on soil-borne fungal pathogens and their function further in the coming years.

Rules of play for plant-fungal interactions

Proof for a steering role of soil-borne plant pathogenic fungi in the spatiotemporal dynamics of natural grassland ecosystems is thus accumulating. We have so far identified three important lines of evidence: a) NGS studies show a diverse soil-borne fungal community associated with roots of grassland plants, b) some fungal isolates negatively affect plant growth in bioassays, and c) the relationship between plant diversity and plant productivity is affected by soil sterilization and fungicide application. For the majority of fungal species, however, knowledge of their interactions with plants and how these are affected by plant diversity and other components of the soil food web still need to be revealed.

Ecologists have explored two facets that shape the interactions between plant species and their natural enemies in natural ecosystems - host specificity and density dependence (Bever et al. 2015; Connell 1971; Janzen 1970). Below, we will provide a brief review of the agricultural and ecological literature on these two topics. Moreover, we also propose a third factor to be important in belowground plant-fungal interactions: plant neighbor effects, either directly or indirectly.

Host specificity

A prerequisite for the 'pathogen hypothesis' is that negative effects of pathogenic fungi on plant species should be species-specific (Fig. 1a). This requires fungal pathogens that are specialist pathogens for each plant species (a single host species, e.g. *Synchytrium endobioticum* on potato; or genus, e.g. *Paraphoma chrysanthemicola* on *Leucanthemum*), or generalist pathogens that have differential effects on multiple host species (e.g. many dicots: *Verticillium dahliae, Rhizoctonia solani*) (Hersh et al. 2012).

High-throughput NGS analysis yielded the first evidence for host specificity in natural grassland species: the roots of 8 different natural grassland species (4 grasses and 4 forbs) harboured unique putative pathogenic fungal communities (based on ITS sequencing), when grown in monoculture (Mommer et al. 2018). There was a clear discrimination between plant functional group (forbs vs. grasses), but also within these two plant functional groups host specificity of the fungal communities was apparent. These patterns of host specificity are consistent with results of plant-soil feedback studies that have shown reduced plant growth on soil with a history of plants of the same species or functional group compared to the average community soil (e.g. Cortois et al. 2016; Hendriks et al. 2013; Mangan et al. 2010; Petermann et al. 2008). It is, however, crucial to reveal the (fungal) actors and their functional role in grassland plant communities, if we want to increase our understanding of the myriad of plant-fungal interactions belowground. This requires that NGS analyses are complemented with classic plant pathology approaches where fungi are isolated from soil and roots and (re-)introduced to determine pathogenicity and host-specificity (Hendriks et al. 2015a; Mommer et al. 2018). For example, Klironomos (2002) isolated fungi from the roots of several rare plant species in Canadian meadows. These fungi were identified as

Verticillium, *Fusarium* and *Cylindrocarpon* species. Although identification of fungi to the genus level limits interpretation from a plant pathology perspective, the ecological principle of host specificity was clearly demonstrated: upon inoculation, species-specific pathogenic effects were found: plant growth was reduced with fungi isolated from conspecific (i.e. the same species) roots, but not with fungi isolated from heterospecific (i.e. another species) roots.

Density-dependence of the conspecific host

The second assumption of the pathogen hypothesis is that disease incidence is reduced with reduced host density (Fig. 1b). Pathogen dilution in diverse plant communities implies that the build-up of species-specific pathogens decreases with decreasing abundance of the host plant. Therefore, disease incidence is expected to be high in monocultures (i.e. high host density) and lower in plant species-rich mixtures (i.e. lower host density) (Bever et al. 2015; Kulmatiski et al. 2012). Indeed, in grassland biodiversity experiments, pathogen dilution has been observed for foliar (Knops et al. 1999; Mitchell et al. 2002; Rottstock et al. 2014) and soil-borne fungal pathogens (Mommer et al. 2018). For example, foliar fungal pathogen incidence (presence or absence per plant) and severity were reduced at higher plant diversities in the study of Rottstock et al. (2014). However, this may be partly a 'sampling' effect, as the number of sampled plants per species greatly differed between the levels of plant diversity. Also, Mommer et al. (2018) demonstrated a reduction of more than 50% of putative pathogenic root-associated fungal OTUs from monocultures to the plots with eight plant species.

Evidence for the role of host density in pathogen dilution also originates from studies investigating seedling mortality as a function of pathogenic soil biota (e.g. *Fusarium oxysporum; Pythium*) and density of (or distance to) adult trees (e.g. Johnson et al. 2012; Liu et al. 2012, 2015a; Mangan et al. 2010). Furthermore, in agricultural systems there has been pioneering experimental and modelling work on the effect of plant density on soil-borne disease dynamics (Hiddink 2008; Otten et al. 2005; Otten and Gilligan 2004). For example, the dispersal of *Pythium irregulare* damping-off disease in small-scale stands of garden cress (*Lepidium sativum*) under controlled conditions was reduced with lower seedling densities (Burdon and Chilvers 1975). Specifically, the relationship between infection rate of

P. irregulare and inter-plant distance of garden cress was linear at plant distances from 1 to 5 cm. Another example - the soil-borne fungus *Aphanomyces euteiches* inducing root rot in pea – showed a similar effect: disease incidence was reduced with increasing interplant distances from 2.5–15 cm under controlled conditions (Willocquet et al. 2007). The same study further explored the effect of pea density in the field, where a low plant density (70 plants/m^2) resulted in a lower rate of pea root rot than the high density (140 plants/m^2). Similarly, a reduced rate of *Sclerotium rolfsii* disease (southern blight) on carrots was observed at a low crop density (26 plants/m) compared to a high density (52 plants/m) in the field (Smith et al. 1988).

In the Wageningen grassland biodiversity experiment (Cong et al. 2014; van Ruijven et al. 2003; van Ruijven and Berendse 2005, 2009), more than half of the variation in fungal community composition could be explained by the variation in belowground host density (i.e. species-specific root biomass) (Mommer et al. 2018), suggesting that host density may be important in regulating fungal communities in more diverse plant communities. However, there were only a few direct links between fungal community composition and the density of specific hosts. Only one (the grass *A. odoratum*) out of eight species had a significant effect on the composition of the putative pathogenic fungal community. When analysing the confirmed specialist pathogen in that system - *Paraphoma chrysanthemicola* – it appeared that the number of sequence reads of this fungus was positively correlated with the density of its host, the forb *Leucanthemum vulgare*.

The effect of heterospecific neighbours

There thus seems to be a clear role for host specificity and conspecific host density in disease dynamics in species-rich grasslands, but the presence of (a wide variety of) heterospecific neighbours (i.e. individuals belonging to other species) may additionally affect belowground disease dynamics and infection of host plants (Eppinga et al. 2006; Otten et al. 2005). Effects of heterospecific neighbouring plants are inherently linked to a pathogens' host range and host density. For example, the inclusion of heterospecific neighbour plants (increasing plant species diversity) may reduce overall host density for a specialist pathogen, but not for a generalist pathogen (Parker et al. 2015).

Therefore, it is important to tease apart additional neighbour effects from the main effects of host specificity and density. There have been only a few studies that disentangled the effect of host density and neighbour identity so far. In one such study in an agricultural system, Burdon and Chilvers (1976) did not find an effect of the presence of resistant ryegrass (*Lolium rigidum*) on the *Pythium* disease spread in their garden cress stands. They, therefore, concluded that host density rather than neighbour identity was the main driving factor for *Pythium* disease dynamics in their experimental system. However, the potential 'neighbour effect' on disease dynamics is probably pathogen and plant species-specific (Garrett and Mundt 1999). Recent agricultural studies describe that heterospecific neighbours indeed can reduce soil-borne fungal pathogens. The presence of the medicinal herb *Atractylodes lancea* reduced root rot infections of *F. oxysporum* in peanut crops (Li et al. 2018), and the presence of maize reduced *Phytophthora* blight severity and spread in pepper intercropping (Yang et al. 2014).

The question is how such additional neighbour effects arise: what are the mechanisms for heterospecific neighbours to influence belowground disease dynamics? We propose several potential mechanisms, directly or indirectly impacting the fungal disease dynamics.

Direct neighbour effects via plant traits and root exudates

The roots of heterospecific neighbours may serve as a direct vector or barrier to soil-borne fungal pathogens. On the one hand, disease transmission is likely affected by the 'contagiousness' of the neighbour (Otten et al. 2005). Therefore, host plants that are surrounded by non-host plants may be in general less likely to become infected than plants surrounded by heterospecific host plants or non-symptomatic plants that host the pathogen as an endophyte (Malcolm et al. 2013). Additionally, a larger phylogenetic distance between plant species could decrease the chance that both species are hosts to the same pathogen species (Gilbert and Webb 2007; Wehner et al. 2014). Plants in (phylogenetically) diverse plant communities may thus be more 'buffered' against their soil-borne pathogens, because their neighbours are more likely to be non-vectors (Gilbert and Parker 2016; Haas et al. 2011).

Roots of different species may act as a physical or chemical "root wall" for fungal pathogens. Disease transmission may be enhanced or reduced depending on the structure of the rooting system traits related to morphological or chemical defence (e.g. root thickness (Newsham et al. 1995a)). In the maize-pepper intercropping system mentioned above, maize plants were planted at different interplant distances, resulting in different degrees of maize root intermingling (Yang et al. 2014). The spread of *Phytopthora* blight between pepper rows was reduced with a higher degree of root intermingling and even totally blocked in the treatment with the tightest root intermingling. Root systems in species-rich grassland communities are often dense and tightly intermingled as well (Kesanakurti et al. 2011; Ravenek et al. 2014; Frank et al. 2015), thus potentially reducing spread of fungal pathogens.

In addition, secreted chemicals of heterospecific neighbours - root exudates (incl. volatiles) – may further directly affect the fungal life cycle such as spore germination, mycelial growth and orientation. Antifungal secondary metabolites in root exudates can directly inhibit fungi (Baetz and Martinoia 2014). For instance, the medicinal herb *Atractylodes lancea* in the peanut intercropping system described above (Li et al. 2018) releases a blend of volatiles that inhibits the growth of *F. oxysporum* mycelia. In the intercropping system with pepper, maize root exudates inhibited zoospores of the pepper pathogen *Phytophthora capsici*, thereby restricting its movement across rows (Yang et al. 2014). Specifically, several benzoxazinoid compounds secreted by the maize roots inhibited *P. capsici* zoospore motility, cystospore germination and hyphal growth (Yang et al. 2014). Complex belowground chemical communication between plant species and fungi may be expected also to occur in species-rich grasslands; but until now it has proven difficult to pinpoint the players and the underlying chemistry in situ under complex field conditions.

Indirect neighbour effects via the root microbiome

A potential indirect mechanism of neighbouring plants to dilute pathogens is through alteration of the root microbiome. The microbes associating with plant roots often affect the belowground interaction between a plant and pathogen (Berendsen et al. 2012). Gilbert et al. (1994) hypothesised already in the '90s that plant root-colonizing bacteria may 'camouflage' the roots against pathogens.

We now know that plants assemble unique rhizosphere microbial communities: root exudates can attract and favour the colonization of specific microbes (Berg and Smalla 2009; Philippot et al. 2013). This process is plant species and genotype specific, but is also influenced by environmental factors such as soil type and temperature (Brader et al. 2017; Philippot et al. 2013; Schlemper et al. 2017). The bacterial rhizobiome is a dynamic microbial network that affects pathogen invasiveness, infection and severity (Chapelle et al. 2016; Raaijmakers et al. 2009). For instance, it can form a barrier against root infection through competitive exclusion of the pathogenic invader (Chapelle et al. 2016; Hacquard et al. 2017) and adapts to pathogen presence, seemingly to battle the invader. For example, fungal invasion of *R. solani* in soil has been found to alter the rhizosphere bacterial community of sugar beet. The relative abundance of specific bacterial families increased in suppressive soils inoculated with *R. solani* and stress-related genes were upregulated in these bacteria, suggesting antagonistic activity against pathogen infection (Chapelle et al. 2016; Mendes et al. 2011; van der Voort et al. 2016). Other recent work shows that *Carex arenaria* roots infected by the pathogen *Fusarium culmorum* release an altered volatile blend that attracts specific bacteria with antifungal properties (Schulz-Bohm et al. 2018). The root microbiome may thus either protect the plant species from fungal infection or battle the fungal pathogens.

The microbiome of the soil, rhizosphere, and roots can be affected by the diversity and identity of plant species in a plant community. In general, it is thought that a larger plant diversity creates more 'niches' for soil microbes and/or promotes multiple microbial activities due to chemically more diverse exudates, thereby increasing soil suppressiveness (Gómez Expósito et al. 2017; Mendes et al. 2011; Schlatter et al. 2017; Steinauer et al. 2016). A higher microbial diversity is expected to reduce invasion of pathogens and increase antagonism in soils, thereby reducing the impact of plant pathogenic fungi (Larkin 2015; Mallon et al. 2015). In fact, an increase in plant diversity in the Jena biodiversity experiment (Weisser et al. 2017) enhanced the activity of antagonistic bacteria in the soil against the soil-borne fungal pathogen *R. solani* (Latz et al. 2012). Also in natural grasslands, the diversity of neighbouring plants has been found to affect *Streptomyces* spp. and fungal communities in soil at the base of specific plant species (Bakker et al. 2013; LeBlanc et al. 2014). Whereas the fungal communities

were distinctly different between two grasses and two legumes grown in monoculture, they became similar when the species where grown in mixtures. Furthermore, plant species identity in 4-species grassland mixtures was associated with bacterial and fungal community composition in the soil (Leff et al. 2018).

Importantly, neighbouring plants indeed appear to also impact the microbial community composition of rhizobiomes. Intercropping of wheat and faba bean changed the bacterial rhizosphere community of both crops compared to monoculture (Song et al. 2007). The study of Li et al. (2018) shows that the composition of the fungal rhizosphere community of peanut was significantly altered by presence of the medicinal herb *A. lancea*, coinciding with *Fusarium* root rot decline. Even microbial root colonization can be altered by neighbouring plants, as already shown in a study on mycorrhizal fungi: mycorrhizal community composition of a perennial natural grassland grass species (*Nassella pulchra*) changed in the presence of three neighbouring grass species (Hausmann and Hawkes 2009).

Given the evidence so far, neighbouring plants thus have the potential to directly (via reduced pathogen transmission and root exudates) or indirectly (via the root microbiome) affect soil-borne disease dynamics in plant hosts.

Bridging the gaps: a future perspective for ecology and plant pathology

Understanding the belowground interactions between plants and fungi and how these interactions influence the spatiotemporal dynamics of soil-borne disease in natural ecosystems is complex due to the vast number of plant and soil-borne fungal species involved, let alone other (a) biotic components that affect these innate interactions. Recently, ecologists have embraced NGS techniques in order to describe overall microbial diversity and community assembly in ecosystems (Dassen et al. 2017; Hannula et al. 2017; Mommer et al. 2018; Prober et al. 2015; Wehner et al. 2014). However, this descriptive step alone will not reveal mechanisms of interaction. Therefore, experimental approaches should be adopted to study the interactions between single fungal species (or even single strains/ genotypes) and individual plant species. Once these baselines have been set, we need to move to other experimental approaches that reveal the more complex interactions between multiple plant species and

different fungal pathogens (e.g. Hersh et al. 2012). Also the role of other players in the root microbiome can be incorporated (Mendes et al. 2011; Berendsen et al. 2018). A multi-species approach, rather than pairwise interactions, can reveal potential (synergistic) mechanisms that act only in diverse systems, as was recently suggested for fungal-bacterial (de Boer 2017) and plant-plant (Levine et al. 2017) interactions.

The belowground chemical communication between plants and fungal pathogens is a main interaction mechanism that ecologists and plant pathologists could jointly investigate. Soil-borne fungi locate and orientate to their host plant via chemotropism: the ability to detect and grow towards a chemical gradient, i.e. root exudates (Turrà and Di Pietro 2015). These host signals from the plants may break fungal dormancy, leading to spore germination and subsequent hyphal growth, or conversely, inhibit these processes (e.g. Yang et al. 2014). The exact components of those processes, such as the plant host signals and fungal receptors, are largely unknown for soil-borne fungi. Recent progress is being made in this field: molecular work on a plant pathogenic strain of the fungal species *F. oxysporum* identified an evolutionary conserved signalling pathway that is triggered by peroxidase proteins present in its host (tomato) root exudates, inducing a chemotrophic response of the fungal hyphae towards these roots (Turrà et al. 2015). In order to get a better grip on the chemical belowground communication in natural grasslands, we need more information on the root exudates and volatiles of plants and their effects on fungal growth; particularly in non-model plant species and fungal strains.

Another potential shared research interest would be predicting host infection-compatibility, although ecologists and plant pathologists appear to have fundamentally different approaches. Plant pathologists use molecular knowledge on the pathogen-host infection process to predict fungal pathogenicity and pathogen-host combinations (e.g. through presence of specific functional genes) (Brader et al. 2017; Rodriguez-Moreno et al. 2018; van Schie and Takken 2014). For instance, specific genomic signatures of pathogenic vs. endophytic lifestyle were detected in the root-colonizing pathogenic fungus *Colletotrichum incanum* and its close relative with an endophytic lifestyle *C. tofieldiae* (Hacquard et al. 2016). This included differences in the repertoire of secreted effector proteins and activity of pathogenicity-related genes. In apparent contrast,

ecologists predict pathogen-host compatibility based on overall plant phylogeny (Gilbert and Webb 2007; Liu et al. 2015b, 2016): more related plants are more likely to be host to the same pathogen (Gilbert and Webb 2007). For instance, Parker et al. (2015) derived a model, based on over 200 known host – fungal pathogen associations, that predicts the probability for two plant species to share the same particular pathogen based on the phylogenetic distance. However, there are quite some cases where overall plant phylogeny is not an accurate predictor for fungal-host plant combinations. An example is *R. solani* subgroup AG2-2IIIB, which is known to have a broad host range among crops from a wide variety of mono and dicot families (Boine et al. 2014).

Although these two approaches of phytopathologists and ecologists may seem entirely different, they are in fact based on the same line of thinking. The likelihood of a compatible pathogen-host combination is affected by the co-evolution of hosts and pathogens, which is represented in both overall phylogeny and presence of specific genes encoding for products involved in infection and defence (Gilbert and Parker 2016). A question is whether 'ecological' plant traits related to morphological or chemical defence (e.g. root thickness (Newsham et al. 1995a)) share the same phylogenetic signal as molecular traits such as R and *avr* genes that evolved through host-pathogen co-evolution (Gilbert and Parker 2016). Another question concerns the predictive power of fungal phylogeny (Gilbert and Parker 2016): do closely related fungi share the same host plants (Kia et al. 2017)?

These knowledge gaps on belowground plant-fungal interactions in diverse ecosystems can be closed through the combined power of ecology and plant pathology. The answers will improve our predictions of potential pathogen-host combinations in species-rich grasslands and aid in the design of effective intercropping strategies. These sustainable cropping systems are urgently required due to the adverse environmental effects of many pesticides and the strict regulation of their use (Hillocks 2012). The 100-yr old insights of Johanna Westerdijk on the importance of complex species interactions in explaining plant disease dynamics will thus remain highly relevant in the next decade of both sustainable agriculture and biodiversity research. Learning from diverse, natural grasslands serves as a scientific basis for the application of crop diversification – and its potentials for reduction of soil-borne disease pressure.

Compliance with ethical standards

Conflict of interest All authors (E.A.A.; J.v.R; J.M.R; A.J.T.; L.M.) declare that they have no conflict of interest. Ethical approval: This article does not contain any studies with human participants or animals performed by any of the authors.

References

Alexander, H. M. (2010). Disease in natural plant populations, communities, and ecosystems: Insights into ecological and evolutionary processes. *Plant Disease, 94*(5), 492–503. https://doi.org/10.1094/PDIS-94-5-0492.

Alexander, H. M., & Mihail, J. D. (2000). Seedling disease in an annual legume: consequences for seedling mortality, plant size, and population seed production. *Oecologia, 122*(3), 346–353. https://doi.org/10.1007/s004420050040.

Anderson, I. C., & Parkin, P. I. (2007). Detection of active soil fungi by RT-PCR amplification of precursor rRNA molecules. *Journal of Microbiological Methods, 68*(2), 248–253. https://doi.org/10.1016/j.mimet.2006.08.005.

Bach, E. M., Williams, R. J., Hargreaves, S. K., Yang, F., & Hofmockel, K. S. (2018). Greatest soil microbial diversity found in micro-habitats. *Soil Biology and Biochemistry, 118*, 217–226. https://doi.org/10.1016/j.soilbio.2017.12.018.

Baetz, U., & Martinoia, E. (2014). Root exudates: The hidden part of plant defense. *Trends in Plant Science, 19*(2), 90–98. https://doi.org/10.1016/j.tplants.2013.11.006.

Bagchi, R., Gallery, R. E., Gripenberg, S., Gurr, S. J., Narayan, L., Addis, C. E., Freckleton, R. P., & Lewis, O. T. (2014). Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature, 506*(7486), 85–88. https://doi.org/10.1038/nature12911.

Bakker, M. G., Bradeen, J. M., & Kinkel, L. L. (2013). Effects of plant host species and plant community richness on streptomycete community structure. *FEMS Microbiology Ecology, 83*(3), 596–606. https://doi.org/10.1111/1574-6941.12017.

Berendsen, R. L., Pieterse, C. M. J., & Bakker, P. A. H. M. (2012). The rhizosphere microbiome and plant health. *Trends in Plant Science, 17*(8), 478–486. https://doi.org/10.1016/j.tplants.2012.04.001.

Berendsen, R. L., Vismans, G., Yu, K., Song, Y., de Jonge, R., Burgman, W. P., Burmølle, M., Herschend, J., Bakker, P. A. H. M., & Pieterse, C. M. J. (2018). Disease-induced assemblage of a plant-beneficial bacterial consortium. *The ISME*

Journal, 12(6), 1496–1507. https://doi.org/10.1038/s41396-018-0093-1.

Berg, G., & Smalla, K. (2009). Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. *FEMS Microbiology Ecology, 68*(1), 1–13. https://doi.org/10.1111/j.1574-6941.2009.00654.x.

Bever, J. D., Mangan, S. A., & Alexander, H. M. (2015). Maintenance of plant species diversity by pathogens. *Annual Review of Ecology, Evolution, and Systematics, 46*(1), 305–325. https://doi.org/10.1146/annurev-ecolsys-112414-054306.

Blackwell, M. (2011). The fungi: 1, 2, 3 ... 5.1 million species? *American Journal of Botany, 98*(3), 426–438. https://doi.org/10.3732/ajb.1000298.

Boine, B., Renner, A. C., Zellner, M., & Nechwatal, J. (2014). Quantitative methods for assessment of the impact of different crops on the inoculum density of *Rhizoctonia solani* AG2-2IIIB in soil. *European Journal of Plant Pathology, 140*(4), 745–756. https://doi.org/10.1007/s10658-014-0506-6.

Boudreau, M. A. (2013). Diseases in intercropping systems. *Annual Review of Phytopathology, 51*(1), 499–519. https://doi.org/10.1146/annurev-phyto-082712-102246.

Brader, G., Compant, S., Vescio, K., Mitter, B., Trognitz, F., Ma, L.-J., & Sessitsch, A. (2017). Ecology and genomic insights into plant-pathogenic and plant-nonpathogenic Endophytes. *Annual Review of Phytopathology, 55*(1), 61–83. https://doi.org/10.1146/annurev-phyto-080516-035641.

Brown, J. K. M., & Hovmøller, M. S. (2002). Aerial dispersal of fungi on the global and continental scales and its consequences for plant disease. *Science, 297*(5581), 537–541. https://doi.org/10.1126/science.1072678.

Bucher, E. S., & Wilkinson, H. T. (2007). The pathogenicity of *Gaeumannomyces incrustans* on turfgrass *Zoysia japonica*. *Canadian Journal of Plant Pathology, 29*(1), 56–62. https://doi.org/10.1080/07060660709507437.

Buée, A. M., Reich, M., Murat, C., Morin, E., Nilsson, R. H., Uroz, S., et al. (2014). 454 Pyrosequencing analyses of forest soils reveal an high fungal diversity unexpectedly. *New Phytologist, 184*(2), 449–456.

Burdon, J. J., & Chilvers, G. A. (1975). Epidemiology of damping-off disease (*Pythium irregulare*) in relation to density of *Lepidium sativum* seedlings. *Annals of Applied Biology, 81*(2), 135–143. https://doi.org/10.1111/j.1744-7348.1975.tb00530.x.

Burdon, J. J., & Chilvers, G. A. (1976). Epidemiology of *Pythium*-induced damping-off in mixed species seedling stands. *Annals of Applied Biology, 82*(2), 233–240. https://doi.org/10.1111/j.1744-7348.1976.tb00558.x.

Burdon, J. J., Thrall, P. H., & Ericson, L. (2006). The current and future dynamics of disease in plant communities. *Annual Review of Phytopathology, 44*(1), 19–39. https://doi.org/10.1146/annurev.phyto.43.040204.140238.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature, 486*(7401), 59–67. https://doi.org/10.1038/nature11148.

Chapelle, E., Mendes, R., Bakker, P. A. H., & Raaijmakers, J. M. (2016). Fungal invasion of the rhizosphere microbiome. *The ISME Journal, 10*(1), 265–268. https://doi.org/10.1038/ismej.2015.82.

Cong, W.-F., van Ruijven, J., Mommer, L., De Deyn, G. B., Berendse, F., & Hoffland, E. (2014). Plant species richness promotes soil carbon and nitrogen stocks in grasslands without legumes. *Journal of Ecology, 102*(5), 1163–1170. https://doi.org/10.1111/1365-2745.12280.

Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In P. J. den Boer & G. R. Gradwell (Eds.), *Dynamics of populations* (pp. 298–312). Wageningen: Center for Agricultural Publishing and Documentation.

Cortois, R., Schröder-Georgi, T., Weigelt, A., van der Putten, W. H., & De Deyn, G. B. (2016). Plant-soil feedbacks: role of plant functional group and plant traits. *Journal of Ecology, 104*(6), 1608–1617. https://doi.org/10.1111/1365-2745.12643.

Dassen, S., Cortois, R., Martens, H., de Hollander, M., Kowalchuk, G. A., van der Putten, W. H., & De Deyn, G. B. (2017). Differential responses of soil bacteria, fungi, archaea and protists to plant species richness and plant functional group identity. *Molecular Ecology, 26*(15), 4084–4098. https://doi.org/10.1111/mec.14175.

de Boer, W. (2017). Upscaling of fungal–bacterial interactions: from the lab to the field. *Current Opinion in Microbiology, 37*, 35–41. https://doi.org/10.1016/j.mib.2017.03.007.

De Deyn, G. B., Raaijmakers, C. E., Zoomer, H. R., Berg, M. P., de Ruiter, P. C., Verhoef, H. A., Bezemer, T. M., van der Putten, W. H. (2003) Soil invertebrate fauna enhances grassland succession and diversity. *Nature 422* (6933):711-713

de Kroon, H., Hendriks, M., van Ruijven, J., Ravenek, J., Padilla, F. M., Jongejans, E., Visser, E. J. W., & Mommer, L. (2012). Root responses to nutrients and soil biota: drivers of species coexistence and ecosystem productivity. *Journal of Ecology, 100*(1), 6–15. https://doi.org/10.1111/j.1365-2745.2011.01906.x.

Dignam, B. E. A., O'Callaghan, M., Condron, L. M., Raaijmakers, J. M., Kowalchuk, G. A., & Wakelin, S. A. (2016). Challenges and opportunities in harnessing soil disease suppressiveness for sustainable pasture production. *Soil Biology and Biochemistry, 95*, 100–111. https://doi.org/10.1016/j.soilbio.2015.12.006.

Eppinga, M. B., Rietkerk, M., Dekker, S. C., & De Ruiter, P. C. (2006). Accumulation of local pathogens: a new hypothesis to explain exotic plant invasions. *Oikos, 114*(1), 168–176.

Fitt, B. D. L., McCartney, H. A., & Walklate, P. J. (1989). The role of rain in dispersal of pathogen inoculum. *Annual Review of Phytopathology, 27*(1), 241–270. https://doi.org/10.1146/annurev.py.27.090189.001325.

Frank, D. A., Pontes, A. W., Maine, E. M., & Fridley, J. D. (2015). Fine-scale belowground species associations in temperate grassland. *Molecular Ecology, 24*(12), 3206–3216. https://doi.org/10.1111/mec.13232.

Gaetán, S., Madia, M., & Cepeda, R. (2004). First report of *Fusarium* crown and root rot caused by *Fusarium solani* on St. John's-Wort in Argentina. *Plant Disease, 88*(9), 1050. https://doi.org/10.1094/PDIS.2004.88.9.1050B.

Garrett, K. A., & Mundt, C. C. (1999). Epidemiology in mixed host populations. *Phytopathology, 89*(11), 984–990. https://doi.org/10.1094/PHYTO.1999.89.11.984.

Gilbert, G. S. (2002). Evolutionary ecology of plant diseases in natural ecosystems. *Annual Review of Phytopathology,*

40(1), 13–43. https://doi.org/10.1146/annurev.phyto.40.021202.110417.

Gilbert, G. S., & Parker, I. M. (2016). The evolutionary ecology of plant disease: a phylogenetic perspective. *Annual Review of Phytopathology, 54*(1), 549–578. https://doi.org/10.1146/annurev-phyto-102313-045959.

Gilbert, G. S., & Webb, C. O. (2007). Phylogenetic signal in plant pathogen-host range. *Proceedings of the National Academy of Sciences of the United States of America, 104*(12), 4979–4983. https://doi.org/10.1073/pnas.0607968104.

Gilbert, G. S., Handelsman, J., & Parke, J. L. (1994). Root camouflage and disease control. *Phytopathology (USA), 84*(3), 222–225.

Gómez Expósito, R., de Bruijn, I., Postma, J., & Raaijmakers, J. M. (2017). Current insights into the role of rhizosphere bacteria in disease suppressive soils. *Frontiers in Microbiology, 8*, 2529. https://doi.org/10.3389/fmicb.2017.02529.

Gordon, T. R., & Martyn, R. D. (1997). The evolutionary biology of *Fusarium oxysporum*. *Annual Review of Phytopathology, 35*, 111–128.

Haas, S. E., Hooten, M. B., Rizzo, D. M., & Meentemeyer, R. K. (2011). Forest species diversity reduces disease risk in a generalist plant pathogen invasion. *Ecology Letters, 14*(11), 1108–1116. https://doi.org/10.1111/j.1461-0248.2011.01679.x.

Hacquard, S., Kracher, B., Hiruma, K., Münch, P. C., Garrido-Oter, R., Thon, M. R., Weimann, A., Damm, U., Dallery, J. F., Hainaut, M., Henrissat, B., Lespinet, O., Sacristán, S., ver Loren van Themaat, E., Kemen, E., McHardy, A. C., Schulze-Lefert, P., & O'Connell, R. J. (2016). Survival trade-offs in plant roots during colonization by closely related beneficial and pathogenic fungi. *Nature Communications, 7*(May), 11362. https://doi.org/10.1038/ncomms11362.

Hacquard, S., Spaepen, S., Garrido-Oter, R., & Schulze-Lefert, P. (2017). Interplay between innate immunity and the plant microbiota. *Annual Review of Phytopathology, 55*(1), 565–589. https://doi.org/10.1146/annurev-phyto-080516-035623.

Hannula, S. E., Morriën, E., De Hollander, M., Van Der Putten, W. H., Van Veen, J. A., & De Boer, W. (2017). Shifts in rhizosphere fungal community during secondary succession following abandonment from agriculture. *ISME Journal, 11*(10), 2294–2304. https://doi.org/10.1038/ismej.2017.90.

Hausmann, N. T., & Hawkes, C. V. (2009). Plant neighbourhood control of arbuscular mycorrhizal community composition. *New Phytologist, 183*(4), 1188–1200.

Hector, A. (1999). Plant diversity and productivity experiments in European grasslands. *Science, 286*(5442), 1123–1127. https://doi.org/10.1126/science.286.5442.1123.

Hendriks, M., Mommer, L., de Caluwe, H., Smit-Tiekstra, A. E., van der Putten, W. H., & de Kroon, H. (2013). Independent variations of plant and soil mixtures reveal soil feedback effects on plant community overyielding. *Journal of Ecology, 101*(2), 287–297. https://doi.org/10.1111/1365-2745.12032.

Hendriks, M., Raaijmakers, J. M., Reijers, V., Mortel, J. van de, Kroon, H. de, & Mommer, L. (2015a). The role of root-associated fungi as drivers of the plant diversity-productivity relationship. In: *Effects of plant-soil feedback on root distribution, plant competition and community productivity*. PhD thesis, Radboud University Nijmegen.

Hendriks, M., Ravenek, J. M., Smit-Tiekstra, A. E., van der Paauw, J. W., de Caluwe, H., van der Putten, W. H., de Kroon, H., & Mommer, L. (2015b). Spatial heterogeneity of plant-soil feedback affects root interactions and interspecific competition. *New Phytologist, 207*(3), 830–840. https://doi.org/10.1111/nph.13394.

Herben, T., Hadincová, F., & Kováříová, V. (1993). Small-scale spatial dynamics of plant species in a grassland community over six years. *Journal of Vegetation Science, 4*, 171–178. https://doi.org/10.2307/3236102.

Hernandez-Escribano, L., Iturritxa, E., Elvira-Recuenco, M., Berbegal, M., Campos, J. A., Renobales, G., García, I., & Raposo, R. (2018). Herbaceous plants in the understory of a pitch canker-affected *Pinus radiata* plantation are endophytically infected with *Fusarium circinatum*. *Fungal Ecology, 32*, 65–71. https://doi.org/10.1016/j.funeco.2017.12.001.

Hersh, M. H., Vilgalys, R., & Clark, J. S. (2012). Evaluating the impacts of multiple generalist fungal pathogens on temperate tree seedling survival. *Ecology, 93*(3), 511–520. https://doi.org/10.1890/11-0598.1.

Hiddink, G. A. (2008). *Suppression of soilborne pathogens in mixed cropping systems*. PhD thesis, Wageningen University.

Hiddink, G. A., Termorshuizen, A. J., & Van Bruggen, A. H. C. (2010). Mixed cropping and suppression of Soilborne diseases. In E. Lichtfouse (Ed.), *Genetic Engineering, Biofertilisation, Soil Quality and Organic Farming. Sustainable Agriculture Reviews* (Vol. 4). Dordrecht: Springer. https://doi.org/10.1007/978-90-481-8741-6.

Hillocks, R. J. (2012). Farming with fewer pesticides: EU pesticide review and resulting challenges for UK agriculture. *Crop Protection, 31*(1), 85–93. https://doi.org/10.1016/j.cropro.2011.08.008.

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist, 104*(940), 501–528. https://doi.org/10.1086/282687.

Jesch, A., Barry, K. E., Ravenek, J., Bachmann, D., Strecker, T., Weigelt, A., et al. (2018). Belowground resource partitioning alone cannot explain the biodiversity-ecosystem function relationship: A field test using multiple tracers. *Journal of Ecology*. https://doi.org/10.1111/1365-2745.12947.

Johnson, D. J., Beaulieu, W. T., Bever, J. D., & Clay, K. (2012). Conspecific negative density dependence and Forest diversity. *Science, 336*(6083), 904–907.

Jumpponen, A., Jones, K. L., & Blair, J. (2010). Vertical distribution of fungal communities in tallgrass prairie soil. *Mycologia, 102*(5), 1027–1041. https://doi.org/10.3852/09-316.

Kesanakurti, P. R., Fazekas, A. J., Burgess, K. S., Percy, D. M., Newmaster, S. G., Graham, S. W., et al. (2011). Spatial patterns of plant diversity below-ground as revealed by DNA barcoding. *Molecular Ecology, 20*(6), 1289–1302. https://doi.org/10.1111/j.1365-294X.2010.04989.x.

Kia, S. H., Glynou, K., Nau, T., Thines, M., Piepenbring, M., & Maciá-Vicente, J. G. (2017). Influence of phylogenetic conservatism and trait convergence on the interactions between fungal root endophytes and plants. *The ISME Journal, 11*(3), 777–790. https://doi.org/10.1038/ismej.2016.140.

Kia, S. H., Jurkechova, M., Glynou, K., Piepenbring, M., & Macia-Vicente, J. G. (2018). The effects of fungal root endophytes on plant growth are stable along gradients of abiotic habitat conditions. *FEMS Microbiology Ecology, 94*(2). https://doi.org/10.1093/femsec/fix162/4654843.

Klironomos, J. N. (2002). Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature, 417*(6884), 67–70. https://doi.org/10.1038/417067a.

Knops, J. M. H., Tilman, D., Haddad, N. M., Naeem, S., Mitchell, C. E., Haarstad, J., Ritchie, M. E., Howe, K. M., Reich, P. B., Siemann, E., & Groth, J. (1999). Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters, 2*(5), 286–293. https://doi.org/10.1046/j.1461-0248.1999.00083.x.

Kos, M., Veendrick, J., & Bezemer, T. M. (2013). Local variation in conspecific plant density influences plant-soil feedback in a natural grassland. *Basic and Applied Ecology, 14*(6), 506–514. https://doi.org/10.1016/j.baae.2013.07.002.

Krupinsky, J. M., Bailey, K. L., Mcmullen, M. P., Gossen, B. D., & Turkington, T. K. (2002). Managing plant disease risk in diversified cropping systems. *Agronomy Journal, 94*(April), 198–209. https://doi.org/10.2134/AGRONJ2002.1980.

Kulmatiski, A., Beard, K. H., & Heavilin, J. (2012). Plant–soil feedbacks provide an additional explanation for diversity–productivity relationships. *Proceedings of the Royal Society of London B: Biological Sciences, 279*(1740), 3020–3026.

Larkin, R. P. (2015). Soil health paradigms and implications for disease management. *Annual Review of Phytopathology, 53*(1), 199–221. https://doi.org/10.1146/annurev-phyto-080614-120357.

Latz, E., Eisenhauer, N., Rall, B. C., Allan, E., Roscher, C., Scheu, S., & Jousset, A. (2012). Plant diversity improves protection against soil-borne pathogens by fostering antagonistic bacterial communities. *Journal of Ecology, 100*(3), 597–604. https://doi.org/10.1111/j.1365-2745.2011.01940.x.

LeBlanc, N., Kinkel, L. L., & Kistler, H. C. (2014). Soil fungal communities respond to grassland plant community richness and soil Edaphics. *Microbial Ecology, 70*(1), 188–195. https://doi.org/10.1007/s00248-014-0531-1.

Leff, J. W., Bardgett, R. D., Wilkinson, A., Jackson, B. G., Pritchard, W. J., de Long, J. R., Oakley, S., Mason, K. E., Ostle, N. J., Johnson, D., Baggs, E. M., & Fierer, N. (2018). Predicting the structure of soil communities from plant community taxonomy, phylogeny, and traits. *ISME Journal, 12*, 1–12. https://doi.org/10.1038/s41396-018-0089-x.

Levine, J. M., Bascompte, J., Adler, P. B., & Allesina, S. (2017). Beyond pairwise mechanisms of species coexistence in complex communities. *Nature, 546*(7656), 56–64. https://doi.org/10.1038/nature22898.

Li, X., de Boer, W., Zhang, Y., Ding, C., Zhang, T., & Wang, X. (2018). Suppression of soil-borne *Fusarium* pathogens of peanut by intercropping with the medicinal herb *Atractylodes lancea*. *Soil Biology and Biochemistry, 116*(May 2017), 120–130. https://doi.org/10.1016/j.soilbio.2017.09.029.

Liu, Y., Yu, S., Xie, Z. P., & Staehelin, C. (2012). Analysis of a negative plant-soil feedback in a subtropical monsoon forest. *Journal of Ecology, 100*(4), 1019–1028. https://doi.org/10.1111/j.1365-2745.2012.01953.x.

Liu, Y., Fang, S., Chesson, P., & He, F. (2015a). The effect of soil-borne pathogens depends on the abundance of host tree species. *Nature Communications, 6*, 10017. https://doi.org/10.1038/ncomms10017.

Liu, X., Etienne, R., Liang, M., Wang, Y., & Yu, S. (2015b). Experimental evidence for an intraspecific Janzen-Connell

effect mediated by soil biota. *Ecology, 96*(August), 662–671. https://doi.org/10.1890/14-0014.1.

Liu, X., Liang, M., Etienne, R. S., Gilbert, G. S., & Yu, S. (2016). Phylogenetic congruence between subtropical trees and their associated fungi. *Ecology and Evolution, 6*(23), 8412–8422. https://doi.org/10.1002/ece3.2503.

Lofgren, L. A., LeBlanc, N. R., Certano, A. K., Nachtigall, J., LaBine, K. M., Riddle, J., Broz, K., Dong, Y., Bethan, B., Kafer, C. W., & Kistler, H. C. (2018). *Fusarium graminearum*: pathogen or endophyte of North American grasses? *New Phytologist, 217*(3), 1203–1212. https://doi.org/10.1111/nph.14894.

Malcolm, G. M., Kuldau, G. A., Gugino, B. K., & Jiménez-Gasco, M. d. M. (2013). Hidden host plant associations of Soilborne fungal pathogens: an ecological perspective. *Phytopathology, 103*(6), 538–544. https://doi.org/10.1094/PHYTO-08-12-0192-LE.

Mallon, C. A., Van Elsas, J. D., & Salles, J. F. (2015). Microbial invasions: the process, patterns, and mechanisms. *Trends in Microbiology, 23*(11), 719–729. https://doi.org/10.1016/j.tim.2015.07.013.

Mandeel, Q., & Baker, R. (1991). Mechanisms involved in biological control of Fusarium wilt of cucumber with strains of nonpathogenic Fusariutn oxysporum. *Phytopathology, 81*, 462–469.

Mangan, S. A., Schnitzer, S. A., Herre, E. A., Mack, K. M. L., Valencia, M. C., Sanchez, E. I., & Bever, J. D. (2010). Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature, 466*(7307), 752–755. https://doi.org/10.1038/nature09273.

Maron, J. L., Marler, M., Klironomos, J. N., & Cleveland, C. C. (2011). Soil fungal pathogens and the relationship between plant diversity and productivity. *Ecology Letters, 14*(1), 36–41. https://doi.org/10.1111/j.1461-0248.2010.01547.x.

McCarthy-Neumann, S., & Ibáñez, I. (2013). Plant–soil feedback links negative distance dependence and light gradient partitioning during seedling establishment. *Ecology, 94*(4), 780–786.

Mendes, R., Kruijt, M., de Bruijn, I., Dekkers, E., van der Voort, M., Schneider, J. H. M., Piceno, Y. M., DeSantis, T. Z., Andersen, G. L., Bakker, P. A. H. M., & Raaijmakers, J. M. (2011). Deciphering the rhizosphere microbiome for disease-suppressive bacteria. *Science, 332*(6033), 1097–1100. https://doi.org/10.1126/science.1203980.

Michielse, C. B., & Rep, M. (2009). Pathogen profile update: *Fusarium oxysporum*. *Molecular Plant Pathology, 10*(3), 311–324. https://doi.org/10.1111/j.1364-3703.2009.00538.x.

Mihail, J. D., Alexander, H. M., & Taylor, S. J. (1998). Interactions between root-infecting fungi and plant density in an annual legume. *Journal of Ecology, 86*, 739–748.

Mills, K. E., & Bever, J. D. (1998). Maintenance of diversity within plant communities: soil pathogens as agents of negative feedback. *Ecology, 79*(5), 1595–1601.

Mitchell, C. E., Tilman, D., & Groth, J. V. (2002). Effects of grassland plant species diversity, abundance, and composition on foliar fungal disease. *Ecology, 83*(6), 1713–1726.

Mommer, L., Cotton, T. E. A., Raaijmakers, J. M., Termorshuizen, A. J., van Ruijven, J., Hendriks, M., van Rijssel, S. Q., van de Mortel, J. E., van der Paauw, J. W., Schijlen, E. G. W. M., Smit-Tiekstra, A. E., Berendse, F., de Kroon, H., & Dumbrell, A. J. (2018). Lost in diversity: The interactions between soil-borne

fungi, biodiversity and plant productivity. *New Phytologist, 218*(2), 542–553. https://doi.org/10.1111/nph.15036.

Moore, S. M., & Borer, E. T. (2012). The influence of host diversity and composition on epidemiological patterns at multiple spatial scales. *Ecology, 93*(5), 1095–1105. https://doi.org/10.1890/11-0086.1.

Mueller, K. E., Tilman, D., Fornara, D. A., & Hobbie, S. E. (2013). Root depth distribution and the diversity–productivity relationship in a long-term grassland experiment. *Ecology, 94*(4), 787–793. https://doi.org/10.1890/12-1399.1.

Newsham, K. K., Fitter, A. H., & Watkinson, A. R. (1995a). Multi-functionality and biodiversity in arbuscular mycorrhizas. *Trends in Ecology & Evolution, 10*(10), 407–411.

Newsham, K. K., Fitter, A. H., & Watkinson, A. R. (1995b). Arbuscular Mycorrhiza protect an annual grass from root pathogenic Fungi in the field. *Journal of Ecology, 83*(6), 991–1000.

Nguyen, N. H., Song, Z., Bates, S. T., Branco, S., Tedersoo, L., Menke, J., Schilling, J. S., & Kennedy, P. G. (2016). FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecology, 20*, 241–248. https://doi.org/10.1016/j.funeco.2015.06.006.

Olff, H., Hoorens, B., de Goede, R. G. M., van der Putten, W. H., & Gleichman, J. M. (2000). Small-scale shifting mosaics of two dominant grassland species: The possible role of soil-borne pathogens. *Oecologia, 125*(1), 45–54. https://doi.org/10.1007/PL00008890.

Otten, W., & Gilligan, C. A. (2004). Empirical evidence of spatial thresholds to control invasion of fungal parasites and saprotrophs. *New Phytologist, 163*(1), 125–132. https://doi.org/10.1111/j.1469-8137.2004.01086.x.

Otten, W., Filipe, J. A. N., & Gilligan, C. A. (2005). Damping-off epidemics, contact structure, and disease transmission in mixed-species populations. *Ecology, 86*(7), 1948–1957. https://doi.org/10.1890/04-1122.

Packer, A., & Clay, K. (2000). Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature, 404*(6775), 278–281. https://doi.org/10.1038/35005072.

Parker, I. M., Saunders, M., Bontrager, M., Weitz, A. P., Hendricks, R., Magarey, R., Suiter, K., & Gilbert, G. S. (2015). Phylogenetic structure and host abundance drive disease pressure in communities. *Nature, 520*(7548), 542–544. https://doi.org/10.1038/nature14372.

Peay, K. G. (2014). Back to the future: natural history and the way forward in modern fungal ecology. *Fungal Ecology, 12*, 4–9. https://doi.org/10.1016/j.funeco.2014.06.001.

Petermann, J. S., Fergus, A. J. F., Turnbull, L. A., & Schmid, B. (2008). Janzen-Connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology, 89*(9), 2399–2406. https://doi.org/10.1890/07-2056.1.

Philippot, L., Raaijmakers, J. M., Lemanceau, P., & van der Putten, W. H. (2013). Going back to the roots: The microbial ecology of the rhizosphere. *Nature Reviews Microbiology, 11*(11), 789–799. https://doi.org/10.1038/nrmicro3109.

Prober, S. M., Leff, J. W., Bates, S. T., Borer, E. T., Firn, J., Harpole, W. S., Lind, E. M., Seabloom, E. W., Adler, P. B., Bakker, J. D., Cleland, E. E., DeCrappeo, N. M., DeLorenze, E., Hagenah, N., Hautier, Y., Hofmockel, K. S., Kirkman, K. P., Knops, J. M. H., la Pierre, K. J., MacDougall, A. S., McCulley, R. L., Mitchell, C. E., Risch, A. C., Schuetz, M., Stevens, C. J., Williams, R. J., & Fierer, N. (2015). Plant diversity predicts beta but not alpha diversity of soil microbes

across grasslands worldwide. *Ecology Letters, 18*(1), 85–95. https://doi.org/10.1111/ele.12381.

Raaijmakers, J. M., Paulitz, T. C., Steinberg, C., Alabouvette, C., & Moënne-Loccoz, Y. (2009). The rhizosphere: a playground and battlefield for soilborne pathogens and beneficial microorganisms. *Plant and Soil, 321*(1–2), 341–361. https://doi.org/10.1007/s11104-008-9568-6.

Ratnadass, A., Fernandes, P., Avelino, J., & Habib, R. (2012). Plant species diversity for sustainable management of crop pests and diseases in agroecosystems: a review. *Agronomy for Sustainable Development, 32*(1), 273–303. https://doi.org/10.1007/s13593-011-0022-4.

Ravenek, J. M., Bessler, H., Engels, C., Scherer-Lorenzen, M., Gessler, A., Gockele, A., de Luca, E., Temperton, V. M., Ebeling, A., Roscher, C., Schmid, B., Weisser, W. W., Wirth, C., de Kroon, H., Weigelt, A., & Mommer, L. (2014). Long-term study of root biomass in a biodiversity experiment reveals shifts in diversity effects over time. *Oikos, 123*(12), 1528–1536. https://doi.org/10.1111/oik.01502.

Rodriguez, R. J., White, J. F., Arnold, a. E., & Redman, R. S. (2009). Fungal endophytes: diversity and functional roles. *The New Phytologist, 182*(2), 314–330. https://doi.org/10.1111/j.1469-8137.2009.02773.x.

Rodriguez-Moreno, L., Ebert, M. K., Bolton, M. D., & Thomma, B. P. H. J. (2018). Tools of the crook- infection strategies of fungal plant pathogens. *Plant Journal, 93*(4), 664–674. https://doi.org/10.1111/tpj.13810.

Rottstock, T., Joshi, J., Kummer, V., & Fischer, M. (2014). Higher plant diversity promotes higher diversity of fungal pathogens, while it decreases pathogen infection per plant. *Ecology, 95*(7), 1907–1917. https://doi.org/10.1890/13-2317.1.

Schlatter, D., Kinkel, L., Thomashow, L., Weller, D., & Paulitz, T. (2017). Disease suppressive soils: New insights from the soil microbiome. *Phytopathology, 107*(11), 1284–1297. https://doi.org/10.1094/PHYTO-03-17-0111-RVW.

Schlemper, T. R., van Veen, J. A., & Kuramae, E. E. (2017). Co-variation of bacterial and fungal communities in different Sorghum cultivars and growth stages is soil dependent. *Microbial Ecology., 76*, 205–214. https://doi.org/10.1007/s00248-017-1108-6.

Schnitzer, S. A., Klironomos, J. N., Hillerislambers, J., Kinkel, L. L., Reich, P. B., Xiao, K., et al. (2011). Soil microbes drive the classic plant-productivity diversity pattern. *Ecology, 92*(2), 296–303.

Schulz-Bohm, K., Gerards, S., Hundscheid, M., Melenhorst, J., de Boer, W., & Garbeva, P. (2018). Calling from distance: attraction of soil bacteria by plant root volatiles. *The ISME Journal., 12*, 1252–1262. https://doi.org/10.1038/s41396-017-0035-3.

Schulze, E.-D., & Mooney, H. A. (1994). *Biodiversity and ecosystem function.* Berlin: Springer-Verlag.

Smiley, R. W., Dernoeden, P. H., & Clarke, B. B. (2005). *Compendium of Turfgrass diseases* (3rd ed.). St. Paul: American Phytopathological Society.

Smith, V. L., Campbell, C. L., Jenkins, S. F., & Benson, D. M. (1988). Effects of host density and number of disease foci on epidemics of southern blight of processing carrot. *Phytopathology, 78*(5), 595–600.

Song, Y. N., Zhang, F. S., Marschner, P., Fan, F. L., Gao, H. M., Bao, X. G., Sun, J. H., & Li, L. (2007). Effect of intercropping on crop yield and chemical and microbiological properties in rhizosphere of wheat (*Triticum aestivum* L.), maize (*Zea mays* L.),

and faba bean (*Vicia faba* L.). *Biology and Fertility of Soils, 43*(5), 565–574. https://doi.org/10.1007/s00374-006-0139-9.

Steinauer, K., Chatzinotas, A., & Eisenhauer, N. (2016). Root exudate cocktails: the link between plant diversity and soil microorganisms? *Ecology and Evolution, 6*(20), 7387–7396. https://doi.org/10.1002/ece3.2454.

Tedersoo, L. (2014). Global diversity and geography of soil fungi. *Science, 346*(6213), 1052–1053. https://doi.org/10.1126/science.aaa1185.

Termorshuizen, A. J. (2014). Root pathogens. In J. A. K. John Dighton (Ed.), *Interactions in soil: promoting plant growth* (Vol. 1, pp. 119–137). https://doi.org/10.1007/978-94-017-8890-8.

Termorshuizen, A. J. (2016). Ecology of fungal plant pathogens. *Microbiology Spectrum, 4*(6). https://doi.org/10.1128/microbiolspec.FUNK-0013-2016.

Tilman, D. (1997). The influence of functional diversity and composition on ecosystem processes. *Science, 277*(5330), 1300–1302. https://doi.org/10.1126/science.277.5330.1300.

Tilman, D. (2001). Diversity and productivity in a long-term grassland experiment. *Science, 294*(5543), 843–845. https://doi.org/10.1126/science.1060391.

Trenbath, B. R. (1993). Intercropping for the management of pests and diseases. *Field Crops Research, 34*(3–4), 381–405. https://doi.org/10.1016/0378-4290(93)90123-5.

Turrà, D., & Di Pietro, A. (2015). Chemotropic sensing in fungus-plant interactions. *Current Opinion in Plant Biology, 26*, 135–140. https://doi.org/10.1016/j.pbi.2015.07.004.

Turrà, D., El Ghalid, M., Rossi, F., & Di Pietro, A. (2015). Fungal pathogen uses sex pheromone receptor for chemotropic sensing of host plant signals. *Nature, 527*(7579), 521–524. https://doi.org/10.1038/nature15516.

Van der Maarel, E., & Sykes, M. (1993). Small scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. *Journal of Vegetation Science, 4*(2), 179–188. https://doi.org/10.2307/3236103.

van der Voort, M., Kempenaar, M., van Driel, M., Raaijmakers, J. M., & Mendes, R. (2016). Impact of soil heat on reassembly of bacterial communities in the rhizosphere microbiome and plant disease suppression. *Ecology Letters, 19*(4), 375–382. https://doi.org/10.1111/ele.12567.

van Ruijven, J., & Berendse, F. (2005). Diversity-productivity relationships: initial effects, long-term patterns, and underlying mechanisms. *Proceedings of the National Academy of Sciences of the United States of America, 102*(3), 695–700. https://doi.org/10.1073/pnas.0407524102.

Van Ruijven, J., & Berendse, F. (2009). Long-term persistence of a positive plant diversity-productivity relationship in the absence of legumes. *Oikos, 118*(1), 101–106. https://doi.org/10.1111/j.1600-0706.2008.17119.x.

Van Ruijven, J., De Deyn, G. B., & Berendse, F. (2003). Diversity reduces invasibility in experimental plant communities: the role of plant species. *Ecology Letters, 6*(10), 910–918. https://doi.org/10.1046/j.1461-0248.2003.00516.x.

van Schie, C. C. N., & Takken, F. L. W. (2014). Susceptibility genes 101: how to be a good host. *Annual Review of Phytopathology, 52*(1), 551–581. https://doi.org/10.1146/annurev-phyto-102313-045854.

Vandenkoornhuyse, P. (2002). Extensive fungal diversity in plant roots. *Science, 295*(5562), 2051. https://doi.org/10.1126/science.295.5562.2051.

Vandermeer, J. H. (2011). *The ecology of agroecosystems*. Massachussetts: Jones and Bartlett Publishers.

Wehner, J., Powell, J. R., Muller, L. A. H., Caruso, T., Veresoglou, S. D., Hempel, S., & Rillig, M. C. (2014). Determinants of root-associated fungal communities within Asteraceae in a semi-arid grassland. *Journal of Ecology, 102*(2), 425–436. https://doi.org/10.1111/1365-2745.12197.

Weisser, W. W., Roscher, C., Meyer, S. T., Ebeling, A., Luo, G., Allan, E., Beßler, H., Barnard, R. L., Buchmann, N., Buscot, F., Engels, C., Fischer, C., Fischer, M., Gessler, A., Gleixner, G., Halle, S., Hildebrandt, A., Hillebrand, H., de Kroon, H., Lange, M., Leimer, S., le Roux, X., Milcu, A., Mommer, L., Niklaus, P. A., Oelmann, Y., Proulx, R., Roy, J., Scherber, C., Scherer-Lorenzen, M., Scheu, S., Tscharntke, T., Wachendorf, M., Wagg, C., Weigelt, A., Wilcke, W., Wirth, C., Schulze, E. D., Schmid, B., & Eisenhauer, N. (2017). Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: Patterns, mechanisms, and open questions. *Basic and Applied Ecology, 23*, 1–73. https://doi.org/10.1016/j.baae.2017.06.002.

Willocquet, L., Jumel, S., & Lemarchand, E. (2007). Spatio-temporal development of pea root rot disease through secondary infections during a crop cycle. *Journal of Phytopathology, 155*(10), 623–632. https://doi.org/10.1111/j.1439-0434.2007.01289.x.

Wilson, J. B., Peet, R. K., Dengler, J., & Pärtel, M. (2012). Plant species richness: The world records. *Journal of Vegetation Science, 23*(4), 796–802. https://doi.org/10.1111/j.1654-1103.2012.01400.x.

Wright, A. J., Wardle, D. A., Callaway, R., & Gaxiola, A. (2017). The overlooked role of facilitation in biodiversity experiments. *Trends in Ecology & Evolution, 32*(5), 383–390. https://doi.org/10.1016/j.tree.2017.02.011.

Wubs, E. R. J., & Bezemer, T. M. (2018). Plant community evenness responds to spatial plant-soil feedback heterogeneity primarily through the diversity of soil conditioning. *Functional Ecology, 32*(2), 509–521. https://doi.org/10.1111/1365-2435.13017.

Yang, M., Zhang, Y., Qi, L., Mei, X., Liao, J., Ding, X., Deng, W., Fan, L., He, X., Vivanco, J. M., Li, C., Zhu, Y., & Zhu, S. (2014). Plant-plant-microbe mechanisms involved in soil-borne disease suppression on a maize and pepper intercropping system. *PLoS One, 9*(12), 1–22. https://doi.org/10.1371/journal.pone.0115052.

Yang, L., Maron, J. L., & Callaway, R. M. (2015). Inhibitory effects of soil biota are ameliorated by high plant diversity. *Oecologia, 179*(2), 519–525. https://doi.org/10.1007/s00442-015-3351-1.

Yang, T., Adams, J. M., Shi, Y., He, J., Jing, X., Chen, L., Tedersoo, L., & Chu, H. (2017). Soil fungal diversity in natural grasslands of the Tibetan plateau: associations with plant diversity and productivity. *New Phytologist, 215*(2), 756–765. https://doi.org/10.1111/nph.14606.

Yu, Y., Stomph, T. J., Makowski, D., & van der Werf, W. (2015). Temporal niche differentiation increases the land equivalent ratio of annual intercrops: a meta-analysis. *Field Crops Research, 184*, 133–144. https://doi.org/10.1016/j.fcr.2015.09.010.

Zimowska, B. (2013). Diversity of fungi colonizing and damaging selected parts of ribwort (*Plantago lanceolata* L.). *Acta Sci. Pol., Hortorum Cultus, 12*(3), 91–103.