

1 *Running header:* Belowground diversity-stability relationships

2 Linking diversity, synchrony and stability in soil microbial communities

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24 dynamics; land management; agriculture, ARISA, qPCR.

25 Abstract

- 26 **1.** It is becoming well established that plant diversity is instrumental in stabilizing the
27 temporal functioning of ecosystems through population dynamics and the so-called
28 insurance or portfolio effect. However, it is unclear whether diversity-stability
29 relationships and the role of population dynamics in soil microbial communities
30 parallel those in plant communities.
- 31 **2.** Our study took place in a long-term land management experiment with and without
32 perturbation to the soil ecosystem by tilling. We assessed the impacts of the soil
33 perturbation on the diversity, synchrony and stability relationships in soil fungal and
34 bacterial communities.
- 35 **3.** We found that the perturbation to the soil ecosystem not only reduced the abundance
36 and richness of the fungal community, but it also reduced the temporal stability in
37 both bacterial and fungal abundance. The fungal community abundance was
38 destabilized by soil tilling due to reduced richness and increased temporal variation
39 of individual taxa. In contrast, soil tilling destabilized the bacterial community
40 abundance by reducing the temporal variation of individual taxa. Both bacterial and
41 fungal community abundances were more temporally variable when taxa fluctuated
42 more synchronously through time.
- 43 **4.** Our results show that land management practices, such as tilling, can destabilize soil
44 microbial abundance by reducing the richness and disrupting the temporal dynamics
45 belowground. However, the differences in the mechanisms that underlie the temporal
46 variations in fungal and bacterial net abundances suggests that the mechanisms that
47 drive the stability can differ among guilds of organisms within the same system. The

48 different temporal responses between the fungal and bacterial communities are likely
49 linked to changes in edaphic properties resulting from the physical alteration of the
50 soil structure.

51

52 INTRODUCTION

53 Understanding the link between an ecosystem's biodiversity and stability is a
54 central question in contemporary ecology (Loreau 2010; de Manzacourt *et al.* 2013;
55 Donohue *et al.* 2013). Much of the headway in conceptualizing and empirically testing
56 biodiversity-stability theory has been developed using plant communities in long-term
57 biodiversity experiments. Over the past few decades these studies have shown that greater
58 plant species richness is required to support greater stability in plant community
59 productivity over many years (Tilman 1996; Tilman, Reich & Knops 2006; Isbell *et al.*
60 2009; Roscher *et al.* 2011; Hector *et al.* 2010; Hautier *et al.* 2014; Hallett *et al.* 2014;
61 Isbell *et al.* 2015). However, the generality of these results has not been as extensively
62 addressed in other systems and a recent synthesis has illustrated that different systems
63 may exhibit different diversity-stability relationships and underlying mechanisms (Gross
64 *et al.* 2014). In particular we know very little about biodiversity-stability relationships in
65 the belowground compartment of terrestrial ecosystems and how they function in nature
66 (Wall, Bardgett & Kelly 2010; Bardgett & van der Putten 2014).

67 The temporal stability in ecosystem functioning, such as the maintenance of net
68 plant community productivity over time, depends upon the temporal fluctuations in the
69 productivity of individual species (Loreau 2010). Moreover, changes in the temporal
70 abundance of different species within a community will likely vary if the species possess

71 different fundamental niches and life histories (Huston 1979; Chesson 2000; Loreau & de
72 Mazancourt 2008). Such asynchronous fluctuations among taxa at the population level
73 can result in the maintenance of the overall functioning of a community where the decline
74 in the functioning of some species are compensated by the increase in the functioning of
75 other community members so that the overall functioning of the community is maintained
76 (Yachi & Loreau 1999; Loreau 2010; Gonzalez & Loreau 2009). Therefore, more diverse
77 communities can enhance the stability of the community as a greater number of species
78 increases the probability that some species will maintain the functioning of the
79 community within a temporally variable environment; often referred to as the insurance
80 or portfolio effect (Doak *et al.* 1998; Tilman *et al.* 1998; Yachi & Loreau 1999; Hector *et*
81 *al.* 2010; Thibaut & Connolly 2013). At the same time, increasing the number of species
82 and their density can result in increased competition that may also increase the temporal
83 variation in the functioning of individual species, and thus their temporal asynchrony
84 (Tilman, Lehman & Bristow 1998; Chesson 2000; Loreau & de Mazancourt 2008).
85 Together both environmental variation and diversity-competition mechanisms can create
86 asynchronous patterns in the temporal functioning of a population that can be quantified
87 and assessed as potential explanations behind the stability in the net functioning of a
88 community (de Mazancourt *et al.* 2013; Thibaut & Connolly 2013; Gross *et al.* 2014).

89 There is growing evidence that soil organisms play key roles in a multitude of
90 ecosystem functions including processes that support plant productivity and maintain the
91 cycling of nutrients between above and belowground communities (van der Heijden,
92 Bardgett & Van Straalen 2008, De Vries *et al.* 2013, Wagg *et al.* 2014; Bradford *et al.*
93 2014; Pelkofer *et al.* 2016). Moreover, the abundance of soil microbes has been

94 associated with a broad spectrum of functions such as soil carbon sequestration,
95 respiration, nutrient cycling processes, and is also intimately linked with plant diversity
96 and productivity (Griffiths *et al.* 2000; Zac *et al.* 2003; Bender & van der Heijden 2014;
97 Wagg *et al.* 2014; Delgado-Baquerizo *et al.* 2016; Legay *et al.* 2016). Yet, disturbance
98 through intense land management practices are often observed to result in lower soil
99 microbial diversity, abundance and induce compositional changes (Oehl *et al.* 2004;
100 Verbruggen *et al.* 2008; Lauber *et al.* 2013; Hartmann *et al.* 2015). Such anthropogenic
101 disturbances that reduce soil biodiversity and alter the composition of fungal and
102 bacterial taxa likely impact the daily, seasonal and annual processes by which resources
103 are cycled and maintained in the system (Bardgett Hobbs & Frostegård 1996; Yeates *et al.*
104 1997; Fierer & Schimel 2002; Wardle *et al.* 2004; Six *et al.* 2006; Bradford *et al.* 2014).
105 The maintenance of a stable abundance of soil biota may be crucial for the efficiency in
106 the cycling of soil resources and the general maintenance of soil health throughout the
107 growing season and contribute to plant productivity and yield. For instance, it has been
108 observed that soil tilling causes short-term changes in soil microbial abundance that
109 coincides with the disruption of nutrient cycling by increasing nutrient leaching and soil
110 denitrification (Calderón *et al.* 2001; Griffiths *et al.* 2004).

111 Previously it has been shown that the temporal changes in soil microbial
112 community composition are influenced by land management practices (Lauber *et al.*
113 2013), and several past studies have assessed the resistance and resilience of microbial
114 communities to soil perturbation (Griffiths *et al.* 2000; Girvan *et al.* 2005; Wertz *et al.*
115 2007; Griffiths & Philippot 2013; Zhang *et al.* 2016). However, the application of
116 diversity-stability analyses, paralleling those developed in long-term plant diversity

117 studies, that links the stability in the net community functioning to the temporal dynamics
118 within the population has never been considered previously in natural soil microbial
119 communities. Thus, there is a need to fill the knowledge gap as to how anthropogenic
120 perturbation to the soil ecosystem might influence the microbial population level
121 mechanisms that maintain the abundance of soil microbial communities through time
122 (Wall, Bardgett & Kelly 2010; Bardgett & van der Putten 2014).

123 Here we address the impact of land management perturbation on the diversity-
124 stability mechanisms in bacterial and fungal soil communities. Our study took place in an
125 experimental agricultural field that was designed to assess the effects of land
126 management practices on ecosystem services and diversity. We quantified the bacterial
127 and fungal community abundances and richness on a monthly basis over nine-months that
128 spanned the entire land-management period. The field experiment included a treatment of
129 soil tilling or no-tilling, a soil perturbation well known to alter soil microbial diversity
130 and abundance (i.e. Oehl *et al.* 2004; Hartmann *et al.* 2015). We anticipate that (i) the
131 tilling perturbation reduces soil microbial community abundance and richness. Moreover,
132 if stability is maintained by greater richness due to its effect on the temporal population
133 variation and asynchrony, we further hypothesize that (ii) the loss of richness due to
134 tilling will also result in greater synchronous variation in the population that in turn
135 decreases the temporal stability of community abundance (Yachi & Loreau 1999; Loreau
136 2010; Thibaut & Connely 2013). Finally, (iii) we assess the direct and indirect pathways
137 by which the tilling disturbance may impact the temporal stability of soil microbial
138 community abundance by altering the relationships among richness, abundance and the
139 temporal variance of the population.

140

141 MATERIALS AND METHODS

142 **Study site and sample collection**

143 Samples were taken from the long-term Swiss Farming Systems and Tillage
144 Experiment (FAST); see Wittwer *et al.* (2017) for a detailed description of the
145 experiment. This experiment consists of 4 main treatments; organically and
146 conventionally managed arable fields, each with and without tillage with the overall aim
147 to investigate the impact of major farming systems (organic, conventional, tillage and no
148 tillage) on ecosystem services, functions and soil biodiversity. The main plots measure 6
149 by 30 metres and are replicated four times using a randomized block design resulting in a
150 total of 16 main plots. Blocks were arranged within the field in order to account for
151 potential edaphic spatial variation within the field site. Each of these main plots is split in
152 four subplots of 3 by 15 metres, which received one of four different cover crop
153 treatments that were sown in August the previous year: no cover crop (fallow), a legume
154 (*Vicia villosa*, winter vetch) or a Brassicaceae (*Sinapis alba*, white mustard), or a mixture
155 of several cover crops: phacelia (*Phacelia tanacetifolia*), hairy vetch (*Vicia villosa*),
156 buckwheat (*Fagopyrum esculentum* Moench) and camelina (*Camelina sativa* L). The
157 whole experiment is composed of two field experiments established on the same field
158 beside each other. The first experiment started in summer 2009 (FAST I) and the second
159 in summer 2010 (FAST II), following a staggered start design. Prior to 2009 the site was
160 an organically managed grassland (Wittwer *et al.* 2017). The results presented in this
161 paper focus on samples taken from the second trial (FAST II).

162 In all plots, the main crop that was grown during the growing season were sown

163 following an annual crop rotation scheme: field pea (*Pisum sativum* L. subsp. *Arvense*),
164 cover crop treatment, wheat (*Triticum aestivum* L. cv. 'Titlis'), cover crop treatment, corn
165 (*Zea mays* L. cv. 'Padrino'), cover crop treatment, faba bean (*Vicia faba*), winter wheat
166 (*Triticum aestivum* L. cv. 'Titlis') followed by a 2 year grass-clover pasture. In the
167 conventional tillage treatment, tilling was performed with a mouldboard plough (Menzi,
168 B. Schnyder Pflugfabrik, Brütten, Switzerland) to a depth of 20 cm followed by a
169 seedbed preparation with a rotary harrow (Amazone, H. Dreyer GmbH & Co. KG,
170 Hasbergen, Germany) just before seeding. In the conventional no tillage treatment there
171 were no soil disturbances during the whole crop rotation period and maize was sown with
172 a no-till single-grain seeder (Amazone, H. Dreyer GmbH & Co. KG, Hasbergen,
173 Germany). The soil type at the experimental site is a calcareous Cambisol containing 1.5%
174 organic C, 24% clay, 34% silt, 42% sand and had a pH of 7.6. The soil contained 64 mg
175 P/kg, 160 mg N/kg, 194 mg K/kg, 519 mg Mg/kg, 4854 mg Ca/kg. Soil properties were
176 assessed in the plots in the following years of our study (tilling treatments maintained
177 yearly) that revealed that tilling reduced the silt ($F_{1, 11} = 11.1$, $P = 0.007$, tilled = 21.3%
178 and non-tilled = 22.1%) and potassium ($F_{1, 11} = 10.1$, $P = 0.009$, tilled = 275 mg/kg and
179 non-tilled = 317 mg/kg) content of the soils, as well as marginally increased the soil pH
180 ($F_{1, 11} = 3.42$, $P = 0.091$, tilled = 7.92 and non-tilled = 7.63, see Table S2 for further
181 details).

182 Here we focus on the conventionally managed tilled and non-tilled plots receiving
183 no cover crop, a legume or white mustard as cover crop. We focused on these plots as
184 they represented the most extreme gradient of soil disturbance (tillage versus no soil
185 movement) and contain clearly defined cover crop treatments. Samples were taken from a

186 total of 24 plots (8 main plots \times 3 subplots with cover crop treatments). The site is located
187 near Zürich, Switzerland (47°26'20.0" N, 8°31'40.1" E) and has an average annual
188 temperature of 8.5°C with 1042 mm precipitation.

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

196

197 **Characterization of soil microbial communities**

198 Approximately 0.75 g of the homogenized fresh soil was transferred to a 2 ml
199 tube and DNA was extracted by bead beating for 45 s at 5.5 m s⁻¹ in a FastPrep FP120 cell
200 disruptor with 0.75 g 0.1 mm diameter glass beads followed by CTAB extraction
201 following Bürgmann *et al.* (2001). DNA extract was purified using the NucleoSpin
202 gDNA Clean-up Kit (Machery-Nagel). DNA was extracted from each soil sample in
203 triplicate technical replicates.

204 Bacterial and fungal community abundances were determined by quantitative
205 PCR (qPCR) using primers targeting the bacterial 16S and the fungal 18S rRNA genes
206 (see Tables S3 and S4 for reagents and cycling conditions). For qPCR, purified DNA
207 extracts were pre-incubated with 3 μ g μ l⁻¹ BSA for 5 min at 92°C to bind PCR inhibiting
208 substances. Bacterial and fungal rRNA genes were amplified using the PCR reagents and

209 cycling conditions listed in Tables S2 and S3. Melting curve analyses were performed at
210 72°C to 99°C with 1°C increments for 10 s each. Because template composition of soil
211 DNA extracts may change over the season (Lauber *et al.* 2013), we generated standard
212 curves from a mixture of the 24 purified DNA extracts of different treatments and time
213 points to reduce amplification bias and ensure the comparability of the relative 16S and
214 18S gene abundances over the whole sampling period. This mixture was adjusted to a
215 concentration of 60 ng μl^{-1} genomic DNA and used in a 2 fold dilution series as universal
216 quantification standard for all qPCR amplifications. The qPCR amplifications were done
217 in duplicate for each sample using a CFX 96 C1000 Cycler with optical module (Bio-
218 Rad). The qPCR based microbial abundance was positively correlated with soil microbial
219 biomass, respiration and microbial N and C in our system (see Fig. S1), all of which can
220 be key predictors of soil microbial mediated ecosystem functions (Graham *et al.* 2016).
221 The microbial biomass, respiration and microbial N and C were only measure at a single
222 time point in the experiment and thus was not used in any further diversity-stability
223 analyses. For practical reasons, we used the qPCR abundance measures as a surrogate for
224 general microbial abundance and functioning as it has been considered to be an indicator
225 of soil microbial biomass and activity (Anderson 2003; Tellenbach *et al.* 2010; Zhang *et*
226 *al.* 2016).

227 To determine population characteristics we used the ribosomal intergenic spacer
228 analyses (RISA; Fisher & Triplett 1999, Ranjard *et al.* 2001) performed with the primers
229 fRISAfor and fRISArev for fungi (Sequerra *et al.* 1997) and bRISAfor and bRISArev for
230 bacteria (Hartmann *et al.* 2005). RISA PCR reagents and cycling conditions are shown in
231 Tables S3 and S4. PCR products were run on capillary electrophoresis in an ABI 3130xl

232 genetic analyzer (Applied Bio Systems) to obtain community profiles. Fungal and
233 bacterial RISA profiles were scored for unambiguous fragment peaks using GeneMarker
234 V1.91 (Softgenetics). Fragments of similar length were binned as one operational
235 taxonomic unit (OTU). Peak intensities of the OTUs were scored as relative florescence
236 units with a threshold value of 50 units. Additionally, OTUs that were negatively
237 correlated, differed by 1 base pair in length and never occurred together within the same
238 sample were considered to be erroneously scored OTUs and were therefore pooled as a
239 single OTU. These OTU groupings were defined as taxa in our study system. Richness is
240 thus, the number of OTUs detected within a sample. Rarefaction analyses revealed a
241 sufficient sampling efficiency of the two management treatments (see Figs. S2 and S3).

242

243 **Temporal community characteristics**

244 To derive the relevant population and community level indices that have been
245 used to assess plant community diversity-stability relationships over the past few decades,
246 it is necessary that the functioning of individual species sum to the overall ecosystem
247 function of interest; such as plant species biomass summing to the net primary
248 productivity of the ecosystem. To obtain an analogous abundance measure for each taxa
249 in our soil samples that sum to the quantified 16S and 18S gene abundances, we
250 multiplied the relative florescence of each taxa in a sample (OTUs measured by RISA)
251 with the overall gene abundances in the sample (measured by qPCR). This yielded
252 population and community level abundances on the same scale leading to population and
253 community level indices that meaningfully relate to one another (i.e. Gonzalez &
254 Descamps-Julien 2004; Loreau & de Mazancourt 2008; Isbell *et al.* 2009; Loreau, M.

255 2010; Gross *et al.* 2014; Thibaut & Connolly 2013). The weighting of taxa abundance by
256 the measured 16S and 18S gene abundances did not dramatically alter the variation in
257 taxa among plots and time points, as both 16S and 18S weighted taxa abundances and the
258 un-weighted relative RISA derived abundances were highly correlated (the average
259 Pearson correlation between the relative abundance and the weighted abundance of a
260 fungal taxa was $\rho = 0.887$ and for bacteria $\rho = 0.880$). Hence, the weighting of relative
261 abundances of taxa by the quantified 16S and 18S genes in a soil sample still reflects the
262 original un-weighted variation in the relative abundances of taxa among plots and time
263 points.

264 Stability in fungal and bacterial community abundances was calculated as the
265 inverse coefficient of variation (CV^{-1}), which is the ratio between the temporal mean (μ)
266 and the temporal variation (σ) in the in fungal or bacterial abundance (Lehman & Tilman,
267 2000) measured as 18S rRNA and 16S gene abundances respectively. We also calculated
268 the average variation in individual taxa (population CV) as the weighted average CV of
269 taxa in a community by weighting the CV of taxa by its overall average abundance. This
270 was done since taxa that are very low in abundance tend to have very high CV values
271 (Gross *et al.* 2014). Synchrony among taxa (η) was calculated as the average correlation
272 coefficient between a particular taxon and the sum of all other taxa within the community
273 following Gross *et al.* (2014), where $\eta = 1$ indicates perfect synchrony and $\eta = -1$
274 indicates perfect asynchrony, while $\eta = 0$ indicates stochasticity. This measure of
275 synchrony allows for convenient tests of whether the population is statistically
276 synchronous or asynchronous; i.e. are estimates statistically different from 0 (stochastic).
277

278 **Analyses**

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

288 To address hypothesis (ii), we tested for an overall effect of tilling on the fungal
289 and bacterial community stability (μ/σ), population variation (population CV) and
290 synchrony (η) as in the ANOVAs above, but without any terms that included month. To
291 test for effects of tilling on stability, population CV and synchrony though altering
292 richness, we also assess their relationship with richness and the interaction with the tilling
293 treatment. To further assess the effect of richness on the fungal and bacterial community
294 stability we ‘unpacked’ the effects of richness on stability (μ/σ) by assessing the
295 relationships between richness and abundance (μ) and richness and the temporal variation
296 of a community (σ) following Gross *et al.* (2014). Specially, the log-abundance (μ) and
297 log-variation (σ) were regressed against richness and the interaction with tilling. The
298 slope coefficients for both regressions are then denoted as $\beta\mu$ and $\beta\sigma$, respectively. Since
299 $\log(\mu/\sigma)$, the log of stability, is the difference in $\log(\sigma)$ from $\log(\mu)$, the difference in the
300 slope coefficients $\beta\mu$ and $\beta\sigma$ is the slope coefficient for the relationship between richness

301 and stability (β_{CV}). Therefore when the β_{μ} is greater than β_{σ} , richness contributes to the
302 community stability by increasing the abundance more than it does the variation (see
303 Gross *et al.* 2014). Furthermore, since richness may increase stability by increasing the
304 population CV and reducing the population synchrony we also assessed the richness-
305 population CV and richness-synchrony relationships and their interactions with the tilling
306 perturbation by regression. The interaction was removed if found to be non-significant
307 ($P > 0.05$).

308 Finally, to assess hypothesis (iii) regarding the indirect effects of the tilling
309 disturbance on stability through its influence on richness, abundance and the population
310 level temporal variation we used piecewise structural equation modelling, using the R
311 package ‘piecewiseSEM’ (Lefcheck 2015), which allows us to incorporate the error
312 structure of cover within blocks as a random effect. Specifically, the variation in the
313 community abundance was assessed as a function of the community richness, the mean
314 abundance of a community, the population CV and the population synchrony. We
315 assessed the temporal variation in fungal and bacterial abundances separately from the
316 mean (instead of their ratio as an indication of stability) in order to further determine the
317 separate effects of the disturbance and richness on stability through their effects on the
318 temporal variation and mean abundance. The paths for the effect of the population CV
319 and synchrony on the community level variation were included since the abundance of
320 individual taxa at the population level sum to the community abundance, and moreover,
321 indicate whether greater asynchronous variation at the population level reduces the net
322 community level variation. Since it is often observed that increased diversity increases
323 the net abundance of the community and that increased richness can also lead to greater

324 variation within the temporal functioning of the population, we also included paths for
325 the effects of richness on synchrony, population CV and the net abundance of the
326 community. Finally, since the synchrony, population CV and the net community
327 abundance and variation can all be influenced by tilling (i.e. through a direct effect on the
328 temporal abundance of individual taxa and thus their sum) we included all paths to the
329 tilling disturbance treatment.

330

331 RESULTS

332 **Disturbance on abundance and richness**

333 The tilling perturbation significantly reduced fungal abundance ($F_{1,9} = 32.1$, $P <$
334 0.001 , Table 1 and Table S4) and fungal richness ($F_{1,9} = 7.93$, $P = 0.020$, Table 1 and
335 Table S4). Fungal abundance was most reduced by the perturbation during the later part
336 of the summer, resulting in a marginally non-significant tilling treatment by month
337 interaction ($F_{8,117.8} = 1.86$, $P = 0.074$, Table S4, Fig. 1a). Fungal richness was also
338 significantly reduced during the latter half of the year causing a significant tilling
339 treatment by month interaction ($F_{8,122.8} = 2.91$, $P = 0.005$, Table S4, Fig. 1b). Bacterial
340 abundance was also influenced by the tilling treatment depending on the month ($F_{8,119.7} =$
341 5.66 , $P < 0.001$, Table 1 and Table S4). In the first half of the year (March-July) bacterial
342 abundance tended to be greater in the tilled soils, while later in the growing season
343 (August and September) the opposite was true (Fig. 1c). Unlike the response in the fungal
344 richness, the bacterial richness was largely unaffected by the tilling treatment ($F_{1,9} = 2.20$,
345 $P = 0.174$, Table 1 & Table S4), but did vary greatly among months ($F_{8,120.2} = 15.50$, $P <$
346 0.001 , Table S4), with the lowest bacterial abundance occurring in April and May (Fig.

347 1d).

348

349 **Diversity driven stability and population dynamics**

350 Both fungal and bacterial community abundances were less stable in the tilled
351 plots (fungi: $F_{1,9} = 7.23$, $P = 0.025$, bacteria: $F_{1,9} = 10.3$, $P = 0.011$, Table 1).

352 Additionally, the fungal community stability was positively related to fungal richness

353 overall (slope = 0.096, SE = 0.031, $P = 0.002$, Fig. 2a). The tilling disturbance had no

354 statistically distinguishable effect on the fungal richness-stability relationship (richness

355 by treatment interaction: $F_{1,15.1} = 0.530$, $P = 0.477$). By ‘unpacking’ the diversity-

356 stability relationship into the separate diversity-abundance and diversity-variation

357 relationships, following Gross *et al.* (2014), we found that the overall positive diversity-

358 stability relationship in the fungal community was driven by the effect of fungal richness

359 on reducing the temporal variation ($\beta_{\sigma} = -0.0271$, SE = 0.0150, $P = 0.084$), which

360 accounted for 65.9% of the positive relationship between fungal richness and fungal

361 stability ($\beta_{CV} = 0.0411$, SE = 0.0130, $P = 0.005$). Additionally, the fungal richness-

362 variance relationship was about twice the magnitude as the fungal richness-abundance

363 relationship, which was not statistically significant ($\beta_{\mu} = 0.0140$, SE = 0.0116, $P = 0.243$).

364 In the bacterial community there was no significant association between bacterial

365 richness and stability (slope = 0.021, SE = 0.032, $P = 0.511$, Fig. 2b), and neither did the

366 tilling treatment affect the richness-stability relationship ($F_{1,14.1} = 0.91$, $P = 0.357$, Fig.

367 2b). Unpacking the bacterial richness-stability relationship into the component richness-

368 abundance and richness-variation relationships revealed that the magnitude in the effect

369 of richness on the bacterial abundance and temporal variation were relatively equivalent
370 ($\beta_{\mu} = 0.0154$, SE = 0.0046, $P = 0.003$; $\beta_{\sigma} = 0.0141$, SE = 0.0112, $P = 0.220$). Thus, the
371 variation consistently scaled with the mean bacterial abundance with the changes in
372 richness (i.e. $\beta_{\mu}:\beta_{\sigma} \approx 1$), such that changes in bacterial richness did not relate to bacterial
373 community stability ($\beta_{CV} = 0.0013$, SE = 0.0109, $P = 0.904$).

374 At the population level, the tilling disturbance resulted in greater fungal
375 population CV, which reflects an increase in the average variation of individual taxa ($F_{1,9}$
376 = 16.9, $P = 0.003$, Table 1 & S4). Moreover, we found that the fungal population CV
377 declined overall with increasing richness (slope = -0.025, SE = 0.005, $P < 0.001$, Fig. 2c).
378 Although, for bacteria the population CV was not significantly affected by the
379 management treatment ($F_{1,9} = 2.16$, $P = 0.176$, Table 1 & S4), the tilling treatment
380 resulted in a steeper richness-population CV (till by richness interaction: $F_{1,15.9} = 5.68$, P
381 = 0.030). However, the richness population CV was significantly positive in both cases
382 (till: slope = 0.038, SE = 0.008, $P < 0.001$, no-till: slope = 0.016, SE = 0.005, $P = 0.002$,
383 Fig. 2d). Overall, richness had a strong positive effect on the bacterial population CV
384 (slope = 0.018, SE = 0.005, $P < 0.001$, Fig. 2d). The population synchrony (η) was not
385 significantly affected by the management treatment in either the fungal community ($F_{1,9}$
386 = 1.68, $P = 0.931$, Table 1) or the bacterial community ($F_{1,9} = 3.85$, $P = 0.081$, Table 1).
387 Fungal richness had no relationship with fungal synchrony (slope = $0.345 \cdot 10^{-3}$, SE =
388 $3.996 \cdot 10^{-3}$, $P = 0.404$, Fig. 2e), but bacterial richness was positively related to synchrony
389 (slope = $5.101 \cdot 10^{-3}$, SE = $2.265 \cdot 10^{-3}$, $P = 0.024$, Fig. 2f).

390

391 **Linking population dynamics and stability**

392 The structural equation model revealed how the temporal variation in the fungal
393 community abundance was indirectly influenced by the management treatment through
394 its effects on the temporal dynamics of the fungal population (Fig. 3a, model fit statistics:
395 Fischer's $C = 3.31$, $P = 0.769$). Specifically, temporal variation in fungal abundance (σ)
396 was most positively related to the temporal mean in fungal abundance (μ), followed by
397 the temporal variation at the population level (population CV) and population synchrony.
398 The population CV was negatively associated to richness, but positively associated to the
399 tilling disturbance indicating that the tilling disturbance indirectly increased the temporal
400 variation in fungal abundance by reducing fungal richness and increasing the population
401 CV. The tilling treatment also strongly reduced the fungal abundance (i.e. Table 1), and
402 thus was indirectly linked to a lower temporal variance in fungal abundance. The
403 synchrony in the fungal population was positively related with the temporal variation in
404 the fungal community abundance. However, fungal synchrony did not create a significant
405 indirect link between the variation in fungal abundance and the tilling treatment or fungal
406 richness (Fig. 3a).

407 The model for the bacterial community revealed that the tilling disturbance
408 increased the temporal variation in the bacterial community abundance indirectly through
409 its negative effect on the temporal variation of individual taxa (Fig. 3b, model fit statistics:
410 Fischer's $C = 1.82$, $P = 0.935$). Specifically, the variation in the bacterial community
411 abundance was negatively, and most strongly, associated with the bacterial population
412 CV, which was positively associated with bacterial richness and negatively affected by
413 the tilling disturbance. Although bacterial richness was not significantly affected by the

414 disturbance treatment, it was found to have a positive effect on the population CV.
415 Therefore, the bacterial richness could be indirectly linked with a lower variation in
416 bacterial abundance through its effect on increasing the population CV. The bacterial
417 population synchrony and the temporal mean abundance were both positively related with
418 the temporal variation in the bacterial community abundance. However, the effect of
419 synchrony and abundance did not reveal any indirect link of the tilling disturbance or
420 changes in bacterial richness on the temporal variation in bacterial community abundance.

421

422 DISCUSSION

423 Here we assessed the link between diversity and stability in the abundance of
424 fungal and bacterial communities over a nine-month period spanning the management
425 and growing season under contrasting agricultural management regimes. We
426 hypothesized that the effect of soil disturbance, imposed by tilling, would impact not only
427 the abundance and diversity in the soil communities, but also alter the temporal dynamics
428 of the communities that underlie the stability of their net abundance. As anticipated (i) the
429 disturbance in our system not only reduced the abundance and richness of soil fungi, as
430 observed in numerous other studies (e.g. Oehl *et al.* 2004; Verbruggen *et al.* 2008;
431 Lauber *et al.* 2013; Hartmann *et al.* 2015), but also destabilized the abundance of both
432 fungal and bacterial communities. Further in support of our hypothesis (ii), we found a
433 positive diversity-stability relationship in the fungal community that resulted from
434 richness having a stronger effect on reducing the temporal variation than increasing the
435 overall mean fungal abundance. Yet, we did not find any bacterial richness-stability
436 relationship, and bacterial richness was generally unrelated directly to the temporal

437 variation in the net bacterial abundance. Moreover, by investigating the indirect effects of
438 the tilling treatment on the population level mechanisms that drive stability (*iii*), we
439 found the population level mechanisms underlying stability differed between fungal and
440 bacterial communities. These differences likely reflect their differing responses to the
441 tilling disturbance and the temporal demographic characteristics of these two guilds of
442 soil organisms. Importantly for the objectives of our current study, our results parallel
443 findings in plant community studies in that changes in the environment, such as those
444 induced by anthropogenic management intensity and extreme climate events along side
445 diversity loss, can destabilize productivity by negatively impacting species richness and
446 altering the temporal community characteristics that drive stability (Hallett *et al.* 2014;
447 Yang *et al.* 2014; Hautier *et al.* 2014; Isbell *et al.* 2015; Wagg *et al.* 2017). Moreover, we
448 observed the fungal and bacterial abundance was associated with microbial respiration,
449 biomass and microbial N and C in our system that are considered to be key characteristics
450 to the functioning of soil ecosystems (Graham *et al.* 2016). Considering this, the
451 destabilization in the abundances of fungal and bacterial communities and their
452 community composition likely reflects the stability in ecosystem functioning, and in
453 particular the efficiency by which soil resources are maintained and recycled within the
454 system through microbial mediated pathways.

455

456 **Contrasting responses in fungal and bacterial communities**

457 Although the stability in fungal abundance was stabilized by greater richness and
458 lower temporal variation in the population, the bacterial community exhibited opposing
459 trends. Firstly, the tilling disturbance had a statistically non-significant effect on the

460 richness and abundance in the bacterial community. The minimal effect of the tilling
461 disturbance on bacterial richness and abundance coincides with previous observations
462 that bacterial richness and abundance may be less negatively impacted by physical soil
463 disturbances compared to fungal communities (Bardgett, Hobbs & Frostegård 1996;
464 Yeates *et al.* 1997; Six *et al.* 2006). Further, the lack of an effect of the tilling disturbance
465 on bacterial richness may reflect the ability of the soil microbial communities to rapidly
466 recover and adapt following environmental perturbations (Jackson *et al.* 2003; Girvan *et*
467 *al.* 2005; Allison & Martiny 2008; Griffiths & Philippot 2013).

468 In contrast to bacteria, fungi have been known to be strongly reduced in
469 abundance and richness following the physical destruction of the soil structure and
470 hyphal networks that may require a longer time to re-establish and recover in abundance
471 (Oehl *et al.* 2004; van der Wal 2006; Rousk *et al.* 2007; Verbruggen *et al.* 2008; Lauber
472 *et al.* 2013; Hartmann *et al.* 2015; Sun *et al.* 2017). Further, soil tilling is well known to
473 alter the abiotic properties of the soil and in our system it was observed that tilling
474 increased soil pH and reduced soil silt content. Such changes in soil pH, clay and silt
475 properties have been linked previously to changes in fungal and bacterial abundances and
476 community composition (Rousk, Brookes & Bååth 2009, Rousk *et al.* 2010) that may
477 have also contributed to the differing responses in abundances and composition between
478 fungal and bacterial communities to soil tilling.

479 Although tilling had no detectible effect on synchrony in either the bacterial or
480 fungal populations, synchrony in both communities was positively related to the temporal
481 variation in the net community abundance. This indicates that the abundance of different
482 taxa at different times (i.e. less synchronous, more stochastic population dynamics) is of

483 key importance for maintaining a stable abundance in both fungal and bacterial
484 communities. This parallels the growing literature that has shown that plant communities
485 are stabilized by greater asynchrony as different species maintain the net community
486 abundance at different times (Isbell *et al.* 2009; Roscher *et al.* 2011; de Mazancourt *et al.*
487 2013; Hautier *et al.* 2014). Yet, although the underlying temporal population variation
488 had a strong influence on the stability in the net community abundance in both fungal and
489 bacterial communities, the effects were in opposite directions.

490

491 **Population mechanisms underlying bacterial stability**

492 In the bacterial community the negative effect of increasing population variation
493 on the variation in the net bacterial abundance, in combination with the positive effect of
494 synchrony, suggests compensatory dynamics occurred within the bacterial community. In
495 other words, greater variation of individual taxa (population CV) at different times (less
496 synchronously) together resulted in the more stable bacterial abundance that is indicative
497 of compensatory dynamics (Loreau & de Mazencourt 2008; Loreau & Gonzales 2009;
498 Loreau 2010). Consequently the bacterial community was destabilized by the tilling
499 disturbance because of the reduced temporal variation in the bacterial population. The
500 effect of the tilling disturbance on the temporal variability in the bacterial population and
501 reduced bacterial stability, lends support to other findings that the temporal variation in
502 bacterial community composition is altered by land management practices (Lauber *et al.*
503 2013). The reduced temporal variation in the bacterial population in soils disturbed by
504 tilling may be linked with the reduced silt content, increased pH and the general soil
505 homogenization caused by the tilling that may have favoured bacterial taxa that are more

506 temporally robust regarding their abundance to environmental changes (Doran 1979;
507 Balesdent, Chenu & Balabane 2000; Calderón *et al.* 2001; Jackson *et al.* 2003; Rousk *et*
508 *al.* 2010). However, we found that the richness had a much greater overall effect on the
509 population level variation, and consequently on the community level variation, then the
510 effect of soil tilling on temporal variation at the population.

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

529 the soil tilling effect.

530

531 **Population mechanisms underlying fungal stability**

532 We found that the positive richness-stability relationship in the fungal community
533 was largely explained through the negative association between richness and the temporal
534 variation in the abundance of individual taxa. Hence, soils with a greater fungal richness
535 also exhibited a more stable abundance in individual taxa. Consequently, the tilling
536 disturbance simultaneously reduced both the fungal richness and increased the variation
537 in the abundance of individual taxa (both directly and indirectly), leading to the lower
538 stability in fungal abundance. This result is in line with the many past studies that have
539 observed that soil tilling reduces soil fungal abundance and richness (Oehl *et al.* 2004;
540 van der Wal 2006; Verbruggen *et al.* 2008; Hartmann *et al.* 2015). Considering the
541 physical destruction of fungal hyphae by tilling, the instability in the fungal abundance
542 likely results from fungi requiring longer periods of time to re-establish hyphal networks
543 post disturbance (Rousk *et al.* 2007; Sun *et al.* 2017). The slow development in fungal
544 abundance post disturbance is also evidenced in our system where the tilling reduced
545 fungal abundance throughout the growing season that only seemed to recover towards the
546 end of the year, six to seven months post tilling. This reduction in fungal abundance
547 throughout most of the growing season may also be indicative of a destabilization, or
548 depression, of fungal mediated ecosystem processes such as litter decomposition,
549 maintaining soil structure and the provisioning of soil phosphorous to plants (Griffiths *et*
550 *al.* 2000; Six *et al.* 2006; Verbruggen *et al.* 2008; Bender & van der Heijden 2014; Wagg
551 *et al.* 2014).

552 Although numerous studies experimentally manipulating species richness in
553 grassland plant communities have illustrated that more species rich communities can
554 result in greater population level variation that consequently stabilizes the net community
555 productivity, such richness-population variation and richness-stability relationships are
556 not always observed (Gross *et al.* 2014). For instance, Sankaran & McNaughton (1999)
557 found that population and compositional stability may also be high at low diversity in
558 natural grassland communities and suggest that environmental characteristics in which
559 communities establish and evolve also play an important role. In our system the tilling
560 disturbance to the soil likely also altered characteristics of the soil environment to support
561 a more rich community and temporally stable composition. For instance, fungal
562 abundance and richness have been observed to positively relate to greater clay and silt
563 content and lower pH (Talley, Coley & Kursar 2002; de Vries *et al.* 2012), which we
564 found to be altered in our system by tilling, and may have contributed to greater fungal
565 community compositional variation and abundance. Although the RISA methods used
566 here likely underestimate fungal and bacterial richness, the methods provides a good
567 estimate for the relative changes in richness and community structure that parallels results
568 using methods to obtain a deeper resolution of the microbial diversity present (van Dorst
569 et al. 2013). Thus, we expect that a finer resolution of the community richness and
570 structure should likely parallel our results, but may provide finer details as to the
571 temporally changing compositions that need further exploration for relating changes in
572 microbial community composition to the broader scale ecosystem functioning in natural
573 systems.
574

575 CONCLUSIONS

576 Here we assessed the diversity-stability relationships in soil communities under
577 differing land management intensities following the biodiversity-stability framework
578 typically applied to aboveground plant productivity. Our results highlight that the
579 disruption of the soil ecosystem through land management practices alters the temporal
580 stability in both fungal and bacterial abundances. Further, we show that changes in
581 taxonomic richness can alter the stability of fungal abundance and the temporal
582 population dynamics in both bacterial and fungal communities. However, we also found
583 that the population level mechanisms that underlie temporal stability differed between
584 fungal and bacterial communities demonstrating that the mechanisms that drive the
585 stability can differ among guilds of organisms within the same system. This last result
586 parallels findings that different systems may exhibit different diversity-stability
587 relationships and underlying mechanisms (Gross *et al.* 2014). The differences between
588 fungal and bacterial communities in the underlying mechanisms that supported the
589 temporal stability of their abundances are likely linked to their fundamentally different
590 life histories, such as growth and turnover rates, that determine the responses in
591 community composition to environmental disturbance. Therefore the relationships
592 between diversity, temporal population dynamics and community stability may be
593 temporally and spatially scale dependant relative to the observed organismal community
594 and the environmental perturbation addressed (Sankaran & McNaughton 1999; Bardgett
595 & van der Putten 2014; Oliver *et al.* 2015). Such scale dependent effects of community
596 diversity have been indicated in other systems (Collins 2000, Chase & Leibold 2002,
597 Chalcraft *et al.* 2004, Ives & Carpenter 2007; Wagg *et al.* 2017). Finally, although

598 microbial abundances have been linked to numerous ecosystem functions, the assessment
599 of the temporal variations we observed in their abundances, and their underpinning
600 population level characteristics, still require further investigation into how these temporal
601 compositional changes influence the long-term nutrient cycling and the maintenance of
602 plant diversity and productivity. In summary, we argue that future applications of
603 diversity-stability assessments across systems under management and climatic
604 perturbations are strongly needed and promise to be a worthwhile avenue to derive
605 general rules relating population and community level temporal dynamics that drive
606 ecosystem functioning in nature.

607

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617

618 AUTHORS' CONTRIBUTIONS

619 CW, JHD, FW and MvdH conceived the ideas and designed methodology; JHD collected
620 the data; CW analysed the data and led the writing of the manuscript. All authors
621 contributed critically to the drafts and gave final approval for publication.

622

623 DATA ACCESSIBILITY

624 Data are available at: DOI: xxxxxxxxxx {will be available upon acceptance}

625

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851 TABLES

852

853 **Table 1.** Summary of results for the overall effect of the tilling disturbance on fungal and
854 bacterial temporal community characteristics. Means are shown for both tilled (T) and
855 non-tilled (NT) communities along with the *P*-value for the difference between the two.

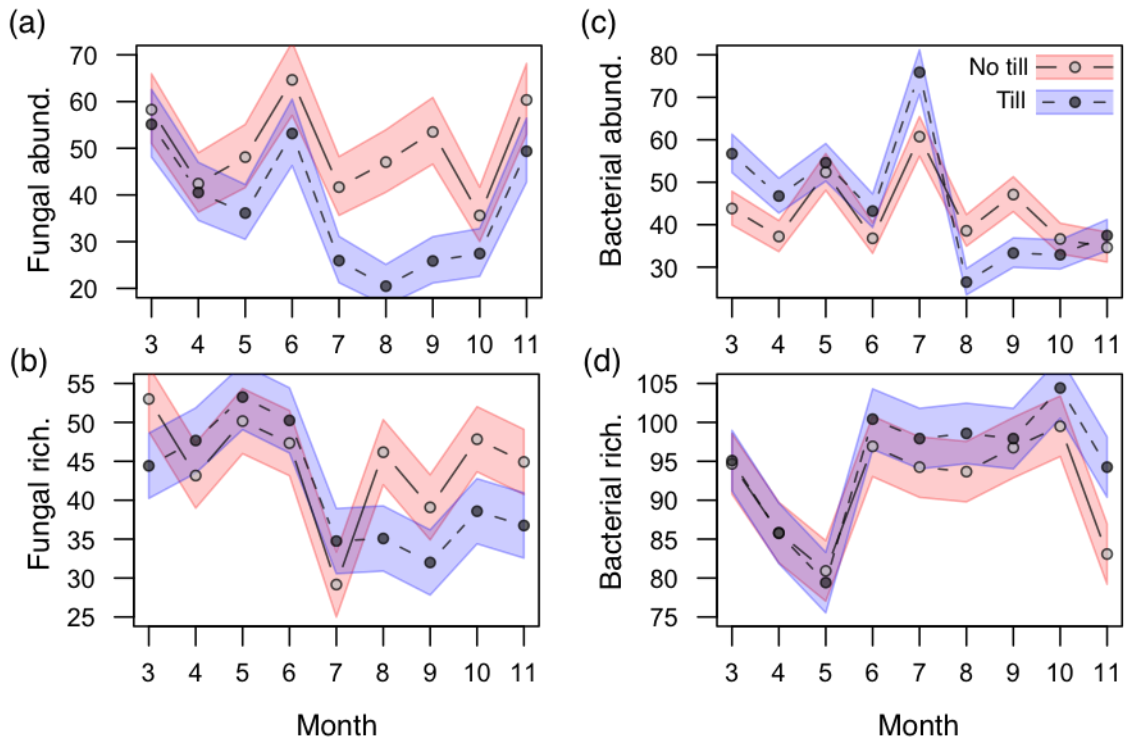
856 Arrows (↑ and ↓) highlight the direction that the tilling disturbance had on the
857 community characteristic

	Fungi			Bacteria		
	T	NT	<i>P</i>	T	NT	<i>P</i>
Richness	↓ 41.42	44.54	0.040	94.86	91.73	0.105
Abundance (μ)	↓ 38.65	51.53	< 0.001	45.93	43.79	0.105
Stability (μ/σ)	↓ 2.23	2.89	0.025	↓ 2.74	3.76	0.011
Population CV	↑ 1.72	1.64	0.002	1.14	1.23	0.176
Synchrony (η)	0.27	0.23	0.227	0.40	0.34	0.081

858

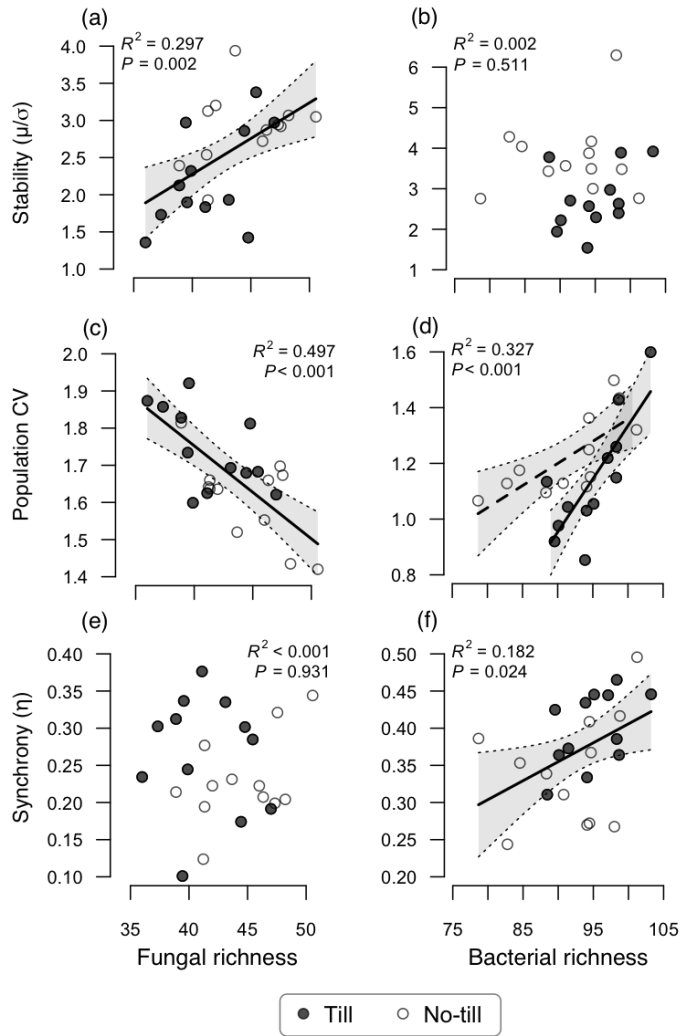
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860 FIGURES



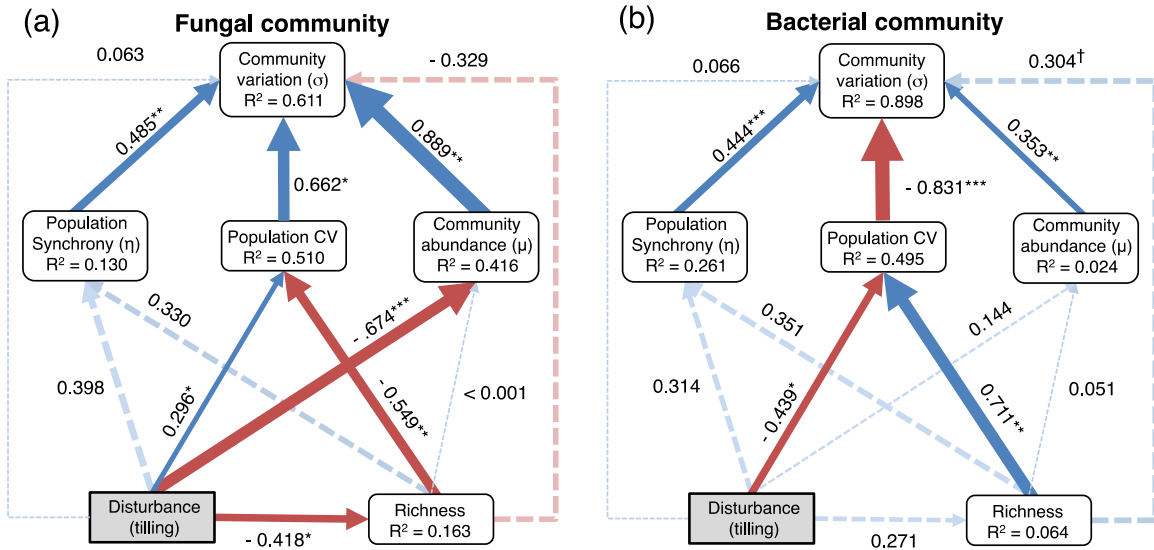
861

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



873

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



883

884 **Figure 3.** Structural equation model results indicating the mechanisms behind the
 885 stability of (a) fungal and (b) bacterial abundances. The effect of disturbance through
 886 tilling is indicated as an exogenous variable highlighted in grey. Blue arrows represent
 887 positive, and red negative, path coefficients and their width reflect the strength of the
 888 standardized path coefficient (shown adjacent to arrows and significance indicated by † P
 889 < 0.1, * P < 0.05, ** P < 0.01, *** P < 0.001). The proportion of variation of each
 890 endogenous variable explained by the paths is shown for each endogenous variable
 891 (marginal R^2). Faded dashed arrows indicate paths coefficients that were not significant.
 892

893 SUPPORTING INFORMATION

894

895 Additional supporting information may be found in the online version of this article:

896

897 **Figure S1.** Correlations between 16S and 18S gene abundance and soil microbial

898 characteristics

899 **Figure S2.** Rarefaction curves for fungal OTUs by month

900 **Figure S3.** Rarefaction curves for bacterial OTUs by month

901 **Table S1.** The management and soil community sampling activities

902 **Table S2.** Soil properties of tilled and non-tilled plots

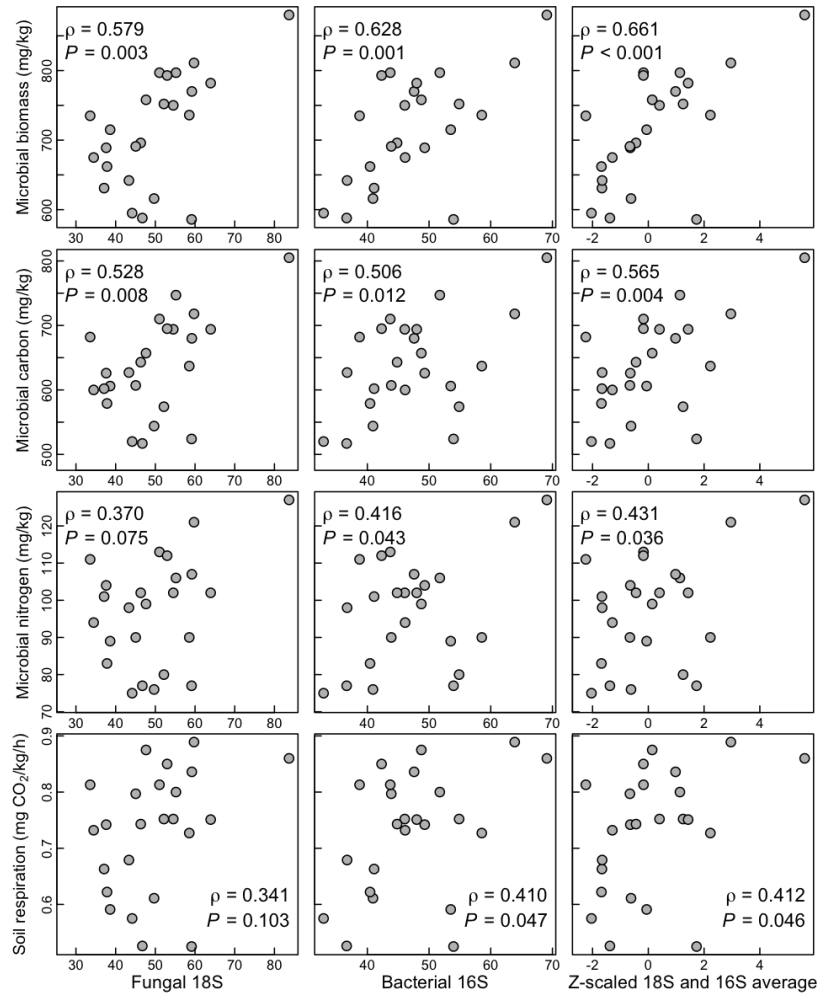
903 **Table S2:** PCR reagents for RISA and qPCR protocols

904 **Table S3.** PCR cycling conditions used for RISA and qPCR

905 **Table S4:** Full ANOVA results for assessing experimental factors on fungal and bacterial

906 abundance and richness

907



908

909 **Figure S1.** Scatterplots showing the correlation (Pearson's rho and associated *P* value)

910 between soil microbial characteristics and qPCR results (18S and 16S copy number

911 averaged across all sampling time points. Both 16S and 18S data are combined into a

912 single index of microbial abundance by averaging the z-scaled, zero mean and unit

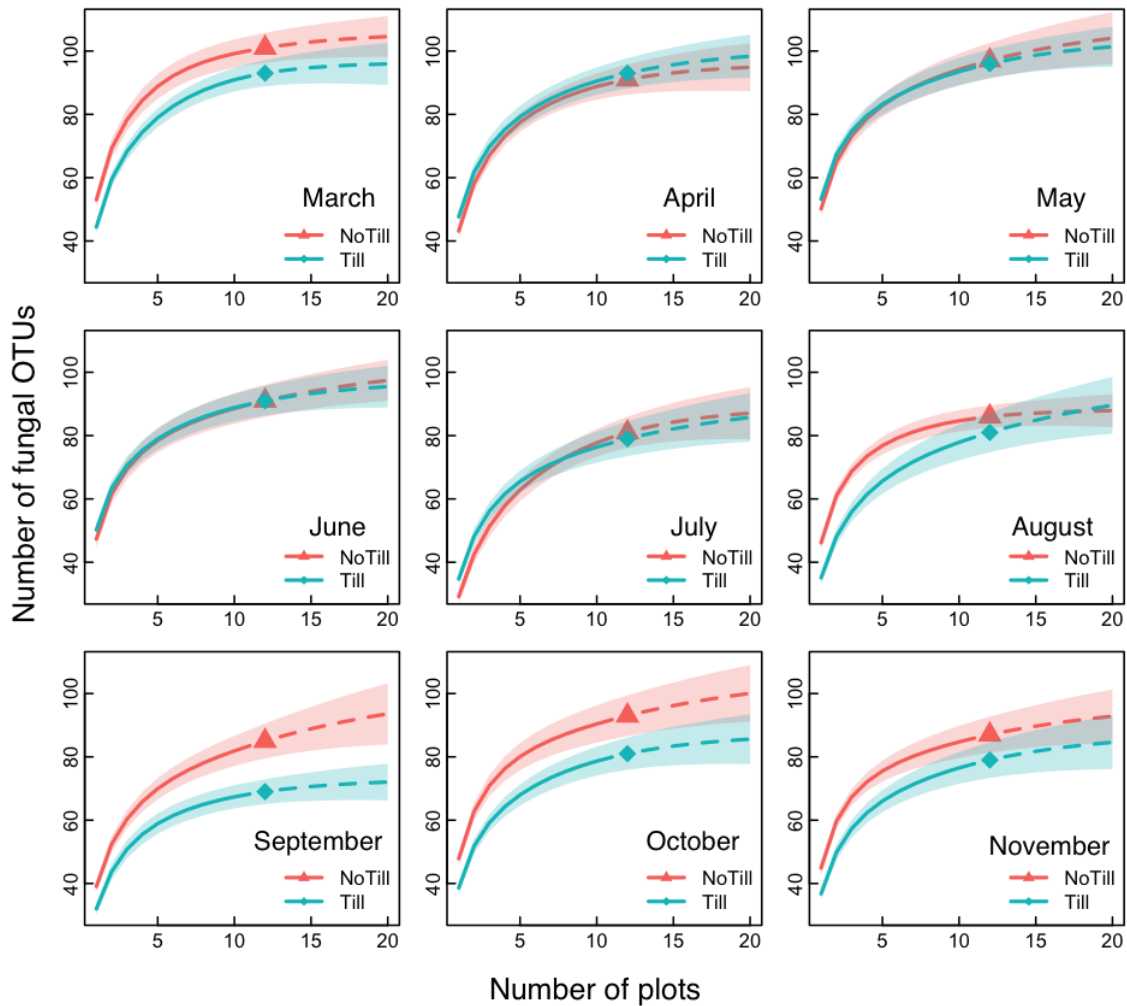
913 variance, data of both). Microbial biomass and soil respiration were quantified using

914 substrate induced respiration methods (Beare *et al.* 1990. *Soil Biology and Biochemistry*

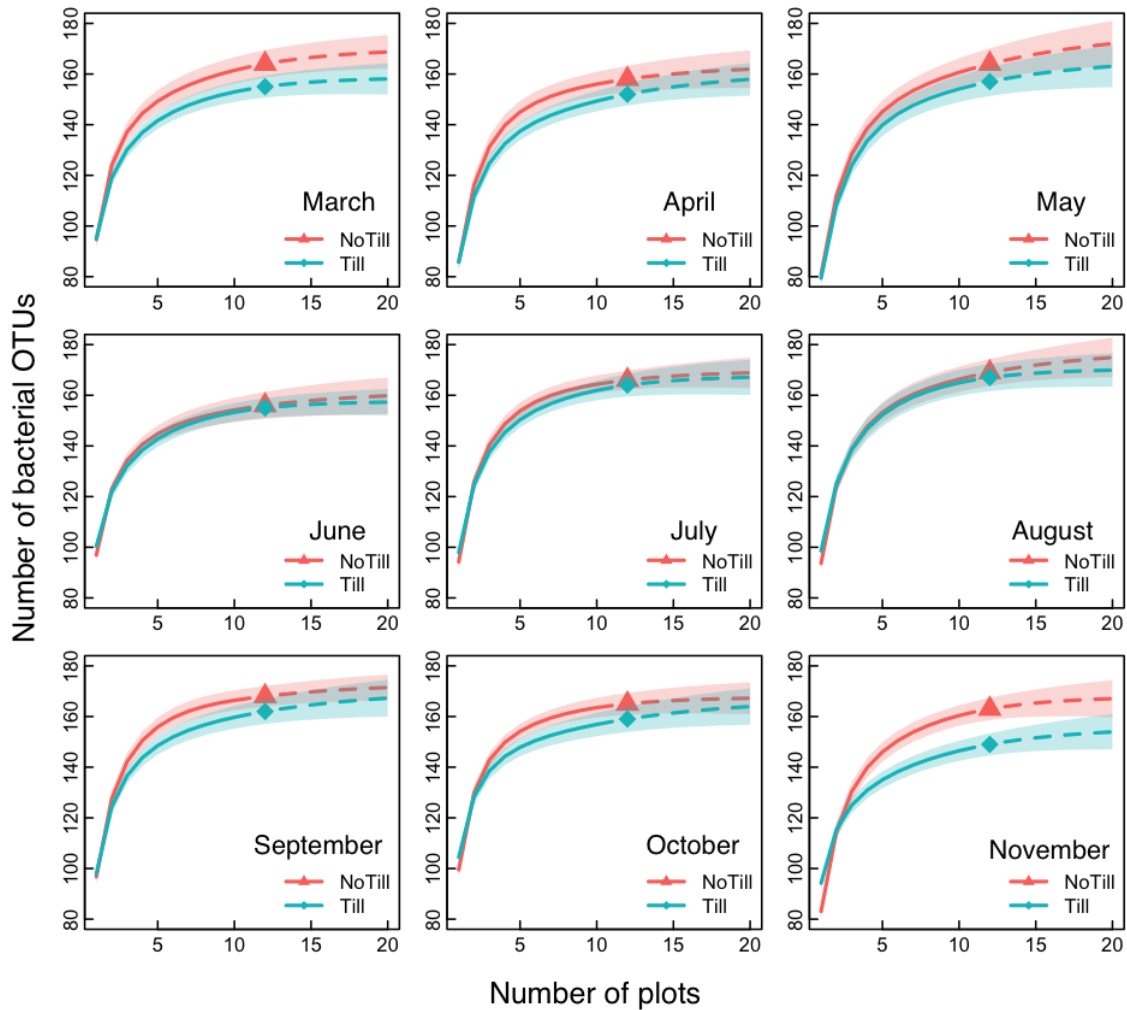
915 **22**, 585-594) and the microbial carbon and nitrogen abundance was quantified by

916 chloroform fumigation extraction methods (see Witt *et al.* 2000. *Biology and Fertility of*

917 *Soils* **30**, 510-519).



918
 919 **Figure S2.** Rarefaction curves showing the accumulating number of fungal OTUs with
 920 the increasing number of plots sampled for tilled and non-tilled plots based on the
 921 frequency of OTUs across the 12 plots under the two tilling treatments. Points indicate
 922 the limit of the 12 plots that were sampled each month. The dashed line is the
 923 extrapolation of the curve (up to 20 plots). The coloured shaded region is the 95%
 924 bootstrapped confidence interval. Plots are generated using the package ‘iNEXT’ for R
 925 (Hsieh *et al.* 2016. *Methods in Ecology and Evolution* **7**, 1451-1456).



926

927 **Figure S3.** Rarefaction curves showing the accumulating number of bacterial OTUs with
 928 the increasing number of plots sampled for tilled and non-tilled plots based on the
 929 frequency of OTUs across the 12 plots under the two tilling treatments. Points indicate
 930 the limit of the 12 plots that were sampled each month. The dashed line is the
 931 extrapolation of the curve (up to 20 plots). The coloured shaded region is the 95%
 932 bootstrapped confidence interval. Plots are generated using the package ‘iNEXT’ for R
 933 (Hsieh *et al.* 2016. *Methods in Ecology and Evolution* **7**, 1451-1456).

934

935

936 **Table S1.** The management and soil community sampling activities are listed with the
 937 corresponding dates (dd.mm.yyyy). The month in which soil communities were sampled
 938 corresponding to months in Fig. 1 are shown in parentheses

Date	Activity
11.08.2011	Cover crops sown
20.03.2012	(3) Soil samples collected
07.04.2012	Glyphosate herbicide applied in the non-tilled plots
19.04.2012	(4) Soil samples collected
28.04.2012	Tilling regime applied in the tilled plots
30.04.2012	Fertilization *
04.05.2012	Main crop sown (<i>Zea maize</i>)§
08.05.2012	Fertilization †
19.05.2012	(5) Soil samples collected
31.05.2012	Herbicide application (Mikado 1 l/ha, Dasul 1 l/ha, Andil 1 kg/ha)
15.06.2012	Fertilization ‡
19.06.2012	(6) Soil samples collected
20.07.2012	(7) Soil samples collected
20.08.2012	(8) Soil samples collected
20.09.2012	(9) Soil samples collected
11.10.2012	Maize kernel harvest
17.10.2012	Maize biomass harvest
20.10.2012	(10) Soil samples collected
20.11.2012	(11) Soil samples collected

939 * 69 kg P₂O₅ / ha, 138 K₂O / ha, † 30 kg N / ha, ‡ 60 kg N / ha, § no-till

940 single-grain seeder (Amazone), 9.5 plants/ m²

941 **Table S2.** Soil property means between tilled and non-tilled plots are provided. Data
 942 were collected in 2014 and *F* and *P* statistics were generated by LMM as described for
 943 the stability in microbial abundance with block included to account for potential spatial
 944 variation in edaphic characteristics within the field site (see Methods). Bold text indicates
 945 characteristics that statistically differed between the Till and No till treatments.

	<i>F</i> _{1,11}	<i>P</i>	Till	No till
Clay (%)	0.69	0.424	21.27	22.06
Silt (%)	11.06	0.007	28.94	31.20
Sand (%)	0.02	0.895	47.39	47.32
pH	3.42	0.091	7.92	7.63
Total C (%)	0.80	0.390	1.72	1.61
Organic C (%)	0.34	0.572	1.39	1.36
Total N (%)	0.00	0.947	0.16	0.16
P (mg/kg)	0.46	0.511	59.73	56.21
K (mg/kg)	10.05	0.009	275.37	317.35
Mg (mg/kg)	0.95	0.350	508.48	458.42
Ca (mg/kg)	0.43	0.525	7474.58	6239.25
Exchangeable cations				
Ca ²⁺	4.38	0.060	12.38	11.07
Mg ²⁺	1.65	0.226	1.91	2.01
Na ⁺	0.00	1.000	0.03	0.03
K⁺	18.02	0.001	0.50	0.61

947

948 **Table S3.** List of reagents and their concentration in the solution mix, as well as the
 949 primer sequences used to amplify bacterial and fungal DNA, used for the extraction of
 950 soil DNA and qPCR and RISA detection of bacterial and fungal communities
 951

Extraction	
CTAB extraction	0.2 M Na ₃ PO ₄ (pH 8), 0.1 M NaCl, 50 mM EDTA, 0.2% CTAB buffer
qPCR (20 µl volume)	
	SsoFast EvaGreen Supermix (Bio-Rad)
0.6 µg µl ⁻¹	Bovine serum albumin (BSA)
0.2 µM	Forward primer
0.2 µM	Reverse primer
<i>Fungi 18S rRNA</i>	
Forward primer	Fung5for (5'-GGGGAACCAGGACTTTTA-3')
Reverse primer	FF390rev (5'-AGGTCTCGTTCGTTATCG-3')
<i>Bacteria 16S rRNA</i>	
Forward primer	Eub338for (5'-ACTCCTACGGGAGGCAGCAG-3')
Reverse primer	Eub518rev (5'-ATTACCGCGGCTGCTGG-3')
RISA (50 µl volume)	
	10 x PCR-buffer (Qiagen)
2 mM	MgCl ₂ (Qiagen)
0.4 mM	DNTP mix (Qiagen)
2 U	HotStar Taq-polymerase (Qiagen)
0.6 mg ml ⁻¹	Bovine serum albumin (BSA)
0.4 mM	Forward primer
0.4 mM	Reverse primer
10 ng	Purified DNA template
<i>Fungi</i>	
Forward primer	fRISAfor (5'-GTTTCCGTAGGTGAACCTGC-3' FAM-labelled)
Reverse primer	fRISArev (5'-ATATGCTTAAGTTCAGCGGGT-3')
<i>Bacteria</i>	
Forward primer	bRISAfor (5'-TGCGGCTGGATCCCCTCCTT-3' FAM-labelled)
Reverse primer	bRISArev (5'-CCGGGTTTCCCCATTCGG-3')

952

953 **Table S4.** PCR cycling conditions for amplifying bacterial and fungal DNA for qPCR
 954 and RISA protocols are listed

955

qPCR	Bacteria		Fungi	
	Time (s)	Temp. (°C)	Time (s)	Temp. (°C)
Initial denaturation	120	98	120	98
40 cycles of:				
Denaturation	40	98	40	98
Annealing	40	53	40	45
Extension	30	61	30	61
<hr/>				
RISA				
Initial denaturation	900	98	900	98
	30 cycles of:		35 cycles of:	
Denaturation	20	92	40	94
Annealing	45	57	40	55
Extension	120	72	120	72
Final extension	300	72	600	72

956

957

958 **Table S5.** Mixed effects model results for the analysis of variance in the abundance and
 959 richness of fungi and bacteria among the cover crops, month in which plots were sampled
 960 and the tilling disturbance, as well as their interactions

	Fungi (18S)				Bacteria (16S)		
Abundance	DF_N	DF_D	F	P	DF_D	F	P
Cover crop (C)	2	9.0	0.60	0.570	9.0	0.15	0.8595
Month (M)	8	117.8	9.49	< 0.001	119.7	31.13	< 0.001
Disturbance (D)	1	9.0	32.12	< 0.001	9.0	2.76	0.1311
M × D	8	117.8	1.86	0.074	119.7	5.66	< 0.001
C × D	2	9.0	1.25	0.331	9.0	5.18	0.0319
C × M	16	122.8	1.02	0.441	124.1	0.76	0.7219
C × M × D	16	122.8	1.11	0.353	124.1	0.61	0.8682
Random terms			Var.	SE		Var.	SE
Subplot			-0.96	16.29		-2.81	6.28
Cover in Block			25.45	20.56		38.68	21.05
Residual			265.84	32.29		106.85	13.25
Month ρ_{AR1}			0.039	0.094		0.095	0.091

	Fungi (# OTUs)				Bacteria (# OTUs)		
Richness	DF_N	DF_D	F	P	DF_D	F	P
Cover crop (C)	2	9.0	0.16	0.852	9.0	0.30	0.737
Month (M)	8	122.8	10.03	< 0.001	120.2	15.50	< 0.001
Disturbance (D)	1	9.0	7.93	0.020	9.0	2.20	0.174
M × D	8	122.8	2.91	0.005	120.2	1.20	0.317
C × D	2	9.0	0.98	0.412	9.0	0.50	0.606
C × M	16	126.4	0.90	0.565	124.5	0.70	0.824
C × M × D	16	126.4	0.27	0.998	124.5	0.80	0.729
Random terms			Var.	SE		Var.	SE
Subplot			-2.82	3.63		18.85	12.12
Cover in Block			7.24	5.26		12.64	13.41
Residual			106.55	12.56		81.16	9.59
Month ρ_{AR1}			-0.115	0.079		-0.163	0.083

961 DF_N = numerator degrees of freedom, DF_D = denominator degrees of freedom, F =
 962 variance ratio, P = error probability, Var. = random term variance component, SE =
 963 standard error of variance component, $AR1\rho_{Month}$ = temporal autocorrelation across
 964 months

965
 966

967