Contrasting management techniques and soil types affect network connections between soil properties and the tulip microbiome

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Abstract

Conventional agriculture relies on high inputs of chemical fertilisers and pesticides, leading to extensive soil damage. As a result, there has been a shift towards organic cultivation to ameliorate these negative effects. However, knowledge gaps remain concerning how different agricultural management regimes can alter soil properties, root-associated biota and relationships between them. We sampled soils and bulbs from clay and sand tulip fields with conventional, organic and hybrid (i.e., intermediate between conventional and organic) management regimes to determine effects on abiotic and biotic soil properties, tulip bulb microbiomes/biota and network connectivity between them. We found that soil abiotic properties were not driven by management. However, soil microbial community composition was determined by interactions between soil type and management. Specifically, conventional management created more heterogeneous and homogenous bacterial and fungal soil communities, respectively, across soil types, while organic and hybrid soil communities differed between soil types. A partial least squares path model revealed that across all fields, soil properties determined the composition of tulip bulb biota (i.e., microorganisms, nematodes), while management techniques did not play a significant role, neither directly nor indirectly. Network analyses revealed more modular (i.e., independent) nodes of association in fields with sandy soils. Specifically, management techniques (i.e., chemical usage, ploughing depth, diminished crop rotation) formed a cluster that was independent from most soil (abiotic and biotic) and bulb biotic properties, while clay field networks showed the opposite. Our results indicate that conventional agriculture can homogenise soil microbial communities, with potential impacts on soil function and buffering capacity to stress. Increased modularity between soil properties, management techniques and tulip bulb biota in sand fields could mean increased resistance to disturbance and abiotic and biotic stress as a result of higher functional redundancy. Interactions between agricultural management regime and soil type must be taken into consideration when determining long-term influences on crop microbiome/biota associations and the potential effects on soil health and productivity.

Keywords: abiotic-biotic interactions; microorganisms; network analyses; organic cultivation; path model; plant microbiome

1 | INTRODUCTION

Modern agriculture relies on high inputs of chemical fertilisers, pesticides, nematicides and fungicides necessary to maintain crop health and soil productivity (Tilman *et al.*, 2002). Intensive agriculture increases nitrogen (N) pollution (Richter and Roelcke, 2000), reduces soil biodiversity (Tsiafouli *et al.*, 2015) and destroys soil fertility (Bünemann *et al.*, 2018). As a result, governments are phasing out damaging chemical inputs (Donley, 2019) and encouraging a shift towards organic agricultural (Palm *et al.*, 2014). The EU defines organic agriculture as: “an agricultural method that aims to produce food using natural substances and processes, [thereby promoting] the maintenance of biodiversity, preservation of regional ecological balances and enhancement of soil fertility”. These techniques can be used in both food and ornamental crop production. Shifting to organic cultivation typically lowers productivity (Palm *et al.*, 2014), but neutral to positive effects have also been observed (Badgley *et al.*, 2007). However, organic practices improve soil quality (Gomiero *et al.*, 2011), enhance ecosystem services (Palm *et al.*, 2014) and provide healthier food (Mie *et al.*, 2017). Organic cultivation can affect the soil microbial community, generating higher fungal abundance and network connectivity (Banerjee *et al.*, 2019), with knock-on effects for plant health (Blundell *et al.*, 2020). Nonetheless, many knowledge gaps remain pertaining to the impacts of such methods on the soil, particularly in relation to flower bulb crops (Sukkel and Hommes, 2009).

Healthy soil is the foundation of sustainable, long-term agricultural productivity. Soil microorganisms such as fungi and bacteria and soil animals such as nematodes, collembola and mites play an integral role in determining soil characteristics such as structure, food web composition, nutrient availability and disease level (Ruf and Beck, 2005; Huhta, 2007; Ferris, 2010). Soil communities with a high level of interdependence between taxonomic groups (i.e., network nodes), but with independence between said nodes (i.e., modularity), create soils that are more resistant to invasion by pathogens (Wei *et al.*, 2015; de Vries and Wallenstein, 2017) and environmental disturbance (de Vries *et al.*, 2012), leading to healthier plants (Bender *et al.*, 2016). Further, management regimes can strongly influence soil network connectivity, with chemical and organic amendments leading to loosely and tightly connected networks, respectively (Ling *et al.*, 2016; Banerjee *et al.*, 2019). The current push by the Dutch and EU governments for more sustainable agricultural practices relies on promoting healthier soils that naturally suppress pests and pathogens (Janvier *et al.*, 2007) and increase the inherent resistance of crops to abiotic and biotic stresses. With integrated knowledge about the relationships between the soil community, soil abiotic properties and plant health, we can build soils that are sustainable and productive. However, current knowledge is lacking about what conditions and management regimes are necessary to create connected, resistant soil networks.

Currently, there is a lack of information on the role soil networks play in determining crop health, in particular that of tulips (Hines *et al.*, 2015). Although a great deal of knowledge exists about the pathogens and pests of tulips (McGovern and Elmer, 2017; Looman *et al.*, 2018), the tulip bulb microbiome and biota (e.g., nematodes) that live on and in the bulbs, remains virtually uncharacterised. The very limited knowledge we do have comes from mixed plant communities in the tulip native range (Pershina *et al.*, 2016), meaning it is impossible to draw species-specific conclusions. Further, key information is missing on how management regimes that affect abiotic and biotic soil properties shape the tulip microbiome and the soil network. Acquiring a better understanding of soil networks in tulip fields is the first critical step towards developing more sustainable cultivation systems in the flower bulb industry, with broader application to other crops.

Here, we analysed soil abiotic and biotic conditions and tulip microbiomes/biota, across both sand and clay fields that employed conventional, organic and hybrid management regimes. We hypothesised: 1) Contrasting management regimes will generate differences in abiotic and biotic soil properties and bulb biota. This is because organic agriculture relies on reduced chemical pesticide and fertilizer inputs, while generally increasing, e.g., the addition of organic matter and the frequency of crop rotation schemes and these management techniques are strong determinants of soil properties (Gomiero *et al.*, 2011) and the microbiomes (Arif *et al.*, 2020). Further, management techniques (e.g., chemical use, crop rotation) are expected to have direct effects on tulip bulb biota and indirect effects mediated through soil abiotic and biotic properties (Figure A.1); 2) Fields with contrasting soil texture (i.e., sand versus clay) will have different responses in abiotic and biotic soil properties to management regime (i.e., contrasting interactions between management regime and soil type). This is because clay soils, as compared to sand soils, have different physical and structural conditions such as poor percolation, reduced oxygen content (Boekel, 1970) and abiotic characteristics (Dexter, 2004), leading to effects on soil-bound pests and diseases (McGovern and Elmer, 2017; Looman *et al.*, 2018) and plant-associated biota (Fierer, 2017); and 3) Across sand versus clay soils, management techniques will create different levels of connectivity between soil abiotic and biotic properties and tulip bulb biota due to inherent differences caused by soil texture (Boekel, 1970; Dexter, 2004) and the known impact of agricultural management on soil networks (de Vries and Wallenstein, 2017).

2 | MATERIALS AND METHODS

2.1 | Experimental setup

Eighteen tulip field representing different soils types and management regimes were selected from North Holland and Flevoland in The Netherlands (Table A.1). Farms were selected that use organic, hybrid and conventional management. Organic farms followed EU regulations for organic cultivation (Meredith and Willer, 2014). Hybrid farms used fewer artificial fertilizers, pesticides, herbicides, etc., but were not certified organic. Conventional farms used standardized agricultural methods, which included chemical inputs. For each management type, farms were selected that have sandy soils (≥75% sand) and clay (>10% clay) soils. In total, this resulted in: 3 management types × 2 soils types × 3 replicates = 18 fields.

2.2 | Soil and bulb sampling

Between 22 May and 4 June 2020, soils and bulbs were collected from 20 locations ranging from approximately 15-30 meters apart across each field in a "W" shaped pattern to capture sufficient heterogeneity (Sabbe and Marx, 1987). Soil samples used to measure all abiotic and biotic soil characteristics (except mites and collembola; see below) were collected from each location to a depth of 25 cm using a 2.4 cm diameter corer. The top 25 cm of soil is considered the most biologically active layer of agricultural soils (Fan *et al.*, 2016a) and encompasses the majority of the rooting depth of tulip bulbs (de Hertogh *et al.*, 1983). Five bulbs were excavated from each of the 20 sampling locations with a hand trowel. Soil was gently shaken off, the leaves and stems removed and bulbs were placed into a paper sack. At each location, a penetrometer measurement was taken to determine soil compaction (Sanglerat, 2012). Samples used for extraction of mites and collembola were collected with a 4 cm diameter corer to a depth of 5 cm because the majority of mite and collembola are found in this upper layer of soil (Römbke *et al.*, 2006). These samples were collected from ten points across each field.

2.3 | Farmer interviews

Farmers were interviewed regarding management techniques such as crop rotation, pesticide use, number of years cultivated, etc. (Table S2).

2.4 | Soil abiotic properties

Soil abiotic (and a few of the biotic) property analyses were performed by Eurofins (Wageningen, The Netherlands) using standard soil abiotic characteristic procedures. For details, see Appendix A.1.

2.5 | Chemical residue analyses

A subsample of soil and bulb material from each field was analysed for chemical residues. Samples were analysed by Eurofins (Wageningen, The Netherlands) using the Mini Luke method (Lozano *et al.*, 2016).

2.6 | Nematode extractions

Nematodes were extracted from soils using a modified version of the Baermann funnel method and from bulbs using a mist chamber (Van Bezooijen, 2006). The number of nematodes in each sample was determined using an inversion microscope (×40-200 magnification). The first 100 nematodes encountered in the counting dish were separated into different feeding groups: plant-feeding, bacterial-feeding, fungal-feeding and omnivore-carnivore (Yeates *et al.*, 1993). For details, see Appendix S2.

2.7 | Mite, collembola and Diptera extraction

Soil samples used to characterise mites, collembola and Diptera were kept refrigerated (5 °C) for one to three days before processing. For details, see Appendix S2.

2.8 | Virus detection in the tulip bulbs

The tulip bulbs were tested in the Bloembollenkeuringsdienst (BKD) laboratory (Lisse, The Netherlands) for the presence of Arabis mosaic virus (ArMV), cucumber mosaic virus (CMV), lily symptomless virus (LSV), tulip breaking virus (TBV), tulip virus X (TVX), tobacco rattle virus (TRV), tobacco necrosis virus (TNV) and tulip mosaic virus (TuMV). The tests were performed using the double-antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA) (Luo *et al.*, 2012) using in-house produced antisera.

2.9 | DNA extraction and sequencing

The microbial community of soil and bulb samples was analysed using high-throughput sequencing. The extraction and isolation of total DNA and the PCRs were done at WUR Glastuinbouw laboratory in Bleiswijk, The Netherlands. Analyses were performed by Utrecht Sequencing Facility (USEQ, UMCU, Utrecht, The Netherlands). For details, see Appendix S3.

2.10 | Statistical analyses

2.10.1 | ANOVAs

Each response variable (chemical, physical, biological, farmer interview responses) was analysed using ANOVA with management regime (organic, hybrid, conventional) and soil type (clay, sand) as fixed factors. All data were checked to ensure all assumptions for ANOVA were met and transformed as necessary (see ANOVA Tables for details). When significant effects were detected, data were subjected to post-hoc tests (Day and Quinn, 1989) using the emmeans/multcomp packages in R (Lenth, 2019) with Tukey HSD adjustment for multiple comparisons. The ANOVAs were performed using R (R Core Team, 2020) with the packages lme4/lmerTest (Bates *et al.*, 2015; Kuznetsova *et al.*, 2017).

2.10.2 | Sequencing data

To process the raw sequences, for both the ITS and 16S reads, Cutadapt (Martin, 2011) was used to remove forward and reverse primers and allow the separation of the fungal reads from the bacterial reads. All raw sequencing data were de-noised with DADA2 (Callahan *et al.*, 2016) following the DADA2 Pipeline Tutorial (1.18). For details, see Appendix S4.

2.10.3 | Partial least squares path model

We used a partial least squares path model (PLS-PM) to investigate the direct and indirect relationships between management regimes, soil abiotic and biotic properties, and tulip biota (Sanchez *et al.*, 2013). This type of structural equation modelling (SEM) is becoming more prominent in natural science (Fan *et al.*, 2016b) and has no distributional or independence requirements (Fornell and Bookstein, 1982; Chin, 2010). For details, see Appendix S5.

2.10.4 | Network and heatmap analyses

The correlation networks and heatmaps were made in R 3.6 (R Core Team, 2020). Networks were based on Veen *et al.* (2019) and heatmaps were made using the cor() and heatmap.2() functions of the R-package "gplots" (Warnes *et al.*, 2020). For details, see Appendix S5.

3 | RESULTS

3.1 | Soil abiotic properties

Soil abiotic properties from clay and sand tulip fields showed many differences (Tables S3-S4). Values from the penetrometer, total N, N supplying capacity, total and available S, total K, Ca and Mg, pH, organic C, soil organic matter, carbonic lime, clay, silt, clay humus and Ca saturation were higher on clay soils. Values for sand, Mg, K and Na saturation and soil friability and slaking were higher on sand soils. No abiotic soil properties differed significantly between management regimes nor were there any significant interactions between soil type and management.

3.2 | Soil and bulb biotic properties

Several soil biotic properties differed by soil type and/or management. The tulip virus tests revealed extremely low infection rates, making these data unfit for statistical analyses. For details, see Appendix S6. See appendices for details on effects on the nematode (Appendix S6, Tables S5-S8) and microarthropod communities (Appendix S6, Tables S9-A.10, Figure S2).

Soil and bulb microbial communities differed between soil type and/or management regime. Here, we present the results germane to our hypotheses, with further details in Appendix S6, Figures S3-S8, Tables A.11-A.12, Supporting Excel Document. Bulb bacterial and fungal community composition were not affected by soil type or management (Figures 1a, 2a). The soil bacterial community was affected by soil type, with communities from clay soils forming a distinct cluster (Figure 1b, Table A.11). However, bacterial communities from organic and hybrid clay fields clustered together, while organic sand field communities formed another distinct cluster and conventionally managed fields showed wide heterogeneity regardless of soil type. Soil fungal communities showed a slightly different pattern: communities from organic and hybrid clay fields formed a cluster separate from their counterparts on sand soils, while fungal communities from conventionally managed clay and sand fields formed a distinct, relatively homogenous cluster (Figure 2b, Table A.11). A number of bacterial and fungal diversity metrics were affected by soil type and management, but no significant interactions were observed (Appendix S6, Table A.12, Figures S3-S4).

The Deseq2 analyses revealed differences between soil and bulb microbial taxa driven by soil type and management (Figures S5-S8, Supporting Excel Document). Soil type did not significantly affect taxonomic abundances of bulb bacterial communities. *Bacillus* and *Streptomyces* were higher in sand soils, while *Fusarium* and *Purpureocillium* were higher in clay soils (Figure S5). Overall, 20 and 16 fungal taxa were more abundant in organic versus conventional and hybrid bulbs, respectively (Figure S6a,b). *Trichoderma* was higher in bulbs from organic versus conventional and hybrid (Figure S6a,b). *Botrytis* and *Fusarium* were lower in bulbs from conventional versus hybrid fields (Figure S6c) and *Fusarium* was more abundant in organic versus conventional and hybrid soils (Figure S8a,b).

3.3 | Management regime properties

Crop rotation was more frequent on clay versus sand soils and on organic versus hybrid and conventional fields. However, sand fields with hybrid and conventional management had more infrequent crop rotation versus organic sand fields and all management regimes on clay fields (soil type × management interaction) (Tables A.13-A.14, Figure S9a). A selection of answers to the interview questions is shown in Table A.1. Of particular noteworthiness, 5 of 6, 1 of 6 and 1 of 6 of the organic, hybrid and conventional farmers added animal manure, respectively. Chemical use and residue in soils and bulbs was higher in conventional and hybrid versus organic (none) fields. For details, see Tables A.15-A.16, Figures A.10-A.11.

3.4 | Partial least squares path model

The final PLS-PM showed abiotic and biotic soil properties explained significant variation in tulip bulb biota (Figure 3, $R^2 = 0.66$). Soil abiotic properties were directly negatively driven by management techniques (NB: considered as individual measures, not categorically) (-0.47). Management directly negatively influenced soil biotic properties (-0.63), but also exerted a weak, indirect negative effect mediated through soil abiotic properties (-0.05). Soil abiotic properties did not significantly directly affect soil biotic properties (-0.11). Soil abiotic properties had negative direct (-0.55) and indirect (-0.05) effects on tulip bulb biota mediated through soil biotic properties. Soil biotic properties had a marginally significant ($p < 0.10$) direct positive effect (0.42) on tulip bulb biota. Finally, management regime did not have a direct effect on tulip bulb biota, but an insignificant negative effect mediated via soil abiotic and biotic properties (-0.38). For loadings and original and bootstrapped path coefficients, see Tables A.17-A.18.

3.5 | Network analyses and heatmaps

The network analysis across different soils types showed connections between soil abiotic and biotic properties, management regime techniques and tulip bulb biota differed between sand and clay soils (Figure 4, Table A.19). Here, we discuss some of the more remarkable patterns. Overall, networks on clay soils were more compact, with multiple links between numerous variables and few distinct nodes, while sand soils showed a looser network, with fewer links between variables and more distinct, separate nodes. In clay networks, the bulb bacterial and fungal taxa were present in nodes that were distinct from nodes that contained bulb chemical resides, but in sand networks, bulb microorganisms were present in nodes more distant from one another, and some were even associated with bulb chemical residues. Further, bulb-associated nematodes in clay soils were loosely clustered, while in sand soils they clustered tightly. Management techniques (i.e., chemical residues, ploughing depth, crop rotation) formed a distinct node in sandy soils, but in clay soils, these parameters broke apart into several different nodes. The six panels to the right in Figure 4 show pair-wise comparisons of how the values of the measured parameters changed between management regimes in clay and sandy soils. Many of the changes between management regime were similar across sand versus clay fields. For correlation heatmaps, see Figures A.12-A.13.

4 | DISCUSSION

We found that abiotic soil properties were driven by soil type and not management. However, the relative abundances of certain microbial bulb and soil taxa were affected by soil type and management. The soil microbial community composition was determined by an interaction between soil type and management regime. A PLS-PM showed a marginally significant indirect, but no direct, effects of management techniques (i.e., contributions of specific techniques, not categorically divided into management regime) on tulip bulb biota, but strong effects of management techniques on soil abiotic and biotic properties. Network analysis showed strong differences in connectivity between soil abiotic and biotic and tulip bulb biotic properties and management techniques across soil types. Below we discuss what these results mean in the context of agricultural management regimes.

4.1 | Effects of management on soil properties and tulip bulb biota

In contrast to our first hypothesis, we found no differences in abiotic soil properties between organic, hybrid and conventional management regimes. Many studies found differences in abiotic soil properties emerge rapidly under organic management (Clark *et al.*, 1998; Gomiero *et al.*, 2011), which contrasts our findings. However, correlation analyses revealed that fewer years between cycles of tulip cultivation resulted in depletion of virtually all soil nutrients. Of the six fields with the lowest frequency in rotation between tulip crops, tulips were grown the previous year, which may have depleted total soil N (Abasi *et al.*, 2016). On two of the remaining four fields with tight crop rotation, narcissus and lily were grown the previous year. Lilies have a high demand for N (Slangen *et al.*, 1989) and narcissus have a high demand for K, Mg and P (Hanks, 2002) relative to tulips (Niedziela *et al.*, 2015; Abasi *et al.*, 2016), This suggests that considering management categorically my partially mask the effects of specific management techniques (i.e., crop rotation).

In partial support of our first hypothesis, we found an effect of management on bulb and soil microorganisms. *Fusarium* and *Botrytis* abundances, two important tulip fungal diseases (Looman *et al.*, 2018), were higher in bulbs from hybrid versus conventional fields and *Fusarium* was more abundant in organic versus conventional and hybrid soils. This could be attributed to two of six hybrid fields having grown tulips the previous year, with these diseases remaining in the soil the following growing season (McGovern and Elmer, 2017) (NB: no differences in *Fusarium* and *Botrytis* were found between hybrid versus conventional soils). Lower fungicide application in hybrid and organic versus conventional fields may have caused these differences, highlighting the need to find alternatives to chemicals to combat fungal diseases. In addition, *Trichoderma* spp. abundance was higher in organic versus hybrid and conventional bulbs. *Trichoderma* spp. can colonise roots, thereby outcompeting pathogens for space (Harman, 2000) and can enhance tulip flower quality and speed up bulb maturation (Mazhabi *et al.*, 2011). Resultantly, compared to hybrid and conventional, organic tulip bulbs might have higher resistance to disease. Finally, more groups of fungal taxa were more abundant in organic versus hybrid and conventional bulbs. This suggests that organic bulbs host a wider range of fungi, but precisely what this means for bulb health remains unknown.

The PLS-PM revealed that tulip bulb biota were not significantly driven by direct or indirect effects of management regime (NB: considered as individual *techniques* and not categorically). This may have occurred for a number of reasons such as tulip bulbs recruiting their own rhizosphere microbiome via root exudates (Berg and Smalla, 2009) or the confounding effect of different cultivars (Jiang *et al.*, 2017). Instead, soil abiotic properties exerted significant direct and indirect effects mediated via soil biotic properties, while soil biotic properties exerted a nearly significant direct effect on tulip bulb biota. It is intuitive that the soil community would be a driver of tulip bulb microbiota since organisms present in bulk soil colonise bulbs and roots (Berg and Smalla, 2009). Future emphasis should be placed on what specifically drives soil and bulb microbiomes towards enhanced resistance and resilience (Berendsen *et al.*, 2012).

4.2 | Interactive effects between management and soil type on soil properties and tulip bulb biota

In partial support of our second hypothesis, we found that interactions between soil type and management influenced certain soil biotic properties. Abiotic properties remained unaffected, possibly due to inherent differences between clay and sandy soils overriding interactions with management (Boekel, 1970). Bulb biota were also unaffected, with soil abiotic and biotic properties acting as stronger determinants. Soil nematodes and arthropods were unaffected by management, possibly due in part to seasonal effects on soil animal populations (Werner and Dindal, 1990). However, bacterial communities from organic soils formed two distinct, tight clusters driven by soil type, but showed considerable heterogeneity in conventional soils. Bacterial communities differ markedly by soil type in arable systems (Girvan *et al.*, 2003), and these distinctions were retained in organic clay versus sand soils, but lost in conventional soils. Fungal communities showed patterns similar to bacterial communities in organic soils, but conventional fungal communities formed a relatively homogenous cluster across soils types. These differences may be due to different life strategies. Bacteria typically grow more quickly with shorter generation times (Rousk and Bååth, 2011) and are less resistant to disturbance (Sun *et al.*, 2017). Therefore, under conventional management in both clay and sand fields, bacterial communities may have diverged as they recovered from disturbance (e.g., chemical input, deeper ploughing) based on random founder effects (Kim *et al.*, 2013), while fungal communities ended up homogenised across soils types perhaps due to a combination between certain taxa being eliminated or enhanced by disturbance (Schnoor *et al.*, 2011) and higher resistance to disturbance (Sun *et al.*, 2017). Contrasting responses between bacterial and fungal communities may have implications for soil functioning (Berga *et al.*, 2012), tulip health and productivity.

4.3 | Soil network connectivity across management regimes and soil types

In support of our third hypothesis, network connectivity between soil properties, management techniques and bulb biota differed between soil types. Overall, networks on clay soils were more compact with fewer distinct nodes compared to those on sand soils. Compact networks can benefit soil ecosystem services, such as carbon storage (Morriën *et al.*, 2017). Clay soils typically contain more organic matter than sand soils, indicating clay fields have greater potential to sequester carbon, thereby providing benefits for climate change-related goals in agriculture (Zaehle *et al.*, 2007). In contrast, there is evidence that soil networks broken into distinct nodes (i.e., modules) have a greater buffering capacity to stress (e.g., drought, pests, pathogens) due to functional redundancy amongst microorganisms (Wei *et al.*, 2015; de Vries and Wallenstein, 2017), which aligns with the higher modularity between distinction nodes in sand soil networks. This supports existing evidence that disease levels are lower in tulip bulbs grown in sand soils (McGovern and Elmer, 2017; Looman *et al.*, 2018) and was also shown here with greater *Fusarium* abundance in clay versus sand soils. Further, management techniques (i.e., chemical input, ploughing, crop rotation) formed a distinct node in sand soils and showed fewer associations with bulb and soil biota. Distinct nodes could contribute to improved tulip bulb harvests on sandy soils because intensive management practices might be "compartmentalised", thereby isolating the negative impacts of intensive management on soil biota. Reversed, in clay soils, intensive management techniques exert influence across multiple soil properties, thereby potentially playing a disruptive role. The next step is to discover how to steer soil networks into the appropriate direction to suppress disease and maximise ecosystem services.

4.4 | Conclusions

We found that management regime did not affect soil abiotic properties, but soil and tulip bulb microbial taxa were driven by management. Bacterial and fungal soil communities formed distinct clusters with organic and hybrid management on clay soils. However, conventional management resulted in heterogeneous and homogenous bacterial and fungal communities, respectively, regardless of soil type. Sandy soil networks showed more distinct nodes, while this was reversed on clay soils. This could increase buffering capacity in sandy soils against abiotic and biotic stresses and disturbances via increased functional redundancy. These findings pull focus on the need to consider interactive effects between soil type and management on the soil microbial community and soil networks. Future research should explore how long-term changes to management regimes interact with different soil types and crop microbiomes/biota and thereby alter the functional relationships between soil network connectivity and crop health and productivity.

Authors' contributions

J.R.D.L., C.B., G.M. and P.v.L. conceived the experimental design; J.R.D.L., C.B., A.P., P.v.L. and K.P. collected the data; J.R.D.L., E.L.F., L.B.S. and M.D. analysed the data; J.R.D.L. led the writing of the manuscript. All authors contributed to revising the manuscript.

Data availability

Data will be made available in the Dryad Digital Data Repository upon acceptance.

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Conflict of interest

The authors declare no conflict of interest.

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Figure legends

FIGURE 1. Bulb (a) and soil (b) bacterial community composition in samples from tulip fields with organic, hybrid and conventional management on sand and clay soils. For F- and p-values, see Table A.11.

FIGURE 2. Bulb (a) and soil (b) fungal community composition in samples from tulip fields with organic, hybrid and conventional management on sand and clay soils. For F- and p-values, see Table A.11.

FIGURE 3. Partial least squares path model showing the relationships between management regime, soil abiotic properties, soil biotic properties and tulip bulb biota in tulip fields with clay and sand soil with organic, hybrid and conventional management regimes. The width of the arrows indicates the strength of the causal relationships supplemented by standardised path coefficients (~$p < 0.10$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). R^2 values indicate the explained variance of the response variables. For details on measured indicator variables, loadings and path coefficients, see Appendix S5, Tables A.17-A.18.

FIGURE 4. Network analysis showing the interactions between soil abiotic and biotic properties and tulip bulb biota in clay and sand fields. Pairwise comparisons (six panels on the right hand side) indicate higher abundance in fields with the first mentioned management regime when variables are green and higher abundance in fields with the second mentioned management regime when variables are magenta, with brighter colours indicating higher abundances. See Table A.19 for numeric coding of variables.