Dryland cropping system, weed communities, and disease status modulate the effect of climate conditions on wheat soil bacterial communities.

Running title: agricultural soil bacteria and climate

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ABSTRACT

Little knowledge exists on whether soil bacteria are impacted by cropping systems and disease status in current and predicted climate scenarios. We assessed the impact of soil moisture and temperature, weed communities, and disease status on soil bacterial communities across three cropping systems: conventional no-till (CNT) utilizing synthetic pesticides and herbicides, 2) USDA-certified tilled organic (OT), and 3) USDA-certified organic with sheep grazing (OG). Sampling date within the growing season, and associated soil temperature and moisture, exerted the greatest effect on bacterial communities, followed by cropping system, Wheat streak mosaic virus (WSMV) infection status, and weed community. Soil temperature was negatively associated with bacterial richness and evenness, while soil moisture was positively associated with bacterial richness and evenness. Both soil temperature and moisture altered soil bacterial community similarity. Inoculation with WSMV altered community similarity, and there was a date x virus interaction on bacterial richness in CNT and OT systems, as well as an interaction between WSMV x climate. In May and July, cropping system altered the effect of climate change on the bacterial community composition in hotter, and hotter and drier conditions not treated with WSMV, as compared to ambient conditions. In areas treated with WSMV, there were interactions between cropping system, sampling date, and climate conditions, indicating the effect of multiple stressors on bacterial communities in soil. Overall, this study indicates that predicted climate modifications as well as biological stressors play a fundamental role in the impact of cropping systems on soil bacterial communities.

IMPORTANCE

Climate change is affecting global moisture and temperature patterns and its impacts are predicted to worsen over time, posing progressively larger threats on food production. In the Northern Great Plains of the United States, climate change is forecasted to increase temperature and decrease precipitation during the summer, and is expected to negatively affect cereal crop production and pest management. In this study, temperature, soil moisture, weed communities, and disease status had interactive effects with cropping system on bacterial communities. As local climates continue to shift, so too will the dynamics of above- and below-ground associated bio-diversity which will impact food production and the need for more sustainable practices.

INTRODUCTION

Climate change affects soil moisture content and temperature which, in turn, impacts: crop production and nutritional value (1–4); pest abundance, dynamics, and management (4–7); as well as overall ecosystem resiliency (8). Determining how climate change modifies multitrophic interactions between crops, weeds, pathogens, and soil microbial communities is complex (9), yet critical, as crop production relies on healthy soil and microbially-mediated nutrient cycling (10, 11). Microbial α-diversity in soil is linked to plant growth stage (12). Low microbial α-diversity in soil is associated with impeded plant growth, and early senescence of *Arabidopsis thaliana* (13). With the knowledge that climate change will fundamentally change the dynamics of agricultural ecosystems, we must increase our understanding of the mechanisms driving biological and environment stress to secure the sustainability of agricultural production, (1, 14, 15).

The Northern Great Plains of the United States is a major global cereal-producing region where the effects of climate change are already being felt (16, 17). Over the next 30 years, mean temperature is predicted to increase by 2.5 – 3.3°C in this region (17, 18). Soil microbial community structure and function may be altered due to their temperature sensitivity (19–21). Coupled with predicted decreases in summer precipitation, hotter and drier conditions during the growing season will result in crop stress (17) which has the potential to further alter soil microbial communities. In periods of drought, microbial diversity is reduced (22, 23) as is their ability to cycle soil nitrogen (24). Drought can also cause plants to prioritize relationships with fungi over bacteria, reducing the transfer of nutrients and contributing to the crash of the bacterial community (25, 26). Further, as climate change alters the composition of plant communities and their nutrient content (27,

28), the composition of plant liter and residues is altered. This change in soil inputs, in turn, modifies plant-microbe relationships (29–31) and reduces the available nutrients recycled into soil (22, 30).

Climate change is also predicted to worsen the effects of plant pathogens, including *Wheat streak mosaic virus* (WSMV; genus *Tritimovirus*), either by altering the dynamics of vector transfer or by decreased plant resistance to infection (7, 32). WSMV is transmitted by wheat curl mites (*Aceria tosichella*), occurs across the North American Great Plains, and can make plants more susceptible to the effects of climate change by hindering root development and water uptake (33). To our knowledge, no study has formally assessed the potential link between WSMV infection and plant-, rhizosphere-, or root-associated microbial communities. While un-explored, it is possible that the WSMV viral infections which alters root structure or function, and thus the capacity for plants to interact with soil microbiota.

In industrial (contemporarily referred to as conventional) cropping systems, management approaches focused on maximizing production are based on regular applications of synthetic inputs in the form of fertilizers and pesticides (34). In recent years, shifted consumer demands and new market opportunities have developed organic production into a major agricultural, economic, and cultural force (35, 36). However, organic cropping systems rely heavily on tillage for weed management and cover-crop termination. Due to the negative consequences that tilling has on the physical, chemical, and biological properties of soils in the semi-arid ecosystems that dominate large sections of the Northern Great Plains, there is a growing interest among farmers and researchers to reduce soil disturbance practices in organic systems (37–39). In this context, the

114 integration of crop and livestock production has been proposed as a sustainable approach
115 to terminate cover crops, manage crop residues, and control weeds while reduce tillage
116 intensity (40–42), yet very few studies exist on the impact of integrated livestock
117 management on soil quality or microbial communities (23) or disease resistance.

118 Differences among cropping systems affect plant communities, including species'
119 abundance, composition, and growth (43, 44) which, in turn, modifies microbial
120 communities in the rhizosphere (23, 45, 46). Although previous studies have evaluated
121 the role of microbial communities in crop yields and crop-weed competition (47), fewer
122 explore the extent to which root-associated bacteria are impacted by cropping systems,
123 weeds, and plant disease in current and predicted climate scenarios. The aim of our study
124 was to assess changes in soil bacterial communities due to warmer and drier climate
125 conditions and the presence of WSMV across contrasting cropping systems and their
126 associated weed communities. We hypothesized that: 1) bacterial community richness
127 and evenness would be reduced by climate or WSMV infection; 2) cropping systems that
128 promote bacterial richness would be more resistant to alterations from climate and
129 WSMV infection; and 3) more diverse bacterial communities would have a more stable
130 bacterial community membership over the growing season and in response to increased
131 soil temperature, decreased precipitation, and WSMV.
132
133

RESULTS

Bacterial diversity and evenness

Soil temperature during the growing season (Fig S1) was a strong driver of bacterial species' richness (Table 1); with fewer bacterial OTUs (97% cutoff) observed in soil during hotter temperatures (Fig 1A). Increased soil temperature reduced the evenness of bacterial species' (Table 1). Hotter soil temperatures were negatively associated with the presence or relative abundance of bacterial taxa that were significantly important features in the model (Figure 1B). The most abundant of those taxa included members of *Blastococcus*, Bacillales, Micromonosporaceae, Intrasporangiaceae, *Sphingomonas*, Microbactericeae, and *Streptomyces* (Fig 1B).

Soil moisture during the growing season (Fig S2) positively impacted total bacterial species' richness (Fig 2A, Table 1) and evenness (Table 1), though not as strongly as temperature did. Across all samples, soil temperature and soil moisture were not correlated with each other (lmer, $p > 0.05$; Fig S3). Soil moisture impacted the relative abundance of bacterial species in different ways (Fig 2B). For example, *Aeromicrobium* were more abundant at low soil moisture levels, *Sphingomonas* were more abundant at high moisture, and *Phenylobacterium* were most abundant at moderate levels of soil moisture (Fig 2B).

Cropping system interacted with climate treatment to affect bacterial richness and evenness (Fig 3; Table 1). Bacterial richness at ambient conditions peaked in early June for all three cropping systems, while richness in both hotter, and hotter and drier conditions peaked in late June in the CNT and OG systems (Fig 3A). Bacterial richness

156 in OG subplots was affected by soil temperature (lmer, Estimate = 35, F = 2.997, p =
157 0.003), and moisture (lmer, Estimate = 6, F = 2.203, p = 0.03).

158 Inoculation with WSMV resulted in 6 CNT positive samples with mean infection
159 rate within subplots of 4.4%, 9 OG positives with mean infection rate of 13.3%, and 7 OT
160 positives with mean infection rate of 3.2% (Table S1). Overall, inoculation with WSMV
161 had no effect on bacterial species' richness or evenness (Fig 3; Table 1). When
162 comparing CNT and OT subplots, there was a date x virus interaction on bacterial
163 richness (lmer, F = 2.6792, p = 0.039). OT subplots at the end of July that had been
164 inoculated with WSMV showed reduced bacterial richness (lmer, F = 2.019, p = 0.046),
165 as did all hotter treatments in July treated with WSMV (F = 3.046, p = 0.003) and hotter
166 OG treatments inoculated with WSMV in April (F = 2.039, p = 0.044), May (F = 2.088 p
167 = 0.039), and late June (F = 2.192, p = 0.03). Weed species' diversity, and percent
168 coverage or biomass, did not alter bacterial richness across all subplots (lm, $p > 0.05$).
169
170 *Bacterial community stability*
171 Soil temperature impacted bacterial community similarity (Table 2). Hotter soil
172 temperatures were associated with increased variation in bacterial community
173 heterogeneity and dispersion (betadisper, F = 3.3579, $p < 0.001$), i.e. in warmer
174 temperatures the bacterial communities were more dissimilar across and within a
175 treatment group. Soil moisture also altered soil bacterial community similarity (Table 2),
176 but did not affect the amount of variation (heterogeneity) within bacterial communities
177 (betadisper, $p > 0.05$). Soil moisture did not have an effect on homogeneity when
178 considering healthy and WSMV subplots separately, to account for the effect of WSMV

179 on plants' abilities to uptake water. Soil bacterial community similarity was impacted by
180 the interaction of cropping system and climate (Table 2).

181 Here, stability (interpreted as no significant difference in bacterial β-diversity)
182 was similar between ambient and treatment subplots over time. Lower OTU richness
183 correlated with a higher similarity between ambient and manipulated hotter and drier
184 subplots (lm, $F = 1291$, $p < 0.001$), and this was most evident early and late in the
185 growing season (Fig 4). The temporal stability of a bacterial community against climate
186 change was not associated with a lower fold difference in OTUs between ambient and
187 hotter, and ambient and hotter and drier subplots (Fig 5). While the most stable soil
188 communities did have more bacterial OTUs, a loss of OTUs was not necessarily
189 associated with having lower community similarity (Fig 5).

190 When comparing bacterial communities in response to climate conditions,
191 cropping system varied how stable bacterial communities remained at different periods in
192 the growing season (Fig 6; Table 3). In May, the bacterial communities in hotter OG
193 samples were less stable compared to the ambient OG samples, as compared to hotter
194 CNT and OT, which were more stable compared to their respective bacterial
195 communities under ambient conditions (Fig 6; Table 3). In July, the bacterial
196 communities in the hotter OT subplots were most stable \, than the hotter CNT or OT
197 subplots and their respective ambient conditions (Fig 6; Table 3). For bacterial
198 communities in hotter and drier subplots as compared to ambient subplots, communities
199 in OT subplots showed the most stability, followed by OG samples, and CNT were least
200 stable (most dissimilar) compared to the respective ambient conditions (Fig 6; Table 3).

Neither WSMV inoculation nor rate of infection (Table S3) within subplots created a definable bacterial community (random forest, data not shown); although WSMV inoculation was negatively associated with a species of *Cellulomonas*, as well as with Actinobacteria clade 480-2 (Fig S4). However, WSMV inoculation significantly affected soil bacterial community similarity (Table 2). Moreover, there was an interaction of WSMV and climate change (Table 2), which was modulated by cropping system (Fig 7; Table 3).

When comparing the change in bacterial communities between ambient conditions and hotter, or hotter and drier climate conditions, cropping system modulated how stable bacterial communities remained in subplots which had been treated with WSMV. In assessing similarity between bacterial communities between ambient and climate conditions, CNT and OT subplots treated with WSMV were significantly different (ANOVA, $p < 0.001$ Tukey) from their non-infected counterparts, indicating that disease status altered the ability of the community to remain stable (i.e. resistance) under changing climate. However, OG subplots did not differ between WSMV-treated and untreated subplots (ANOVA, $p > 0.05$ Tukey) in terms of the similarity between ambient and climate-conditioned soil.

WSMV made it more difficult for bacterial communities to remain stable under climate conditions, across the growing season, and between cropping systems (Fig 7; Table 3). When comparing ambient to hotter conditions in subplots treated with WSMV, in April, CNT subplots were more stable than OG or OT; in early June, OG was more stable than OT; in late June, CNT and OG were more stable than OT; and in late July, CNT subplots were most stable, followed by OT, and then OG subplots (Fig 7, Table 3).

Comparing hotter and drier to ambient conditions in WSMV-treated subplots, in April, CNT subplots were more stable than OG or OT; in late June, CNT and OG were more stable than OT; and in late July, CNT was again more stable than OG or OT (Fig 6; Table 3).

Weed communities in the organic systems were more diverse than the CNT subplots, though OG and CNT had similar relative species abundance (28). Climate conditions had minor impacts on weed communities (28). Weed species' diversity, as well as percent or biomass from subplots negatively impacted the similarity between ambient and climate-treated subplots across the growing season (Fig S5), including weed diversity (lm, F = 79.153, $p < 0.001$) and percent coverage (F = 26.516, $p < 0.001$) the prior fall on Oct 25, 2015, diversity (F = 25.637, $p < 0.001$) and coverage (F = 119.78, $p < 0.001$) early in the growing season on Apr 8, 2016, diversity on 6/14/2016 (F = 68.888, $p < 0.001$), and weed biomass on June 29, 2016 (F = 30.807, $p < 0.001$).

Individual weed species were associated with membership of the soil bacterial community (Table 4) including *Asperugo procumbens, Bromus tectorum, Capsella brusa-pastoris, Chenopodium album, Cirsium arvense, Descurainia sofia, Galium aparine, Lactuca serriola, Lamium ampleuxicaule, Malva neglecta, Monolepsis nuttaliana, Poa annua, Solanum triflorum, Taraxacum officinale, Thlaspi arvense, Tragopogon dubious,* and *Trifolium pretense.* Of these, three weed species had definable effects on bacterial community structure (Fig S6; $p < 0.05$). Winter annuals, *Bromus tectorum* cover in mid-June (Fig S6A), as well as cover of *Capsella bursa-pastoris* (Fig S6B) and *Descurainia sofia* (Fig S6C) in the previous fall had a predictable impact on the rhizosphere community. *Bromus tectorum* had a U-shaped relationship with bacterial

247 relative abundance, while *C. bursa-pastoris* and *D. sofia* showed more of a positive
248 correlation. *Capsella bursa-pastoris* cover in subplots associated with an increase in
249 *Rubrobacter*, *Nocardioides*, *Illumatobacter*, the family-level clade FFCH13075 in the
250 order Solirubrobacteriales, and others (Fig S6B). *Descurainia sofia* coverage of subplots
251 associated with an increase in the KD4-96 clade in the Chloroflexi phylum, FFCH13075,
252 *Blastococcus*, *Nocadioides*, *Oryzihumus*, and others (Fig S6C).
253
254
255 **DISCUSSION**
256 This study evaluated the effects of climate conditions, WSMV inoculation,
257 cropping system and associated *in situ* weed communities on wheat soil bacterial
258 communities over the course of a growing season. We hypothesized that 1) bacterial
259 community richness and evenness would be reduced by climate or WSMV infection, 2)
260 cropping systems which promote bacterial richness would be more resistant to alterations
261 from climate and WSMV infection, and 3) more diverse bacterial communities would
262 have a more stable bacterial community membership over the growing season and in
263 response to increased soil temperature, decreased precipitation, and WSMV. In summary,
264 sampling date within the growing season, soil temperature, and soil moisture exerted the
265 greatest effect on soil bacterial communities, followed by cropping system, WSMV
266 infection status, and weed community characteristics.
267 Changes in precipitation and soil moisture, atmospheric gas concentration, soil
268 salinity, and soil temperature can affect bacterial diversity (19, 20, 48). In particular, soil
269 temperature can be a stronger driver of bacterial diversity and functionality than soil

moisture (49). Even after weeks of warmer temperatures, soils microbiota do not appear to develop functional resistance to the heat and maintain stable communities (49), yet soils which experience frequent wet-dry cycles, such as grassland soils, host microbial communities which remain more stable under drought conditions (50). Physical or chemical disturbance can further prevent a stable soil community which is adapted to warmer temperatures from forming (51). In this study, and in accordance previous studies (52, 53), soil temperature was found to be a stronger driver of bacterial species' diversity and abundance than soil moisture. This may reflect the more complex interaction between plants, microorganisms, and soil conditions, as soil moisture can somewhat stabilize soil temperature (54). Plant foliation, which increases with air temperature, in turn shades soil and can buffer further increases in soil temperature (54), thus better supporting microbial communities.

Cropping systems are known to be associated with particular soil microbial communities (23, 46, 55). In particular, the use of plant- or manure-based fertilizer can increase microbial diversity while chemical-based fertilizers select for acid-tolerant species (46, 56, 57), leading to the trend of organic systems to harbor more diverse microbial communities than conventional (industrial) ones (56, 58, 59). Further, tillage and herbicides reduce microbial diversity (60, 61). Soil microbial α-diversity has been used as a topical application to rescue plants from drought, salt stress, or disease (62–64) and may be used to remediate soils after chemical or physical disruption (65–68). Thus, management practices which promote microbial diversity have the potential to be used as an *in situ* method to moderate the effect of stressors such as climate change, pathogens, or weeds (47, 55).

We previously assessed the impact of these cropping systems over the course of the growing season (23) and observed that under ambient conditions, cropping system did not alter bacterial richness or evenness but did affect β-diversity. In particular, organic tilled subplots contained more putative nitrogen-fixing bacterial genera (23). In the present study, the bacterial community in all cropping systems changed over the course of the growing season, as well as in response to increased soil temperature or decreased soil moisture. However, the interaction between cropping systems and climate conditions, which was not identical across systems. The peak in bacterial richness in CNT and OG systems was delayed in the hotter and hotter and drier conditions as compared to their respective ambient subplots. From observations, wheat in these systems developed more slowly than in OT subplots. The peak in bacterial richness is likely tied to peak growth and development of wheat, when plant-bacterial nutrient exchange is greatest. In OT subplots, the earlier peak and subsequent drop in bacterial richness may be associated with an more advanced growth stage and earlier senescence (13). Cropping system affected the stability of bacterial communities when comparing ambient to climate-treated conditions, with the conventional no-till system remaining more stable than the organic ones. This may reflect the more intense selective pressure exerted by chemical inputs on the community, and the recruitment of a more resilient microbiota.

Cropping system can indirectly alter soil microbial α-diversity via crop disease susceptibility. For example, direct nitrogen fertilization can increase WSMV disease transmission (69). Using livestock grazing to terminate cover crops and control weed residues can reduce wheat mite populations (70), although this has not been shown to reduce virus transmission (71). In the present study, there were interactions between

316 WSMV application and soil moisture, soil temperature, and cropping system X soil
317 moisture, pointing to the importance of multiple concurrent stressors in shaping soil
318 communities. The effect of different cropping systems on viral infection in crops is
319 complex (72) and is largely modulated by the extent of crop diversification, crop residue
320 removal strategy, and pest control (73).

321 As early successional species, agricultural weeds establish quickly in newly-
322 disturbed soil and sometimes earlier in the growing season than spring or summer crops
323 (74). In climate change scenarios which predict warmer, wetter springs, and higher
324 atmospheric CO_2, the alteration of the local environmental conditions can give weeds a
325 greater advantage over crops (75). Changing environmental conditions and crop-weed
326 competition may, in turn, alter the soil microbial community, further making conditions
327 less favorable for crop germination, growth, and competitive ability (76). As with all
328 plant species, agricultural weed species associate with particular microbial communities
329 in their rhizosphere (23, 55, 74, 77). It is generally thought that weed diversity in
330 agricultural settings could increase microbial diversity in soil, and potentially increase the
331 functionality and stability of soil microbial communities. In this study site, ambient
332 subplots were previously showed to have weak positive correlations between weed
333 diversity and soil bacterial richness (23). In the present study, weed diversity or biomass
334 did not alter soil bacterial richness or evenness, although bacterial β-diversity was
335 affected, and weed diversity was inversely related to the stability of bacterial
336 communities in response to climate treatment. This may reflect the temporary increases
337 in bacterial richness during periods of weed growth which are not sustained during the

338 hottest part of the season when bacterial communities are more susceptible to temperature
339 and moisture stress.

340 Environmental conditions or disease status on bacterial communities had
341 interactive effects with cropping system. This has implications for soil bacterial
342 communities and plant performance (78), both within the growing season and in
343 successive plantings, as the legacy of these altered bacterial communities persists (8). As
344 local climates continue to shift, so too will the dynamics of above- and below-ground
345 diversity which will impact food production and the need for more sustainable practices
346 (5, 16, 18).

347

348 **MATERIALS AND METHODS**

349 *Experimental Design*

350 This study was conducted in 2015 and 2016 at an agricultural field experiment
351 that was implemented since July 2012 at the Montana State University Fort Ellis
352 Research and Teaching Center, Bozeman, MT (45.652664056 N -110.97249611 W,
353 elevation 1500 m a.s.l.) to test production of three dryland cropping systems using a 5-
354 year crop rotation. The Fort Ellis site is a Blackmore silt loam soil type (a fine-silty,
355 mixed, superactive, frigid Typic Arguistoll) with a consistent ratio of 1 part sand, 2 parts
356 silt, 1 part clay, by weight, at 0 to 4% slopes (79). The monthly air temperature in
357 Bozeman in 2016 was higher than historic maximum and minimums from 1981 – 2010,
358 and the mean monthly precipitation [Table S2, reproduced from (23)] was lower by 18
359 mm in May, 16 mm in June, and 14 mm in July (80).

The cropping systems at the studied site consisted of 1) conventional no-till system (CNT), in which synthetic inputs were used in the form of fertilizers, herbicides, and fungicides, 2) USDA-certified tilled organic (OT), and 3) USDA-certified organic with grazing (OG), which integrates sheep grazing to terminate cover crops and manage weeds, with the overall goal of reducing tillage intensity in organic production. Chemical inputs utilized in the CNT system included 2,4-D, bromoxynil, dicamba, fluroxypyr, glyphosate, MCPA, pinoxaden, and urea for winter wheat rotations [see Tables 2.7 and 2.8 in (81)]. The organic plots began the organic transition process in July 2012, and completed in 2015. In the OT system, tillage was performed with a chisel plow, tandem disk, or field cultivator, as needed for to control weeds, prepare the seedbed, and to incorporate cover crops and crop residues. Weed control was enhanced with a rotary harrow. In the OG system, targeted sheep grazing was used to reduce tillage intensity for pre-seeding and post-harvest weed control and to terminate the cover crops, with duration and intensity of grazing based on weed biomass (5). Grazing was minimally supplemented with tillage, based on soil conditions and weed pressure. For all systems, seeding was done with a low-disturbance no-till double-disk seeder. Outside of normal farm management activities, soil disturbance and compaction were minimized during sampling procedures. Further details of the management practices, both historical and at the time of experimentation, can be found elsewhere (5, 43, 81).

Each system was replicated three times (i.e. blocks) with cropping systems (75 x 90 m) as the main plots, each of which was further divided into 5 split plots (13 x 90 m), with a 2m fallow buffer in between. Split plots were each following a 5 yr rotation which consisted of: year 1 – safflower (*Carthamus tinctorius* L.) under-sown to yellow sweet

383 clover (*Melilotus oficinalis* (L.) Lam.), year 2 – sweet clover cover crop, year 3 – winter
384 wheat (*Triticum aestivum* L.), year 4 – lentil (*Lens culinaris* Medik.), and year 5 – winter
385 wheat (5).

386 Within each the year 3 – winter wheat fields, subplots (1 m diameter) were
387 randomly established to assess the impact of climate conditions and disease status on
388 wheat soil bacteria across cropping systems. Two subplots were marked with flags and
389 used as control or ambient climate conditions (ambient), two subplots were enclosed with
390 an open-top chamber (OTC, hotter) made from 18 in high plastic that reflected heat back
391 on the subplot to increase air temperature and soil temperature by 1 - 2° C (82), and two
392 subplots were enclosed with OTCs and partially covered with rain-out shelters (OTC-
393 ROS, hotter and drier) which reduced rainfall by 50% using transparent polyurethane
394 [Fig S7, similar to (83)]. For each of the three climate treatments, one of the subplots
395 was randomly inoculated with WSMV (see below).

396

397 *Wheat streak mosaic virus inoculation and data collection*

398 Following previous work (84), prior to the WSMV inoculations, spring wheat
399 (variety Chouteau) was grown in the greenhouse in flat trays (30 x 10 cm), where plants
400 were maintained under a 16-h photoperiod of sunlight supplemented with mercury
401 vapour lamps (165 uE m^{-2} s^{-1}) at 10°C/25°C day/night. When the wheat was at Feekes
402 stage 4 - 6, an inoculum of WSMV was created from the 'Conrad' isolate line (85).
403 Infected wheat was harvested from the greenhouse and frozen for 1 - 2 days until use. To
404 create the WSMV inoculum, 300 g of infected wheat clippings were ground to reduce
405 particle size using a food processor, then blended with buffer (3.2 L of de-ionized water +

406 600 ml of 5X PBS, pH 7.2) until smooth. Slurry was filtered through cheesecloth to
407 remove particulate matter which would clog the spray hose, and refrigerated for up to 1 h
408 until use. Immediately prior to use, 2 g carborundum (ground glass) was added per 3.78
409 L of slurry as an abrasive to slightly injure wheat enough for the virus to infect. Slurry
410 was sprayed onto subplots using an air compressor (275 kilo Pascals) travelling at a rate
411 of 0.5 m/s and sprayed at a height of 20 cm above the canopy. Control subplots were
412 sprayed with water in which 2 g carborundum was added per 3.78 L (no-template
413 control). Spraying occurred the last week of April, one week after the first soil sampling
414 date (April 21) and two weeks prior to the second sampling date (May 12).

415 Infection of WSMV in subplots was evaluated in July by using an indirect ELISA,
416 with 10 leaves sampled from each subplot and assessed separately (Ito et al. 2012).
417 Within a plate, every 10th well contained a negative control (i.e., sample from healthy
418 wheat plant) to reduce potential bias in values of optical density caused by position of
419 samples. The mean and standard deviation of the negative control on each plate were
420 calculated. Samples above three standard deviations were considered infected with
421 WSMV (Miller et al. 2014). ELISA results are provided in Table S1.

422

423 *Crop and weed evaluations*

424 Percent coverage of weeds in subplots was assessed visually in October 2015,
425 April 2016, and June 2016. Aboveground biomass of all weed species within sampled
426 areas was harvested by hand in late June 2016. Within each 0.75 m^2 subplot, weed
427 biomass was cut at ground level and separated by species. The individual biomass of each
428 species was dried for 2 weeks at 55° C, and weighed (28). Wheat biomass was harvested

429 from sampled areas by hand on July 25, 2016, once the crop had completely senesced and
430 ripened. The two center rows (75 cm each) of wheat in the subplot were harvested, for a
431 total of 1.5 row meters. All the aboveground biomass was harvested, dried for 1 week at
432 55° C and threshed to determine biomass and grain yields (28)
433
434 *Soil assessment*
435 Soil moisture was measured weekly using gypsum blocks buried at 5 cm below
436 ground (86). Soil temperature was measured with buried iButtons (Maxim Integrated),
437 with data obtained every four hours between April 14, 2016 (one week prior to the first
438 sampling) and July 25, 2016 (final sampling date). In each subplot, three cores were
439 taken from around wheat plants to a depth of 15 cm, then homogenized into one
440 composite sample, which was used for bacterial community sampling (stored at -20°C)
441 and nutrient analysis (stored at 4°C). Soil cores were obtained from all 54 subplots at
442 five time-points over the growing season: April 21 before the WSMV inoculations were
443 applied; May 12, one week post-WSMV infection; June 1, three weeks post-WSMV
444 infection; June 22, six weeks post-WSMV infection; and July 25th, 10 weeks post-
445 WSMV infection and immediately prior to wheat harvesting. Additional soil was
446 collected at wheat harvest for nutrient analysis, presented in Table S3 (Agvise
447 Laboratories, Northwood, North Dakota, US).
448 DNA extraction from soil samples, library preparation, sequencing, and sequence
449 analysis protocols were as previously described (23). Illumina MiSeq (Montana State
450 University, Bozeman, MT) was used to sequence the V3-V4 region of the 16S rRNA
451 gene, using primers 341F (5'-CCTACGGGAGGCAGCAG-3') and 806R (5'-

452 GGACTACHVGGGTWTCTAAT-3') (87). Sequencing output data can be found in the
453 Sequence Read Archive (SRA) at NCBI under BioProject PRJNA383161
454 (https://www.ncbi.nlm.nih.gov/bioproject/?term=PRJNA383161).

455 Linear mixed effects models and distance based redundancy models (vegan) (88),
456 random forest with permutation (89, 90), PERMANOVA (adonis) (91), and ggplot2 (92)
457 were used in the R statistical package (93). Linear mixed models used cropping system,
458 soil moisture and soil temperature on the day of sampling, and WSMV application as
459 random effects. Sampling date and subplot identity nested with block were included to
460 control for repeated sampling. Some variables were aliased in the distance-based
461 redundancy analysis and therefore were removed from the model: *Capsella brusa-*
462 *pastoris*, *Cirsium arvense*, *Galium aparine*, and *Tragopogon dubious* biomass on June 29,
463 2016; *Chenopodium album*, *Lamium ampleuxicaule*, *Malva neglecta*, *Poa annua*, and
464 *Solanum triflorum* coverage October 25, 2015; *C. arvense*, *T. dubious*, and *Trifolium*
465 *pretense* coverage April 8, 2016; and *Chenopodium album* and *Tragopogon dubious*
466 coverage June 14, 2016. Plant coverage has been shown to have a linear correlation with
467 plant aboveground biomass (94, 95) and, weed senescence may negate the effect on soil
468 microorganisms (95). Thus, as coverage was measured at multiple timepoints but
469 biomass only once, coverage was used as a more accurate measure of the weed-soil
470 microbe relationship with respect to sampling date when coverage and biomass were both
471 significant.

472 Random forest was performed with 500 trees and 100 permutations. Replicate
473 block did not affect numerical diversity and was included as a random effect in those
474 models, but did affect bacterial communities when comparing ambient systems (23), and

475 was included as a fixed effect in those models. Unweighted Jaccard similarity was used
476 to determine effect of factors on community structure, and tested with PERMANOVA
477 (adonis), with replicate block as a stratification. When comparing climate to ambient
478 conditions, we utilized analysis of variance (ANOVA) and Tukey's Honest Significant
479 Differences to assess the variables determining soil bacterial communities. The
480 comparison and visualization of ambient to climate conditions was based on R code
481 developed by Drs. Ashkaan Fahimipour and Roo Vandegrift.
482

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765 **TABLES**

766 **Table 1. Effect of treatment factors and their interactions on observed soil bacterial**

767 **richness and evenness.**

768 Richness is measured as bacterial taxa counts and evenness of taxa abundance on a scale

769 from 0 to 1 (each species having equal abundance). Comparisons were made using a

770 linear mixed effects model accounting for repeated measures of subplots within

771 replicated blocks and significance was determined via Type III ANOVA with

772 Satterthwaite's approximation.

773

	Observed Richness			Shannon Evenness		
	Sum Sq	**F value**	**P value**	**Sum Sq**	**F value**	**P value**
Cropping System (C)	275,240	4.53	0.012	0.051	6.28	0.002
Soil Temperature (T)	2,513,973	82.82	<0.001	0.080	19.64	<0.001
Soil Moisture (M)	1,201,709	39.59	<0.001	0.028	6.97	0.009
WSMV (V)	56,697	1.87	0.173	0.001	0.14	0.708
Date*	2,203,758	28.71	<0.001	0.104	8.6	<0.001
C:T	442,913	7.30	0.001	0.072	8.84	<0.001
C:M	217,218	3.58	0.029	0.015	1.89	0.154
T:M	845,614	27.86	<0.001	0.025	6.07	0.014
C:V	110,178	1.81	0.165	0.001	0.17	0.844
T:V	49,186	1.62	0.204	0.001	0.32	0.571
M:V	23,029	0.76	0.385	0.001	0.17	0.683
C:T:M	179,405	2.96	0.054	0.010	1.24	0.293
C:T:V	59,576	0.98	0.376	0.008	0.96	0.385
C:M:V	11,219	0.18	0.831	0.002	0.21	0.812
T:M:V	4,413	0.15	0.703	0.001	0.37	0.546
C:T:M:V	8.038	0.13	0.876	0.005	0.59	0.556

774 *Factor used in simple model.

775 **Table 2. PERMANOVA of treatment factors and their interactions on soil bacterial**

776 **communities.**

777 Comparisons were made accounting for repeated measures of subplots and with replicate

778 blocks as a stratification. Significance was determined as: < 0.001 = ***, 0.001 – 0.009

779 = **, 0.01 – 0.05 = *, 0.05 - 0.1 = t (trending).

	Bray-Curtis			
	F	**R^2**	**P value**	
Cropping system (C)	0.88	0.007	0.001	***
Soil Moisture (M)	3.67	0.014	0.001	***
Soil Temperature (T)	2.00	0.007	0.004	**
Virus (V)	1.63	0.006	0.001	***
Date*	5.27	0.077	<0.001	***
C:M	1.15	0.008	0.213	
C:T	1.69	0.012	0.005	**
M:T	2.88	0.011	0.001	***
C:V	1.00	0.007	0.189	
M:V	1.82	0.007	0.015	*
T:V	2.93	0.011	0.001	***
C:M:T	1.03	0.008	0.411	
C:M:V	1.56	0.011	0.009	**
C:T:V	1.25	0.009	0.107	
M:T:V	2.22	0.008	0.001	***
C:M:T:V	1.25	0.009	0.093	t

780 *Factor used in simple model.

781

782

783

Table 3. Effect of climate conditions, cropping system, and sampling date on soil bacterial community composition.

Unweighted Jaccard was used to calculate bacterial community composition and comparisons were made between ambient and hotter, or ambient and hotter and drier conditions within each sampling date. Comparisons were tested with analysis of variance and P-values adjusted with Tukey's Honest Significant Differences.

Cropping System	Date	Virus	Adj. *p* value
	Ambient vs. Hotter		
OG-CNT	12-May	none	0.002
OT-OG	12-May	none	0.001
OT-CNT	25-Jul	none	< 0.001
OT-OG	25-Jul	none	< 0.001
OG-CNT	21-Apr	WSMV	< 0.001
OT-CNT	21-Apr	WSMV	0.001
OT-OG	1-Jun	WSMV	0.032
OT-CNT	22-Jun	WSMV	< 0.001
OT-OG	22-Jun	WSMV	0.007
OG-CNT	25-Jul	WSMV	< 0.001
OT-CNT	25-Jul	WSMV	< 0.001
OT-OG	25-Jul	WSMV	0.003
	Ambient vs. Hotter and Drier		
OG-CNT	25-Jul	none	0.006
OT-CNT	25-Jul	none	< 0.001
OT-OG	25-Jul	none	< 0.001
OG-CNT	21-Apr	WSMV	0.001
OT-CNT	21-Apr	WSMV	0.002
OT-OG	22-Jun	WSMV	0.001
OT-CNT	22-Jun	WSMV	0.007
OG-CNT	25-Jul	WSMV	< 0.001
OT-CNT	25-Jul	WSMV	< 0.001

Table 4. PERMANOVA of weed species' identity and percent coverage (cov) on soil bacterial communities at different times over a growing season.

Comparisons were made accounting for repeated measures of subplots, and with replicate blocks as a stratification. Only significant comparisons are shown. Significance was determined as: < 0.001 = ***, 0.001 – 0.009 = **, 0.01 – 0.05 = *, 0.05 - 0.1 = t (trending).

Weed	F.Model	R2	*p* value	Sig
Asperugo procumbens cov Oct 2015	1.212	0.00474	0.047	*
Bromus tectorum cov Oct 2015	0.819	0.0032	0.001	***
Bromus tectorum cov Jun 2016	1.016	0.00397	0.005	**
Bromus tectorum biomass late Jun 2016	1.1495	0.00449	0.001	***
Capsella bursa-pastoris cov Oct 2015	0.7862	0.00307	0.035	*
Capsella bursa-pastoris cov Apr 2016	1.0965	0.00429	0.001	***
Capsella brusa-pastoris biomass late Jun 2016	1.0236	0.004	0.001	***
Chenopodium album cov Apr 2016	1.1424	0.00447	0.05	*
Chenopodium album cov Jun 2016	1.0397	0.00407	0.001	***
Cirsium arvense biomass late Jun 2016	0.8499	0.00332	0.03	*
Descurainia sofia cov Oct 2015	0.7804	0.00305	0.003	**
Galium aparine cov Apr 2016	0.7757	0.00303	0.049	*
Lactuca serriola biomass late Jun 2016	0.9691	0.00379	0.042	*
Lamium ampleuxicaule cov Oct 2015	1.0349	0.00405	0.047	*
Malva neglecta cov Oct 2015	1.129	0.00441	0.019	*
Malva neglecta cov Apr 2016	0.6295	0.00246	0.009	**
Monolepsis nuttaliana cov Jun 2016	0.9573	0.00374	0.009	**
Poa annua cov Oct 2015	0.8321	0.00325	0.001	***
Poa annua cov Apr 2016	0.7457	0.00292	0.022	*
Solanum triflorum cov Oct 2015	0.8559	0.00335	0.044	*
Taraxacum officinale cov Oct 2015	0.8523	0.00333	0.002	**
Taraxacum officinale cov Jun 2016	0.7226	0.00283	0.021	*
Thlaspi arvense cov Apr 2016	1.3834	0.00541	0.002	**
Thlaspi arvense cov Jun 2016	0.8235	0.00322	0.047	*
Tragopogon dubious biomass late Jun 2016	0.799	0.00312	0.002	**
Trifolium pratense biomass late Jun 2016	0.8271	0.00323	0.001	***
Trifolium pratense cov Apr 2016	0.813	0.00318	0.024	*

801

802 **FIGURE LEGENDS**

803 **Fig 1. Effect of soil temperature on soil bacterial communities.** A) Soil temperature
804 was negatively correlated with soil bacterial richness. B) Relative abundance of soil
805 bacterial by temperature over the 2016 growing season, selected as important features by
806 random forest classification. Taxa are arranged by total relative abundance, and only
807 statistically significant taxa features are shown. Model explained 45% of variance.

808

809 **Fig 2. Effect of soil moisture on soil bacterial communities.** A) Soil moisture (% of
810 saturation) was positively correlated with soil bacterial richness. B) Relative abundance
811 of rhizosphere bacteria affected by soil moisture from all subplots across the 2016
812 growing season, selected as important features by random forest classification ($p < 0.05$).
813 Model explained 32% of variance.

814

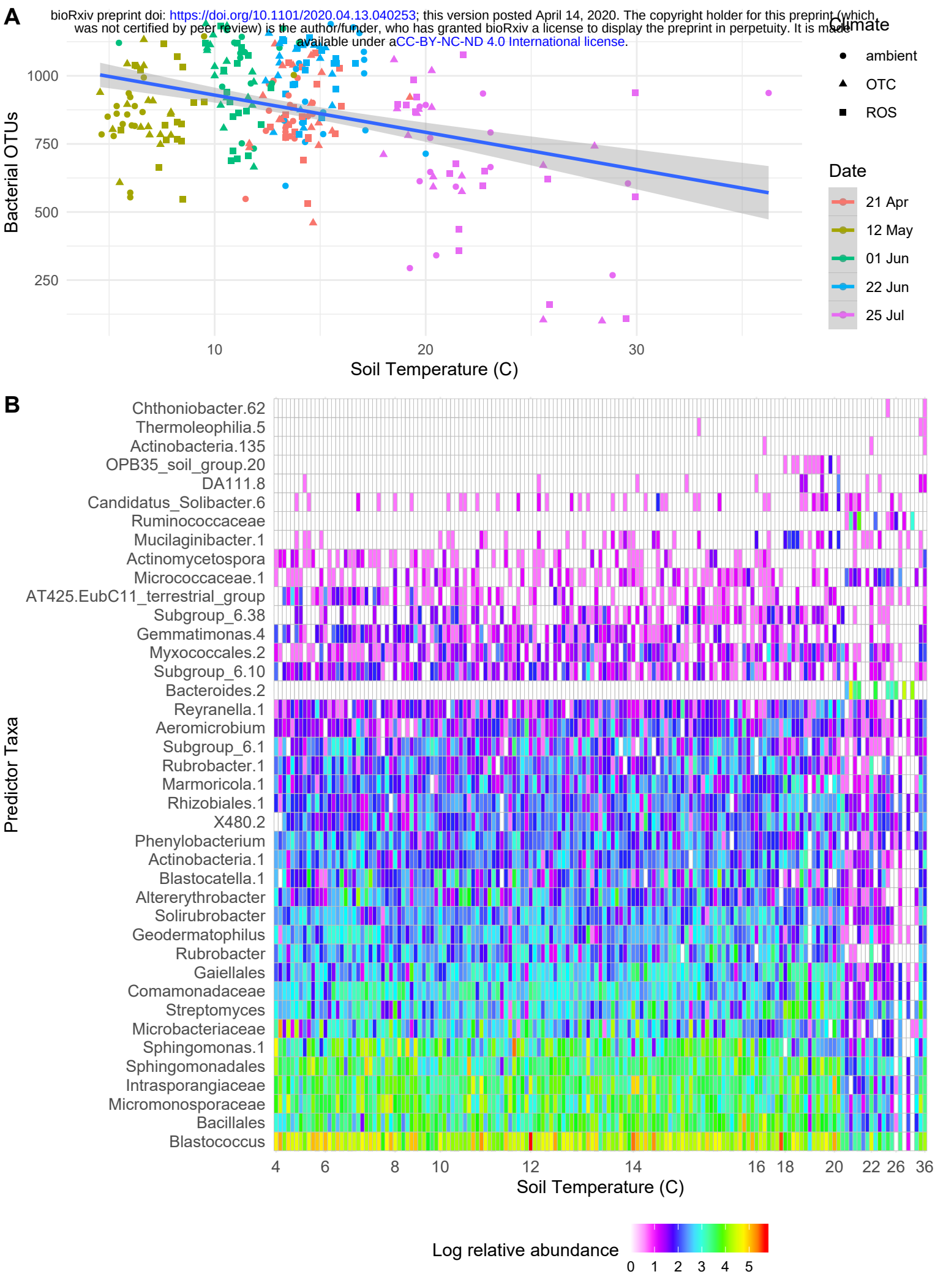
815 **Fig 3. Soil bacterial richness and evenness over the 2016 growing season.** A) species-
816 level richness and B) species-level evenness by cropping system (conventional no-till,
817 CNT; organic grazed, OG; organic tilled, OT), climate conditions (ambient, hotter, hotter
818 and drier), and pathogen infection (Wheat streak mosaic virus, WSMV; no WSMV,
819 none). Error bars show Standard Error of Means (SEM).

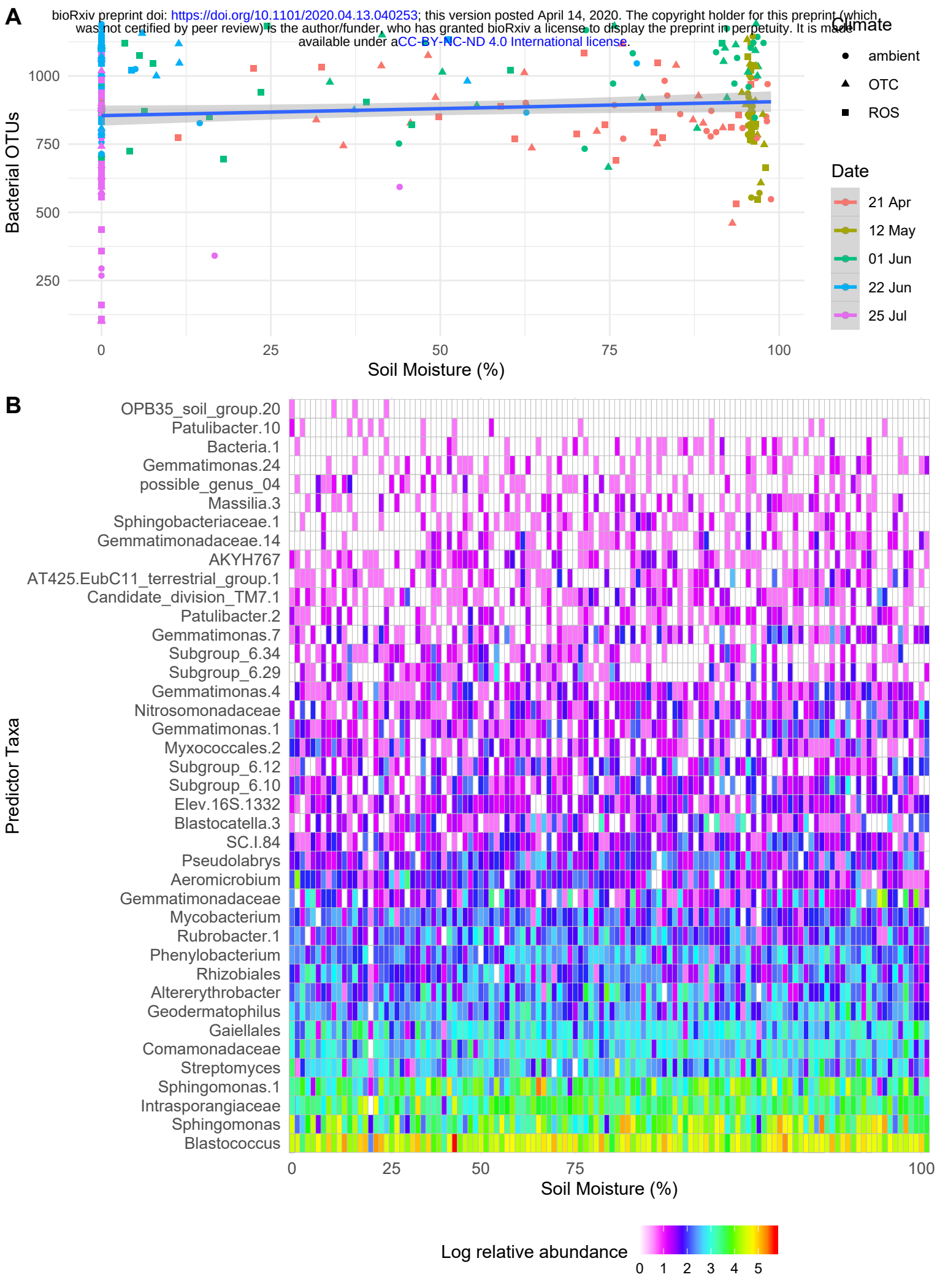
820

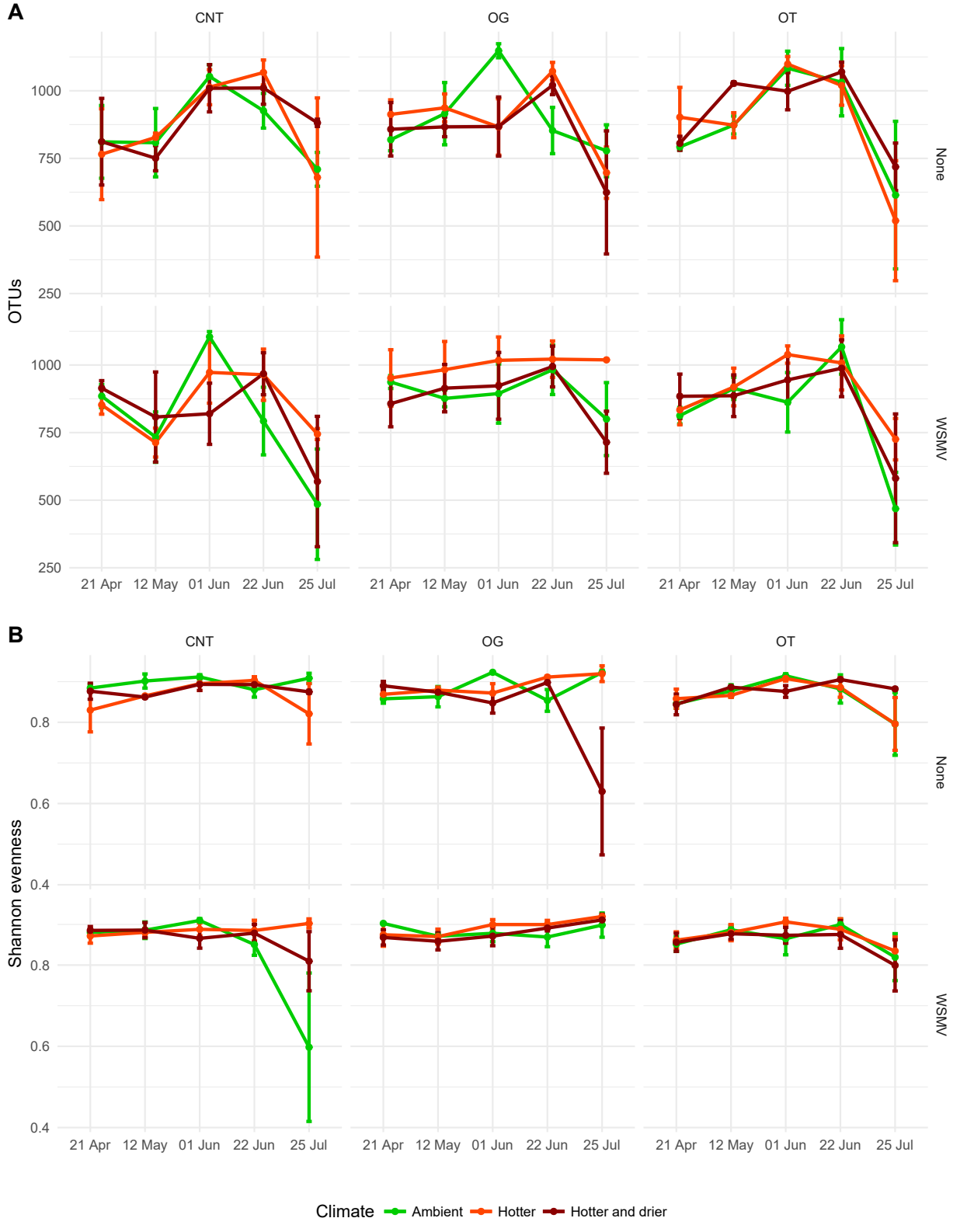
821 **Fig 4. Soil bacterial community similarity between ambient and climate-treated**
822 **subplots correlation with bacterial OTUs.** Cropping systems include conventional no-
823 till (CNT), organic grazed (OG), and organic tilled (OT).

824

825 **Fig 5. Soil bacterial community similarity against the fold change in number of**
826 **OTUs in comparing ambient to hotter, and ambient to hotter and drier subplots**
827 **across the 2016 growing season.** Difference in OTUs is measured as fold change, or
828 ratio of the OTU abundance in ambient subplots over the OTU abundance in climate
829 scenario subplots. Viral treatment includes Wheat streak mosaic virus (WSMV) and no-
830 template control (none). Cropping systems include conventional no-till (CNT), organic
831 grazed (OG), and organic tilled (OT).
832
833 **Fig 6. Soil bacterial community similarity between ambient and hotter, and ambient**
834 **and hotter and drier conditions, subplots from three cropping systems across the**
835 **2016 growing season.** Plots were not treated with Wheat streak mosaic virus.
836 Significance is provided in Table 4. Cropping systems include conventional no-till (CNT),
837 organic grazed (OG), and organic tilled (OT).
838
839 **Fig 7 Soil bacterial community similarity between ambient and hotter, and ambient**
840 **and hotter and drier conditions, in subplots treated with Wheat streak mosaic virus**
841 **from three cropping systems across the 2016 growing season.** Significance is
842 provided in Table 4. Cropping systems include conventional no-till (CNT), organic
843 grazed (OG), and organic tilled (OT).






A
CNT
OG
OT
None
WSMV
OTUs
1000
750
500
250
21 Apr
12 May
01 Jun
22 Jun
25 Jul
B
Shannon evenness
0.8
0.6
0.4
Climate
Ambient
Hotter
Hotter and drier