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Linking diversity, synchrony and stability in soil microbial communities

Cameron Wagg[1,2] | Jan-Hendrik Dudenhöffer[3] | Franco Widmer[4] | Marcel G. A. van der Heijden[1,5,6]

[1]Department of Evolutionary Biology and Environmental Sciences, University of Zürich, Zürich, Switzerland; [2]Institute of Ecology, University of Jena, Jena, Germany; [3]Chair of Nature Conservation and Landscape Ecology, Institute of Earth and Environmental Sciences, University of Freiburg, Freiburg, Germany; [4]Molecular Ecology, Agroscope, Institute for Sustainability Sciences, Zürich, Switzerland; [5]Plant-Soil Interactions, Agroscope, Institute for Sustainability Sciences, Zürich, Switzerland and [6]Plant-Microbe Interactions, Institute of Environmental Biology, Faculty of Science, Utrecht, The Netherlands

Correspondence
Cameron Wagg
Email: cameron.wagg@ieu.uzh.ch

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Abstract

1. It is becoming well-established that plant diversity is instrumental in stabilizing the temporal functioning of ecosystems through population dynamics and the so-called insurance or portfolio effect. However, it remains unclear whether diversity–stability relationships and the role of population dynamics in soil microbial communities parallel those in plant communities.
2. Our study took place in a long-term land management experiment with and without perturbation to the soil ecosystem by tilling. We assessed the impacts of the soil perturbation on the diversity, synchrony and stability relationships in soil fungal and bacterial communities.
3. We found that the perturbation to the soil ecosystem not only reduced the abundance and richness of the fungal community, but it also reduced the temporal stability in both bacterial and fungal abundance. The fungal community abundance was destabilized by soil tilling due to reduced richness and increased temporal variation in individual taxa. In contrast, soil tilling destabilized the bacterial community abundance by reducing the temporal variation in individual taxa. Both bacterial and fungal community abundances were more temporally variable when taxa fluctuated more synchronously through time.
4. Our results show that land management practices, such as tilling, can destabilize soil microbial abundance by reducing the richness and disrupting the temporal dynamics below-ground. However, the differences in the mechanisms that underlie the temporal variations in fungal and bacterial net abundances suggest that the mechanisms that drive the stability can differ among guilds of organisms within the same system. The different temporal responses between the fungal and bacterial communities are likely linked to changes in edaphic properties resulting from the physical alteration of the soil structure.

KEYWORDS
agriculture, ARISA, biodiversity, community ecology, environmental perturbation, land management, qPCR, soil dynamics

1 | INTRODUCTION

Understanding the link between an ecosystem's biodiversity and stability is a central question in contemporary ecology (Donohue et al., 2013; de Mazancourt et al., 2013; Loreau, 2010). Much of the headway in conceptualizing and empirically testing bio diversity–stability theory has been developed using plant communities in long-term biodiversity experiments. Over the past few decades these studies have shown that greater plant species richness is required to support greater stability in plant community productivity over many years (Hallett et al., 2014; Hautier et al., 2014; Hector et al., 2010; Isbell, Polley, & Wilsey, 2009; Isbell et al., 2015; Roscher et al., 2011; Tilman, 1996; Tilman, Reich, & Knops, 2006). However, the generality of these results has not been as extensively addressed in other systems and a recent synthesis has illustrated that different systems may exhibit different diversity–stability relationships and underlying mechanisms (Gross et al., 2014). In particular we know very little about bio diversity–stability relationships in the below-ground compartment of terrestrial ecosystems and how they function in nature (Bardgett & van der Putten, 2014; Wall, Bardgett, & Kelly, 2010).

The temporal stability in ecosystem functioning, such as the maintenance of net plant community productivity over time, depends upon the temporal fluctuations in the productivity of individual species (Loreau, 2010). Moreover, changes in the temporal abundance of different species within a community will likely vary if the species possess different fundamental niches and life histories (Chesson, 2000; Huston, 1979; Loreau & de Mazancourt, 2008). Such asynchronous fluctuations among taxa at the population level can result in the maintenance of the overall functioning of a community where the decline in the functioning of some species are compensated by the increase in the functioning of other community members so that the overall functioning of the community is maintained (Gonzalez & Loreau, 2009; Loreau, 2010; Yachi & Loreau, 1999). Therefore, more diverse communities can enhance the stability of the community as a greater number of species increases the probability that some species will maintain the functioning of the community within a temporally variable environment; often referred to as the insurance or portfolio effect (Doak et al., 1998; Hector et al., 2010; Thibaut & Connolly, 2013; Tilman, Lehman, & Bristow, 1998; Yachi & Loreau, 1999). At the same time, increasing the number of species and their density can result in increased competition that may also increase the temporal variation in the functioning of individual species, and thus their temporal asynchrony (Chesson, 2000; Loreau & de Mazancourt, 2008; Tilman et al., 1998). Together both environmental variation and diversity–competition mechanisms can create asynchronous patterns in the temporal functioning of a population that can be quantified and assessed as potential explanations behind the stability in the net functioning of a community (Gross et al., 2014; de Mazancourt et al., 2013; Thibaut & Connolly, 2013).

There is growing evidence that soil organisms play key roles in a multitude of ecosystem functions including processes that support plant productivity and maintain the cycling of nutrients between above and below-ground communities (Bradford et al., 2014; de Vries et al., 2013; Pellkofer, van der Heijden, Schmid, & Wagg, 2016; van der Heijden, Bardgett, & Van Straalen, 2008; Wagg, Bender, Widmer, & van der Heijden, 2014). Moreover, the abundance of soil microbes has been associated with a broad spectrum of functions such as soil carbon sequestration, respiration, nutrient cycling processes, and is also intimately linked with plant diversity and productivity (Bender & van der Heijden, 2014; Delgado-Baquerizo, Grinyer, Reich, & Singh, 2016; Griffiths et al., 2000; Legay et al., 2016; Wagg et al., 2014; Zak, Holmes, White, Peacock, & Tilman, 2003). Yet, disturbance through intense land management practices are often observed to result in lower soil microbial diversity, abundance and induce compositional changes (Hartmann, Frey, Mayer, Mäder, & Widmer, 2015; Lauber, Remirez, Aanderund, Lennon, & Fierer, 2013; Oehl et al., 2004; Verbruggen et al., 2010). Such anthropogenic disturbances that reduce soil biodiversity and alter the composition of fungal and bacterial taxa likely impact the daily, seasonal and annual processes by which resources are cycled and maintained in the system (Bardgett, Hobbs, & Frostegård, 1996; Bradford et al., 2014; Fierer & Schimel, 2002; Six, Frey, Thiet, & Battan, 2006; Wardle et al., 2004; Yeates et al., 1997). The maintenance of a stable abundance of soil biota may be crucial for the efficiency in the cycling of soil resources and the general maintenance of soil health throughout the growing season and contribute to plant productivity and yield. For instance it has been observed that soil tilling causes short-term changes in soil microbial abundance that coincides with the disruption of nutrient cycling by increasing nutrient leaching and soil denitrification (Calderón, Jackson, Scow, & Rolston, 2001; Griffiths et al., 2004).

Previously it has been shown that the temporal changes in soil microbial community composition are influenced by land management practices (Lauber et al., 2013), and several past studies have assessed the resistance and resilience of microbial communities to soil perturbation (Griffiths & Philippot, 2013; Griffiths et al., 2000; Girvan, Campbell, Killham, Prosser, & Glover, 2005; Wertz et al., 2007; Zhang et al., 2016) . However, the application of diversity–stability analyses, paralleling those developed in long-term plant diversity studies, that links the stability in the net community functioning to the temporal dynamics within the population has never been considered previously in natural soil microbial communities. Thus, there is a need to fill the knowledge gap as to how anthropogenic perturbation to the soil ecosystem might influence the microbial population level mechanisms that maintain the abundance of soil microbial communities through time (Bardgett & van der Putten, 2014; Wall et al., 2010).

Here we address the impact of land management perturbation on the diversity–stability mechanisms in bacterial and fungal soil communities. Our study took place in an experimental agricultural field that was designed to assess the effects of land management practices on ecosystem services and diversity. We quantified the bacterial and fungal community abundances and richness on a monthly basis over 9 months that spanned the entire land management period. The field experiment included a treatment of soil tilling or no-tilling, a soil perturbation well known to alter soil microbial diversity

and abundance (i.e. Hartmann et al., 2015; Oehl et al., 2004). We anticipate that (i) the tilling perturbation reduces soil microbial community abundance and richness. Moreover, if stability is maintained by greater richness due to its effect on the temporal population variation and asynchrony, we further hypothesize that (ii) the loss of richness due to tilling will also result in greater synchronous variation in the population that in turn decreases the temporal stability of community abundance (Loreau, 2010; Thibaut & Connolly, 2013; Yachi & Loreau, 1999). Finally, (iii) we assess the direct and indirect pathways by which the tilling disturbance may impact the temporal stability of soil microbial community abundance by altering the relationships among richness, abundance and the temporal variance of the population.

2 | MATERIALS AND METHODS

2.1 | Study site and sample collection

Samples were taken from the long-term Swiss Farming Systems and Tillage Experiment (FAST); see Wittwer, Dorn, Jossi, and van der Heijden (2017) for a detailed description of the experiment. This experiment consists of four main treatments; organically and conventionally managed arable fields, each with and without tillage with the overall aim to investigate the impact of major farming systems (organic, conventional, tillage and no tillage) on ecosystem services, functions and soil biodiversity. The main plots measure 6 by 30 m and are replicated four times using a randomized block design resulting in a total of 16 main plots. Blocks were arranged within the field to account for potential edaphic spatial variation within the field site. Each of these main plots is split in four subplots of 3 by 15 m, which received one of four different cover crop treatments that were sown in August the previous year: no cover crop (fallow), a legume *Vicia villosa*, winter vetch or a Brassicaceae *Sinapis alba*, white mustard, or a mixture of several cover crops: phacelia *Phacelia tanacetifolia*, hairy vetch *Vicia villosa*, buckwheat *Fagopyrum esculentum* Moench and camelina *Camelina sativa* L. The whole experiment is composed of two field experiments established on the same field beside each other. The first experiment started in summer 2009 (FAST I) and the second in summer 2010 (FAST II), following a staggered start design. Prior to 2009 the site was an organically managed grassland (Wittwer et al., 2017). The results presented in this paper focus on samples taken from the second trial (FAST II).

In all plots, the main crop that was grown during the growing season were sown following an annual crop rotation scheme: field pea *Pisum sativum* L. subsp. *Arvense*, cover crop treatment, wheat *Triticum aestivum* L. cv. "Titlis", cover crop treatment, corn *Zea mays* L. cv. "Padrino", cover crop treatment, faba bean *Vicia faba*, winter wheat *Triticum aestivum* L. cv. "Titlis" followed by a 2 year grass-clover pasture. In the conventional tillage treatment, tilling was performed with a mouldboard plough (Menzi, B. Schnyder Pflugfabrik, Brütten, Switzerland) to a depth of 20 cm followed by a seedbed preparation with a rotary harrow (Amazone, H. Dreyer GmbH & Co. KG, Hasbergen, Germany) just before seeding. In the conventional no tillage treatment there were no soil disturbances during the whole crop rotation period and maize was sown with a no-till single-grain seeder (Amazone, H. Dreyer GmbH & Co. KG). The soil type at the experimental site is a calcareous Cambisol containing 1.5% organic C, 24% clay, 34% silt, 42% sand and had a pH of 7.6. The soil contained 64 mg P/kg, 160 mg N/kg, 194 mg K/kg, 519 mg Mg/kg, 4854 mg Ca/kg. Soil properties were assessed in the plots in the following years of our study (tilling treatments maintained yearly) that revealed that tilling reduced the silt ($F_{1,11} = 11.1$, $p = .007$, tilled = 21.3% and non-tilled = 22.1%) and potassium ($F_{1,11} = 10.1$, $p = .009$, tilled = 275 mg/kg and non-tilled = 317 mg/kg) content of the soils, as well as marginally increased the soil pH ($F_{1,11} = 3.42$, $p = .091$, tilled = 7.92 and non-tilled = 7.63, see Table S2 for further details).

Here we focus on the conventionally managed tilled and non-tilled plots receiving no cover crop, a legume or white mustard as cover crop. We focused on these plots as they represented the most extreme gradient of soil disturbance (tillage vs. no soil movement) and contain clearly defined cover crop treatments. Samples were taken from a total of 24 plots (8 main plots × 3 subplots with cover crop treatments). The site is located near Zürich, Switzerland (47°26′20.0″N, 8°31′40.1″E) and has an average annual temperature of 8.5°C with 1,042 mm precipitation.

Soil samples were collected monthly in 2012 between March and November when maize was the main crop. The dates for the monthly sampling and the management activities for the 2012 in the sampled plots are listed in Table S1 in Supporting Information. Eight soil cores per plot were taken with a soil corer (2.5 cm diameter) to a depth of 15 cm and were pooled and homogenized by sieving through a mesh size of 2.5 mm directly after sampling. This yielded a total of 216 soil samples: 4 blocks × 2 tilling treatments × 3 cover crops × 9 months.

2.2 | Characterization of soil microbial communities

Approximately 0.75 g of the homogenized fresh soil was transferred to a 2 ml tube and DNA was extracted by bead beating for 45 s at 5.5 m/s in a FastPrep FP120 cell disruptor with 0.75 g 0.1 mm diameter glass beads followed by CTAB extraction following Bürgmann, Pesaro, Widmer, and Zeyer (2001). DNA extract was purified using the NucleoSpin gDNA Clean-up Kit (Machery–Nagel). DNA was extracted from each soil sample in triplicate technical replicates.

Bacterial and fungal community abundances were determined by quantitative PCR (qPCR) using primers targeting the bacterial 16S and the fungal 18S rRNA genes (see Tables S3 and S4 for reagents and cycling conditions). For qPCR, purified DNA extracts were pre-incubated with 3 μg/μl BSA for 5 min at 92°C to bind PCR inhibiting substances. Bacterial and fungal rRNA genes were amplified using the PCR reagents and cycling conditions listed in Tables S2 and S3. Melting curve analyses were performed at 72°C to 99°C with 1°C increments for 10 s each. Because template composition of soil DNA extracts may change over the season (Lauber et al., 2013), we generated standard curves from a mixture of the 24 purified DNA extracts of different treatments and time points to reduce amplification bias

and ensure the comparability of the relative 16S and 18S gene abundances over the whole sampling period. This mixture was adjusted to a concentration of 60 ng/μl genomic DNA and used in a twofold dilution series as universal quantification standard for all qPCR amplifications. The qPCR amplifications were done in duplicate for each sample using a CFX 96 C1000 Cycler with optical module (Bio-Rad). The qPCR-based microbial abundance was positively correlated with soil microbial biomass, respiration and microbial N and C in our system (see Figure S1), all of which can be key predictors of soil microbial mediated ecosystem functions (Graham et al., 2016). The microbial biomass, respiration and microbial N and C were only measure at a single time point in the experiment and thus were not used in any further diversity–stability analyses. For practical reasons, we used the qPCR abundance measures as a surrogate for general microbial abundance and functioning as it has been considered to be an indicator of soil microbial biomass and activity (Anderson, 2003; Tellenbach, Grünig, & Sieber, 2010; Zhang et al., 2016).

To determine population characteristics we used the ribosomal intergenic spacer analyses (RISA; Fisher & Triplett, 1999; Ranjard et al., 2001) performed with the primers fRISAfor and fRISArev for fungi (Sequerra et al., 1997) and bRISAfor and bRISArev for bacteria (Hartmann, Frey, Kölliker, & Widmer, 2005). RISA PCR reagents and cycling conditions are shown in Tables S3 and S4. PCR products were run on capillary electrophoresis in an ABI 3130xl genetic analyser (Applied Bio Systems) to obtain community profiles. Fungal and bacterial RISA profiles were scored for unambiguous fragment peaks using GeneMarker V1.91 (Softgenetics). Fragments of similar length were binned as one operational taxonomic unit (OTU). Peak intensities of the OTUs were scored as relative florescence units with a threshold value of 50 units. In addition, OTUs that were negatively correlated, differed by 1 base pair in length and never occurred together within the same sample were considered to be erroneously scored OTUs and were therefore pooled as a single OTU. These OTU groupings were defined as taxa in our study system. Richness is thus, the number of OTUs detected within a sample. Rarefaction analyses revealed a sufficient sampling efficiency of the two management treatments (see Figures S2 and S3).

2.3 | Temporal community characteristics

To derive the relevant population and community level indices that have been used to assess plant community diversity–stability relationships over the past few decades, it is necessary that the functioning of individual species sum to the overall ecosystem function of interest; such as plant species biomass summing to the net primary productivity of the ecosystem. To obtain an analogous abundance measure for each taxa in our soil samples that sum to the quantified 16S and 18S gene abundances, we multiplied the relative florescence of each taxa in a sample (OTUs measured by RISA) with the overall gene abundances in the sample (measured by qPCR). This yielded population and community level abundances on the same scale leading to population and community level indices that meaningfully relate to one another (i.e. Gonzalez & Descamps-Julien, 2004; Gross et al., 2014; Isbell et al., 2009; Loreau, 2010; Loreau & de Mazancourt, 2008; Thibaut & Connolly, 2013). The weighting of taxa abundance by the measured 16S and 18S gene abundances did not dramatically alter the variation in taxa among plots and time points, as both 16S and 18S weighted taxa abundances and the unweighted relative RISA derived abundances were highly correlated (the average Pearson correlation between the relative abundance and the weighted abundance of a fungal taxa was $\rho = 0.887$ and for bacteria $\rho = 0.880$). Hence, the weighting of relative abundances of taxa by the quantified 16S and 18S genes in a soil sample still reflects the original un-weighted variation in the relative abundances of taxa among plots and time points.

Stability in fungal and bacterial community abundances was calculated as the inverse coefficient of variation (C/V), which is the ratio between the temporal mean (μ) and the temporal variation (σ) in the in fungal or bacterial abundance (Lehman & Tilman, 2000) measured as 18S rRNA and 16S gene abundances respectively. We also calculated the average variation in individual taxa (population CV) as the weighted average CV of taxa in a community by weighting the CV of taxa by its overall average abundance. This was done since taxa that are very low in abundance tend to have very high CV values (Gross et al., 2014). Synchrony among taxa (η) was calculated as the average correlation coefficient between a particular taxon and the sum of all other taxa within the community following Gross et al. (2014), where $\eta = 1$ indicates perfect synchrony and $\eta = -1$ indicates perfect asynchrony, whereas $\eta = 0$ indicates stochasticity. This measure of synchrony allows for convenient tests of whether the population is statistically synchronous or asynchronous; i.e. are estimates statistically different from 0 (stochastic).

2.4 | Analyses

All analyses were performed in R 3.02 (R Core Team, 2013) and all ANOVA models were performed using the R package "ASREML" (VSN International Ltd., Herts, UK) and "PASCAL" (accessible at www.github.com/pascal-niklaus/pascal). To assess (i) the effects of the tilling perturbation on the richness and abundance of fungal and bacterial communities we used mixed effect ANOVAs with month, tilling and the interactions with the cover crop treatment as fixed effects. The plot and the error structure for cover crop within block were included as random terms. The first-order auto-regression for the serial correlation at the resampled plot level was included in all repeated measures models.

To address hypothesis (ii), we tested for an overall effect of tilling on the fungal and bacterial community stability (μ/σ), population variation (population CV) and synchrony (η) as in the ANOVAs above, but without any terms that included month. To test for effects of tilling on stability, population CV and synchrony though altering richness, we also assess their relationship with richness and the interaction with the tilling treatment. To further assess the effect of richness on the fungal and bacterial community stability we "unpacked" the effects of richness on stability (μ/σ) by assessing the relationships between richness and abundance (μ) and richness and the temporal variation

TABLE 1 Summary of results for the overall effect of the tilling disturbance on fungal and bacterial temporal community characteristics. Means are shown for both tilled (T) and non-tilled (NT) communities along with the *p*-value for the difference between the two. Arrows (↑ and ↓) highlight the direction that the tilling disturbance had on the community characteristic

	Fungi			Bacteria		
	T	NT	*p*	T	NT	*p*
Richness	↓ 41.42	44.54	.040	94.86	91.73	.105
Abundance (μ)	↓ 38.65	51.53	<.001	45.93	43.79	.105
Stability (μ/σ)	↓ 2.23	2.89	.025	↓ 2.74	3.76	.011
Population CV	↑ 1.72	1.64	.002	1.14	1.23	.176
Synchrony (η)	0.27	0.23	.227	0.40	0.34	.081

in a community (σ) following Gross et al. (2014). Specially, the log-abundance (μ) and log-variation (σ) were regressed against richness and the interaction with tilling. The slope coefficients for both regressions are then denoted as βμ and βσ respectively. Since log(μ/σ), the log of stability, is the difference in log(σ) from log(μ), the difference in the slope coefficients βμ and βσ is the slope coefficient for the relationship between richness and stability (β_{CV}). Therefore when the βμ is greater than βσ, richness contributes to the community stability by increasing the abundance more than it does the variation (see Gross et al., 2014). Furthermore, since richness may increases stability by increasing the population CV and reducing the population synchrony we also assessed the richness–population CV and richness–synchrony relationships and their interactions with the tilling perturbation by regression. The interaction was removed if found to be non-significant ($p > .05$).

Finally, to assess hypothesis (iii) regarding the indirect effects of the tilling disturbance on stability through its influence on richness, abundance and the population level temporal variation we used piecewise structural equation modelling, using the R package "piecewiseSEM" (Lefcheck, 2016), which allows us to incorporate the error structure of cover within blocks as a random effect. Specifically, the variation in the community abundance was assessed as a function of the community richness, the mean abundance of a community, the population CV and the population synchrony. We assessed the temporal variation in fungal and bacterial abundances separately from the mean (instead of their ratio as an indication of stability) to further determine the separate effects of the disturbance and richness on stability through their effects on the temporal variation and mean abundance. The paths for the effect of the population CV and synchrony on the community level variation were included since the abundance of individual taxa at the population level sum to the community abundance, and, moreover, indicate whether greater asynchronous variation at the population level reduces the net community level variation. Since it is often observed that increased diversity increases the net abundance of the community and that increased richness can also lead to greater variation within the temporal functioning of the population, we also included paths for the effects of richness on synchrony, population CV and the net abundance of the community. Finally, since the synchrony, population CV and the net community abundance and variation can all be influenced by tilling (i.e. through a direct effect on the temporal abundance of individual taxa and thus their sum) we included all paths to the tilling disturbance treatment.

3 | RESULTS

3.1 | Disturbance on abundance and richness

The tilling perturbation significantly reduced fungal abundance ($F_{1,9} = 32.1$, $p < .001$, Tables 1 and S4) and fungal richness ($F_{1,9} = 7.93$, $p = .020$, Tables 1 and S4). Fungal abundance was most reduced by the perturbation during the later part of the summer, resulting in a marginally non-significant tilling treatment by month interaction ($F_{8,117.8} = 1.86$, $p = .074$, Table S4, Figure 1a). Fungal richness was also significantly reduced during the latter half of the year causing a significant tilling treatment by month interaction ($F_{8,122.8} = 2.91$, $p = .005$, Table S4, Figure 1b). Bacterial abundance was also influenced by the tilling treatment depending on the month ($F_{8,119.7} = 5.66$, $p < .001$, Tables 1 and S4). In the first half of the year (March–July) bacterial abundance tended to be greater in the tilled soils, whereas later in the growing season (August and September) the opposite was true (Figure 1c). Unlike the response in the fungal richness, the bacterial richness was largely unaffected by the tilling treatment ($F_{1,9} = 2.20$, $p = .174$, Tables 1 and S4), but did vary greatly among months ($F_{8,120.2} = 15.50$, $p < .001$, Table S4), with the lowest bacterial abundance occurring in April and May (Figure 1d).

3.2 | Diversity driven stability and population dynamics

Both fungal and bacterial community abundances were less stable in the tilled plots (fungi: $F_{1,9} = 7.23$, $p = .025$, bacteria: $F_{1,9} = 10.3$, $p = .011$, Table 1). In addition, the fungal community stability was positively related to fungal richness overall (slope = 0.096, $SE = 0.031$, $p = .002$, Figure 2a). The tilling disturbance had no statistically distinguishable effect on the fungal richness–stability relationship (richness by treatment interaction: $F_{1,15.1} = 0.530$, $p = .477$). By "unpacking" the diversity–stability relationship into the separate diversity–abundance and diversity–variation relationships, following Gross et al. (2014), we found that the overall positive diversity–stability relationship in the fungal community was driven by the effect of fungal richness on reducing the temporal variation ($\beta_{\sigma} = -0.0271$, $SE = 0.0150$, $p = .084$), which accounted for 65.9% of the positive relationship between fungal richness and fungal stability ($\beta_{CV} = 0.0411$, $SE = 0.0130$, $p = .005$). In addition, the fungal

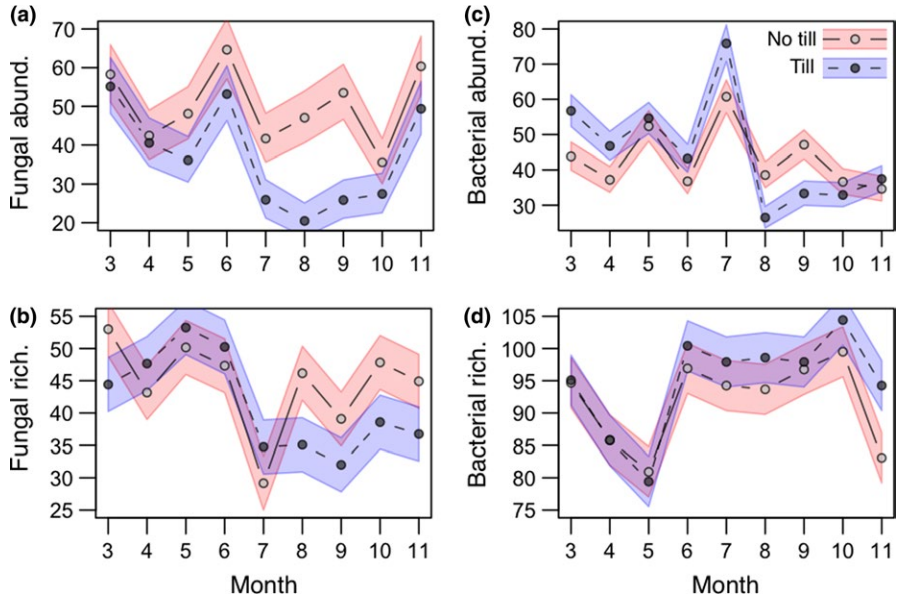

FIGURE 1 Mean fungal abundance (a) and richness (b) as well as bacterial abundance (c) and richness (d) are shown for each month spanning the management period from March to November (months 3–11 on the *x*-axis). Means from the undisturbed (no till) treatment are indicated by the lightly shaded points and highlighted in red, whereas the tilled (disturbed) treatment are indicated by the dark points and highlighted in blue. The tilling disturbance occurred between months 4 and 5. The width in the red and blue shading above and below the means is the standard error for the pairwise difference between the till (red) and no till (red) treatments for a given month, such that overlapping shading indicates no difference between means at $\alpha < 0.05$. Fungal and bacterial abundances were determined by quantifying the abundance of 18S and 16S genes respectively. Richness is the number of taxa detected by ribosomal intergenic spacer analyses

richness–variance relationship was about twice the magnitude as the fungal richness–abundance relationship, which was not statistically significant ($\beta_\mu = 0.0140$, $SE = 0.0116$, $p = .243$).

In the bacterial community there was no significant association between bacterial richness and stability (slope = 0.021, $SE = 0.032$, $p = .511$, Figure 2b), and neither did the tilling treatment affect the richness–stability relationship ($F_{1,14.1} = 0.91$, $p = .357$, Figure 2b). Unpacking the bacterial richness–stability relationship into the component richness–abundance and richness–variation relationships revealed that the magnitude in the effect of richness on the bacterial abundance and temporal variation were relatively equivalent ($\beta_\mu = 0.0154$, $SE = 0.0046$, $p = .003$; $\beta_\sigma = 0.0141$, $SE = 0.0112$, $p = .220$). Thus, the variation consistently scaled with the mean bacterial abundance with the changes in richness (i.e. β_μ:$\beta_\sigma \approx 1$), such that changes in bacterial richness did not relate to bacterial community stability ($\beta_{CV} = 0.0013$, $SE = 0.0109$, $p = .904$).

At the population level, the tilling disturbance resulted in greater fungal population CV, which reflects an increase in the average variation in individual taxa ($F_{1,9} = 16.9$, $p = .003$, Tables 1 and S4). Moreover, we found that the fungal population CV declined overall with increasing richness (slope = −0.025, $SE = 0.005$, $p < .001$, Figure 2c). Although, for bacteria the population CV was not significantly affected by the management treatment ($F_{1,9} = 2.16$, $p = .176$, Tables 1 and S4), the tilling treatment resulted in a steeper richness–population CV (till by richness interaction: $F_{1,15.9} = 5.68$, $p = .030$). However, the richness population CV was significantly positive in both cases (till: slope = 0.038, $SE = 0.008$, $p < .001$, no-till: slope = 0.016, $SE = 0.005$, $p = .002$, Figure 2d). Overall, richness had a strong positive effect on the bacterial population CV (slope = 0.018, $SE = 0.005$, $p < .001$, Figure 2d). The population synchrony (η) was not significantly affected by the management treatment in either the fungal community ($F_{1,9} = 1.68$, $p = .931$, Table 1) or the bacterial community ($F_{1,9} = 3.85$, $p = .081$, Table 1). Fungal richness had no relationship with fungal synchrony (slope = 0.345×10^{-3}, $SE = 3.996 \times 10^{-3}$, $p = .404$, Figure 2e), but bacterial richness was positively related to synchrony (slope = 5.101×10^{-3}, $SE = 2.265 \times 10^{-3}$, $p = .024$, Figure 2f).

3.3 | Linking population dynamics and stability

The structural equation model revealed how the temporal variation in the fungal community abundance was indirectly influenced by the management treatment through its effects on the temporal dynamics of the fungal population (Figure 3a, model fit statistics: Fischer's $C = 3.31$, $p = .769$). Specifically, temporal variation in fungal abundance (σ) was most positively related to the temporal mean in fungal abundance (μ), followed by the temporal variation at the population level (population CV) and population synchrony. The population CV was negatively associated to richness, but positively associated to the tilling disturbance indicating that the tilling disturbance indirectly increased the temporal variation in fungal abundance by reducing fungal richness and increasing the population CV. The tilling treatment also strongly reduced the fungal abundance (i.e. Table 1), and thus was indirectly linked to a lower temporal variance in fungal abundance. The synchrony in the fungal population was positively related with the temporal variation in the fungal community abundance. However, fungal synchrony did not create a significant indirect link between the variation in fungal abundance and the tilling treatment or fungal richness (Figure 3a).

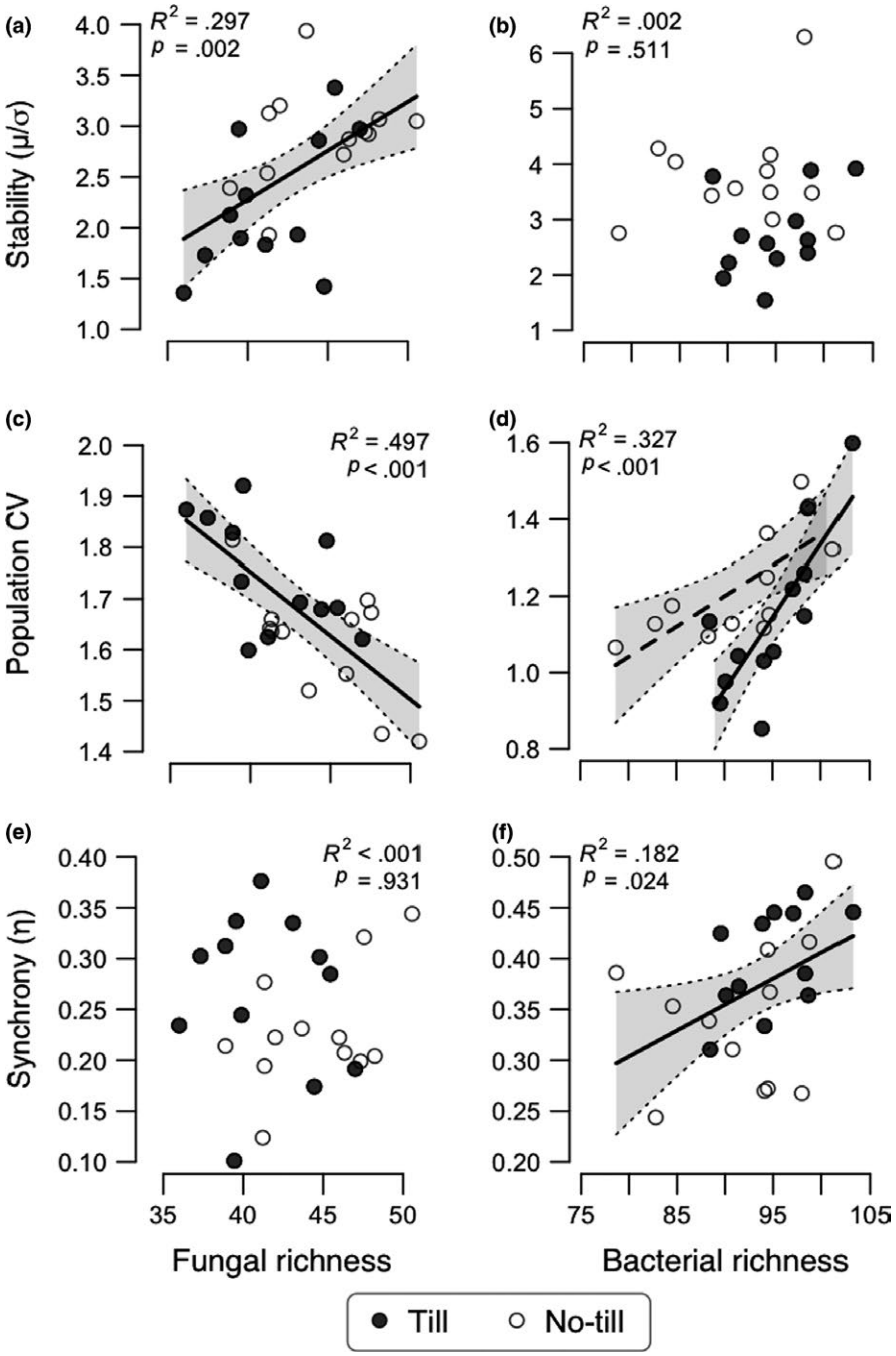

FIGURE 2 Relationships between richness and the temporal stability in (a) fungal and (b) bacterial abundance, as well as the average temporal coefficient of variation in individual taxa (population CV) are shown for fungi (c) and bacteria (d). The relationships between richness and the temporal synchrony among fungal (e) and bacteria (f) taxa are also shown. Data were obtained from tilled (Till) or non-tilled plots (No-till). Regression lines are shown where relationships were found to be significant with 95% confidence bands shaded in grey. The marginal R^2 and *p*-values indicate the fit for the overall relationship with richness. In (d) the relationships differed between tilled (solid regression line) and no-till (dashed regression line) treatments

The model for the bacterial community revealed that the tilling disturbance increased the temporal variation in the bacterial community abundance indirectly through its negative effect on the temporal variation of individual taxa (Figure 3b, model fit statistics: Fischer's C = 1.82, p = .935). Specifically, the variation in the bacterial community abundance was negatively, and most strongly, associated with the bacterial population CV, which was positively associated with bacterial richness and negatively affected by the tilling disturbance. Although bacterial richness was not significantly affected by the disturbance treatment, it was found to have a positive effect on the population CV. Therefore, the bacterial richness could be indirectly linked with a lower variation in bacterial abundance through its effect on increasing the population CV. The bacterial population synchrony and the temporal mean abundance were both positively related with the temporal variation in the bacterial community abundance. However, the effect of synchrony and abundance did not reveal any indirect link of the tilling disturbance or changes in bacterial richness on the temporal variation in bacterial community abundance.

4 | DISCUSSION

Here we assessed the link between diversity and stability in the abundance of fungal and bacterial communities over a 9-month period spanning the management and growing season under

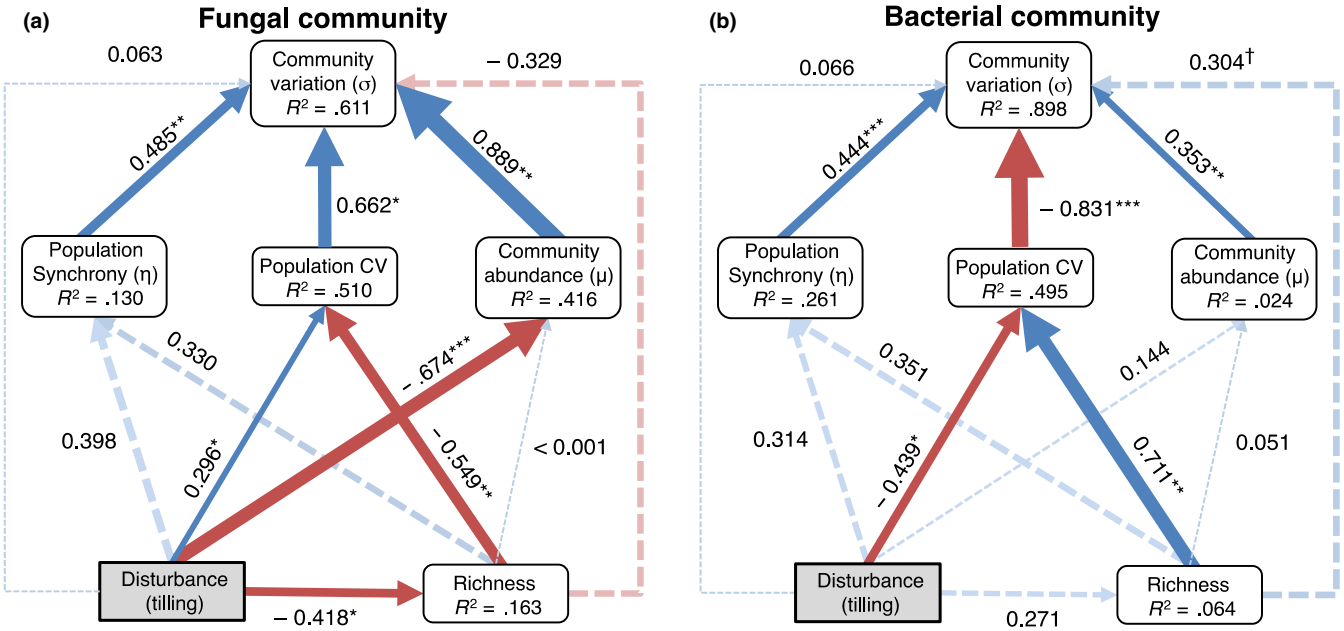

FIGURE 3 Structural equation model results indicating the mechanisms behind the stability of (a) fungal and (b) bacterial abundances. The effect of disturbance through tilling is indicated as an exogenous variable highlighted in grey. Blue arrows represent positive, and red negative, path coefficients and their width reflect the strength of the standardized path coefficient (shown adjacent to arrows and significance indicated by $^{\dagger}p < .1$, $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$). The proportion of variation in each endogenous variable explained by the paths is shown for each endogenous variable (marginal R^2). Faded dashed arrows indicate paths coefficients that were not significant

contrasting agricultural management regimes. We hypothesized that the effect of soil disturbance, imposed by tilling, would impact not only the abundance and diversity in the soil communities, but also alter the temporal dynamics of the communities that underlie the stability of their net abundance. As anticipated (i) the disturbance in our system not only reduced the abundance and richness of soil fungi, as observed in numerous other studies (e.g. Hartmann et al., 2015; Lauber et al., 2013; Oehl et al., 2004; Verbruggen et al., 2010), but also destabilized the abundance of both fungal and bacterial communities. Further in support of our hypothesis (ii), we found a positive diversity–stability relationship in the fungal community that resulted from richness having a stronger effect on reducing the temporal variation then increasing the overall mean fungal abundance. Yet, we did not find any bacterial richness–stability relationship, and bacterial richness was generally unrelated directly to the temporal variation in the net bacterial abundance. Moreover, by investigating the indirect effects of the tilling treatment on the population level mechanisms that drive stability (iii), we found the population level mechanisms underlying stability differed between fungal and bacterial communities. These differences likely reflect their differing responses to the tilling disturbance and the temporal demographic characteristics of these two guilds of soil organisms. Importantly for the objectives of our current study, our results parallel findings in plant community studies in that changes in the environment, such as those induced by anthropogenic management intensity and extreme climate events along side diversity loss, can destabilize productivity by negatively impacting species richness and altering the temporal community characteristics that drive stability (Hallett et al., 2014; Hautier et al., 2014; Isbell et al., 2015; Wagg et al., 2017; Yang et al., 2014). Moreover, we observed the fungal and bacterial abundance was associated with microbial respiration, biomass and microbial N and C in our system that are considered to be key characteristics to the functioning of soil ecosystems (Graham et al., 2016). Considering this, the destabilization in the abundances of fungal and bacterial communities and their community composition likely reflects the stability in ecosystem functioning, and in particular the efficiency by which soil resources are maintained and recycled within the system through microbial mediated pathways.

4.1 | Contrasting responses in fungal and bacterial communities

Although the stability in fungal abundance was stabilized by greater richness and lower temporal variation in the population, the bacterial community exhibited opposing trends. Firstly, the tilling disturbance had a statistically non-significant effect on the richness and abundance in the bacterial community. The minimal effect of the tilling disturbance on bacterial richness and abundance coincides with previous observations that bacterial richness and abundance may be less negatively impacted by physical soil disturbances compared to fungal communities (Bardgett et al., 1996; Six et al., 2006; Yeates et al., 1997). Furthermore, the lack of an effect of the tilling disturbance on bacterial richness may reflect the ability of the soil microbial communities to rapidly recover and adapt following environmental perturbations (Allison & Martiny, 2008; Girvan et al.,

2005; Griffiths & Philippot, 2013; Jackson, Calderon, Steenwerth, Scow, & Rolston, 2003).

In contrast to bacteria, fungi have been known to be strongly reduced in abundance and richness following the physical destruction of the soil structure and hyphal networks that may require a longer time to re-establish and recover in abundance (Hartmann et al., 2015; Lauber et al., 2013; Oehl et al., 2004; Rousk & Bååth, 2007; Sun, Li, Avera, Strahm, & Badgley, 2017; van der Wal et al., 2006; Verbruggen et al., 2010). Furthermore, soil tilling is well known to alter the abiotic properties of the soil and in our system it was observed that tilling increased soil pH and reduced soil silt content. Such changes in soil pH, clay and silt properties have been linked previously to changes in fungal and bacterial abundances and community composition (Rousk, Brookes, & Bååth, 2009; Rousk et al., 2010) that may have also contributed to the differing responses in abundances and composition between fungal and bacterial communities to soil tilling.

Although tilling had no detectible effect on synchrony in either the bacterial or fungal populations, synchrony in both communities was positively related to the temporal variation in the net community abundance. This indicates that the abundance of different taxa at different times (i.e. less synchronous, more stochastic population dynamics) is of key importance for maintaining a stable abundance in both fungal and bacterial communities. This parallels the growing literature that has shown that plant communities are stabilized by greater asynchrony as different species maintain the net community abundance at different times (de Mazancourt et al., 2013; Hautier et al., 2014; Isbell et al., 2009; Roscher et al., 2011). Yet, although the underlying temporal population variation had a strong influence on the stability in the net community abundance in both fungal and bacterial communities, the effects were in opposite directions.

4.2 | Population mechanisms underlying bacterial stability

In the bacterial community the negative effect of increasing population variation on the variation in the net bacterial abundance, in combination with the positive effect of synchrony, suggests compensatory dynamics occurred within the bacterial community. In other words, greater variation of individual taxa (population CV) at different times (less synchronously) together resulted in the more stable bacterial abundance that is indicative of compensatory dynamics (Gonzalez & Loreau, 2009; Loreau, 2010; Loreau & de Mazancourt, 2008). Consequently the bacterial community was destabilized by the tilling disturbance because of the reduced temporal variation in the bacterial population. The effect of the tilling disturbance on the temporal variability in the bacterial population and reduced bacterial stability, lends support to other findings that the temporal variation in bacterial community composition is altered by land management practices (Lauber et al., 2013). The reduced temporal variation in the bacterial population in soils disturbed by tilling may be linked with the reduced silt content, increased pH and the general soil homogenization caused by the tilling that may have favoured bacterial taxa that are more temporally robust regarding their abundance to environmental changes (Balesdent, Chenu, & Balabane, 2000; Calderón et al., 2001; Doran, 1979; Jackson et al., 2003; Rousk et al., 2010). However, we found that the richness had a much greater overall effect on the population level variation, and consequently on the community level variation, then the effect of soil tilling on temporal variation at the population.

The strong positive effect of bacterial richness on the temporal variation in the bacterial population indicates soils with a more rich bacterial community also have a highly variable composition and more stable net abundance. This may be explained by greater richness providing a greater insurance that some taxa benefit over others through temporal environmental variations in a compensatory manner so that the net functioning of the community is maintained (Doak et al., 1998; Hallett et al., 2014; Isbell et al., 2009; Lehman & Tilman, 2000; Loreau, 2010; Loreau & de Mazancourt, 2008; Yachi & Loreau, 1999). Furthermore, the richness driven variation in the bacterial population, that was independent of the tilling treatment in our system, was likely also affected by the monthly environmental and climatic changes in our system that result in the decline in abundance of some taxa and coinciding increases in other taxa. The influence of such temporal variations in climatic conditions on species asynchrony and population level variation has also been observed in plant communities (de Mazancourt et al., 2013; Hallett et al., 2014). Considering that changes in soil temperature and moisture are known to have strong impacts on soil bacterial community abundance, composition and function (Barnard, Osborne, & Firestone, 2013; Castro, Classen, Austin, Norby, & Schadt, 2009; Fierer & Schimel, 2002; Griffiths & Philippot, 2013; Talley, Coley, & Kursar, 2002), it is likely that monthly changes in precipitation and soil temperature also played a key role in the bacterial population variation independently of the soil tilling effect.

4.3 | Population mechanisms underlying fungal stability

We found that the positive richness–stability relationship in the fungal community was largely explained through the negative association between richness and the temporal variation in the abundance of individual taxa. Hence, soils with a greater fungal richness also exhibited a more stable abundance in individual taxa. Consequently, the tilling disturbance simultaneously reduced both the fungal richness and increased the variation in the abundance of individual taxa (both directly and indirectly), leading to the lower stability in fungal abundance. This result is in line with the many past studies that have observed that soil tilling reduces soil fungal abundance and richness (Hartmann et al., 2015; Oehl et al., 2004; van der Wal et al., 2006; Verbruggen et al., 2010). Considering the physical destruction of fungal hyphae by tilling, the instability in the fungal abundance likely results from fungi requiring longer periods of time to re-establish hyphal networks post disturbance (Rousk & Bååth, 2007; Sun et al., 2017). The slow development in fungal abundance post disturbance is also evidenced in our system where the tilling reduced fungal

abundance throughout the growing season that only seemed to recover towards the end of the year, 6–7 months post tilling. This reduction in fungal abundance throughout most of the growing season may also be indicative of a destabilization, or depression, of fungal mediated ecosystem processes such as litter decomposition, maintaining soil structure and the provisioning of soil phosphorous to plants (Bender & van der Heijden, 2014; Griffiths et al., 2000; Six et al., 2006; Verbruggen et al., 2010; Wagg et al., 2014).

Although numerous studies experimentally manipulating species richness in grassland plant communities have illustrated that more species rich communities can result in greater population level variation that consequently stabilizes the net community productivity, such richness–population variation and richness–stability relationships are not always observed (Gross et al., 2014). For instance Sankaran and McNaughton (1999) found that population and compositional stability may also be high at low diversity in natural grassland communities and suggest that environmental characteristics in which communities establish and evolve also play an important role. In our system the tilling disturbance to the soil likely also altered characteristics of the soil environment to support a more rich community and temporally stable composition. For instance fungal abundance and richness have been observed to positively relate to greater clay and silt content and lower pH (de Vries et al., 2012; Talley et al., 2002), which we found to be altered in our system by tilling, and may have contributed to greater fungal community compositional variation and abundance. Although the RISA methods used here likely underestimate fungal and bacterial richness, the methods provides a good estimate for the relative changes in richness and community structure that parallels results using methods to obtain a deeper resolution of the microbial diversity present (van Dorst et al., 2013). Thus, we expect that a finer resolution of the community richness and structure should likely parallel our results, but may provide finer details as to the temporally changing compositions that need further exploration for relating changes in microbial community composition to the broader scale ecosystem functioning in natural systems.

5 | CONCLUSIONS

Here we assessed the diversity–stability relationships in soil communities under differing land management intensities following the bio diversity–stability framework typically applied to above-ground plant productivity. Our results highlight that the disruption of the soil ecosystem through land management practices alters the temporal stability in both fungal and bacterial abundances. Furthermore, we show that changes in taxonomic richness can alter the stability of fungal abundance and the temporal population dynamics in both bacterial and fungal communities. However, we also found that the population level mechanisms that underlie temporal stability differed between fungal and bacterial communities demonstrating that the mechanisms that drive the stability can differ among guilds of organisms within the same system. This last result parallels findings that different systems may exhibit different diversity–stability relationships and underlying mechanisms (Gross et al., 2014). The differences between fungal and bacterial communities in the underlying mechanisms that supported the temporal stability of their abundances are likely linked to their fundamentally different life histories, such as growth and turnover rates, that determine the responses in community composition to environmental disturbance. Therefore the relationships between diversity, temporal population dynamics and community stability may be temporally and spatially scale dependant relative to the observed organismal community and the environmental perturbation addressed (Bardgett & van der Putten, 2014; Oliver et al., 2015; Sankaran & McNaughton, 1999). Such scale dependent effects of community diversity have been indicated in other systems (Chalcraft, Williams, Smith, & Willig, 2004; Chase & Leibold, 2002; Collins, 2000; Ives & Carpenter, 2007; Wagg et al., 2017). Finally, although microbial abundances have been linked to numerous ecosystem functions, the assessment of the temporal variations we observed in their abundances, and their underpinning population level characteristics, still require further investigation into how these temporal compositional changes influence the long-term nutrient cycling and the maintenance of plant diversity and productivity. In summary, we argue that future applications of diversity–stability assessments across systems under management and climatic perturbations are strongly needed and promise to be a worthwhile avenue to derive general rules relating population and community level temporal dynamics that drive ecosystem functioning in nature.

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AUTHORS' CONTRIBUTIONS

C.W., J.H.D., F.W. and M.v.d.H. conceived the ideas and designed methodology; J.H.D. collected the data; C.W. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data are available at the Dryad Digital Repository: https://doi.org/10.5061/dryad.kg262 (Wagg, Dudenhöffer, van der Widmer, & Heijden, 2018).

ORCID

Cameron Wagg http://orcid.org/0000-0002-9738-6901

Jan-Hendrik Dudenhöffer http://orcid.org/0000-0003-1548-1436

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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