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Plant host domestication and soil nutrient availability determine positive plant microbial response across the Solanum genus.

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Peer reviewed

1 **Title:** Plant host domestication and environmental factors determine positive plant microbial
2 response across potato (*Solanum tuberosum*) domestication

3

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32 **Highlight**

33 Potato domestication has altered the host response to its rhizosphere microbiome in
34 nutrient-dependent ways. Differences or lack thereof in the rhizosphere microbial community did
35 not determine similar functionality for plant host health.

36

37 **Abstract**

38 Domestication of crops has changed how crops shape their associated microbial communities
39 compared to their progenitors. However, studies testing how crop domestication driven
40 differences in rhizosphere microbial communities affect plant health are limited mostly to
41 specific symbiont pairings. By conducting a soil manipulation greenhouse study, we examined
42 plant growth and yield in response to differences in microbial communities and nutrient
43 availability across a variety of wild, landrace, and cultivated potatoes. Coupled with this, we
44 conducted 16S and ITS amplicon sequencing to examine plant host and soil treatment driven
45 differences in microbial community composition on potato plant roots. Our results found the
46 plant response to microbes (PRM) is context dependent. In low nutrient conditions, landraces
47 responded positively to the presence of live soil microbial inocula. Conversely, modern potato
48 varieties positively responded in high nutrient conditions. Amplicon sequencing found
49 differences in bacterial communities due to environmental and temporal factors. However, potato
50 clade (e.g. *Andigenum*, *Chiletanum*, *S. berthaulti*, and *Modern*) alone did not lead to differences
51 in microbial communities that accounted for PRM differences. Differences in PRM between
52 landraces and modern potatoes, and the correlation of PRM to microbial diversity, suggest that
53 domestication has altered the *S. tuberosum* response to rhizosphere microbiomes.

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56 **Keywords:** crop domestication, fertilization, landraces, microbial community, microbiome,
57 nutrient acquisition, plant microbial response, potato

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63 **Introduction**

64 Over millions of years, plants have coevolved with soil microbes to respond to challenges from
65 pathogens, environmental stress, and nutrient scarcity (Perez Jaramillo et al 2015, Liu et al
66 2020). However, human intervention in plant evolution may have altered the nature of plant-
67 microbe interactions in domesticated crop species. Artificial selection for higher yields in an
68 environment less conducive for beneficial microbial associations, due to high fertilization and
69 soil disturbance, may have changed the diversity, assembly, and function of the associated
70 microbiome of crop plants and altered the corresponding plant response (Perez Jaramillo et al
71 2015). For instance, domestication and breeding in wheat may have resulted in reduced
72 dependence on mycorrhizal interactions (Bulgarelli et al. 2013, Hetrick et al 1992). However, the
73 reduction in beneficial plant-microbe interactions can be environmentally dependent. For
74 example, in soybean newer cultivars were found to be less able to sanction ineffective rhizobia,
75 potentially due to breeding under high fertilizer regimes (Kiers et al 2007). The increased
76 availability of mineral nutrients in fertilized fields may reduce the benefits of nutrient trading
77 microbial partners (Perez-Jaramillo et al. 2015, Porter and Sachs et al 2020, Saleem et al 2019).
78 In absence of these microbial benefits, the costs of maintaining microbial symbionts could
79 compromise yield, resulting in inadvertent selection against the plant traits maintaining these
80 interactions (Perez-Jaramillo et al. 2015, Porter and Sachs et al 2020).

81
82 Agricultural practices may also limit the available pool of microbial taxa for plants to use.
83 Studies between managed vs unmanaged prairie fields showed significant shifts in microbial
84 function and composition (Fierer et al 2013). The constant soil disruption from agricultural land
85 use results in more homogenous bulk soil microbial communities with less C and N content, and
86 more K and Mg despite differences in original plant communities (Jangid et al 2011). Other
87 agricultural practices such as tillage, crop diversification, fertilizer input, and organic soil
88 amendments have positive and negative effects on the crop microbiome (French et al 2021).
89 Thus, agricultural cultivation practices may have implications on physiochemical and biological
90 properties of crop soils.

91
92 The general hypothesis that modern breeding has led to elite crop varieties that are less

93 responsive to microbes can be explained by two general mechanisms. One potential mechanism
94 is that modern crops fail to recruit or support beneficial microbes present in the soil (Porter and
95 Sachs 2020). The absence of such microbes in their rhizospheres then leads to poorer plant
96 performance compared to more ancestral genotypes, at least in low-input conditions.
97 Alternatively, when encountering similar microbial communities modern crop varieties may be
98 less responsive than their ancestral relatives (Porter and Sachs, 2020). This could arise in
99 multiple ways; for instance, modern varieties might fail to enforce fair trading relations with
100 symbionts or have altered root traits that make nutrient-acquiring microbial relationships less
101 important. Both proposed mechanisms for loss in microbial responsiveness have been
102 documented and are not mutually exclusive of each other.

103

104 The ‘host determinism hypothesis’ states that plant genotype plays a role in beneficial plant-
105 microbial community associations, and interactions can vary even at the cultivar or subspecies
106 level (Bouffaud et al 2014, Anacker et al 2014, Wagner et al 2016, Leff et al 2017). Moreover,
107 variation in microbial community assembly among plant hosts may cause differences in plant
108 health outcomes such as phytopathogen suppression (Zachow et al 2014, Carrion et al 2019,
109 Carrillo et al 2019). To date, few studies have investigated the effect of plant domestication on
110 both the variation in plant-microbial community interactions and their consequences for plant
111 health outcomes. In common bean (*Phaseolus vulgaris*), breeding for resistance to *Fusarium*
112 pathogens was linked to recruitment of specific microbial taxa that express anti-fungal
113 compounds (Mendes et al. 2017). In potato, levels of predicted microbial phosphatases differed
114 between cultivated and uncultivated potatoes (Pantigoso et al 2020). In rice, relative abundance
115 of the plant mutualist *Azoarcus sp.* decreased between wild and domesticated rice varieties
116 (Engelhard et al 2000). Overall, these studies indicate that landraces and wild relatives may
117 potentially contain traits useful for plant breeding efforts aimed at improving crop benefits from
118 their associated microbial communities.

119

120 Alternatively, the ‘host-insensitivity’ hypothesis states that while symbiont recruitment
121 traits have not diminished through domestication, the ability to respond to (and benefit from)
122 recruited microbes is reduced in modern lines. (Martin-Robles et al. 2019, Hetrick et al 1992,
123 Porter and Sachs et al 2020). Closer examination reveals that selection for higher performing

124 crops appears to be driven by increased performance in symbiont free environments (Sawers et
125 al. 2010, Porter and Sachs et al 2020). For example, modern soybean varieties have a reduced
126 ability to sanction poor rhizobial symbiotic partners compared to their ancestors (Kiers et al.
127 2007). Modern breeding may also lead to new kinds of beneficial interactions. For example, the
128 *fox* bean cultivar, bred for resistance to a fungal pathogen, had elevated expression of microbial
129 anti-fungal genes in its rhizosphere microbiome compared to wild varieties (Mendes et al 2018).
130 Similarly in rice, domestication may have led to recruitment of more diverse diazotrophic
131 microbes and nitrogenase genes (Engelhard et al 2000). Recruitment of potential beneficial
132 microbes may remain intact even in the high input conditions if the costs to the host plant is low
133 (Emmett et al 2018).

134
135 However, careful consideration is needed on how microbial communities affect plant
136 performance. Plant responses to microbial communities (or subsets, such as arbuscular
137 mycorrhizal fungi) are often measured as the proportional difference in growth in the presence
138 vs. absence of the microbe. This metric is thus sensitive to two separate phenomena: the growth
139 benefit provided by the microbe, and the ability of the host plant to maintain growth in the
140 absence of the microbe. We define Plant Microbial Dependence (PMD) as an inability for a host
141 plant to survive or grow normally in the absence of microbial symbionts. It is well documented
142 that domestication has reduced PMD for many crop species (Martin-Robles et al. 2019, Hetrick
143 et al 1992). Specifically, many wild relatives maintain interactions with mycorrhizal partners in
144 high phosphorus conditions, even in the absence of growth benefits, while more domesticated
145 relatives exhibit, on average, decreased levels of mycorrhizal colonization in high phosphorus
146 conditions (Martin-Robles et al. 2019). In some cases, mycorrhizal root colonization adversely
147 affected plant growth (Hetrick et al 1992). Collectively, these studies have shown mycorrhizal
148 dependence in more ancestral plants and potentially a tradeoff between plant performance and
149 PMD. While maximizing the benefits crop plants gain from microbial symbionts could be useful
150 for agricultural systems, maximizing PMD on its own is not likely to be useful. Despite evidence
151 for reductions in PMD in elite crops, there is also evidence suggesting a true loss of plant traits
152 favoring beneficial interactions between crops and their respective microbes. Hence, the
153 influence of crop breeding on rhizosphere microbial community composition and plant health
154 outcomes will require crop-specific exploration.

155

156 Here, we tested whether domestication of *Solanum tuberosum* (potato) has led to changes in
157 plant-microbial interactions, specifically examining the plant's positive or negative responses to
158 soil microbial communities. In *S. tuberosum*, host genotype has a documented role in shaping the
159 rhizosphere microbiome (Pfeiffer et al. 2017, Weinert et al 2011, Pantigoso 2020), but no studies
160 have determined the impact of this host driven variation in microbial communities on plant
161 performance. Sawers et al. (2010) suggest an alternative way to compare plant responses to
162 microbes across host genotypes by assessing whether a plant genotype's performance in the
163 symbiotic state is significantly larger or smaller than predicted by that genotype's performance in
164 the non-symbiotic state. To date, we are unaware of any studies documenting reductions in plant
165 responses to whole microbial communities in elite crop varieties compared to wild or landrace
166 ancestors, using methods that can distinguish between a loss of beneficial plant response from a
167 reduction in plant microbial dependence.

168

169 We used modern and landrace potato varieties, along with a wild ancestor species, to test the
170 hypothesis that domestication and modern breeding have altered both the crop response to, and
171 effect on, rhizosphere microbial communities. We performed a greenhouse experiment
172 measuring plant tuber yield in live and sterilized soils in nutrient-rich or nutrient-poor conditions.
173 We then characterized bacterial and fungal rhizosphere community composition at two time
174 points, in order to illustrate how the plant host is shaping the rhizosphere microbial community
175 composition given our environmental conditions. Specifically, we hypothesized that wild and
176 landrace potato varieties would have greater positive responses to soil microbial communities
177 compared to modern varieties, especially in nutrient poor conditions. Additionally, we tested
178 whether the change in plant response to microbes was consistent with either the "host
179 determinism hypothesis" and/or the "host insensitivity hypothesis" by testing whether 1) Wild
180 and landrace potato varieties recruit different rhizosphere microbial communities from modern
181 varieties, and 2) Modern varieties are less sensitive to the soil microbial community.

182

183 **Materials and Methods:**

184 **Study system:** Plant genotypes representing wild, landrace, and modern potato genotypes were
185 selected for the experiment based on the phylogeny of potato domestication (Spooner et al. 2007,

186 Rodriguez et al. 2010, Spooner and Janksy 2017). We selected four genotypes of *Solanum*
187 *tuberosum* sp. *andigenum* as the most ancestral potato genotypes (PI 281208, PI 281038, PI
188 280995, PI 619141), four genotypes of the wild species *Solanum berthaultii* due its involvement
189 in potato domestication (PI 566799, PI 545922, PI 545851, PI 498096), four genotypes of
190 Chiletanum landraces (*S. tuberosum* sp. *tuberosum*), which are the most recent ancestors of
191 modern ‘European’ potato (PI 245796, PI 245835, PI 245940, PI 611078), and five genotypes of
192 modern potatoes spanning the range from early to recently released varieties (‘Garnet Chili’,
193 ‘Russet Burbank’, ‘Snowden’, ‘Russet Ranger’, ‘Russet Norkotah’). This sample set provides
194 comparisons among original domestication, secondary domestication events, and more recent
195 modern breeding efforts. All genotypes except for modern potatoes were sourced from the US
196 Potato Genebank (NRSP-6) in Sturgeon Bay, Wisconsin, while modern potato germplasm was
197 obtained through the Wisconsin Clean Seed Program.

198

199 **Greenhouse Experiment:** We performed a greenhouse experiment to test for differences in
200 plant responses to soil microbial communities across potato varieties. We factorially crossed the
201 initial soil microbial source in each pot (sterilized soil only, microbial inoculum from a native
202 prairie, or microbial inoculum from a working potato field) with a nutrient treatment (high vs.
203 low). The two soil inoculation sources represent two different initial microbial communities, one
204 from a highly managed system versus an unmanaged prairie (See Soil Inoculation). High nutrient
205 pots were fertilized once with 53 grams of Nutricote slow-release fertilizer (13-13-13, Arysta
206 LifeSciences). Low nutrient pots were given no additional nutritional input. High versus low
207 nutrients treatments were used to compare potato genotypes’ response to microbial communities
208 in nutrient limiting and non-limiting conditions. We grew all 17 potato varieties spanning wild
209 relatives, landraces, and modern varieties in each treatment combination. There were four
210 replicates of each treatment combination for each genotype for a total of 432 pots.

211

212 The plants grew for four months in 3.78 L pots and were watered every two to three days. At
213 four and 12 weeks, plants were measured for shoot length and width, and fine roots were
214 sampled and immediately frozen for subsequent DNA extraction. At 12 weeks, shoot, tuber, and
215 underground root biomass were measured from each plant. Plants were constantly exposed to at
216 least 500 gHz of lighting for a 12-hour light and dark cycle at 22°C to promote tuberization. At

217 the end of the experiment we excluded plants that died due to injury during initial planting (n =
218 50).

219
220 **Soil Inoculation:** Microbial community inocula were sourced from a native tallgrass prairie
221 (Mudd Lake Wildlife Area; Rio, Wisconsin, USA) and an intensively managed potato field
222 (University of Wisconsin's Hancock Research Station; Hancock, Wisconsin, USA) to provide
223 extremes in microbial composition. We verified microbial taxonomic richness using 16S and ITS
224 sequencing from two locations (see 'Amplicon preparation and sequencing'), finding that the
225 'Prairie' inocula (Mudd Lake Wildlife Area) contained a bacterial phyla richness of 34.2 versus
226 26.7 for the "Field" inocula. Topsoil (0-20cm depth) was collected from three different sites at
227 each location and mixed thoroughly within a source site to produce two live inoculum
228 treatments. Treatment pots contained 90% volume of a standard, sterilized background soil
229 (50/50 mixture of sand and field soil sourced from the University of Wisconsin's West Madison
230 Research station, Madison, WI, autoclaved for two hours) and 10% volume of either live soil
231 inoculum from one of the two sources or more sterilized background soil (control) to initiate
232 differing microbial communities while maintaining common abiotic soil conditions.

233
234 **Plantlet and Tissue Culture:** Plants were obtained from Sturgeon Bay United States
235 Department of Agriculture Agricultural Research Station Potato Genebank (USDA-ARS NR6).
236 Seventeen potato genotypes were selected as described above. Potato plants were grown from
237 true seed (*Andigenum*, *S. berthaultii* and *Chiletanum* genotypes) or from tissue-culture derived
238 plantlets obtained through the WI clean seed certification program (Modern genotypes). True
239 seed was surface sterilized with bleach and incubated in 2000 ppm gibberellic acid solution
240 overnight before being placed in a humid chamber for germination. Germinated seedlings were
241 placed into tissue culture (MS media Caisson mix). To ensure minimal genetic variability within
242 each potato genotype, only one seedling individual was selected and continuously propagated
243 through cuttings to produce plantlets for use in the greenhouse experiment. All potato tissue
244 cultures were grown in a growth chamber at 22°C on a 16/8-hour day/night cycle.

245
246 **Nutrient Analysis:** Leaf samples were collected after 12 weeks of growth. Leaf tissue from 333
247 samples were dried, ground and tinned prior to analysis. Samples were flash combusted for total

248 N and C nutrient analysis using a Flash EA 1112 Flash Combustion Analyzer. Leaf nitrogen
249 concentrations averaged 3-3.5% N concentration in high nutrient samples and 1-1.5% N in low
250 nutrient samples. These results confirmed that low nutrient plants were nutrient deficient, while
251 high nutrient plants were within the recommended range for modern potatoes to maximize tuber
252 yields without excessive vine growth (Rosen 2018).

253

254 **Amplicon preparation and sequencing:** Fine root samples were collected at four weeks and 12
255 weeks. We extracted DNA from each root tip sample using OMEGA Plant DNeasy extraction
256 kit (Omega Bio-tek, Norcross, GA) according to the manufacturer's directions. To characterize
257 bacterial and archaeal communities, the prokaryotic 16S-V4-V5 region was amplified using the
258 515F forward primer (5'-GTGYCAGCMGCCGCGGTAA, Caporaso et al 2011) and 926R
259 reverse primer (5'-CCGYCAATTYMTTTRAGTTT, Parada et al 2016). For fungal community
260 characterization, the fungal ITS2 sequence was amplified using the ITS3-KYO2 forward primer
261 (5'- GATGAAGAACGYAGYRAA, Toju et al 2012) and the ITS4 reverse primer (5'
262 TCCTCCGCTTATTGATATGC, White et al 1990). External fusion PCR primers contained a
263 14-bp overlap to the trailing end of internal primers with 12bp i7 index and P7 flow cell adaptor
264 or an i5 index, 7-bp spacer and P5 adapter (See Lankau and Keymer 2015).

265 Amplicon library preparation was composed of two PCR steps. The first round of PCR amplified
266 the ITS2 or 16S V4-5 region along with associated Nextera read primers. PCR was performed in
267 10 µl reactions using 0.2 µL of a hot-start, high fidelity polymerase (Cloneteck Prime Star GLX,
268 Fitchburg, WI) with 2 µL of its 5X buffer, 0.8 µL dNTPs (at 10 nM concentration), 0.25 µL of
269 each primer (at 10 nM), 0.7 µg T4 gene 32 protein, and 10 ng of template DNA. The
270 thermocycling program for the ITS2 region was a 5-minute hot start at 98°C, 35 cycles of
271 denaturing (98°C, 0:30), annealing (50°C, 0:45), and extension (68°C, 1:00) and a final extension
272 of 15 minutes at 68°C. The thermocycling program for the 16S region was 5-minute hot start at
273 98°C, 35 cycles of denaturing (98°C, 0:45), annealing (50°C, 0:45), and extension (68°C, 1:00)
274 and a final extension of 15 minutes at 68°C. Successful amplification was verified using agarose
275 gel electrophoresis. The second round of PCR added the P5 and P7 flowcell adapters to prepare
276 the library for sequencing on an Illumina MiSeq, along with an external set of sample barcodes
277 located between the flowcell adaptors and read primers. Fungal ITS2 and 16S amplicons were
278 cleaned with the Omega BioTek E-Z 96 Cycle Pure kit. Purified products were quantified using a

279 Qubit 2.0 fluorometer with the Qubit dsDNA HS assay and then pooled at equal concentrations
280 (Thermo Scientific, Grand Island, NY). Amplicon products were then sequenced on Illumina
281 Miseq using a 300 cycle Paired-End run at the University of Wisconsin-Madison Biotechnology
282 Center.

283

284 **Bioinformatics:** Raw external sequences were initially trimmed at both the 5' and 3' ends using
285 Cutadapt (version 1.18). The Qiime 2(v2017.12) pipeline was used to processed trimmed reads
286 using DADA2. Samples were filtered and further trimmed by DADA2 using the following
287 parameters (16S-V4 sequences: truncLen = (0, 240), p-max-ee = 10, and truncQ = 2; ITS2
288 sequences: truncLen = (258,232), p-max-ee = 10, and truncQ = 2). We used the RDP Naïve
289 Bayesian Classifier to assign taxonomy to bacterial and fungal amplicon sequence variants
290 (AVS) using the Greengenes (version 13.8) and UNITE (version 8.0) reference databases for
291 bacteria and fungi, respectively. However, a large amount of 16S reads remained unidentified.
292 As a result, for the top 50 most abundant unidentified bacterial reads we used the Basic Local
293 Alignment Search Tool against the NCBI nucleotide database (blastn, NCBI genebank, Clark et
294 al 2016) for identification and verification of microbial taxa. Reads assigned to chloroplast and
295 mitochondria were removed. Samples with fewer than 300 reads were removed for 16S samples
296 based on inspection of rarefaction curves, while samples below 200 reads were removed for ITS
297 samples. In the end, this resulted in a total of 128 16S and 366 ITS samples for analysis.

298

299 **Statistical Analysis** We performed a linear mixed model using lmer and lm4test packages in R
300 to compare differences in plant biomass and allocation to tubers, shoots and roots among potato
301 clades and nutrient treatments. Mixed models included nutrient treatment, soil inocula source,
302 and potato clade as fixed effects, and potato genotype nested within clades as a random effect.

303

304 To test our hypothesis that rhizosphere microbial communities affect plant fitness/health, we
305 examined potato plant response to soil inoculation treatments. Potato plant response to microbes
306 (PRM) was calculated using a method described by Sawers et al. 2010. We accounted for
307 intrinsic differences in plant performance in sterile control pots by using a residual based
308 method. Accounting for these differences allowed us to focus on specific plant traits that bolster
309 plant microbe interactions for our phenotype of interest (Sawers et al 2010). First, we calculated

310 the average tuber mass for the four replicates of each genotype in each unique treatment
311 combination, giving six values for each of the 17 genotypes. Then, we regressed the genotype
312 average tuber mass values in live soil treatments against the genotype average tuber mass values
313 in the sterile soil treatment, separately for each nutrient treatment. We used the residual values
314 for each genotype by soil inocula combination as our metric of plant response to microbes.
315 Positive residual values indicate that a genotype produced a higher tuber mass in live soils than
316 expected based on its tuber production in sterile soils, and thus showed a benefit from the
317 presence of soil microbes. A negative residual value indicates the opposite. The residuals were
318 then used as the dependent variable in our statistical model with nutrient treatment, potato clade
319 (*S. berthaultii*, *Andigenum*, *Chiletanum*, and *Modern*), and soil inocula source as fixed effects
320 using the `lmer` function with genotype nested within clade as a random effect. P values were
321 calculating using the `lmerTest` package with the Satterthwaite approximation of degrees of
322 freedom.

323
324 We used permutation MANOVA to test for differences in microbial community composition due
325 to soil inoculation, nutrient treatments and potato clades using the `adonis` function in the `vegan`
326 package (Oksanen et al 2019). Alpha diversity was measured using the Shannon Weiner Index
327 calculated by the `diversity` function in the `vegan` package and compared among experimental
328 treatments and potato clades using linear mixed models as described above. Contrasts and
329 pairwise analysis were performed with the `pairwise.adonis` package (Martinez 2017) and t-tests
330 using base R respectively. Differences in the relative abundance of specific bacterial phyla
331 among treatments and potato clades were tested using linear mixed models as described above.

332
333 To test how plant response to microbes correlated with rhizosphere diversity, and whether the
334 direction or magnitude of that correlation differed among treatments or potato clades, we fit a
335 linear mixed model with the PRM metric (residual values, see above) as the dependent variable,
336 and used genotype average bacterial diversity as the independent variable, along with nutrient
337 treatment, potato clade, and all two and three way interactions. A significant, positive effect of
338 average bacterial diversity in this model indicates that genotypes with higher rhizosphere
339 microbial diversity tended to also have more positive responses to the presence of a live soil

340 microbial community. A significant interaction between diversity and potato clade in this model
341 indicates that this correlation differs in size and/or magnitude between potato clades.

342

343 **RESULTS:**

344 **Potato plants differed in resource use across domestication history:** Domestication has
345 changed plant morphology and allocation among potato clades irrespective of the presence of
346 microbial communities. We found that potato clade predicted phenotypic differences in tuber
347 mass, nutrient responses, and overall dry mass (Figure S1). Tuber mass followed a consistent
348 pattern of most ancestral (smallest) to modern (largest) regardless of nutrient regime (Figure
349 S1 and $p < 0.0001$, ANOVA). In high nutrient conditions, the modern potato clade allocated a
350 greater proportion of resources towards tuber mass versus shoot or root mass compared to
351 ancestral potato clades (Figure S1A). However, in low nutrient conditions, Chiletanum landraces
352 produced the most tuber mass (Figure S1B).

353

354 **Chiletanum Landrace responded positively to microbes in low nutrient conditions:** We
355 measured plant response to microbes (PRM) as the potato genotype's tuber mass in live soils
356 after controlling for that genotype's tuber mass in sterile soils. In low nutrient conditions we
357 found differences in PRM among different potato clades (Figure 1B, Table 1A, Table 1B). The
358 Chiletanum clade in low nutrient conditions had a significantly positive PRM (95% CI: $9.311 \pm$
359 6.089), while the Andigenum clade exhibited a weak neutral to positive PRM (95% CI: $1.49 \pm$
360 6.02 , Figure 1B). *S. berthaultii* had a significantly negative PRM (95% CI: -8.576 ± 4.99 , Figure
361 1B), while Modern potatoes had a neutral to negative PRM (95% CI: -3.793 ± 8.19 , Figure 1B).
362 Chiletanum potatoes showed a more positive PRM than modern genotypes in low nutrient
363 conditions (t-statistic (df)= 13, $\beta = 9.991$, $p=0.0295$, Table 1B, Figure 1B).

364

365 The PRM of modern potato genotypes tended to increase (become more positive) in high,
366 compared to low, nutrient conditions (95% CI: 13.219 ± 24.54 , Figure 1D). However, the
367 landrace and wild clades showed the opposite pattern, all displaying PMR values that were lower
368 (more negative) in high, compared to low, nutrient conditions, and none were significantly
369 different from zero; *S. berthaultii* (95% CI: -20.293 ± 5.855 , Figure 1D), Andigenum (95% CI: $-$
370 1.893 ± 7.753 , Figure 1D) and Chiletanum landraces (95% CI: 1.063 ± 16.97 , Figure 1D). The

371 divergent effect of the nutrient treatment on the PRM of modern vs. landrace or wild clades
372 resulted in a significant nutrient treatment by clade interaction (Table 1A). Plant microbial
373 response (PRM) did not differ between the two soil inocula in either nutrient condition ($p = 0.29$,
374 Table 1A).

375

376 **Rhizosphere microbial community composition differed across time and nutrients but not**
377 **potato clades.** We found that timepoint (4 vs 12 weeks) and soil inocula affected bacterial ASV
378 community composition on potato roots in both nutrient conditions (perMANOVA, $p < 0.001$ for
379 all, Table S2 and Table S3). There was weak evidence that potato clade affected the rhizosphere
380 microbial community in low (perMANOVA, $p = 0.101$, Table 2A), but not high nutrients (Table
381 2B) after 12 weeks of growth. Microbial communities on modern genotypes were similar to
382 those of landraces (Andigenum and Chiletanum) based our NMDS plot and pairwise
383 perMANOVA analysis. There were no significant differences in microbial structure between
384 Modern genotypes and either Chiletanum, Andigenum, or *S. berthaultii* genotypes in either
385 nutrient condition at either time point (F-test, pairwise permutation, $p > 0.05$ Table 3-4 and
386 Figure 2A, 2B). We found no significant differences in fungal communities between *S.*
387 *berthaultii*, Andigenum, Chiletanum and Modern samples (Supplement Table S4, perMANOVA,
388 $p = 0.157$).

389

390 Despite detecting few significant differences in community composition at fine scales, the
391 relative abundance of some microbial phyla differed among landraces and wild species in low
392 nutrient condition differences (Figure 3). Over time, there was an increase in the relative
393 abundance of Bacteroidetes in landraces relative to the modern clade in low nutrients (Figure 3,
394 Table 5A). Specifically, Bacteroidetes relative abundance increased more between time points
395 for Andigenum landraces compared to Modern counterparts at low nutrients (Table 5A, p -value
396 = 0.027), but this effect was not evident in high nutrient conditions (Figure 3, Table 5B). Other
397 major phyla (Proteobacteria and Actinobacteria) did not differ in relative abundance between
398 different potato clades (Supplement Table S4-7).

399

400 **Potato clade did not shape rhizosphere microbial diversity:** Shannon-Weaver diversity of
401 bacteria did not differ among potato clades (Table 6, Supplement Table S9). Although only

marginally statistically significant, a time by nutrient interaction effect on microbial diversity saw a decrease in diversity between 4 to 12 weeks in low nutrient conditions but an opposite pattern in high nutrient conditions (ANOVA, $p = 0.07859$, Table S8). Shannon diversity of root bacterial communities did not differ between initial inocula from either prairie and potato field soils ($p > 0.05$, Table 6).

407

Positive link between PRM and microbial diversity was host and nutrient dependent:

Shannon diversity of root-associated bacterial communities, measured at 4 weeks of growth, was negatively correlated with PRM across genotypes in the Modern clade, weakly in high nutrient and strongly in low nutrient conditions ($p = 0.0568$ and 0.0051 , respectively, Table 7A-B, Figure 4). In low nutrient conditions there was strong evidence that Shannon diversity was more positively associated with PRM for Chiletanum and Andigenum clades compared to the modern clade (t-test, $\beta_{Chiletanum} = 42.996$, $p_{chiletanum} = 0.01441$ and $\beta_{Andigenum} = 28.282$, $p_{Andigenum} = 0.01754$ Table 7A, and Figure 4A). This indicates that in low nutrient conditions Chiletanum and Andigenum landrace genotypes that harbored more bacterial diversity on their roots tended to show greater positive PRM than genotypes of that same clade that harbored a lower diversity. However, among modern potato genotypes there was a negative link between a genotype's PRM and the diversity of bacteria on that genotype's roots. This was consistent across both high and low nutrient conditions. Bacterial diversity was not found to significantly associate with PRM among genotypes of *S. berthaulti*.

422

DISCUSSION

In summary, our results confirmed that potato domestication has altered how different lineages of *S. tuberosum* respond to their respective soil microbial communities in a nutrient-dependent way. The mechanism for the difference in plant responsiveness to microbes was more consistent with changes in the plant host's (in)ability to respond to the rhizosphere microbial community rather than host driven changes in the microbial community composition.

Wild and landrace potato varieties have greater positive response to soil microbes in nutrient poor conditions. Most studies examining domestication effects on plant response to microbes have focused on a narrow subset of root associated microbial communities, namely rhizobia and

432 mycorrhizal fungi (Hetrick et al 1992, Zhu et al 200, Kiers et al 2007). Collectively, these studies
433 have demonstrated greater plant beneficial response to inoculated microbes in some ancestral
434 plant genotypes compared to modern counterparts, generally due to increased performance of
435 modern varieties in the non-symbiotic state (Hetrick et al 1992, Sawers et al. 2010, Potter and
436 Sachs 2020). However, no studies to our knowledge have documented changes in plant host
437 responses to the whole microbial community as a result of plant domestication.

438 We attempted to address this gap by examining how plant responses to microbial communities
439 differed among genotype groups (potato clades). The Chiletanum landraces had a more positive
440 response to their microbial community than their modern counterparts in low nutrient conditions.
441 Importantly, this was not due solely to poor performance in sterile soils, suggesting that the
442 beneficial plant response to microbes observed was not linked to plant microbial dependence
443 (PMD).

444

445 However, two distant ancestral relatives, Andigenum landraces and the wild *S. berthaulti*, did not
446 show significantly positive plant responses to live soils. Our experiment may have failed to
447 replicate the relevant context necessary to detect positive plant response to microbes in these
448 groups, either due to the use of non-native microbial communities or inappropriate
449 environmental conditions. For instance, in Andigenum landraces, Gumiere (2019) found
450 recruitment of microbial communities was linked to drought stress tolerance and high tuber
451 production (Gumiere et al 2019). Davies et al (2005) noted that Andigenum variety ‘Yungay’
452 was particularly responsive to native Andean AMF strains. The ecological context of these
453 Andigenum landraces and wild *S. berthaulti*, which grow at high altitudes, may have led to
454 different plant response towards their microbial partners (Aleti et al 2017).

455

456 On the other hand, the more positive plant response to microbes in modern potatoes in high
457 nutrient levels may suggest artificial selection for potatoes that respond positively to the
458 microbial taxa that thrive in high nutrient conditions. Modern potato genotypes may still require
459 certain services from their respective rhizosphere microbiomes independent of nutrient
460 acquisition. Over multiple generations of selection, crops may have adapted to develop
461 relationships with microbes found in agricultural soils. This was suggested for common bean

462 where modern resistance breeding inadvertently selected for plants traits enriching beneficial
463 phytopathogen antagonists (Mendes et al 2017).

464

465 *Mechanism for positive plant response to microbial composition is driven by presence or*
466 *absence of plant host traits.* We hypothesized that differences in PRM along the domestication
467 gradient would reflect differences in the composition of rhizosphere microbial communities
468 among clades (“host determinism hypothesis”). Other studies have found differences in
469 rhizosphere microbial community structure between wild, landrace, and modern crop
470 counterparts (Bouffaud et al 2004, Mendes et al 2017, Brisson et al 2019, Engelhard et al 2020).
471 In common bean, the phylogenetic distance between plant hosts, as well as morphological traits
472 like root length were correlated with rhizosphere microbial composition (Perez-Jaramillo et al
473 2017). We found a difference in relative abundance of the Bacteroidetes phylum between
474 Andigenum landraces versus modern genotypes, but only in low nutrient conditions.
475 Nevertheless, we did not detect any differences in microbial community composition between
476 the modern and Chiletanum clades, which were the two clades showing divergent responses to
477 microbes (PRM) across nutrient levels. Thus, host driven changes, or the lack thereof, in
478 microbial community composition was not predictive of plant host response, and thus did not
479 support the host determinism hypothesis. While our results suggest that plant domestication may
480 not have had a strong effect on the recruitment of abundant microbial taxa, our study lacked the
481 necessary depth and resolution to investigate rare taxa. The microbial differences from
482 domestication may lie in more rare microbial taxa (Johnston-Monje et al 2014, Brisson et al
483 2019). Absolute abundance of microbial taxa may also have differed between potato clades but
484 measuring absolute abundance was unfortunately beyond the scope of this experiment.

485

486 Previous studies investigating host determinism in maize found inbred lines found differences in
487 microbial beta diversity among lines (Peiffer et al 2013, Favela et al 2021). Specifically, in
488 certain maize genotypes, microbial taxa were identified as heritable symbionts at the genus level
489 (Walter et al 2018). However, Walter et al (2018) did not find genetic dissimilarity among maize
490 lines to be predictive of rhizosphere microbial community composition, consistent with our
491 findings. In other systems, barley rhizosphere diversification led to distinct microbial
492 communities between wild and domesticated genotypes (Bulgarelli et al 2015). The lack of

493 differences amongst our potato clades may reflect the breeding history of potatoes. Most of the
494 major North American varieties used in this study are only 4 or 5 generations descended from
495 landraces and displayed low levels of heterozygosity (Janksy et al 2016, Hirsch et al 2013). With
496 clonal propagation, domesticated populations may have had too few recombination-and-selection
497 cycles to have accumulated numerous differences from their wild ancestors (McKey et al 2010,
498 Hirsch et al 2013). As a result, rhizosphere microbial communities may not significantly differ
499 amongst potato clades.

500

501 We found more support for the “host insensitivity hypothesis”, in that modern and Chiletanum
502 clades displayed different PRM despite recruiting similar microbial communities. Instead,
503 environmental factors (nutrient levels) played a stronger role in shaping the microbial
504 community composition in our study. In doing so, the environmental conditions determined what
505 microbes were available for the plant host to utilize. Other studies have also observed that
506 environmental factors played a more significant role in determining rhizosphere microbial
507 community composition than host genotype (Turner et al 2013, Johnston-Monje et al., 2014,
508 Brisson et al 2019, Pantigoso et al 2020).

509

510 In further support of host insensitivity, and against the host determinism, hypothesis, we saw no
511 differences in the average bacterial diversity between potato clades, but there were differences in
512 the way that a genotype’s PMR correlated with the diversity of their root-associated microbial
513 communities among clades. Within the Chiletanum and Andigenum clades, genotypes displayed
514 generally positive correlations between each genotype’s response to microbes and the diversity
515 of their rhizosphere communities in low nutrient conditions. In contrast, for modern varieties
516 there was negative correlation between these metrics in both nutrient conditions. Importantly, we
517 used genotype averages for both traits (PRM and rhizosphere microbial diversity), so these
518 relationships represent genetic correlations rather than phenotypic correlations induced by
519 environmental variation.

520

521 The differences in how PRM correlates to rhizosphere diversity among genotypes may indicate
522 differences in how the potato clades affect rhizosphere microbial community assembly.

523 Specifically, the significant interaction effects between diversity and specific potato clade

524 highlight these clade specific differences to diverse microbial communities. Plants have varying
525 ways to either exclude or recruit microbes in the rhizosphere via root exudates, signaling
526 molecules, and rhizodeposition (Cordovez et al 2019, Beilsmith et al 2019, Jacoby et al 2020).
527 The distinctly different patterns of co-variation between microbial diversity and PRM between
528 modern and landrace clades (highlighted by the significant diversity by potato clade interaction
529 on PRM) may have resulted from differing levels of exclusion and recruitment of microbes.
530 Specifically, the positive co-variation between PRM and diversity among Chiletanum and
531 Andigenum landraces may have resulted from the genotype's recruiting a diversity of
532 complementary microbial taxa creating a more multi-functioning community that ultimately
533 leads to greater plant productivity (Saleem et al 2019). Meanwhile, among modern potato
534 genotypes, the negative co-variation with microbial diversity may reflect the exclusion, or failure
535 to exclude, of detrimental microbial taxa. If increasing diversity occurred in part through the
536 accumulation of parasitic or pathogenic microbes, this could lead to an overall negative impact
537 on plant health outcomes (Franzini et al 2013).

538
539 *Trade-off between environmental factors and plant response amongst potato clades:* The
540 differences in how the potato clades responded to microbes in high versus low nutrient
541 conditions points to a tradeoff, which may be a consequence of potato domestication. Microbial
542 community composition in soils is shaped by environmental factors, including agricultural
543 management, and this determines the pool of microbes the plant host can use. This then sets the
544 stage upon which artificial selection for potato tuber quantity and quality is exerted. The loss of
545 positive responses to microbes in low nutrient conditions seen in modern potato varieties could
546 then have arisen either through multiple bottlenecking events (Genetic cost hypothesis, Porter
547 and Sachs 2020), through a loss of positive selection because this trait was not linked to breeding
548 targets in high nutrient conditions (Selection relaxation hypothesis, Porter and Sachs 2020), or
549 because this trait directly traded off with other traits that were linked to breeding targets,
550 resulting in direct selection against this trait (Genetic trade-off hypothesis, Porter and Sachs
551 2020).

552
553 Plant response to microbes did not differ between our two soil inocula sources, despite clear
554 differences in the composition and diversity of these inocula. This suggests some degree of

555 functional redundancy in the microbial communities that allows plants to recruit different sets of
556 microbes to achieve the same results. Soil is known to have great functional redundancy. Rather,
557 the nutrient conditions in our experimental pots seemed to drive differences in plant response to
558 microbes that were clade specific. This agrees with the literature that fertilization has a profound
559 impact on microbial communities in cultivated systems (French et al 2021). These findings may
560 suggest a microbiome core based on function in addition to composition.

561
562 Our findings highlight the need to examine environmental and genetic host factors influencing
563 plant microbial community interactions. Quantitative genetics techniques such as genome-wide
564 association sites (GWAS) performed across nutrient and microbial contexts could potentially
565 utilize these findings for breeding purposes (Beilsmith et al 2019, Jacoby et al 2020).

566 Importantly, in our study differences in microbial composition among varieties were not linked
567 to plant responses. Future studies should aim to document both host plant effects on microbial
568 community composition (via metabarcoding or metagenomic sequencing) as well as microbial
569 effects on plant hosts (via experimental manipulations). Together, these techniques may aid in
570 developing crop varieties that can better capitalize on positive plant–microbe responses for
571 greater agricultural yields.

572

573 **Supplementary Data:**

574 Supplementary Data is available online at JXB online

575

576 Table S1: Permutational MANOVA ITS (Fungal) community structure results for root-
577 associated bacterial ASVs.

578 Table S2: 95% Confidence Interval of Plant Response to Microbes (PRM) amongst potato clades
579 in high and low nutrient conditions

580 Figure S1: Plant response to microbes in terms of root mass low nutrient conditions

581 Figure S2: Dry Weight Root Biomass (Low Nutrient Conditions)

582 Figure S3: Absolute Total dry weight biomass versus potato clade in low nutrient conditions
583 after 12 weeks of growth

584 Figure S4: Absolute Total Biomass versus potato clade in high Nutrient Conditions after 12
585 weeks of growth.

586 Table S3: ANOVA results for Total Plant Dry Biomass after 12 weeks of growth across potato
587 clade, nutrient, and soil inocula
588 Table S4: ANOVA results for Plant Response to Microbes (PRM) in terms of tuber response to
589 Shannon diversity in low nutrient condition
590 Table S5: Differential abundance of Proteobacteria phyla in low nutrient conditions
591 Table S6: Differential abundance of Proteobacteria phyla in high nutrient conditions
592 Table S7: Differential abundance of Actinobacteria phyla in low nutrient conditions
593 Table S8: Differential abundance of Actinobacteria phyla in high nutrient conditions
594 Table S9: ANOVA result for Shannon diversity as a function of time (Week 4 vs Week 12
595 Table S10 PerMANOVA results for root-associated bacterial ASVs, across week 4 and week 12
596 in Low Nutrient Conditions

597

598 **Data Availability**

599 The scripts that support the findings of this study are openly available in Github at
600 https://github.com/maxmiao/GH_2017_exmpt. The data that support the findings of this study
601 are openly available in Dryad at <https://doi.org/10.5061/dryad.pzgmsbcmf>, and
602 doi:10.5061/dryad.2jm63xspw.

603

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608

609 **Author Contribution:**

610 MM conceived this study with RAL advisement. Greenhouse and laboratory work was
611 performed primarily by MM. Data analysis was conducted by MM with aid from RAL. MM led
612 the writing with RAL providing critical feedback. All authors agreed in submission of final draft.

613

614 **Conflicts of Interest Statement**

615 All authors declare no potential, perceived, or real conflict of interest regarding the content of
616 this paper. The funding agencies did not have any role in design and conduct of the study;

617 collection, management, and interpretation of the data; or preparation, review, or approval of the
618 paper.
619
620

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Tables

Table 1A-B: Regression estimates with SE and t-tests for multiple regression of Plant Response to Microbes against soil inocula, potato clades, and nutrient treatments and their interactions (A), or soil inocula and potato clade separately in low nutrients (B) or high nutrients (C). Estimates indicate deviations from the default group – soil inocula from the agricultural site, modern potato clade, and high nutrient conditions. Bold text = $P < 0.05$.

Table 1A: Regression table for analysis of Plant Response to Microbes by clade and nutrient treatment

	Estimate	Std. Error	df	t value	Pr(> t)	
(Intercept)	9.991	7.776	33.174	1.285	0.20772	
Soil Inocula (Virgin)	6.455	6.098	45	1.058	0.29548	
Potato Clade (Chiletanum)	-12.156	10.73	25.731	-1.133	0.26769	
Potato Clade (Andigenum)	-15.112	10.116	25.731	-1.494	0.14739	
Potato Clade (<i>S. berthaulti</i>)	-33.512	11.681	25.731	-2.869	0.00812	**
Nutrient Treatment (Low)	-11.749	9.045	45	-1.299	0.20058	
Soil Inocula : Nutrient Treatment	-10.526	8.624	45	-1.221	0.22861	
Potato Clade (Chiletanum):Nutrient Trt	25.26	11.926	45	2.118	0.03973	*
Potato Clade (Andigenum):Nutrient Trt	20.394	11.244	45	1.814	0.07639	.
Potato Clade (<i>S. berthaulti</i>):Nutrient Trt	28.729	12.984	45	2.213	0.03203	*

Table 1B: Regression Table Plant Response to Microbes in Low Nutrients

	Estimate	Std. Error	df	t value	Pr(> t)	
(Intercept)	-1.757	3.906	18.019	1.285	0.6582	
Soil Inocula (Virgin)	-4.071	3.159	16	1.058	0.2158	
Potato Clade (Chiletanum)	13.104	5.359	13	-1.133	0.0295	*
Potato Clade (Andigenum)	5.282	5.053	13	-1.494	0.3149	
Potato Clade (<i>S. berthaulti</i>)	-4.782	5.834	13	-2.869	0.4271	

Table 2A-B: Permutational MANOVA results for root-associated bacterial ASVs, analyzed after 12 weeks of growth separately for low (A) and high (B) nutrient conditions. Bold text = $P < 0.05$.

Table 2A: PerMANOVA Low Nutrients at Week 12

	Df	SumsOfSqs	MeanSqs	Psuedo-F	R ²	Pr(>F)	
Soil Inocula	1	1.0181	1.0181	2.7832	0.07672	0.001	***
Potato Clade	3	1.278	0.42601	1.1646	0.09631	0.101	
Residuals	27	10.9742	0.36061		0.7337		
Total	34	13.2703			1		

Table 2B: PerMANOVA High Nutrients at Week 12

	Df	SumsOfSqs	MeanSqs	Psuedo-F	R ²	Pr(>F)	
Soil Inocula	1	0.6598	0.65975	1.97896	0.07153	0.001	***
Potato Clade	3	0.8954	0.29847	0.89526	0.09708	0.756	
Residuals	23	7.6678	0.33338		0.83138		
Total	27	9.2229			1		

Table 3: Pair-wise comparisons of root-associated bacterial ASV community composition between Modern each land-race or wild potato clade at week 4 and 12 in low nutrients. Bold text = P <0.05.

Table 3: PerMANOVA Pair-wise Contrasts					
Low Nutrients					
Week 4					
pairs	Df	SumsOfSqs	F.Model	R2	p.value
Andigenum vs Elite	1	0.00268	1.252118	0.05627	0.215
Chiletanum vs Elite	1	0.002402	1.278154	0.069928	0.19
Elite vs S. berthaulti	1	0.001669	0.80388	0.054302	0.618
Week 12					
Andigenum vs Elite	1	0.003539	0.940373	0.040992	0.45
Chiletanum vs Elite	1	0.003845	1.181159	0.058528	0.282
Elite vs S. berthaulti	1	0.006784	2.042533	0.10191	0.067

Table 4: Pair-wise comparisons of root-associated bacterial ASV community composition between Modern each land-race or wild potato clade, in high nutrient conditions, and for each time point (week 4 or 12). Bold text = P <0.05.

Table 4: PerMANOVA Pair-wise Contrasts					
High Nutrients					
Week 4					
pairs	Df	SumsOfSqs	F.Model	R2	p.value
Andigenum vs Elite	1	0.001559	0.86233	0.022775	0.48
Chiletanum vs Elite	1	0.003557	2.137769	0.073368	0.055
Elite vs S. berthaulti	1	0.001216	0.660437	0.025738	0.696
Week 12					
Andigenum vs Elite	1	0.002359	0.627373	0.037731	0.871
Chiletanum vs Elite	1	0.004291	1.201931	0.084632	0.268
Elite vs S. berthaulti	1	0.003448	0.85096	0.096143	0.64

Table 5A-B: Differential abundance of Bacteroidetes phyla in low nutrient conditions (**A**) and high nutrient conditions (**B**). Regression estimates with SE and t-tests for multiple regression of Bacteroidetes relative abundance against time point, potato clade, and their interaction, separately for low and high nutrient conditions. Estimates indicate deviations from the default group – the week 4 time point and the Modern potato clade. Bold text = $P < 0.05$.

Table 5A: Differential Abundance of Bacteroidetes (Low)

	Estimate	Std. Error	df	t value	Pr(> t)	
(Intercept)	0.34536	0.05947	71	5.807	1.65E-07	***
Time point (Week 12)	0.03842	0.07979	71	0.482	0.6316	
Potato Clade (Chiletanum)	-0.10704	0.086	71	-1.245	0.2173	
Potato Clade (Andigenum)	-0.14672	0.07867	71	-1.865	0.0663	
Potato Clade (<i>S. berthaulti</i>)	-0.12575	0.10966	71	-1.147	0.2553	
Time point: Potato Clade (Chiletanum)	0.12414	0.13152	71	0.944	0.3485	
Time point: Potato Clade (Andigenum)	0.26467	0.1172	71	2.258	0.027	*
Time point: Potato Clade (<i>S. berthaulti</i>)	0.16001	0.15279	71	1.047	0.2985	

Table 5B: Differential Abundance of Bacteroidetes (High)

	Estimate	Std. Error	df	t value	Pr(> t)	
(Intercept)	0.22003	0.04182	9.60217	5.261	0.00042	***
Time point (Week 12)	0.13705	0.06209	46.24055	2.207	0.0323	*
Potato Clade (Chiletanum)	-0.02178	0.07023	18.32075	-0.31	0.76	
Potato Clade (Andigenum)	-0.03312	0.05781	10.21838	-0.573	0.5791	
Potato Clade (<i>S. berthaulti</i>)	-0.05776	0.0707	15.30511	-0.817	0.42647	
Time point: Potato Clade (Chiletanum)	-0.04383	0.09709	53.34004	-0.451	0.65349	
Time point: Potato Clade (Andigenum)	-0.06526	0.08353	54.95962	-0.781	0.43801	
Time point: Potato Clade (<i>S. berthaulti</i>)	0.13719	0.11142	54.38172	1.231	0.22351	

Table 6: Regression estimates with SE and t-tests for multiple regression of bacterial Shannon-Weiner diversity against potato clade and soil inocula source, separately for low and high nutrient conditions and each time point. Estimates indicate deviations from the default group – agricultural source soil and the Modern potato clade. Bold text = $P < 0.05$.

Low Nutrients					
Week 4					
	Estimate	Std. Error	df	t-value	Pr(> t)
(Intercept)	2.82487	0.23934	18.81108	11.803	3.87E-10
Soil Inocula (Virgin)	-0.07946	0.21248	28.85155	-0.374	0.711
Potato Clade (Chiletanum)	-0.05586	0.29492	11.67958	-0.189	0.853
Potato Clade (Andigenum)	-0.32949	0.27135	11.04078	-1.214	0.25
Potato Clade (<i>S. berthaulti</i>)	-0.29577	0.36207	9.91398	-0.817	0.433
Week 12					
	Estimate	Std. Error	df	t-value	Pr(> t)
(Intercept)	2.79446	0.18641	30	14.99	1.78E-15
Soil Inocula (Virgin)	-0.41453	0.20968	30	-1.977	0.573
Potato Clade (Chiletanum)	-0.02145	0.2791	30	-0.077	0.9392
Potato Clade (Andigenum)	-0.24803	0.2488	30	-0.997	0.3269
Potato Clade (<i>S. berthaulti</i>)	-0.28872	0.30347	30	-0.951	0.349

Table 7A-B: Regression estimates with SE and t-tests for multiple regression of Plant Response to Microbes against root-associated bacterial diversity (Shannon-Weiner), potato clade, and their interaction separately for (A) low nutrient and (B) high nutrient conditions. Estimates indicate deviations from the default modern potato clade. Bacterial diversity metric measured at week 4. Bold text = P<0.05.

Table 7A Low Nutrient

Fixed Effects	Estimate	Std. Error	df	t-value	Pr(> t)	
(Intercept)	82.375	26.948	15	3.057	0.00799	**
Shannon Diversity	-30.272	9.241	15	-3.276	0.0051	**
Potato clade (Chiletanum)	-104.49	43.541	15	-2.4	0.02984	*
Potato clade (Andigenum)	-75.028	30.01	15	-2.5	0.0245	*
Potato clade (<i>S. berthaulti</i>)	-77.104	50.014	15	-1.542	0.14398	
Diversity: Potato clade (Chiletanum)	42.996	15.544	15	2.766	0.01441	*
Diversity: Potato clade (Andigenum)	28.282	10.6	15	2.668	0.01754	*
Diversity: Potato clade (<i>S. berthaulti</i>)	24.022	19.478	15	1.233	0.23643	

Table 7B High Nutrients

Fixed Effects	Estimate	Std. Error	df	t-value	Pr(> t)	
(Intercept)	142.627	62.754	9.05	2.273	0.049	*
Shannon Diversity	-50.466	23.144	9.093	-2.181	0.0568	
Potato clade (Chiletanum)	-343.104	179.268	5.684	-1.914	0.1068	
Potato clade (Andigenum)	-141.113	78.312	9.789	-1.802	0.1024	
Potato clade (<i>S. berthaulti</i>)	-226.336	126.018	9.591	-1.796	0.104	
Diversity: Potato clade (Chiletanum)	146.331	81.471	5.195	1.796	0.1302	
Diversity: Potato clade (Andigenum)	50.156	29.781	9.985	1.684	0.1231	
Diversity: Potato clade (<i>S. berthaulti</i>)	75.35	52.27	9.231	1.442	0.1825	

Figure Legends

Figure 1A-D: Tuber yields in live versus sterilized soils and resulting Plant Response to Microbe metrics per potato clade. Circle (●) indicates soil inocula sourced from Hancock research station while triangle (▲) indicates soil sourced from Mudd Lake Nature reserve. Orange symbols refer to accessions that are considered part of the ‘Modern’ clade, green to accessions that are considered part of the ‘Chiletanum’ clade, black to accessions that are considered part of the ‘Andigenum’ clade, and blue to accessions that are considered part of ‘*S. berthaulti*’ clade. A) Tuber mass in low nutrient conditions. Each dot represents average tuber biomass weight for a particular accession in a particular soil inocula source in live soil treatments (y-axis) versus its tuber biomass in sterilized soil treatments (x-axis). B) Plant Response to Microbes (PRM) in low nutrient conditions – Mean \pm SE per clade of residual values from the regression of tuber yield in live vs. sterilized soil shown in 1A; C) Tuber mass in high nutrient conditions; D) PRM in high nutrient conditions

Figure 2A-B. Non-metric multidimensional scaling ordinations of root-associated bacterial communities: A) Low Nutrients (top); B) High Nutrients (bottom). Orange symbols refer to accessions that are considered part of the ‘Modern’ clade, green to accessions that are considered part of the ‘Chiletanum’ clade, black to accessions that are considered part of the ‘Andigenum’ clade, and blue to accessions that are considered part of ‘*S. berthaulti*’ clade. Square symbols = time point 1 (week 4), Circular symbols = time point 2 (week 12). Ellipses are 95% confidence intervals around clade X time point centroids.

Figure 3: Heat map of relative abundance of bacterial phyla based on 16S amplicon sequencing, separately for low and high nutrients, and for timepoints 1 (week 4) and 2 (week 12). Blue to red gradient indicates increased to decreased relative abundance. The color bar below each heat map indicates potato clades: Blue (*S.berthaulti*), Black (Andigenum), Green (Chiletanum), Orange (Modern).

Figure 4A-B: Plant Response to Microbes (PRM) versus bacterial diversity (Shannon-Weiner) by accession in A) low nutrient conditions; B) high nutrient conditions. Each symbol represents the average Shannon diversity (x-axis) and PRM (y-axis) for a given potato accession. Orange represents 'Modern' clade. Green represents 'Chiletanum' clade. Black represents 'Andigenum' clade. 'Blue' represents '*S. berthaulti*' clade.

Figure 1A-D: Tuber yields in live versus sterilized soils, and resulting Plant Response to Microbe metrics per potato clade. Circle (●) indicates soil inocula sourced from Hancock research station while triangle (▲) indicates soil sourced from Mudd Lake Nature reserve. Orange symbols refer to accessions that are considered part of the ‘Modern’ clade, green to accessions that are considered part of the ‘Chiletanum’ clade, black to accessions that are considered part of the ‘Andigenum’ clade, and blue to accessions that are considered part of ‘*S. berthaulti*’ clade. A) Tuber mass in low nutrient conditions. Each dot represents average tuber biomass weight for a particular accession in a particular soil inocula source in live soil treatments (y-axis) versus its tuber biomass in sterilized soil treatments (x-axis). B) Plant Response to Microbes (PRM) in low nutrient conditions – Mean \pm SE per clade of residual values from the regression of tuber yield in live vs. sterilized soil shown in 1A; C) Tuber mass in high nutrient conditions; D) PRM in high nutrient conditions

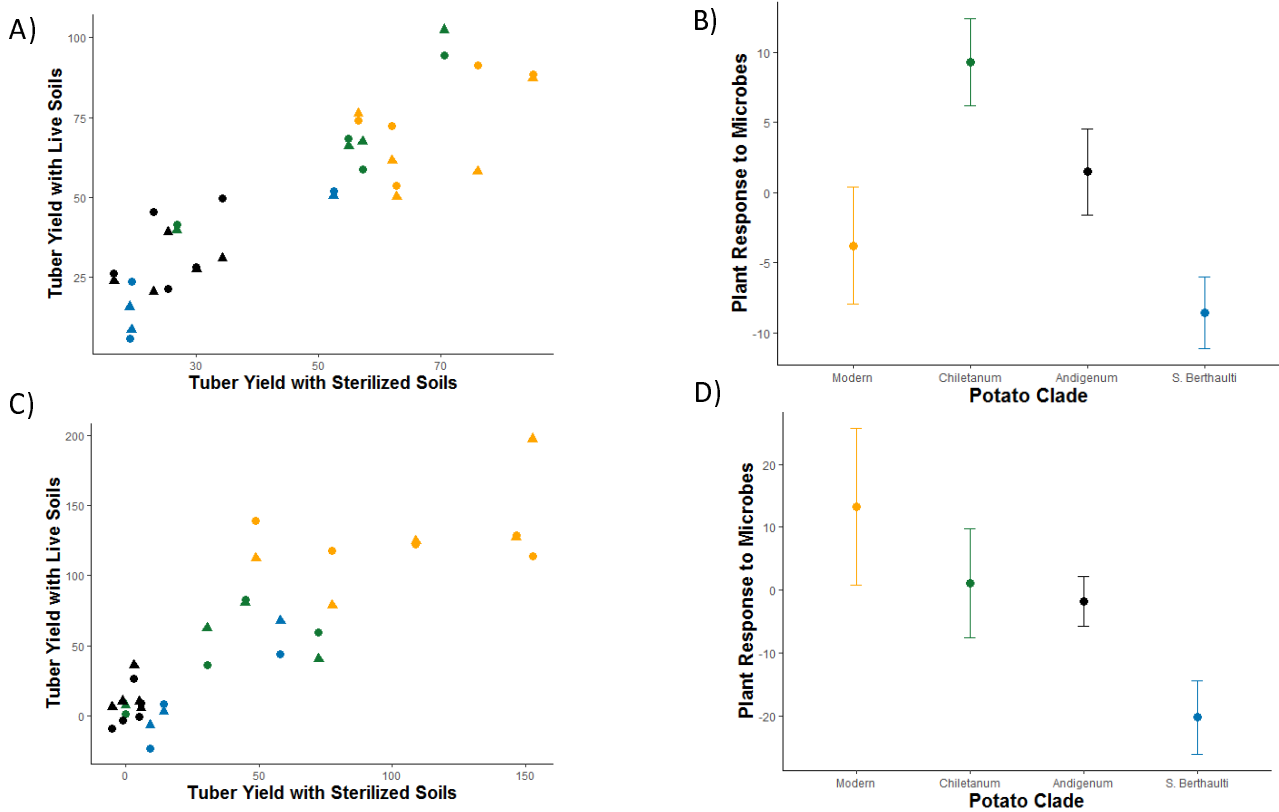
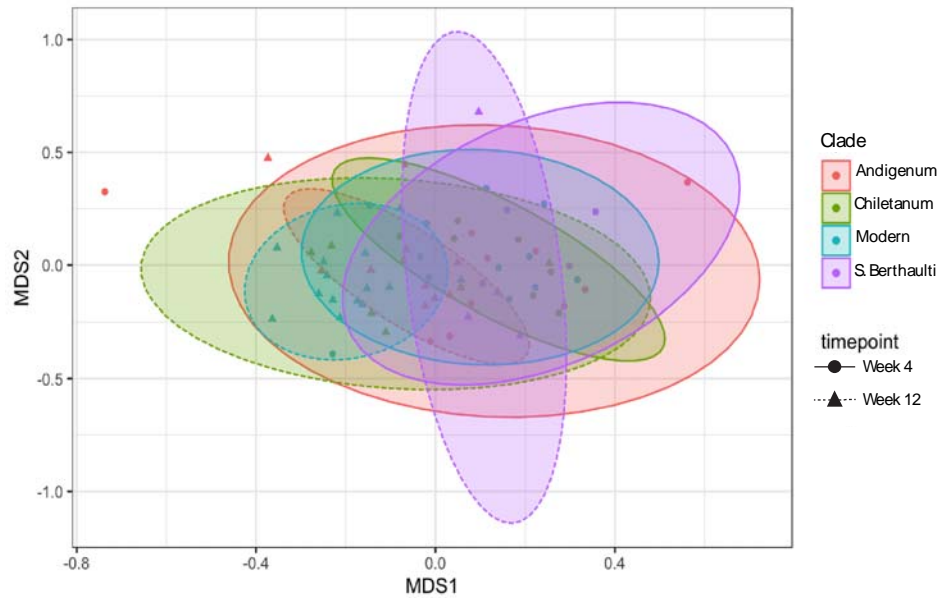


Figure 2A-B. Non-metric multidimensional scaling ordinations of root-associated bacterial communities: 2A) Low Nutrients (top); 2B) High Nutrients (bottom). Teal symbols refer to accessions that are considered part of the ‘Modern’ clade, green to accessions that are considered part of the ‘Chiletanum’ clade, Red to accessions that are considered part of the ‘Andigenum’ clade, and Purple to accessions that are considered part of ‘*S. berthaulti*’ clade. Square symbols = time point 1 (week 4), Circular symbols = time point 2 (week 12). Ellipses are 95% confidence intervals around clade X time point centroids. Solid ellipses represent timepoint week 4. Dashed ellipses represent timepoint week 12.

2A)



Solid ellipses represent timepoint week 4. Dashed ellipses represent timepoint week 12.

2B)

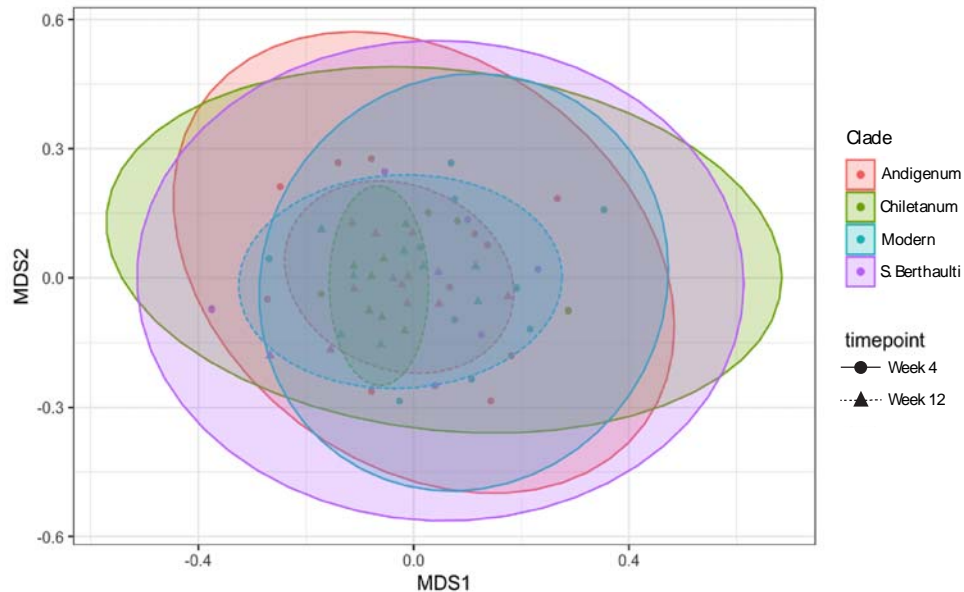


Figure 1: Heat map of relative abundance of bacterial phyla based on 16S amplicon sequencing, separately for low and high nutrients, and for timepoints 1 (week 4) and 2 (week 12). Blue to red gradient indicates increased to decreased relative abundance. The colored outlines indicate potato clades : Blue (*S.berthauti*), Black (Andigenum), Green (Chiletanum), Gold (Modern).

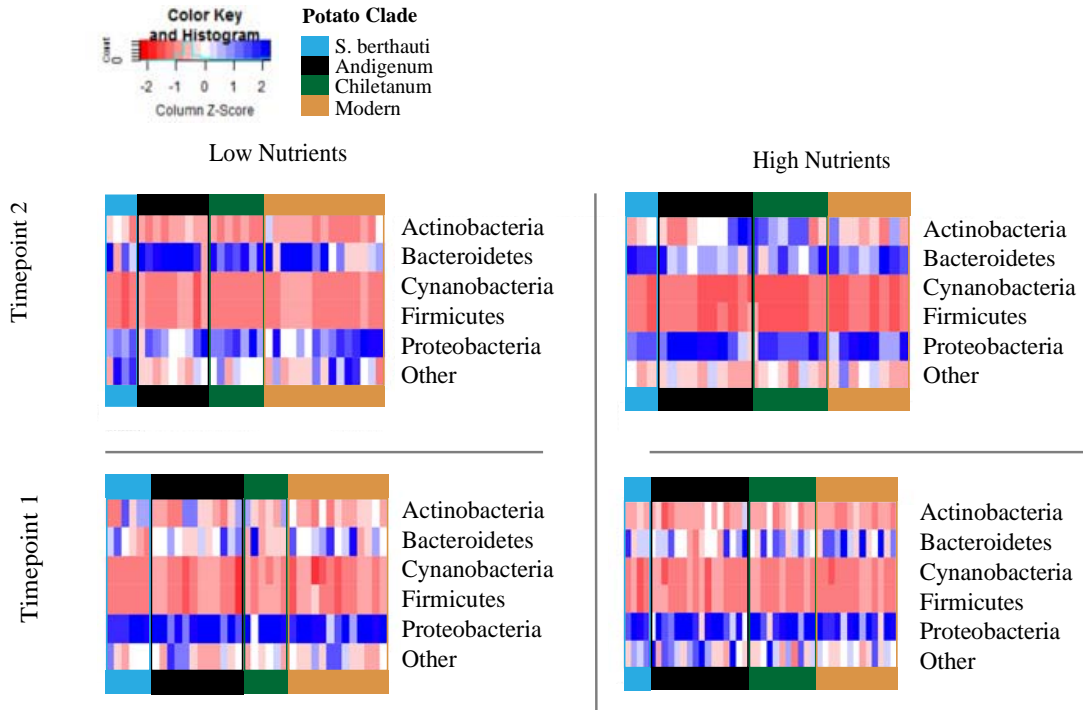
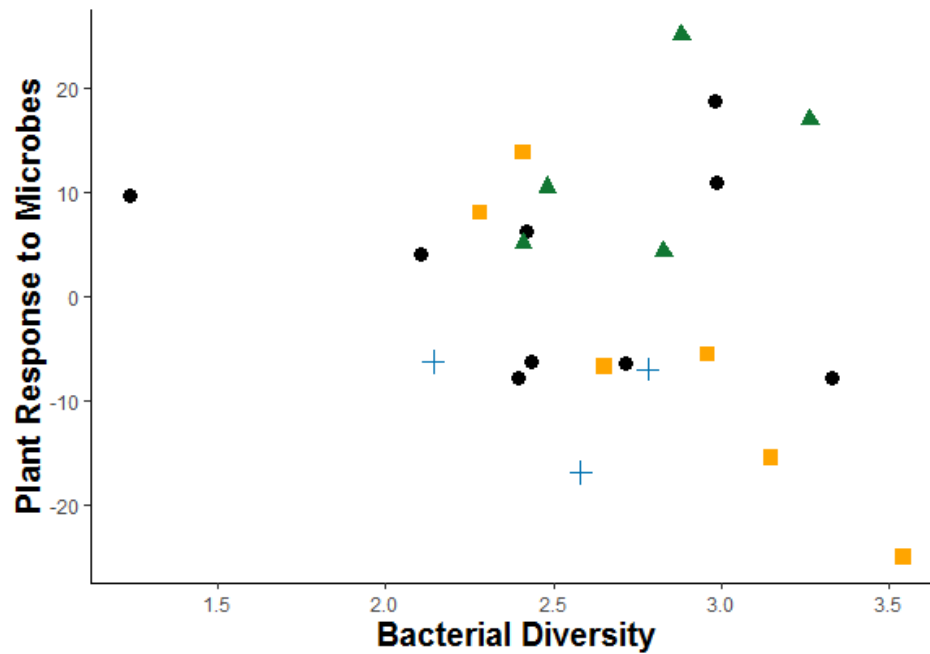


Figure 4A-B: Plant Response to Microbes (PRM) versus bacterial diversity (Shannon-Weiner) by accession in 4A) low nutrient conditions (top); 4B) high nutrient conditions (bottom). Each symbol represents the average Shannon diversity (x-axis) and PRM (y-axis) for a given potato genotype. Orange represents 'Modern' clade. Green represents 'Chiletanum' clade. Black represents 'Andigenum' clade. 'Blue' represents '*S. berthaulti*' clade.

4A)



4B)

