Crop performance is predicted by soil microbial diversity across phylogenetic scales

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Abstract

Soils contain diverse living communities that provide key ecosystem functions in agroecosystems. In many systems, ecosystems functions are positively related to the taxonomic, phylogenetic, and functional diversity of the community. Despite calls to incorporate microbial diversity in measures of soil health, whether increased microbial diversity *per se* can predict increased crop health and productivity has rarely been documented. Here we used microbial communities from commercial potato fields varying in diversity and composition, and experimentally assessed their ability to promote crop yield under low or high nutrient conditions and to suppress a soil-borne pathogen. Across two independent sets of communities, we found that yields under low nutrient conditions were predicted by high initial microbial diversity measured at broad phylogenetic levels, consistent with greater niche complementarity among unrelated taxa leading to greater total resource use. However, disease suppression was inconsistently linked to diversity and explained as well or better by microbial composition rather than diversity *per se*. Ecosystem multifunctionality was predicted by high diversity at broad to intermediate phylogenetic scales. These results indicate that the diversity of microbial taxa may influence multiple soil functions; however, the mechanisms underlying the diversity-function relationships may vary.

Keywords

Microbial community, diversity, ecosystem function, disease suppression, potato

Introduction

Soils are the base of agricultural ecosystems, and many of the most important limitations to plant growth are soil based (Clermont-Dauphin et al. 2014, Lehman et al. 2015). Soils contain highly diverse microbial communities, and research has documented that microbial communities play a vital role in promoting key plant functions (Janvier et al. 2007, Hinsinger et al. 2009, Richardson et al. 2009, Mendes et al. 2011, Berendsen et al. 2012, Ellouze et al. 2014). Researchers have made great strides in understanding the physiological, genetic, and biochemical mechanisms underlying these relationships for model systems involving one or a few targeted microbial taxa (Bloemberg and Lugtenberg 2001, Lugtenberg et al. 2001, Persello-Cartieaux et al. 2003, Somers et al. 2004, Stacey et al. 2006, Barret et al. 2011, Udvardi and Poole 2013, Garcia et al. 2015, Peix et al. 2015). However, as complex systems the functions of soil microbial communities may not be predictable from investigations of individual components in isolation, but rather reflect emergent properties resulting from interactions among community members.

In many systems, ecosystem functions are positively related to the taxonomic, phylogenetic, and functional diversity of the community (Cadotte et al. 2011, Cardinale et al. 2012, Tilman et al. 2014, Wagg et al. 2019). Despite calls to incorporate microbial diversity in measures of soil health (Lehman et al. 2015), whether increased microbial diversity *per se* predicts increased crop health and productivity has rarely been documented (Nielsen et al. 2011, Bardgett and van der Putten 2014, Wagg et al. 2019). Theory predicts that ecosystem functions that result from resource utilization, such as nitrogen mineralization via the decomposition of soil organic matter, are optimized by broad taxonomic, phylogenetic, and/or functional diversity. Higher diversity can increase function via sampling effects (greater likelihood of including a

highly functional species) or complementarity (resource partitioning among species, leading to more complete use of the resource base) (Loreau and Hector 2001). Complementarity has consistently been shown to be the most important component of biodiversity effects on ecosystem productivity (Cardinale et al. 2007), since productivity is increased when limiting resources are used in the most complete and efficient way.

However, other ecosystem functions rely not on the most efficient use of the entire resource base, but on competitive exclusion of undesirable community members. Positive diversity-invasibility relationships, in which more taxonomically, phylogenetically, or functionally diverse communities are less susceptible to invasion by novel species, generally derive from competitive exclusion of the potential invader by resident community members (Levine and D'Antonio 1999, Tilman 2004, Fargione and Tilman 2005). In this case, overall diversity is less important than the presence of strong competitors in the precise niche required for the invasive species. Exclusion of any particular invasive species correlates positively with diversity primarily through sampling effects, as more diverse communities will be more likely to include a native species occupying the precise niche of the invader (Fargione and Tilman 2005).

In agricultural systems, soil communities are needed to provide a suite of ecosystem functions, but two crucial ones are support of crop growth through the mineralization and acquisition of growth limiting soil nutrients and suppression of soil borne plant pathogens. These two functions likely represent examples of the two phenomenon discussed above. Promotion of plant growth should be maximized by the most complete and efficient decomposition and cycling of soil organic matter by microbial communities, as this is the process that releases growth limiting nutrients (N, P, and K) into plant available forms. Soil microbial communities contain high levels of functional redundancy (Allison and Martiny 2008). Thus, diversity at fine

taxonomic scales may not correlate with the functional diversity necessary to create the niche complementarity that drives positive diversity-ecosystem function relationships (Nielsen et al. 2011). Alternatively, diversity at higher phylogenetic scales is more likely to reflect diversity in important functional traits (Maherali and Klironomos 2007, Cadotte et al. 2008), since microbial responses to environmental variation tend to be phylogenetically conserved (Isobe et al. 2020). In contrast, suppression of soil-borne plant pathogens requires exclusion of specific community members. Specific suppression, in which a soil community displays suppression ability against a particular pathogen, can result from direct microbe-microbe inhibitory interactions, often through the production of antibiotic compounds (Raaijmakers and Mazzola 2016, Schlatter et al. 2017). While decomposition and N and C cycling are likely to be optimized by resource partitioning among functionally distinct microbial groups (Miki et al. 2014, Wagg et al. 2014, Wagg et al. 2019), specific suppression is likely to depend on the presence or absence of specific inhibitors of the pathogen, as has been documented with simplified artificial communities (Wei et al. 2015, Yang et al. 2017).

Truly healthy soils must perform multiple functions simultaneously. Accumulating evidence suggests that while the relationship between diversity and any one function may be weak or saturate at low levels of richness/diversity, the relationship saturates at high levels of diversity when considering multiple functions (Lefcheck et al. 2015), including for soil communities (Wagg et al. 2014, Delgado-Baquerizo et al. 2016, Wagg et al. 2019). However, if crop growth and disease suppression relate to opposing components of microbial community structure, e.g. broad vs. narrow diversity, then simultaneous optimization of both functions may require promoting diversity within communities at multiple scales.

Here, we investigated the ecosystem function of soil microbial communities present in active potato production fields in Wisconsin, U.S.A to test three hypotheses:

1) A microbial community's ability to promote crop yield will be optimized by diversity at broad phylogenetic levels when nutrients are limited, but be unrelated to diversity when nutrients are in excess, consistent with niche complementarity effects.
2) Suppression of soil-borne pathogens will instead depend on fine scale diversity of taxa and the specific composition of communities, consistent with sampling effects.
3) The sum of the yield promotion and disease suppression functions will correlate positively with diversity at multiple scales

Rigorously examining diversity-ecosystem function relationships in soil microbial communities is challenging, as it is not possible to independently manipulate microbial taxa in order to create replicated levels of diversity across distinct compositions as is done in plant (Tilman et al. 2001), animal (Cardinale et al. 2002), or culture-based microbial communities (Wei et al. 2015). Other approaches have involved filtering whole soil guilds by size (Wagg et al. 2014, Wagg et al. 2019) or dilution-to-extinction methods (Wertz et al. 2006, Philippot et al. 2013, Maron et al. 2018) to create high and low diverse communities. While these approaches have proven powerful and led to important insights, these approaches can lead to unrealistically low levels of diversity, potentially biasing outcomes towards results irrelevant to field conditions. We took an alternative approach, in which we sampled intact soil communities from a variety of commercial potato fields where we suspected differences in soil properties and management practices had resulted in large differences in microbial diversity and composition. This approach ensures that we investigated ecological responses to relevant gradients in microbial diversity. We used these communities to inoculate pots in controlled conditions to isolate biotic effects on crop yield and

disease symptoms. Because diversity may be correlated with composition differences, we repeated the experiment with a completely new set of microbial communities to ensure that the relationship between diversity and ecosystem function was not due to the particular mix of microbial community compositions present in our first experiment. Finally, we used linear models incorporating metrics for both diversity and compositional variation to further disentangle effects of diversity from compositional variation on plant outcomes.

We used the results from our exploratory and confirmatory greenhouse experiments for the following objectives:

1) Determine whether increasing microbial diversity consistently promotes greater crop yield under low and/or high nutrient conditions, and the phylogenetic scale at which microbial diversity is most predictive of yield promotion
2) Determine whether increasing microbial diversity consistently promotes greater suppression of crop disease, and the phylogenetic scale at which microbial diversity is most predictive of disease suppression.
3) Determine how microbial diversity at multiple phylogenetic scales relates to the sum of yield promotion and disease suppressive functions.

Materials and Methods

To address hypotheses 1-3, potato plants were grown in controlled conditions in pots inoculated with microbial communities sourced from commercial potato fields throughout Wisconsin, USA (Fig. 1). We performed a two stage experiment. The first stage ("exploratory experiment"), occurred in 2015 using soil from 13 fields across 8 farms. The second stage ("confirmatory experiment"), occurred in 2017 using soil 12 new fields across 10 farms. No

fields were repeated between the two stages, to provide an independent confirmation of any diversity-plant performance relationships observed in the exploratory experiment.

Soil community sources.

We source live microbial communities from thirteen fields actively growing a potato crop in 2015 through Wisconsin, USA. Fields varied in management practices (USDA certified organic or conventionally managed), soil types, and potato varieties. A summary of the source fields is presented in the Table S1. At each field, we took samples from multiple locations (2-4 locations depending on field size, see Table S1 for exact values per field), with each location separated by at least 100m. At each location, we took three soil cores (2 cm diameter, 15 cm depth) pulled from the base of three adjacent potato plants (within 10 cm of the plant stem). Root fragments were present in soil cores and not intentionally removed. The three cores per sampling location were homogenized in the field, but distinct sampling locations within a single field were collected and processed separately for molecular characterization of microbial communities. Soils were kept on ice until transported to our laboratory, where they were frozen at -80° C until analyzed. Bulk soils (~10 L) were collected from these locations to use as inoculum for our greenhouse experiment. Bulk soil was collected from each sampling location but homogenized into one sample per field for the experiment.

Soil sampling occurred similarly in 2017, with the exception that in this case we collected soil from only one location per field. Again, three soil cores were collected from the single location in each field, and were homogenized within a field and a 15 mL subset frozen at -80° C for later DNA extraction. Bulk soils were stored at 4° C until used in the greenhouse experiment. For this experiment, we also included an additional soil source taken from a remnant sand prairie in central Wisconsin.

Molecular characterization of microbial communities

Microbial communities were characterized via metabarcoding of the bacterial 16S and fungal ITS2 gene regions using Illumina Miseq sequencing. Raw sequences were demultiplexed, filtered for quality, and assigned to exact amplicon sequence variants using the Qiime2 pipeline (Bolyen E 2018). A phylogenetic tree of the resulting 16S ASV sequences was created using the "align-to-tree-mafft-fasttree" function in the "phylogeny" plug-in for QIIME2. For the exploratory experiment, we sequenced 2-4 distinct locations in each field separately (see Table S1 for exact numbers per field). However, since we homogenized the soil from these locations into one bulk sample for inoculation in our greenhouse experiment (see below), we bioinformatically pooled the resulting ASV tables for the replicate locations in a given field, to yield one community per field that matches with the inocula used in the greenhouse experiment. See Supplemental Information for details on molecular protocols and bioinformatic analyses.

Greenhouse experiment

We used two parallel greenhouse experiments to measure the ability of each of the 13 microbial communities per experiment to 1) support potato yield under high nutrient conditions, 2) support potato yield under low nutrient conditions, and 3) suppress the tuber blemish disease, common scab, caused by the pathogen *Streptomyces scabies*. Each experiment consisted of three experimental conditions: fertilization with a NPK fertilizer, no additional nutrients, or fertilization (as above) combined with inoculation of a highly virulent strain of *S. scabies*. These three experimental conditions were factorially crossed with inoculation with one of the 13 soil microbial communities sourced from the field, or a non-inoculated (sterilized soil) control.

In the exploratory experiment (2015), we grew 4-5 replications of each combination of condition and soil community for a total of 182 pots (3 treatments X 13 microbial communities X 4-5 replicates). Each 11.3 L plastic pot was filled with 9.5 L of a sterilized background soil, consisting of a 50%/50% mixture of field soil collected from the West Madison Agricultural Research Station and river sand, which was autoclaved for 2 hours after mixing. To this soil we added 500 mL (5% pot volume) of live soil from one of the 13 source fields, or an additional 500 mL of the sterilized background soil for the sterilized soil control pots. By adding only a small volume of live soil to each pot, we greatly minimize the impact of any abiotic differences between the source soils on plant growth/disease. Therefore, we assume that any consistent differences in plant growth or disease between pots inoculated with different field soils stem primarily from differences in the biological communities added to each pot.

For pots in the two fertilized treatments, we added 11 g of 13-13-13 Nutricote slow release fertilizer pellets (1.43 g N, 1.43 g P, and 1.43 g K, Arysta LifeScience). Non fertilized pots received no additional nutrients beyond those available in the sterilized background soil. Fertilizer rates were chosen based on recommendations for field applications in the northern Midwest of the United States (Colquhoun et al. 2017). The background field soil had an organic matter concentration of 3%, P concentration of 297 ppm, and K concentration of 990 ppm, levels higher than almost all field soils (see Supplemental Information). Analysis of leaf nitrogen content suggested that plants faced severe nitrogen limitation in non-fertilized pots (see Supplemental Information).

For pots in the *S. scabies* inoculation treatment, we added 5×10^7 cells of a highly virulent strain of *S. scabies*, kindly provided by A. Gevens (see Webster et al. (2018) for isolate

description). Cells were suspended in 50 mL of water and added to the center of the pots immediately prior to planting the seed tuber.

One first generation minituber of cv. Snowden was added to each pot. Minitubers were generously donated by the Wisconsin Potato Seed Certification Program. First generation minitubers are produced under axenic conditions from plants derived from tissue culture, and so are free of any seed-borne pathogens. Potato plants were grown for 4 months at 26° C/16° C with 16 hour days. Pots were watered 2-3 per week or as necessary to prevent water stress. After 4 months, all aboveground biomass was harvested. Pots were left for an additional week to allow hardening of tuber periderms before soil was washed free of roots and root and tuber biomass was separately harvested. Roots and aboveground vegetative mass were dried for 48 hours at 60° C and weighed. Tubers were weighed fresh, and each tuber above 1 cm diameter was visually assessed for common scab symptoms following (Webster et al. 2018).

The confirmatory experiment (2017) followed the same basic design but had several methodological differences. Due to space constraints, potato plants were grown in smaller pots (7.5 L). To further reduce any potential influence of abiotic differences among the soil microbial inocula, we reduced the volume of live soil added to each pot to 67 mL (~0.88% pot volume), which we added by mixing 1 L of live soil from a source to 2 L of sterile water, mixing well, and adding 200 mL of the slurry to each pot. Because we saw some symptoms of nitrogen limitation in potato plants in the "high nutrient" treatment in 2015, we increased the fertilization rate to 15.4 g of the 13-13-13 slow release fertilizer (2.002 g each of N, P, K). As before, pots in the low nutrient treatment received no additional nutrient inputs. Finally, due to limited *S. scabies* inoculum, we added 3 x 10^6 cells of the same strain to each pot in the pathogen inoculation treatment. On average, severity of common scab symptoms in the confirmatory experiment were

lower than in the exploratory experiment, likely as a result of the reduced pathogen inoculation (average Common Scab severity score: exploratory experiment = 2.122 + 0.38, confirmatory experiment = 1.043 + 0.32, t-test P value = 0.04). Nevertheless, disease symptoms were observed consistently in control pots lacking field microbial community inoculations, suggesting that our reduced S. scabbies inoculation was sufficient to provide consistent pathogen pressure and allow for the expression of quantitative differences in disease suppressiveness among microbial community sources. All other details of the growing conditions and measurements were as described above.

Statistical Analysis

Measuring microbially mediated ecosystem functions using plant responses: We measured a microbial community's ability to promote tuber yield in high nutrient conditions as the mean of tuber yield of the replicate potato plants grown with a given microbial community inoculum in the fertilized, no pathogen treatment. Prior to averaging tuber yields among replicates, we first detrended yields for the effects of greenhouse position and mass of the initial seed tuber. Similarly, a microbial community's ability to promote tuber yield in low nutrient conditions was calculated as the mean of tuber yield of the replicate potato plants grown in the unfertilized, no pathogen treatment. Finally, we calculated the ability of a given microbial community to suppress common scab disease by estimating the severity of common scab symptoms on all tubers from a given plant in the *S. scabies* inoculated treatment, then taking the average per plant. Severity was estimated according to methods described in Webster et al. (2018), incorporating both the tuber surface area covered by lesions and the phenotype of the lesions (see Supplementary Information for details).

Calculating community diversity across phylogenetic scales

We hypothesized that different ecosystem functions (tuber yield under high nutrient conditions, tuber yield under low nutrient conditions, and suppression of common scab disease) would relate to microbial diversity at different phylogenetic scales. We used the branch length from the tree node in the phylogenetic tree estimated from our 16S sequences to provide a quantitative measure of phylogenetic resolution. In brief, we used a given branch distance from the tree root to define clades, then collapsed all ASVs present within a given clade into one "operational phylogenetic unit" and remade our community matrix using these new units. We then calculated the Shannon-Weiner diversity for each sample based on this new community matrix. To create a gradient in phylogenetic resolution, we performed this process using bacterial clades defined by a distance of 0.1, 0.15, 0.2, 0.25, 0.3, 0.35, 0.4, 0.45, 0.5, 0.55, 0.6, and 0.7 units distance from the tree root (Fig 2). Beyond 0.7 units, "clades" were nearly identical to individual ASVs. For more detailed description and R code, see Supplemental Information. For comparison, we also calculated community richness and diversity summarized at each taxonomic scale (phylum, class, order, family, genus, species) using the taxonomic identifications of each ASV generated by the naïve Bayesian classifier. Since the fungal ITS2 sequences are not phylogenetically informative, for fungal diversity we used taxonomic identifications and calculated Shannon-Weiner diversity of fungal classes and ASVs.

Testing hypotheses of diversity-ecosystem function relationships

We used these measures of ecosystem function along with the data on microbial community diversity to test our three hypotheses (see Introduction). We first tested how the three crop performance metrics (tuber yield under low nutrients, tuber yield under high nutrients, and suppression of common scab disease) related to bacterial community diversity measured across a gradient of phylogenetic resolution. We used weighted linear regressions to regress each

ecosystem function on bacterial Shannon-Weiner diversity measured at each of 13 levels of phylogenetic resolution (see above), with weights equal to the inverse of the variance of the ecosystem function metric among the replicate pots sharing the same microbial community, with one exception. In the confirmatory experiment (2017), all replicate pots for three of the 12 microbial communities were free of any common scab symptoms, resulting in a variance estimate of 0 for these communities. Therefore, it was not possible to weight by the inverse of variance, and so we used unweighted regression for the analysis of disease suppression for the confirmatory experiment. We additionally regressed outcomes against Faith's phylogenetic diversity index (Faith 1992), but Faith's PD was nearly perfectly correlated with the Shannon-Weiner diversity measured at the finest phylogenetic resolution, and so the results are not presented here.

We intentionally chose to regress final plant outcomes on the diversity and composition of the initial inoculated soil microbial community, rather than the final community that developed in the experimental pots. This allows us to make stronger causal conclusions, as the growth and development of the potato plant during the experiment cannot have shaped the initial inoculated microbial community, but it almost certainly affected the structure of the final community. Thus, we can be confident that any significant relationship detected must reflect the impact of the initial microbial community on plant growth or disease, and not the other way around. This does not imply that microbial communities were static during the course of the experiment; rather, we investigated the effect of variation in the initial community state on functional outcomes (e.g. crop health metrics), likely as a result of constraining the microbial community assembly process occurring within the pots. Unfortunately, we did not measure microbial composition in the final soils or rhizospheres of our experiments, as this was not the focus of the study. However, in a

different study using very similar experimental methods and growing conditions, we found that the initial field soil source used to inoculate the pots remained the most important factor explaining rhizosphere microbial composition on potato roots after 4 and 12 weeks of growth in both high and low nutrient conditions (Miao and Lankau, in review), indicating that the community that develops in our experimental pots reflects the initial inoculated community even after 3 months of plant growth.

Regressions were performed separately for the exploratory (2015) and confirmatory (2017) experiments. To test whether the effect of diversity on ecosystem function changed in a linear or non-linear fashion across phylogenetic scales, we used the standardized regression estimates from each of the 13 linear models per experiment and ecosystem function as dependent variables in a secondary model, which included phylogenetic scale (defined by the numeric branch length cut-off described above) as the predictor variable, either as a linear term or as a linear and quadratic term. Regressions were weighted by the inverse of the standard error of the individual standardized regression estimates.

We used the formula for "ecosystem multifunctionality" in Maestre et al. (2012) to summarize our three measured functions (yield promotion under low nutrients, yield promotion under high nutrients, and disease suppression) into a single metric. We calculated the summed function of each microbial community as the sum of the Z-scores of each of the three measured functions (tuber yield under high nutrients, tuber yield under low nutrients, and disease suppression). For disease suppression, we multiplied the common scab severity score by -1 to align directions (lower disease = higher ecosystem function). For each function, Z-scores were calculated as the observed value minus the mean value of the function, divided by the standard deviation of the observed values. This acted to set each function on a standardized scale to allow direct

combination into one metric. We calculated an average variance for each microbial community by first dividing the variance in each ecosystem function for each microbial community by the mean variance for that function in the experiment, then taking the average of these relative variances across the three ecosystem functions. We then used the same series of weighted multiple regression models as described for Hypothesis 1.

Assessing effect of diversity versus composition

Since we could not manipulate diversity directly, any relationships between observed diversity and ecosystem function may be due to diversity *per se* (niche complementarity, sampling effects), or may reflect differences in community composition (relative abundance of different taxa) that correlated with diversity. To investigate this possibility, we used Principal Coordinates Analysis to summarize variation in composition among the microbial communities in each experiment, taking the first two eigenvectors of the dissimilarity matrix as proxies for the dominant gradients in composition (explaining 20.2% and 10.1% of total inertia in the exploratory experiment, and 22.1% and 14.4% in the confirmatory experiment). We then used the individual community scores on these two eigenvectors as additional covariates in a multiple regression that also included clade diversity (at the broadest phylogenetic scale for tuber yield, and narrowest phylogenetic scale for disease symptoms). In both the exploratory and confirmatory dataset, the first PCoA axes strongly correlated with broad scale diversity, making interpretation of model parameters challenging in some cases. Therefore, we also present AIC values for models that included all three predictor variables (clade diversity and PCoA axes 1 and 2), as well as all two parameter models and all single parameter models. We use the AIC values as additional evidence for whether diversity or composition provide better predictors of ecosystem function.

Additionally, we assessed the individual relationship of each of the three ecosystem functions with the relative abundance of each microbial clade separately in each experiment, using the same weighted linear regression models as used to analyze the effects of diversity. We used clades defined as unique ASVs, or at 0.4 and 0.1 branch units from the phylogenetic tree node (see above). Resulting P values from each regression were adjusted with the false discovery rate using the p-adjust function in the stats package in R.

Data accessibility: Raw data for plant responses, microbial community composition (ASV table), R scripts, and phylogenetic trees are available at (https://doi.org/10.5061/dryad.qbzkh18hh).

Results

Hypothesis 1: A microbial community's ability to promote crop yield under nutrient limiting conditions will be optimized by diversity at broad phylogenetic levels.

Tuber yields under low nutrient conditions were positively correlated to the Shannon-Weiner diversity of bacterial communities measured at broad phylogenetic scales in both the exploratory and the confirmatory experiment (Fig. 3,4), while relationships with diversity at finer scales were weaker and inconsistent across experiments. The standardized slopes of the diversity-tuber yield relationship estimated across the phylogenetic scale gradient declined linearly with increasing phylogenetic resolution in both experiments (exploratory experiment: estimate = -1.530 + 0.228, $P < 0.0001$, $R^2 = 0.804$; confirmatory experiment: estimate = -0.762 + 0.209, $P = 0.004$, $R^2 = 0.548$). Similar results were seen when analyzing diversity at distinct taxonomic levels (Table S2). Fungal diversity had inconsistent relationships with yield under low nutrient conditions, showing no relationship at either class or ASV levels in the exploratory

experiment ($R^2 < 0.19$, $P > 0.14$ for both). In the confirmatory experiment, tuber yield was positively correlated with diversity of fungal classes (estimate = 29.5 + 10.8, $P = 0.02$, $R^2 = 0.43$), but not fungal ASVs (estimate = -1.03 + 6.53, $P = 0.88$, $R^2 = 0.002$). In the confirmatory experiment, we included an additional microbial community sourced from a native sand prairie. Due to its large differences in land use history and microbial composition, this treatment was not included in our statistical analyses. However, it is interesting to note that the native prairie microbial community led to the highest tuber yields under low nutrient conditions (Fig 4).

In high nutrient conditions, there were no consistent relationships between microbial community diversity and tuber yield. In the exploratory experiment, yield was significantly positively correlated with bacterial diversity measured at the very broadest phylogenetic scale (Fig. 5,6), but significantly negatively correlated with diversity at finer scales. However, in the confirmatory experiment neither of these relationships was reproduced. Similarly, correlations with fungal diversity were inconsistent, being marginally significant in the exploratory experiment (fungal ASV diversity: estimate = 24.2 + 0.117, $P = 0.06$, $R^2 = 0.28$; fungal class diversity: estimate = 69.9 + 34.9, $P = 0.07$, $R^2 = 0.27$), but unrelated in the confirmatory experiment (fungal ASV diversity: estimate = 14.6 + 11.7, $P = 0.24$, $R^2 = 0.13$; fungal class diversity: estimate = 27.3 + 34.5, $P = 0.45$, $R^2 = 0.06$). The native prairie microbial community was not remarkable in high nutrient conditions, leading to near average tuber yields (Fig. 6)

The bacterial diversity-function relationship observed under low nutrient conditions was robust to variation in community composition across the two iterations of the experiment. To further investigate the role of bacterial composition vs. diversity, we compared bacterial composition to tuber yields under high and low nutrient conditions using permutation MANOVA – these relationships were marginally significant in the exploratory experiment (low nutrient

conditions: R^2= 0.116, F=1.439, P = 0.0498; high nutrient conditions, R^2 = 0.110, F=1.362, P = 0.0676), but were not reproducible in the confirmatory experiment (low nutrient conditions: R^2= 0.109, F=1.229, P = 0.152; high nutrient conditions, R^2 = 0.108, F=1.207, P = 0.182). Additionally, we used principal coordinates analysis to summarize the major gradients in bacterial composition in each experiment, and used the first two axes as covariates in a multiple regression to test whether the observed effects of broad scale diversity were better explained by compositional variation. In the exploratory experiment, regression models containing broad scale diversity outperformed all models using only compositional variables (Table S3). Similarly, in the confirmatory experiment broad scale diversity was always retained in the best regression models, although the second PCoA axis also explained some of the variation in tuber yield. For tuber yield under high nutrients, the best models in the exploratory experiment contained both diversity and compositional variables, while in the confirmatory experiment the best model contained only a single compositional variable (Table S3).

No single microbial clade, defined at any phylogenetic scale, was a significant predictor of yield under low nutrients in the exploratory experiment. In the confirmatory experiment, 24 out of 7379 ASVs, 16 out of 1504 clades defined at an intermediate resolution, and 8 out of 44 clades defined at the broadest resolution were significant predictors of yield under low nutrients. We saw an opposite pattern for yield under high nutrients: 131 (out of 2401), 82 (out of 1504), and 12 (out of 40) clades defined at fine, intermediate, and broad resolutions, respectively, were significant predictors of yield in the exploratory experiment. However, only one clade, defined at the broadest phylogenetic resolution, was a significant predictor in the confirmatory experiment, which did not overlap with the significantly predictive clades in the exploratory experiment (full results available at https://doi.org/10.5061/dryad.qbzkh18hh).

Hypothesis 2: Suppression of soil-borne pathogens will instead depend on fine scale diversity of taxa and the specific composition of communities, consistent with sampling effects.

In contrast to tuber yields, suppression of common scab symptoms in pots inoculated with the *Streptomyces scabies* pathogen displayed inconsistent relationships to bacterial diversity across phylogenetic scales, and across the two experiments (Fig 7,8). In the exploratory experiment, disease symptoms negatively correlated with fine scale, but not broad scale, diversity, as predicted (Fig. 7). In the confirmatory experiment, disease symptoms were weakly negatively correlated with bacterial diversity across phylogenetic scales, although the regression slope was only statistically significantly different from zero (at $P<0.05$) for intermediate levels of phylogenetic resolution (Fig 8). The standardized slopes of the diversity- disease symptom relationship estimated across the phylogenetic scale gradient displayed linear declines with increasing phylogenetic resolution in the exploratory experiment (estimate = -1.01 + 0.065, $P < 0.0001$, $R^2 = 0.8164$), but not the confirmatory experiment: estimate = 0.103 + 0.065, $P = 0.143$, $R^2 = 0.18$). However, in both experiments the diversity-disease relationships displayed a statistically significant positive quadratic trend, indicating a tendency for an initial decline with increasing phylogenetic resolution followed by a flat (exploratory experiment) or upward curving (confirmatory experiment) pattern (exploratory experiment: quadratic estimate = 1.684 + 0.454, $P =0.004$, $R^2 = 0.915$; confirmatory experiment: quadratic estimate = 0.70163 + 0.245, $P = 0.017$, $R^2 = 0.55$, Fig. 7,8). Fungal diversity was unrelated to common scab symptoms at either level of diversity in either experiment ($P>0.65$, $R^2 < 0.019$ for all). Interestingly, common scab symptoms were highest in plants inoculated with the native prairie microbial community (Fig. 8).

As predicted, in both experiments the relationship between common scab symptoms and bacterial diversity could be explained as well or better by bacterial composition rather than diversity *per se*. As above, we used the first two principle coordinates axes as covariates along with fine-scale bacterial diversity in a multiple regression of common scab symptoms. In the exploratory experiment, the best supported model included only the second PCoA axis (explaining 65% of the variation in disease symptoms, Table S3). In the confirmatory experiment, neither fine-scale diversity nor the PCoA axes explained a high amount of variation in common scab symptoms ($R^2 < 0.3$, $P>0.05$ for all models, Table S3).

Common scab symptoms were not well predicted by the relative abundance of individual bacterial clades. In the exploratory experiment, no individual ASVs or clade defined at an intermediate level of phylogenetic resolution was a significant predictor of common scab severity. Fifteen clades (out of 40) defined at the broadest phylogenetic resolution were significant predictors of disease severity in the exploratory experiment, with most (10/15) showing positive correlations with disease severity. However, no clades, at any level of phylogenetic resolution, were predictive of disease severity in the confirmatory experiment (full results available at https://doi.org/10.5061/dryad.qbzkh18hh).

Hypothesis 3) The sum of the yield promotion and disease suppression functions will correlate positively with diversity at multiple scales

The sum of the yield promotion and disease suppression functions was positively correlated with broad scale bacterial diversity in both the exploratory and confirmatory experiments (Fig 9,10, see Methods for calculations). In the exploratory experiment, this relationship disappeared with fine-scale diversity, even trending toward a negative relationship (Fig 9), while in the confirmatory experiment the sum of the functions tended to be positively correlated with

bacterial diversity at all phylogenetic scales, but with the highest correlations at broad and intermediate phylogenetic scales (Fig. 10) . In the exploratory experiment, contradictory relationships with broad vs. fine-scale diversity reflect the opposing responses of underlying functions – especially tuber yield under high nutrients which also showed a positive response to broad scale diversity but negative response to fine-scale diversity. Fungal diversity did not correlate with the summed functions in any case ($R^2 < 0.15$, $P>0.19$ for all models).

Discussion

Here we show that two primary functions provided by soil communities to crops, yield promotion under nutrient stress and disease suppression, both responded positively to increasing diversity in the soil bacterial community. However, the two functions differed in the scale of diversity to which they showed positive responses, and in the consistency of these responses across experiments.

Yield under low nutrient conditions was increased when crops were inoculated with bacterial communities with a high diversity of deep phylogenetic clades, similar to phylum and class. Beyond this deep phylogenetic diversity, the diversity of bacterial species/strains was not predictive of yield. It is unclear which specific microbial functions determined tuber yield in our experiment, although it is likely that multiple mechanisms were involved. Possible microbial community effects include mineralization of nitrogen and phosphorous from organic matter, acquisition of mineral nutrients by root symbionts, and production of plant growth promoting hormones. In the low nutrient conditions, plants were strongly limited by N (see *Supplemental Information*), and thus mineralization of N from soil organic matter and transfer to host plants was likely a key attribute of the growth promotive ability of the microbial communities.

Phylogenetic diversity measured at broad scales, similar to phyla or class distinctions, is more likely to serve as a proxy for functional diversity for microbial communities (Powell et al. 2009, Isobe et al. 2020), but how well phylogenetic and functional diversity correlate depends on the specific functional traits involved and their phylogenetic conservatism (Flynn et al. 2011). The value of using phylogenetic diversity as a predictor of ecosystem functions likely increases with more broadly defined "functions" that integrate across many lower level processes. For example, diversity of arbuscular mycorrhizal families (not species) may be a better predictor of plant growth because each AMF family provides distinct benefits (nutrient acquisition, pathogen protection) that integrate together to increase host performance (Maherali and Klironomos 2007).

Alternatively, suppression of the potato disease common scab was highest when soils were inoculated with bacterial communities that had high diversity of bacterial species/strains, independent of the diversity of higher phylogenetic levels. This pattern is consistent with theory regarding diversity and ecosystem function. On one hand, functions that are optimized by greater resource utilization will respond positively to complementarity among community members in their resource use, reducing competition among species (Cardinale et al. 2007, Tilman et al. 2014, Turnbull et al. 2016). On the other hand, exclusion of species from a community is optimized by intense competition among species, which requires high niche overlap between the excluded species and at least some community members (Fargione and Tilman 2005, Wei et al. 2015, Yang et al. 2017).

The ability of a community to provide multiple functions simultaneously was positively correlated with broad scale diversity of the initial bacterial community consistently in both experiments; however, the relationship with finer scale diversity was inconsistent. The divergent patterns across the phylogenetic resolution gradient also reflects different patterns in community

structure in the two sample sets. In the set of 13 communities used in the exploratory experiment, broad scale and fine scale diversity were uncorrelated ($r = 0.01$), with the positive correlation between diversity measured at different phylogenetic scales declining steeply (Supplemental Information). However, in the set of 12 communities used for the confirmatory experiment, broad and fine scale diversity were highly correlated at even the most disparate phylogenetic scales ($r = 0.73$, Table S4). Thus, in the confirmatory experiment we had little power to distinguish the independent relationships of ecosystem functions to broad vs. fine scale diversity. While ecosystem functions may show varying mechanistic responses to diversity measured at different phylogenetic or functional scales, our ability to detect these differential responses will depend on the variation present in the particular set of communities investigated in any given study.

We used a two-stage experimental approach along with statistical procedures to separate the effects of diversity *per se* from compositional variation among communities. The relationship between diversity and tuber yield under low nutrients, and ecosystem multifunctionality, was best explained by broad-scale diversity *per se*, consistent with an underlying mechanism of niche complementarity. Alternatively, disease suppression was explained as well or better by the bacterial community composition, consistent with the observed diversity-disease suppression relationship deriving from a sampling effect. Sampling effects occur when diverse communities are more likely to include particular high functioning taxa – in this case, taxa that can effectively inhibit the pathogen *S. scabies*.

Mechanistically, ecosystem functions must result from the activities of particular microbial populations – diversity is, after all, simply a calculated number. However, when taxonomic membership varies widely across communities, and functional abilities are shared

among taxa, then diversity may prove a more useful predictor of ecosystem function than composition. Associating individual bacterial populations, defined at varying levels of phylogenetic resolution, with ecosystem functions illustrated this phenomenon. While a number of individual populations correlated significantly with yield promotion or disease suppression in any one experiment, we did not detect a single case of a microbial taxonomic unit, defined at any phylogenetic scale, that displayed a consistent correlation across experiments. In the vast majority of cases, the significantly correlated taxa were detected in a single community. It is unsurprising that such patterns would not be reproducible across experiments. These results indicate that the ecosystem functions in question (yield promotion and disease suppression) cannot be attributed to specific microbial taxa; rather, they result from either the integrated activity of many community members, or from distinct taxa that lead to similar functions in different communities. In these cases, diversity (measured at the appropriate phylogenetic scale) may prove a more consistent predictor of ecosystem functions than composition despite its lack of mechanistic basis.

The microbial community sourced from a native prairie provides an interesting, although qualitative, contrast to the general patterns present among the two sets of agricultural soil communities. The prairie community was on outlier from the diversity-function relationships for both tuber yield under low nutrients and common scab suppression, but in opposite directions; resulting in a higher than expected yield of tubers, but also higher levels of disease. While we cannot draw strong conclusions from this single community, it is important to consider how land use history may shape a microbial community's functional ability independent of the effects on microbial diversity.

Achieving the necessary yield increases to keep pace with a growing population while minimizing environmental and economic costs will require optimizing the ecosystem functions provided by agroecosystems. Soils provide the base for these systems, and so optimizing ecosystem functions will require improving soil function. Here we show that the diversity of microbial taxa is a key predictor of multiple soil functions; however, different soil functions may be related to microbial diversity for different reasons. Whether or not it will be possible to manage soil communities to optimally provide multiple functions will depend on our understanding of these diverse mechanisms and the impact of management decisions on diversity at multiple biological scales.

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Conflicts of Interest Statement

All authors declare no potential, perceived, or real conflict of interest regarding the content of this paper. The funding agencies did not have any role in design and conduct of the study; collection, management, and interpretation of the data; or preparation, review, or approval of the paper.

Data Availability

Raw sequences for bacterial and fungal metabarcoding are available at the NCBI Short Read Archive under BioProjects PRJNA484023 (Exploratory experiment, bacteria),

PRJNA4840210 (Exploratory experiment, fungi), and PRJNA759148 (Confirmatory experiment, bacteria and fungi). Data on crop responses, as well as R scripts to replicate analyses, is available at the Dryad data repository at https://doi.org/10.5061/dryad.qbzkh18hh.

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Figure Legends

Figure 1: Schematic of experimental design. Map shows approximate location of commercial potato fields used as source of soil microbial communities. Each soil microbial community was used to inoculate either 4 or 5 replicate pots (varied among inocula) in each of three growing conditions (High Nutrient, Low Nutrient, and + Disease). Orange diamonds = fields used in the exploratory experiment. Blue circles = fields used in the confirmatory experiment. Arrows indicate just one example inoculation procedure. The soil microbial community from each commercial field was used to inoculate a similar set of pots in each experiment.

Figure 2. Approximately Maximum-Likelihood Phylogenetic tree of the bacterial amplicon sequence variants detected in this study based on the V4-V5 region of the 16S rRNA gene. Branches are colored according to the phylum designation of each ASV as estimated by the RDP Naïve Bayesian Classifier – for clarity, minor phyla are all left black. X-axis displays branch length distance from the tree root, and dashed lines illustrate how the tree was "sliced" to create collapsed clades of varying phylogenetic resolution.

Figure 3 Relationship between potato tuber yield (g) under low nutrients and bacterial clade diversity in the exploratory experiment. Clade diversity refers to the Shannon-Weiner diversity of phylogenetic clades delineated broadly (A, clades defined by collapsing all tips beyond 0.1 units of branch length above the root, roughly equivalent to phylum), intermediately (B, clades collapsed at 0.4 units above root) or finely (C, using unique amplicon sequence variants as clades). D) standardized parameter estimates of the regression of tuber yield under low nutrients on clade diversity, measured across a range of phylogenetic resolutions (branch length above root at which clades were collapsed). Clades collapsed at a branch length >0.7 are equivalent to

amplicon sequence variants. Black symbols = regression parameters significantly different from zero at P<0.05. White symbols = regression parameters not significantly different from zero at P<0.05

Figure 4 Relationship between potato tuber yield (g) under low nutrients and bacterial clade diversity in the confirmatory experiment. Clade diversity refers to the Shannon-Weiner diversity of phylogenetic clades delineated broadly (A; clades defined by collapsing all tips beyond 0.1 units of branch length above the root, roughly equivalent to phylum), intermediately (B, clades collapsed at 0.4 units above root) or finely (C using unique amplicon sequence variants as clades). Red symbols = microbial community sourced from native prairie, not included in statistical analyses. D) standardized parameter estimates of the regression of tuber yield under low nutrients on clade diversity, measured across a range of phylogenetic resolutions (branch length above root at which clades were collapsed). Clades collapsed at a branch length >0.7 are equivalent to amplicon sequence variants. Black symbols = regression parameters significantly different from zero at P<0.05. White symbols = regression parameters not significantly different from zero at P<0.05

Figure 5 Relationship between potato tuber yield (g) under high nutrients and bacterial clade diversity in the exploratory experiment. Clade diversity refers to the Shannon-Weiner diversity of phylogenetic clades delineated broadly (A, clades defined by collapsing all tips beyond 0.1 units of branch length above the root, roughly equivalent to phylum), intermediately (B, clades collapsed at 0.4 units above root) or finely (C, using unique amplicon sequence variants as clades). D) standardized parameter estimates of the regression of tuber yield under low nutrients on clade diversity, measured across a range of phylogenetic resolutions (branch length above root at which clades were collapsed). Clades collapsed at a branch length >0.7 are equivalent to

amplicon sequence variants. Black symbols = regression parameters significantly different from zero at P<0.05. White symbols = regression parameters not significantly different from zero at P<0.05

Figure 6 Relationship between potato tuber yield (g) under high nutrients and bacterial clade diversity in the confirmatory experiment. Clade diversity refers to the Shannon-Weiner diversity of phylogenetic clades delineated broadly (A; clades defined by collapsing all tips beyond 0.1 units of branch length above the root, roughly equivalent to phylum), intermediately (B, clades collapsed at 0.4 units above root) or finely (C using unique amplicon sequence variants as clades). Red symbols = microbial community sourced from native prairie, not included in statistical analyses. D) standardized parameter estimates of the regression of tuber yield under low nutrients on clade diversity, measured across a range of phylogenetic resolutions (branch length above root at which clades were collapsed). Clades collapsed at a branch length >0.7 are equivalent to amplicon sequence variants. Black symbols = regression parameters significantly different from zero at P<0.05. White symbols = regression parameters not significantly different from zero at P<0.05

Figure 7 Relationship between common scab severity and bacterial clade diversity in the exploratory experiment. Clade diversity refers to the Shannon-Weiner diversity of phylogenetic clades delineated broadly (A, clades defined by collapsing all tips beyond 0.1 units of branch length above the root, roughly equivalent to phylum), intermediately (B, clades collapsed at 0.4 units above root) or finely (C, using unique amplicon sequence variants as clades). D) standardized parameter estimates of the regression of tuber yield under low nutrients on clade diversity, measured across a range of phylogenetic resolutions (branch length above root at which clades were collapsed). Clades collapsed at a branch length >0.7 are equivalent to

amplicon sequence variants. Black symbols = regression parameters significantly different from zero at P<0.05. White symbols = regression parameters not significantly different from zero at P<0.05

Figure 8 Relationship between common scab severity and bacterial clade diversity in the confirmatory experiment. Clade diversity refers to the Shannon-Weiner diversity of phylogenetic clades delineated broadly (A; clades defined by collapsing all tips beyond 0.1 units of branch length above the root, roughly equivalent to phylum), intermediately (B, clades collapsed at 0.4 units above root) or finely (C using unique amplicon sequence variants as clades). Red symbols = microbial community sourced from native prairie, not included in statistical analyses. D) standardized parameter estimates of the regression of tuber yield under low nutrients on clade diversity, measured across a range of phylogenetic resolutions (branch length above root at which clades were collapsed). Clades collapsed at a branch length >0.7 are equivalent to amplicon sequence variants. Black symbols = regression parameters significantly different from zero at P<0.05. White symbols = regression parameters not significantly different from zero at P<0.05

Figure 9 Relationship between ecosystem multifunctionality and bacterial clade diversity in the exploratory experiment. Clade diversity refers to the Shannon-Weiner diversity of phylogenetic clades delineated broadly (A, clades defined by collapsing all tips beyond 0.1 units of branch length above the root, roughly equivalent to phylum), intermediately (B, clades collapsed at 0.4 units above root) or finely (C, using unique amplicon sequence variants as clades). D) standardized parameter estimates of the regression of tuber yield under low nutrients on clade diversity, measured across a range of phylogenetic resolutions (branch length above root at which clades were collapsed). Clades collapsed at a branch length >0.7 are equivalent to

amplicon sequence variants. Black symbols = regression parameters significantly different from zero at P<0.05. White symbols = regression parameters not significantly different from zero at P<0.05

Figure 10 Relationship between ecosystem multifunctionality and bacterial clade diversity in the confirmatory experiment. Clade diversity refers to the Shannon-Weiner diversity of phylogenetic clades delineated broadly (A; clades defined by collapsing all tips beyond 0.1 units of branch length above the root, roughly equivalent to phylum), intermediately (B, clades collapsed at 0.4 units above root) or finely (C using unique amplicon sequence variants as clades). Red symbols = microbial community sourced from native prairie, not included in statistical analyses. D) standardized parameter estimates of the regression of tuber yield under low nutrients on clade diversity, measured across a range of phylogenetic resolutions (branch length above root at which clades were collapsed). Clades collapsed at a branch length >0.7 are equivalent to amplicon sequence variants. Black symbols = regression parameters significantly different from zero at P<0.05. White symbols = regression parameters not significantly different from zero at P<0.05