Host genomic influence on bacterial composition in the switchgrass rhizosphere

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Keywords: switchgrass, rhizosphere, microbiome, host genomic influence, heritability

Abstract

Host genetic variation can shape the diversity and composition of associated microbiomes, which may reciprocally influence host traits and performance. While the genetic basis of phenotypic diversity of plant populations in nature has been studied, comparatively little research has investigated the genetics of host effects on their associated microbiomes. Switchgrass (*Panicum virgatum*) is a highly outcrossing, perennial, grass species with substantial locally adaptive diversity across its native North American range. Here, we compared 383 switchgrass accessions in a common garden to determine the host genotypic influence on rhizosphere bacterial composition. We hypothesized that the composition and diversity of rhizosphere bacterial assemblages would differentiate due to genotypic differences between hosts (potentially due to root phenotypes and associated life history variation). We observed higher alpha diversity of bacteria associated with upland ecotypes and tetraploids, compared to lowland ecotypes and octoploids, respectively. Alpha diversity correlated negatively with flowering time and plant height, indicating that bacterial composition varies along switchgrass life history axes. Narrow-sense heritability (h^2) of the relative abundance of twenty-one core bacterial families was observed. Overall compositional differences among tetraploids, due to genetic variation, supports wide-spread genotypic influence on the rhizosphere microbiome. Lastly, a genome-wide association study identified 1,861 single-nucleotide polymorphisms associated with 110 families and genes containing them related to potential regulatory functions. Our findings suggest that switchgrass genomic and life-history variation influences bacterial composition in the rhizosphere, potentially due to host adaptation to local environments.

Introduction

Macroscopic organisms host diverse microbiomes, which often differ substantially among individuals (Smith et al., 2015; Trivedi et al., 2020; Wilson et al., 2020). Some of the proximate causes of this variation in microbiome composition arise from differences between host environments and traits, the latter of which can be divided into genetic and plastic components. Host genetic differences can affect a wide range of traits that influence associated microbiome composition, including traits that determine the supply of resources used by microbes or traits that control environmental variables affecting microbial fitness in other ways (e.g. pH) (Lebeis et al., 2015; Sasse et al., 2018). These host genetic influences on microbiomes may arise from different evolutionary processes.

For example, host traits that affect microbiome composition may evolve neutrally or in response to non-microbial components of the local environment (Zeng et al., 2015). Alternatively, host trait variation could have evolved as a direct response to beneficial interactions with microbes in the environment (Gould et al., 2018). In the latter case, hosts could either influence the abundance of microbes that are simply present in the environment, and functionally important to the host, or hosts could form species or strain-specific symbiotic relationships where the host depends on and influences the abundance of those taxa for reproductive success (Parker et al., 2006).

Because of environmental and dispersal limitations, the same microbes may not be present across the entire range of a host, although functionally similar ones might be. It has been shown that reciprocal interactions between host immune systems and host-associated microorganisms can lead to preferential recruitment of beneficial microbial types and repel pathogenic types, to varying degrees (Hacquard et al., 2017; Jones et al., 2019). This suggests that hosts might (directly or indirectly) select for functional microbial traits from certain lineages. Several studies have observed the presence of ‘core microbiota’ – persistent members of the microbiome that appear across a large portion of a host’s population or species (Risely, 2020), but it is often unclear whether these microorganisms are functionally important or commensal to the host. Yet, because microbial traits are often phylogenetically conserved and host selection of microbes can occur in related microbial lineages (Lemanceau et al., 2017; Martiny et al., 2015), a core microbiome might be preserved for higher taxonomic levels but undetectable for lower ones, at the same occupancy frequency threshold. The study of diverse host genotypes and phenotypes in common environments could reveal the genetic and host physiological drivers of variation in associated microbiomes and, potentially, types of microbes that are functionally important to the host.

The demonstrated influence of host trait variation on microbial assemblages (Hestrin et al., 2021; Jones et al., 2019; Wagner et al., 2016) suggests that microbiome composition can be treated as an extension of host phenotype, one that may be under selective pressure by both the host and the environment (Bordenstein & Theis, 2015; Hunter, 2018; Moran & Sloan, 2015; Wagner et al., 2016; Whitham et al., 2003). Genome-wide association studies (GWAS) have shown that the relationship between hosts and specific microbial taxa can be linked to single-nucleotide polymorphisms (SNPs) (Beilsmith et al., 2019). However, at the microbiome level, it becomes challenging to directly link host genotype and microbial composition, due to the high diversity and dimensionality of microbiomes (Wray et al., 2013). Common garden experiments and genetic mapping offer a window into host

genetic impacts on host-associated microbial composition. The resolution of association mapping can be improved by exploiting high levels of genomic diversity within and between populations (Holland, 2007).

Switchgrass (*Panicum virgatum*) is a C4 perennial grass species that has been extensively studied as a bioenergy crop since 2005 (Bouton, 2007; McLaughlin & Kszos, 2005; Parrish & Fike, 2005; Sanderson et al., 2006). Unlike first generation biofuels, switchgrass can be grown on marginal land with minimal inputs while also providing ecological services (e.g. wildlife habitat and soil erosion mitigation) (Werling et al., 2014). In addition to its ecological and agricultural value, switchgrass provides an ideal system for studying the influence of host genotypic diversity on rhizosphere bacterial composition (i.e., bacteria living on or in close proximity to the root system of the plant) because of the high degree of genotypic diversity in the species.

Switchgrass is primarily an outcrossing species with high genetic diversity within populations, showing evidence of inbreeding depression, which increases heterozygosity in the genome (Sharma et al., 2012). The species is comprised of two locally-adapted ecotypes, upland and lowland, based on differences in phenotype, physiology, and habitat (Das et al., 2004). Separate migration events fostered by interglacial periods, in addition to gene duplication through polyploidization, have also played a major role in shaping the genomic diversity of switchgrass (Casler et al., 2015). Lowland switchgrass is primarily allotetraploid (4X: $n = 36$) and exhibits disomic inheritance – chromosome inheritance that follows diploid association patterns. Upland accessions tend to vary in their ploidy level (4X: $n = 36$, 6X: $n = 54$, 8X: $n = 72$) and exhibit widespread aneuploidy between and within localized populations (Costich et al., 2010). Additionally, populations of switchgrass are adapted to local climate conditions and linkage mapping suggests a polygenic basis to this local adaptation (Lowry et al., 2019). Here, we studied genotypes largely from the geographically Northeastern, upper Southern, and Midwestern United States that can be genetically clustered into five groups (roughly North, South, East, West, and Northeast, with some geographic overlap) (Supplemental Figure 1) (Lu et al., 2013). Genetic variation in switchgrass has been linked to measures of plant fitness and performance, including biomass production (Lowry et al., 2019) and soil carbon inputs (Adkins et al., 2016; Stewart et al., 2017). While substantial research has explored the switchgrass microbiome, key gaps remain, including the functional role of non-fungal microorganisms and host mechanisms that underly switchgrass–microbiome interactions (Hestrin et al., 2021).

Vascular plants influence microbes in the rhizosphere through rhizodeposits (Dennis et al., 2010) and carbon-based root exudates (Compant et al., 2010; Hu et al., 2018; Yu & Hochholdinger, 2018). Root exudates

provide signaling and substrate compounds for beneficial microbial recruitment (Carvalhais et al., 2013; Lakshmanan et al., 2012), and antibiotic compounds that defensively modulate the microbiome composition against pathogenic taxa (Baetz & Martinoia, 2014; Lebeis et al., 2015). When available, root exudates potentially represent a larger portion of carbon in the soil compared to other carbon inputs from the environment (e.g. leaf litter) (Heijboer et al., 2018). Switchgrass can benefit from a range of microbes that are influenced by root exudates (Hestrin et al., 2021).

In this study, we analyzed bacterial 16S rRNA gene sequences from total DNA extracted from rhizosphere soil samples for 383 switchgrass accessions from 63 local populations planted within a common garden in Ithaca, NY, USA. Our aim was to better understand the influence of switchgrass genotype on the composition of bacteria in the rhizosphere. We hypothesized that overall bacterial composition and diversity within the growing site would differentiate due to host genetic variation along the three dimensions of switchgrass genetic diversity (ecotype, ploidy level, and genetic cluster), as is true for multiple fitness-related traits (Lovell et al., 2021). Separately, bacteria experience higher rates of gene loss, horizontal gene transfer, and shorter generation times compared to their hosts. So, microbial specialization on a given host can be evolutionarily fast compared to changes in the plant community (Bever et al., 2012). Given that the evolutionary response rate is mismatched between switchgrass genotypes and their microbiomes, we sought to determine the lowest taxonomic level for which a potential host influence could be detected. We show that switchgrass genotype influences bacteria in the rhizosphere at, at least, the family level. Our findings demonstrate how plant host genotype can influence host-associated microbiomes, the taxonomic level at which the microbiome is influenced, and the host genetic architecture involved.

Materials and Methods

Switchgrass Germplasm Data

Previously, exome capture sequencing was used to characterize variation in the genic regions of the genome from the Northern Switchgrass Association Panel used in this study ($n = 537$) (Evans et al., 2018). For this study, the HapMapv2 matrix was obtained from the Dryad Digital Repository (10.5061/dryad.mp6cp) in 2019. Several modifications were made to the original dataset. The dataset was modified in *python* (G. Van Rossum & Drake, 2009) to reflect heterozygote positions more conservatively than the original, unfiltered, dataset, such that heterozygote positions with read count ratios greater than 0.75 or less than 0.25 were called homozygous relative to

the appropriate allele (e.g. A(20)/T(1) = A). SNPs with a minor-allele frequency (MAF) below 0.05 were excluded, resulting in 103,776 SNPs for all genotypes studied here ($n = 362$) spanning eighteen chromosomes: Chr01- 09 (subgenomes a and b) of the v1.1 *P. virgatum* reference genome (www.phytozome.net) and fifteen unanchored scaffolds (Evans et al., 2018). The unanchored scaffolds of Evans et al. (2018) were renamed to the corresponding contig names within the v1.1 reference genome using *python*. Phylogenetic tree generated in Tassel v5 (Bradbury et al., 2007).

We compared bacterial composition to published data on several important switchgrass functional and life history traits, using data from 2009, 2010, and 2011 field seasons at the common garden in Ithaca, NY (genetic variation in these traits is largely consistent from year to year) (Lipka et al., 2014). The 2011 measurements for anthesis date and full plant height were used to identify correlations with rhizosphere alpha diversity present in 2016.

Rhizosphere sampling of switchgrass accessions

The original switchgrass association panel consisted of 3-10 clonally propagated individuals each from 66 discrete switchgrass local populations grown from seed in the greenhouse of the USDA-ARS Dairy Forage Research Center in Madison WI in 2007 (Lu et al., 2013). The accessions were sourced from much of the natural range of switchgrass in the eastern and midwestern United States. Young plants were deposited in the common garden in Ithaca, NY, USA in 2008. In 2016, plugs were collected for transplanting from 525 cloned accessions, representing all but two (perished) original populations. Prior to replanting the plugs, soil samples were collected into a polythene bag from each of the switchgrass accessions by vigorously shaking off soil attached to the roots. The bags with soil and fine roots were initially stored at 4°C while being processed - each soil sample was thoroughly mixed into a uniform distribution and then transferred to 50 ml conical cryogenic tubes and stored at -80°C prior to soil DNA extraction.

Soil DNA extractions

To determine the composition of bacteria established in the switchgrass rhizosphere, we selected soil samples from 383 of the 525 cloned switchgrass accessions, based on a phylogenetically determined set of clones from 63 of the local populations in the association panel. Total DNA was extracted from ~300 mg of soil using the

NucleoSpin Soil 96 kit (Macherey-Nagel, Düren, Germany). Lysis was performed using the Buffer SL with Enhancer SX, and was performed on the FastPrep 24 homogenizer (MP Biomedicals, Santa Ana, CA, USA) at 4.0 m/s for 30 s.

Amplicon Sequencing

Briefly, amplicons targeting the V3-V4 region of the 16S rRNA gene were generated from all 383 samples using universal bacterial primers 515F (5'-GTGYCAGCMGCCGCGGTAA-3') and 806R (5'-GGACTACNVGGGTWTCTAAT-3') (Apprill, McNally, Parsons, & Weber, 2015; Parada, Needham, & Fuhrman, 2016) with overhangs for attaching barcodes and standard Illumina overhang adaptors in a second PCR step (full protocol outlined in the supplemental methods of Trexler & Bell (2019)). Sequencing was performed on an Illumina MiSeq using the 2 × 250 cycle v2 kit. Raw reads are available through NCBI SRA under project number PRJNA689762.

Amplicon sequence analysis pipeline

The raw 16S rRNA gene sequences were analyzed using an adapted version of the *dada2* pipeline (Callahan et al., 2016). *dada2* was used to process the raw sequences into Amplicon Sequence Variants (ASVs). Reads were truncated above 240 bp and below 160 bp. Sequences with any missing reads after truncation were discarded. Reads were then truncated at the first instance of a quality score less than 2. After truncation, reads that matched against the phiX Genome were discarded. Reads with higher than two "expected errors" were also discarded. Expected errors are calculated from the nominal definition of the quality score: $EE = \sum(10^{-(Q/10)})$. Filtered sequences were used to determine the error rate using the *dada2* function: `learnErrors()`. The filtered sequences were then processed with the core sample inference algorithm, *dada()*, incorporating the learned error rates. Forward and reverse sequence reads were then merged. A sequence table was made and chimeras were removed using the "consensus" method. Taxonomic assignments for the ASVs were defined against the SILVA 138 ribosomal RNA gene database (Quast et al., n.d.) using DECIPHER v2.14.0 (Wright, n.d.). The sequence variant table and taxonomy table were exported for downstream processing in *phyloseq* (McMurdie & Holmes, 2013).

In *phyloseq*, ASVs designated "NA" at the phylum level, non-Bacterial entries at the domain level, and those associated to chloroplasts and mitochondria were removed from the taxonomy file before further processing.

Finally, we also removed samples with no ASVs remaining after pruning. Rarefying samples has been shown to effectively reduce false discovery rates when there are large differences between the average sample library size (Weiss et al., 2017). Our data was characteristic of this scenario. Therefore, we rarefied samples to 1000 sequences, to retain as many samples as possible while also maintaining a sufficient sampling depth to detect the most prevalent taxa comprising the switchgrass core microbiome (See below).

Alpha diversity analysis

Using the rarefied ASV dataset, we generated alpha diversity metrics using *phyloseq* (McMurdie & Holmes, 2013). Statistical significance was calculated using the *vegan* 2.5.6 package (Oksanen et al., 2019), and other core functions in R version 3.6.3 (Ihaka & Gentleman, 1996). The Chao1 and Shannon diversity indices were calculated using the `estimate_richness()` function in *phyloseq* and then used to test for differences in alpha diversity between genotypes differing in ecotype, ploidy level, and genetic cluster groups using an analysis of variance (ANOVA) (R version 3.6.3). Correlations between diversity metrics, anthesis date and full plant height were generated using the Pearson correlation test.

Beta diversity and core microbiome analysis

Bacterial diversity data rarely conform to the assumptions of MANOVA-like procedures, largely due to inflated zero values among rare taxa that skew the distribution, thus non-parametric methods based on permutation tests are preferred (M. J. Anderson, 2001). A non-parametric, one-way analysis of variance (NPMANOVA) is also tolerant of non-independent observations (e.g. microbe-microbe interactions). We therefore calculated an NPMANOVA using the *adonis2* function in *vegan* to test for significant differences between the ecotype, ploidy level, and genetic cluster groups on the overall rhizosphere microbiome composition using pairwise Bray-Curtis distances at the ASV level.

The ‘core microbiome’ can be defined as microbial taxa that associate with a host above a particular occupancy frequency threshold (i.e. their prevalence). Biological justifications for such thresholds tend to be subjective, often ranging between 30% and 95% (Risely, 2020). However, core taxa prevalence within a population could be a reflection of an environmental response by the host due to local adaptation, resulting in higher intergroup prevalence of certain ‘core taxa’ relative to the whole population. Thus, we determined two core microbiomes: A

high-fidelity core (prevalence $\geq 90\%$), to determine taxa that reliably associate with the vast majority of our panel, and a low-fidelity core (prevalence $\geq 10\%$), to study host genetic variation effects on bacterial composition. Taxa present within our rarefied dataset were initially agglomerated using the `tax_glom()` function at all taxonomic levels in *phyloseq*. Sample counts were then transformed to relative abundances. A filter was applied to subset phylogenetic groups in abundance greater than 2%. Each core microbiome was determined using the *microbiome* package in R (Lahti, Shetty, & Blake, 2017). The `core()` function in the *microbiome* package (detection = 0, prevalence = 0.9 and 0.1, respectively) was applied at each taxonomic level to determine the core taxa among all genotypes.

Heritability Estimates

Heritability is an estimate that describes the proportion of phenotypic variance that is due to genetic variance. Narrow-sense SNP-based heritability (h^2) was estimated using the *sommer* package in R as: σ_A^2 / σ_p^2 , where σ_A^2 is the additive variance and σ_p^2 is the total phenotypic variance (additive + dominance) (Covarrubias-Pazaran, 2016). The core function of the *sommer* package is the ‘mmer’ function that fits multivariate linear mixed models. The modified exome capture SNP dataset, described above, was used to generate a kinship matrix used in ‘mmer’ to estimate narrow-sense heritability for each of bacterial families’ abundance. The *sommer* package includes a tolerance parameter for the matrix inverse when singularities are encountered in the estimation procedure. Here, inversion tolerance parameters were adjusted to 10 to avoid model singularity.

Redundancy Analysis (RDA) and variance partitioning

To determine how whole microbiome variation changed across host genomic variation, much of which is due to population structure, we implemented redundancy analysis (RDA). RDA models variation in a set of response variables as a function of a set of explanatory variables. We used the first 10 principal components of switchgrass SNPs (Evans et al. 2014) as explanatory variables that describe population structure in switchgrass (Brown, Bray, & Pachter, 2018) and log-scaled ASV counts for each switchgrass genotype as the response variables. We performed the RDA to explain the relative proportion of total genotypic variance on the overall microbiome composition. The `rda()` function in *vegan* (Oksanen et al., 2019) was used to perform the RDA for the tetraploid accessions. For host genomic analyses like this RDA, we focused on tetraploids; since they (1) represent both upland

and lowland ecotypes, (2) exhibit disomic inheritance unlike octoploids, and (3) exhibit more inter-group alpha diversity variation compared to octoploids.

We identified outlier ASVs with the strongest loadings, based on inter-quartile range criteria, on the first two RDA canonical axes; these ASVs are those most representative of microbiome-wide turnover across switchgrass hosts of different genomic background. ASVs that were labeled as outliers were then assigned taxonomic rank using the *phyloseq* method described above and compared to families in the original ASV dataset.

To dissect how genomic variation combined with ecotype, ploidy, and phenotypes to explain bacterial compositional turnover we also implemented variance partitioning of the RDA. Variance partitioning allows one to estimate the portions of compositional turnover explained by multiple sets of factors (Peres-Neto et al., 2006), which here were the first 10 principal components of SNPs, ecotype, geography-of-origin (latitude, longitude, and their squared values), and our two focal phenotypes (anthesis date and height). We implemented two versions of variance partitioning with RDA: one on ASV counts and the other on family abundances, to test whether family-level composition was differently associated with these factors than was ASV level composition.

Genome-wide association study (GWAS)

To identify specific loci in the switchgrass genome linked to variation in rhizosphere bacterial composition, a genome-wide association study (GWAS) was conducted using the *statgenGWAS* package in R (Rossum et al., 2020). This fast single trait GWAS method was developed by Biometris, following the method described in Kang et al. (2010). The modified SNP dataset, described above, was once again used for this analysis.

Family-level abundance counts data (1) were imported from *phyloseq* using the rarified *phyloseq* object and a chromosome positional map (2) was generated from the SNP matrix (3). These three components were used to construct the R object used by *statgenGWAS*. Initial results from the heritability estimates and RDA indicated that certain core families of bacteria were influenced by switchgrass genotype. Therefore, to determine associated genes, a single trait GWAS, where the trait was the abundance of each of the families, was completed using a Generalized Least Squares (GLS) method for estimating the marker effects and corresponding p-values. Our GWAS included random effects correlated according to the kinship matrix, which was calculated with the VanRaden method (VanRaden, 2008). A p-value threshold is required for this method to minimize the False Discovery Rate (FDR) following the algorithm proposed by Brzyski et al. (2017). The method limits the number of SNPs in statistical

linkage with each other passing FDR control. Significant SNPs were identified using a 0.01 threshold for the false-discovery rate (FDR). Linkage disequilibrium (LD) in switchgrass decays over kilobase length. Following Grabowski et al. (2017), we used a window of 25kb to identify genes potentially linked to significant SNPs. Thus, in this study, we defined SNPs within 25 kb as being “within LD of significant SNPs”. For each trait, *statgenGWAS* outputs significant SNPs and SNPs within the defined cutoff. A full description of the method can be found in Rossum et al. (2020).

GO Enrichment Analysis

Significant SNPs associated with bacterial family abundance and positions within 25 kb of significant SNPs were then used to identify associated genes and gene ontologies. Here, we focused on three families: Xanthobacteraceae, Sphingomonadaceae, and Micromonosporaceae. The Xanthobacteraceae and Sphingomonadaceae families were chosen because they represent the high-fidelity core microbiome. Micromonosporaceae was chosen due to its high relative heritability within our panel and its importance in agriculture applications (Trujillo, Hong, & Genilloud, 2014). *Phytomine* was used to identify Gene IDs for each family using the *P. virgatum* v1.1 reference genome at www.phytozome.net. Gene IDs for corresponding SNPs were then used to perform a Singular Enrichment Analysis (SEA) against the gene ID (ver. 4) background for *P. virgatum* using the agrigo v2 web program (Du, Zhou, Ling, Zhang, & Su, 2010). Default parameters were used.

Results

Amplicon Sequence Analysis

For 383 initial rhizosphere soil samples, 96,902 amplicon sequences variants (ASVs) were obtained following initial quality filtering and sequence processing in *dada2* (Callahan et al., n.d.). After sample pruning (removing non-bacteria from the taxonomy table) and rarefaction (1,000 sequences/sample) in *phyloseq*, 365 samples containing 31,181 ASVs remained. Counts for unique phylogenetic classifications are as follows: Domain: 1, Phylum: 26, Class: 59, Order: 142, Family: 268, Genus: 510.

Alpha diversity analysis

We detected significant differences in alpha diversity (Chao1 and Shannon Diversity) between groups. Upland ecotypes, which are adapted to regions at higher latitudes and those geographically closer to our growing site, exhibited higher rhizosphere diversity compared to lowland ecotypes (Figure 1A, Upland-Lowland: p_{adj} (Shannon) = $1.58e^{-2}$). Tetraploids, which are present in both upland and lowland ecotype groups, also exhibited higher diversity overall, compared to octoploids, which are exclusively upland (Figure 1B, 4X-8X: p_{adj} (Shannon) = <0.001). Finally, the North genetic cluster, primarily comprised of upland tetraploids, exhibited the highest rhizosphere diversity among all of the genetic clusters and there was a significant difference between the East and West genetic clusters (Figure 1C, North-East: p_{adj} (Shannon) = <0.001 , North-West: p_{adj} (Shannon) = <0.001 , North-Northeast: p_{adj} (Shannon) = <0.001 , North-South: p_{adj} (Shannon) = <0.001 , East-West: p_{adj} (Shannon) = $5.92e^{-2}$). All diversity measurements for accessions can be found in Supplemental Table 1.

We found that Chao1 and Shannon diversity were negatively correlated with anthesis date (Chao1: $r = -0.17$, p -value = 0.0014; Shannon: $r = -0.18$, p -value = <0.001) and full plant height (Chao1: $r = -0.18$, p -value = 0.0012; Shannon: $r = -0.13$, p -value = 0.017). We also considered these trait-diversity associations stratified by ecotype, ploidy, and genetic cluster (Figure 2). In general, the negative diversity association with anthesis date and height was broadly consistent, with Shannon diversity negatively correlated with plant height for Upland ecotypes ($r = -0.25$, p -value = <0.001), octoploids ($r = -0.23$, p -value = 0.0045), hybrids ($r = -0.73$, p -value = 0.016), the North genetic cluster ($r = -0.27$, p -value = 0.011), the Northeast genetic cluster ($r = -0.22$, p -value = 0.061), and the West genetic cluster ($r = -0.24$, p -value = 0.032) (Figure 2A,B,C). Likewise, Shannon diversity negatively correlated with anthesis date for Upland ecotypes ($r = -0.19$, p -value = 0.002), tetraploids ($r = -0.23$, p -value = 0.0025), hybrids ($r = -0.94$, p -value = <0.001), and the Northeast genetic cluster ($r = -0.45$, p -value = <0.001) (Figure 2D,E,F). A subset ($n = 7$) of ecotype/ploidy/genetic cluster combinations showed positive trait correlations with Shannon diversity, but these were not significant.

Beta diversity analysis

We performed separate multivariate analyses of variance on a Bray-Curtis distance matrix using the NPMANOVA test. There were significant differences in overall bacterial composition between ecotypes ($p < 0.001$), ploidy levels ($p < 0.001$), and genetic clusters ($p < 0.001$), indicating differences in overall composition associated with switchgrass genetics and life-history.

Although all taxonomic levels were tested, the family level was identified as the lowest taxonomic rank with the ability to retain a high-fidelity core (Supplemental Figure 2). The high-fidelity core microbiome ($\geq 90\%$ of samples) contained two families: Xanthobacteraceae and Sphingomonadaceae. The low-fidelity core microbiome ($\geq 10\%$ of samples) contained 110 families (Supplemental Table 2).

Host Genomic Influence

Of the 110 families in the core microbiome, twenty-one showed narrow-sense SNP-based heritability (h^2) significantly greater than zero (Figure 3). The standard errors of narrow-sense heritability estimates are very large and there is considerable uncertainty in the estimate overall (Furlotte, Heckerman, & Lippert, 2014). Therefore, we consider estimates with standard errors that do not intersect zero as showing evidence of heritability (i.e. heritable). Heritability estimates for low-fidelity core taxa in the switchgrass rhizosphere ranged from 0.106 to 0.539, with a mean of 0.241. Heritability estimates presented here for bacterial lineages have a range similar to that of corn and sorghum (Deng et al., 2021). The heritability estimates indicate that, in part, switchgrass genotype influences the variability in the relative abundance of certain families within our growing site. Heritability estimates for all bacterial families can be found in Supplemental Table 2.

Next, we performed a redundancy analysis (RDA) to characterize how the whole rhizosphere bacterial assemblage changes in association with host genomic background (Figure 4, Supplemental Figure 3). The RDA results indicate that genotypic variability among tetraploids (i.e. first 10 PCs of SNPs) had modest influences on bacterial ASV composition ($R^2 = 0.063$, $R^2_{\text{adjusted}} = 0.007$). Switchgrass SNP PC1, which is associated with separation between the North and the Northeast and South genetic clusters, loaded most strongly to the first primary canonical axis (RDA1, PC1 = 0.99, the next strongest loaded PC was PC10, with a 0.097 loading). Switchgrass SNP PC7, which is associated the variance in the North genetic cluster, loaded most strongly to the second canonical axis (RDA2, PC7 = 0.899). The proportion of explained variance in bacterial ASV composition was fairly low along these individual canonical axes (RDA1 = 0.9%, RDA2 = 0.7%), which was unsurprising given the large diversity in the bacterial composition. Still, the RDA identified bacterial ASV compositional turnover in association with switchgrass population structure, as shown by the turnover between the North and the Northeast and South switchgrass genetic clusters (Figure 4).

Outlier ASVs were determined for each of the first two canonical RDA axes ($n = 9,215$). These outlier ASVs are most representative of the variation in bacterial composition among the tetraploid genotypes. We then identified the taxonomic ranks for the outlier ASVs. Our results show that Xanthobacteraceae and Sphingomonadaceae represent the high-fidelity core for both the outlier ASV dataset and the original ASV dataset, signifying host genotypic influence might be strongest on these families. When we consider the low-fidelity core ($n = 110$ families), 70.9% of families in the RDA outlier ASV core microbiome are in original core microbiome (Supplemental Table 2). When we consider just the heritable families, 80.95% of heritable families in the outlier ASV core microbiome are in the original core microbiome (Supplemental Table 2).

When we applied variance partitioning to estimate the portion of ASV-level compositional turnover explained by SNP PCs, ecotype, geographic origin (i.e. latitude and longitude coordinates), and the two phenotypes, we found that the total R^2_{adjusted} was low, approximately %1 of ASV composition. However, variance partitioning of family-level turnover found these 4 factors explained a larger portion, with $R^2_{\text{adjusted}} = 0.096$ (Figure 4). This variance partitioning found that the largest portion of bacterial compositional variation was explained by the collinear portion of SNP PCs, ecotype, and geographic origin ($R^2_{\text{adjusted}} = 0.0866$), suggesting that geographic population structure associated with ecotypic variation explains a large portion of turnover in bacterial family composition.

Genome-wide association study

A primary limitation of heritability estimates and the RDA was that we could not account for which SNPs have the greatest effect on compositional variation. To overcome this, a genome-wide association study (GWAS) was conducted to identify specific loci associated with the relative abundance of families in the core microbiome. In total, 1,861 SNPs were found to be associated with the abundance of the 110 tested core families. 878 SNPs were found to be associated with the abundance of the 21 heritable core families. Furthermore, 36 SNPs were found to be associated with the abundance of the two families (Xanthobacteraceae and Sphingomonadaceae) that represent the high-fidelity core microbiome (Figure 6, Supplemental Table 2).

GO Enrichment Analysis

Despite the general difficulty identifying specific molecular functions or pathways in non-model plant species, resources for gene ontology (GO) still remain useful for biological inference (Tian et al., 2017). Therefore,

we completed a GO enrichment analysis for genes harboring significant SNPs and positions within 25kb of significant SNPs to determine possible cellular processes (P), cellular components (C), and molecular functions (F) associated with three core family abundances (Supplemental Table 3). Primarily, we identified two types of cellular processes: metabolic and stimuli response processes. Broadly, we identified several molecular functions relating to ATPase activity, hydrolase activity, and pyrophosphatase activity (Supplemental Figure 4, Supplemental Table 3). Functions involving ATP hydrolysis as an energy source either typically catalyze a reaction or drive membrane transport against a concentration gradient (Berg, Tymoczko, & Stryer, 2002). In the context of our GWAS, this could suggest possible root exudate activity whereby switchgrass genotypes differentially transport exudates against a lower soil compound gradient influencing core family abundances. Perturbing these regions in future studies could reveal the underlying pathways and mechanisms. Lastly, genes harboring SNPs associated with Sphingomonadaceae abundance, in particular, were enriched for GO terms associated with cellular membrane components, metalloproteinase and metalloendopeptidase activity, and cellular processes that relate to metabolism and response to stimuli (Supplemental Table 3). Again, given the context of our GWAS, we suspect that the genes associated with these GO terms could interact with Sphingomonadaceae populations in the soil. More work involving these genes could expose perturbations that more predictably affect Sphingomonadaceae abundance in switchgrass.

Discussion

Macroscopic organisms often exhibit striking variation among individuals in the microbial assemblages they host, but the genetic basis and ecological relevance of this variation is often unclear. Common garden experiments with diverse genotypes offer a powerful window into dissecting the ecological genomics of host influences on their microbiomes. Previous studies have demonstrated that genomic differences among switchgrass genotypes and populations may, in part, have led to much of the adaptive phenotypic differences observed between switchgrass populations (Adkins et al., 2016; Lowry et al., 2019). We add to these observations by showing a similar phenomenon within a less visible portion of the switchgrass phenotype. We found that switchgrass genotype influences the rhizosphere microbiome in a variety of ways relative to bacterial alpha and beta diversity as a result of variability within the switchgrass genome.

We demonstrated that the alpha diversity (Chao1 and Shannon diversity) of rhizosphere bacteria within a common garden was significantly differentiated between switchgrass ecotypes, ploidy levels, and genetic clusters.

These groupings with distinct bacterial assemblages are associated with life history variation and locally-adapted traits in this species. Furthermore, alpha diversity within each group typically had no correlation with, or was negatively correlated with, anthesis date and plant height (Figure 2). Flowering time is an important adaptation to local growing conditions and has major fitness consequences for the plant (Grabowski et al., 2017b). In general, in common garden experiments, upland ecotypes have an anthesis date 2–4 weeks earlier than lowland ecotypes (Schwartz & Amasino, 2013). As plants move through different developmental stages the diversity and availability of metabolites influencing the rhizosphere microbiome shifts (Wagner, 2021). Rhizosphere sampling in this study occurred in May, 2016. Therefore, it's reasonable to expect genotypes at different stages of development at the time of sampling to exert different selective pressure on the microbiome composition. Future research examining temporal exudate availability in the rhizosphere of switchgrass could expand on this hypothesis.

It is already widely hypothesized that hosts mediate their microbiomes relative to environmental conditions, resource availability, and microbial function, not necessarily always a specific species or strain (Lemanceau et al., 2017; Martiny et al., 2015). Thus, some basis for comparing taxa between host groupings becomes important when determining the taxonomic level at which host influence is detectable. A “core” microbiome can be defined in a variety of ways, and may not represent microbes that have the most important functional impacts on a system (Bell & Bell, 2021). For example, commensal microorganisms remain widespread throughout host populations (Zeng et al., 2015). Still, the consistent occurrence of microbial taxa provides an opportunity to assess relationships between host genetics and microbial recruitment. Here, we applied the “common core” concept (Risely, 2020) to identify bacterial taxa that were consistently associated with diverse switchgrass genotypes in a common garden. Given the disparity in evolutionary pace (i.e. there are many bacterial generations during the lifecycle of a switchgrass plant), it is unlikely that switchgrass has mechanisms to distinguish between closely related bacterial taxa unless doing so provided a substantial fitness advantage (Yin et al., 2021). Therefore, the core microbiome provides both a basis for measuring bacterial abundance across multiple switchgrass genotypes as well as a means to detect host genomic influence at the lowest possible taxonomic rank.

For example, Singer et al. (2019) observed a large core endophytic switchgrass microbiome dominated by root-colonizing bacterial genera such as *Streptomyces*, *Pseudomonas*, and *Bradyrhizobium*, while rhizosphere diversity was more variable between their two sampling sites. Likewise, Singer et al. (2019b) observed different core bacterial classes associated with upland and lowland switchgrass ecotypes, with each ecotype preferentially

enriched for Alphaproteobacteria and Actinobacteria, respectively. For our study, out of 268 families, only two associated with the majority ($\geq 90\%$) of our rhizosphere samples (Xanthobacteraceae and Sphingomonadaceae) and less than half ($n = 110$) associated with more than 10% of our samples. Xanthobacteraceae and Sphingomonadaceae are families in the Alphaproteobacteria class. We were unable to detect any genera or species associated with our genotypes at the 90% occupancy threshold. This indicates that a large swath of the switchgrass rhizosphere microbiome assembly is stochastic and only certain lineages were able to consistently associate with our genotypes in the common garden.

The abundance of twenty-one of the 110 families were determined to show evidence of heritability. After reasonably establishing heritability of select core families, the RDA allowed us to identify how genome-wide variation in switchgrass influenced the rhizosphere microbiome composition. RDA methods used in microbial ecology typically explain the variance in microbiome composition due to environmental variables, such as temperature or pH (Paliy & Shankar, 2016). However, here, we modeled microbial compositional data as a function of host genomic data. As such, the RDA in this study represents the compositional variance of the microbiome due to genetic variation in the hosts. We then extended the analysis to explore outlier ASVs along each of the first two RDA axes, because those ASVs represent taxa associated with host genomic influence on overall turnover in bacterial composition. Once clustered at the family level, we determined that seventeen out of the 21 heritable families were in the outlier ASV dataset. Additionally, the results of the variance partitioning suggest that geographic population structure associated with ecotypic variation explains a larger portion of turnover in bacterial family composition compared to ASV composition. Thus, we determined that genotypic variability in switchgrass sampled from across its natural range influences the composition of the rhizosphere bacterial microbiome, particularly for tetraploids.

The ecophysiology of host-microbe interactions in our study is unclear, requiring detailed investigation, but there may be hints in the function of switchgrass genes that are strongly associated with core family abundances. We conducted a GWAS to identify potential loci that strongly associate with core family abundances. The outcrossing nature of switchgrass and its rapid decay in LD can help pinpoint causal loci with GWAS. Several considerations had to be made though, in order to reliably trust the significance of the resulting QTLs. First, we considered only tetraploids for the same reasons as the RDA, that they (1) represent both upland and lowland ecotypes, (2) exhibit disomic inheritance unlike octoploids, increasing the effect size of additive effects, and (3) exhibit the most inter-

group alpha diversity variation compared to octoploids or hybrids. We used exome capture SNPs (Evans et. al. (2018), which are more effective than genotype-by-sequencing (GBS) in their ability to tag causal polymorphisms, compared to GBS SNPs that are often far from any genes (Kaur et al., 2014). The identification of genes containing significant SNPs could provide insights into potential host-microbe interaction pathways. To explore this relationship further, we chose to focus on three core families: Xanthobacteraceae, Sphingomonadaceae, and Micromonosporaceae.

We identified hundreds of switchgrass genes containing SNPs (including those within 25 kb of significant SNPs) associated with Micromonosporaceae (n = 315), Xanthobacteraceae (n = 578), and Sphingomonadaceae (n = 718) abundance in the rhizosphere. Many species within the Micromonosporaceae family degrade chitin, cellulose, lignin, and pectin, and play an important role in the turnover of organic plant material. Moreover, many strains produce useful secondary metabolites and enzymes used by plants (Trujillo et al., 2014). Members of Xanthobacteraceae have been experimentally identified as nitrate reducers (C. R. Anderson et al., 2011) and therefore their regulation could be important to host metabolic activity. Our GO enrichment analysis indicates that genes associated with Micromonosporaceae and Xanthobacteraceae abundance are involved in hydrolase, pyrophosphatase, and ATPase activity suggesting that the enrichment for this set of genes plays an important role in overall plant fitness. Members of the Sphingomonadaceae family are known to be antagonistic against plant pathogens and induce plant growth promotion (Glaeser & Kämpfer, 2014). GO terms for genes associated with this family are enriched for metallopeptidase and metalloendopeptidase activity, membrane cellular components, and processes involved in stimuli response. Altogether, this suggests that the activity of these genes is linked to environmental stimuli, possibly initiated by Sphingomonadaceae, and interacting with plant cell membranes. Future work examining these families could make these connections to plant function more robust.

In conclusion, bacterial composition in the switchgrass rhizosphere is influenced by host genotypic variability. Rhizosphere diversity shows major differences among switchgrass ecotypes, ploidy levels, genetic clusters, and life-history axes. In particular, the North switchgrass genetic cluster was most distinct at our common garden site. Two high-fidelity core families, Xanthobacteraceae and Sphingomonadaceae, were observed across the majority of our switchgrass genotypes. Twenty-one bacterial families were found to exhibit evidence for heritability. Though the explained variance was low, a redundancy analysis revealed widespread genotypic influence on the composition of the rhizosphere bacterial microbiome and outlier ASVs along each primary axis belonged largely to

our defined core microbiome. Finally, we identified 1,861 SNPs associated with the abundance of core microbiome families and discussed potential pathway mechanisms that could influence a subset of those families that we expected could influence host fitness. A GO enrichment analysis determined several functional and cellular processes for which host genotypic influence could be expressed, notably by hydrolase activity. This study should function as a foundation on which further exploration can be achieved investigating the relationship between switchgrass genotype and its associated rhizosphere microbiome in different environmental contexts or under artificial genetic perturbation.

Acknowledgements

We thank Wanyan Wang for assistance in collecting and cataloging the soil samples from the GWAS panel and selecting samples for metagenome analysis. We thank Maureen Mailander for conducting the initial rhizosphere soil DNA extractions. We are also grateful to our entire project team (investigators Marvin Hall, Stacy Bonos, Julie Hanson, Don Viands, and their students and staff for the collection of the GWAS family plants from the common garden site at Ithaca, NY). We greatly appreciate the opportunity provided by Dr. Michael Casler for allowing us to collect samples of all of the genotypes in this range-wide collection of switchgrass genotypes and check cultivars at Cornell University for this project. This research was supported by the National Institute of Food and Agriculture, U.S. Department of Agriculture, under award number 2019-67009-29006 to JEC, TBH, and JRL. Seed support was provided by the Northeast Woody/warm-season BIOMass consortium, funded by USDA-AFRI Grant #2012-68005-19703. Program support to JEC was provided through the USDA National Institute of Food and Agriculture Federal Appropriations under Project PEN04532 and Accession number 1000326. JRL was also supported by NIH award 1R35GM138300-01.

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Data Availability

Raw amplicon sequence reads are deposited in the SRA (BioProject PRJNA689762).

Figure and Table Captions

Figures:

Figure 1:

A: Alpha diversity by Ecotype. Alpha-diversity, measured by Chao1 and Shannon diversity Index, plotted for switchgrass ecotypes with Lowland (purple), Both (brown), and Upland (green). **B: Alpha diversity by Ploidy.** Alpha-diversity, measured by Chao1 and Shannon diversity Index, plotted for switchgrass ploidy levels with Tetraploid - Four (pink), Hybrid (maroon), and Octoploid - Eight (olive). **C: Alpha diversity by Genetic cluster.** Alpha-diversity, measured by Chao1 and Shannon diversity Index, plotted for switchgrass genetic clusters with North (red), South (dark blue), Northeast (beige), West (light blue), and East (black).

Figure 2:

Relationships between Shannon diversity and plant height. **A: Ecotype:** plotted for switchgrass ecotypes with Lowland (purple), Both (brown), and Upland (green). **B: Ploidy:** plotted for switchgrass ploidy levels with Tetraploid - Four (pink), Hybrid (maroon), and Octoploid - Eight (olive). **C: Genetic cluster:** plotted for switchgrass genetic clusters with North (red), South (dark blue), Northeast (beige), West (light blue), and East (black). **Relationships between Shannon diversity and anthesis date.** **D: Ecotype:** plotted for switchgrass ecotypes with Lowland (purple), Both (brown), and Upland (green). **E: Ploidy:** plotted for switchgrass ploidy levels with Tetraploid - Four (pink), Hybrid (maroon), and Octoploid - Eight (olive). **F: Genetic cluster:** plotted for switchgrass genetic clusters with North (red), South (dark blue), Northeast (beige), West (light blue), and East (black).

Figure 3:

Heritability estimates for bacterial families in the switchgrass rhizosphere. For 110 bacterial families that were observed in more than 10% of switchgrass samples, narrow-sense heritability (h^2) was calculated using a mixed linear model. 21 families had heritability estimates with standard error greater than zero. Families observed in more than 90% of our samples are represented in red.

Figure 4:
Redundancy Analyses and Variance Partitioning. **A:** Results of RDA analysis presenting amplicon sequence variants (Grey) and the North (Red), Northeast (Beige), and South (Blue) genetic clusters. **B:** Results of variance partitioning analysis for ASVs presenting Ecotype (Red), SNP PCs (Grey), Phenotypes (Blue), and Geographic Origin (White). **C:** Results of RDA analysis presenting rhizosphere bacterial families (Grey) and the North (Red), Northeast (Beige), and South (Blue) genetic clusters. **D:** Results of variance partitioning analysis for rhizosphere bacterial families presenting Ecotype (Red), SNP PCs (Grey), Phenotypes (Blue), and Geographic Origin (White).

Figure 5:

Genome-wide association study (GWAS): **A:** Manhattan plot presenting significant SNPs (Red) associated with Xanthobacteraceae rhizosphere abundance. **B:** Manhattan plot presenting significant SNPs (Red) associated with Sphingomonadaceae rhizosphere abundance. **C:** Manhattan plot presenting significant SNPs (Red) associated with Micromonosporaceae rhizosphere abundance.

Supplemental Figures:

Switchgrass Genetic Clusters

Supplemental Figure 1:

Phylogenetic analysis: Results of phylogenetic analysis based on exome capture dataset from Evans et al. 2018 with switchgrass genetic clusters colored as North (red), South (dark blue), Northeast (beige), West (light blue), and East (black).

Supplemental Figure 2:

Prevalence of rhizosphere bacterial taxa: The prevalence of rhizosphere bacterial taxa in greater than 50% of switchgrass samples shown for **A: Genus**, **B: Family**, **C: Order**, **D: Class**, and **E: Phylum**. The 90% occupancy threshold for each group is indicated by a vertical red line.

Supplemental Figure 3:
Redundancy Analyses (PCs): Results of RDA analysis presenting SNP PCs (grey) and the North (red), Northeast (beige), and South (dark blue) genetic clusters.

Supplemental Figure 5:

821 **Genome-wide association study (GWAS): A:** QQ plot presenting significant SNPs (red) associated with
 822 Xanthobacteraceae rhizosphere abundance. **B:** QQ plot presenting significant SNPs (red) associated with
 823 Sphingomonadaceae rhizosphere abundance. **C:** QQ plot presenting significant SNPs (red) associated with
 824 Micromonosporaceae rhizosphere abundance.

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 826 Supplemental Tables:
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Accession	Observed	Chao1	se.chao1	ACE	se.ACE	Shannon	Simpson	InvSimpson	Fisher
Blackwell.01			23.394779	354.272	8.002603	5.3424889			132.26882
.2	284	369.56	1	918	93	2	0.993834	162.179695	2
			1.4225048	82.8502	4.475540				21.150173
Blackwell.01	82	82.75	7	641	56	4.215349	0.983254	59.715753	3
		157.090	13.659610	145.800	5.671623	4.5370031			40.732534
Blackwell.02	132	909	4	369	98	7	0.986778	75.6315232	1
		128.111	4.9758218	125.653	4.950851	4.5327523			36.441366
Blackwell.03	122	111	9	226	1	3	0.986856	76.0803408	1
		196.576	9.7584752	194.578	5.869440	4.8451448			61.407364
Blackwell.04	175	923	9	467	07	3	0.990238	102.438025	3
					0.960768	2.3923152			2.1091676
Blackwell.05	13	13	0	13	92	4	0.899676	9.96770464	9
		232.689	12.043015	226.089	5.819401	5.0021228			76.920499
Blackwell.06	203	655	2	895	91	9	0.991456	117.041199	8
Carthage.01					2.229670	3.3590414			7.0549535
.2	35	35	0	35	06	2	0.960402	25.2538007	3
		33.3333	0.9230919	34.6522	2.343733	3.1504598			6.5554321
Carthage.01	33	333	6	222	59	5	0.94669	18.7582067	1
			0.4923659	33.4661	1.792922	3.2537473			6.5554321
Carthage.02	33	33	6	103	95	8	0.95452	21.9876869	1
			0.4946522	47.1796	3.028009	3.6323294			10.234894
Carthage.03	47	47	5	516	26	5	0.969314	32.588151	7
			0.4898979		1.147710	2.9982538			4.6508688
Carthage.04	25	25	5	26.12	2	8	0.941572	17.1150818	2
					0.966091	2.4329510			2.5030219
Carthage.05	15	15	0	15	78	3	0.900104	10.0104108	3
			0.2472676	46.3328	2.872233	3.5933987			9.9583175
Carthage.06	46	46	8	042	76	1	0.967658	30.9195473	9
CaveinRock.		241.217	22.700631	225.941	7.275428	4.7746719			63.520861
01	179	391	8	994	77	3	0.988734	88.7626487	7
CaveinRock.					2.222875	3.3010188			6.8040632
03	34	34	0	34	72	5	0.957934	23.7721676	3
CaveinRock.					2.0135421				
04	11	11	0	NA	NA	4	0.816972	5.46364491	1.7290385
CaveinRock.			1.4216995	52.5269	3.487480	3.5505624			
06	51	51.75	5	868	35	7	0.964654	28.2917445	11.361576
CaveinRock.					1.589438	2.5947938			3.3283031
07	19	19	0	19	83	6	0.906036	10.6423737	1
CaveinRock.					2.026144	2.3547577			3.3283031
08	19	19	0	19	9	9	0.872682	7.85434895	1
		756.309	50.450369	725.718	14.55862				342.72404
Dacotah.02	468	278	9	703	1	5.9079517	0.996468	283.125708	4
		1277.42	77.663680	1308.02	17.00212	6.3979261			916.05373
Dacotah.03	676	424	8	044	02	8	0.998092	524.109015	4

		624.741	38.926336	620.717	13.96987	5.7900730			276.56328
Dacotah.04	423	573	4	968	77	9	0.99604	252.525253	7
		674.666	37.119183	708.293	15.52590	5.9068336			337.92165
Dacotah.05	465	667	8	812	06	3	0.996498	285.551114	5
		1104.38	65.879614	1139.99	17.53679	6.2936985			713.14069
Dacotah.07	625	71	1	626	3	4	0.997828	460.405157	8
			221.95544	2679.47	13.78880	6.6552991			2260.3525
Dacotah.08	828	2680.32	6	419	54	8	0.9986	714.285714	9
					2.304418	3.0658291			5.5839911
ECS.1.05	29	29	0	29	54	5	0.942692	17.4495707	2
			2.2998855	20.5890	1.683910				3.1175139
ECS.1.06	18	19	8	909	07		0.914612	11.7112475	4
					2.788866	3.6244770			9.6838002
ECS.12.01	45	45	0	45	76	8	0.969748	33.0556657	4
		183.769	17.238614	165.971	5.763388	4.6236123			
ECS.12.02	148	231	5	715	15	2	0.987436	79.5924865	47.997644
				92.3956	4.726708				
ECS.12.03	92	92.2	0.6211081	644	63		0.983272	59.7800096	24.694105
		135.312	1.6025110	136.017	4.915418	4.6706732			41.613637
ECS.12.05	134	5	7	432	19	1	0.988754	88.9205051	9
			0.6211025	91.4664	4.756108	4.3463872			24.331359
ECS.12.07	91	91.2	9	354	06	3	0.985614	69.5120256	3
		126.583	5.4482389	125.221	5.179940	4.4153944			35.190936
ECS.2.02	119	333	4	544	28	3	0.984792	65.7548659	6
		290.454		272.205	6.573931	5.1440032			
ECS.2.03	235	546	18.730274	486	01	3	0.992416	131.85654	96.81155
			0.7360481	81.5651	4.487695	4.1634070			20.806009
ECS.2.04	81	81.25	2	007	33	4	0.981912	55.285272	8
			0.3817603	76.5797	4.342524				19.113207
ECS.2.06	76	76.1	9	785	45		0.977958	45.3679339	7
			2.3326329	67.2962	3.995960	4.0140341			16.184541
ECS.2.07	67	68	5	963	89	7	0.979062	47.7600535	4
			0.2472066	45.3072	2.933789	3.5627293			9.6838002
ECS.10.01	45	45	2	902	86	5	0.967504	30.7730182	4
					1.624807	2.9845207			4.6508688
ECS.10.03	25	25	0	25	68	5	0.940842	16.9038845	2
			4.5993925	32.8037	2.514591	3.0079953			
ECS.10.07	31	34	4	5	17	2	0.937756	16.0658055	6.0650427
			0.4909902	28.2733	2.356810	3.0237944			5.3470387
ECS.10.08	28	28	5	113	57	5	0.943754	17.7790421	8
					3.089571	3.5389183			9.4113548
ECS.10.09	44	44	0	44	9	4	0.966258	29.6366546	7
			2.3232382	39.4975	2.415816	3.3910601			7.8209646
ECS.10.10	38	39	4	37	29	4	0.961654	26.0783393	9
		117.833	1.2604964	118.395	4.950770	4.5256214			34.366727
ECS.11.01	117	333	7	017	42	5	0.987064	77.3036487	8
			0.0988571	44.4333	2.851068	3.5181090			9.4113548
ECS.11.02	44	44	1	048	81	1	0.96517	28.7108814	7
					2.053959	3.2729350			6.3090836
ECS.11.04	32	32	0	32	59	9	0.957414	23.4818955	3
					1.337712	2.6862938			3.3283031
ECS.11.05	19	19	0	19	11	4	0.92127	12.7016385	1

			25.182649	196.417	6.860286	4.5762160			52.304464
ECS.11.07	157	218.875	8	512	26	5	0.986162	72.2647782	6
						2.2086196			
HighTide.02	11	11	0	NA	NA	1	0.86129	7.20928556	1.7290385
					1.345185	2.8546305			3.7583769
HighTide.03	21	21	0	21	42	9	0.9339	15.128593	1
					1.788854	2.6534529			3.5419457
HighTide.05	20	20	0	20	38	5	0.913368	11.5430788	8
					0.953462	2.0604604			
HighTide.09	11	11	0	11	59	1	0.848558	6.60318802	1.7290385
					0.968245	2.5352006			2.7047898
HighTide.10	16	16	0	16	84	8	0.909588	11.0604787	6
			5.7942620	136.481	5.060855	4.6272811			40.732534
Kanlow.01	132	139.8	5	022	93	3	0.988286	85.3679358	1
				59.2239	3.562309	3.8346694			13.710755
Kanlow.02	59	59	0.1652482	335	36	8	0.974376	39.0259132	8
			2.3277386	48.5768	3.106327	3.6482240			10.513519
Kanlow.03	48	49	8	655	2	8	0.970032	33.3689269	9
					2.034190	3.0615609			5.5839911
Kanlow.04	29	29	0	29	51	8	0.943474	17.6909741	2
		197.676	8.8938170	202.486	6.234049	4.7330135			62.459927
Kanlow.05	177	471	5	714	7	2	0.987688	81.2215725	9
					2.304418	3.0572103			5.5839911
Kanlow.06	29	29	0	29	54	4	0.944458	18.0043931	2
					3.016620	3.2779203			8.3425609
Kanlow.08	40	40	0	40	63	6	0.950638	20.2584984	6
					1.951800	2.4982881			3.7583769
Kanlow.10	21	21	0	21	15	9	0.87997	8.33125052	1
					2.236067	3.3007340			7.3080809
KY1625.01	36	36	0	36	98	1	0.955154	22.2985328	3
					1.609630	2.8223172			
KY1625.02	22	22	0	22	11	1	0.930418	14.3715329	3.9775371
			0.4885042	22.5871	1.832393				
KY1625.03	22	22	1	936	2	2.8498394	0.93646	15.7381177	3.9775371
			2.3145502	28.1911	2.095781	3.0126158			5.1125109
KY1625.04	27	28	5	385	78	9	0.944648	18.0661945	2
			0.4952605	53.1403	3.309600	3.7910374			11.936998
KY1625.06	53	53	6	509	16	2	0.974256	38.8440025	1
			0.2465033	36.3734	2.316959				7.3080809
KY1625.07	36	36	2	074	53	3.323476	0.957368	23.4565585	3
Pathfinder.0			0.4894725	25.1111	1.066883				4.4238312
1	24	24	1	111	2	2.8738709	0.931104	14.5146308	1
Pathfinder.0			0.4918693	31.3805	1.810100	3.2172318			
2	31	31	8	41	82	1	0.952968	21.2621194	6.0650427
Pathfinder.0			0.4960158	63.1347	3.615392	4.0034066			14.932265
3	63	63	7	518	81	9	0.979342	48.4073967	5
Pathfinder.0			0.1653594	64.1680	3.910412	3.9565316			15.242462
4	64	64	6	336	95	2	0.97814	45.7456542	8
Pathfinder.0		497.149	32.223917	481.942	10.68062	5.5926925			195.49644
5	354	254	2	64	65	1	0.995268	211.327134	5
Pathfinder.0			0.0992619	68.3272	4.026175	3.9687013			16.502381
6	68	68	8	39	65	1	0.977834	45.1141388	4

		266.675		262.922	6.869075				88.440004
Shelter.01	222	676	15.401994	522	03	5.0768225	0.992116	126.839168	9
		148.157	4.7464328	147.604	5.125929	4.6565174			44.758093
Shelter.04	141	895	2	547	49	1	0.988222	84.9040584	5
		107.111	4.9755659	105.959	5.042556	4.3239777			28.042367
Shelter.05	101	111	3	064	18	8	0.984116	62.9564342	7
					2.620767	3.4252775			7.8209646
Shelter.06	38	38	0	38	26	8	0.962992	27.0211846	9
				41.3370	2.594245	3.4853419			8.6065827
Shelter.07	41	41	0.1646216	185	3	4	0.964894	28.4851592	4
					2.247805	3.4858016			7.8209646
Shelter.08	38	38	0	38	95	3	0.965726	29.1766354	9
					0.980580	3.1696484			4.8804419
Sunburst.01	26	26	0	26	68	6	0.955562	22.503263	6
					1.615145	2.9328576			4.1993718
Sunburst.02	23	23	0	23	71	3	0.94052	16.8123739	9
			0.4890096	24.0864	1.483973	3.0044659			4.1993718
Sunburst.04	23	23	5	198	93	3	0.946512	18.6957822	9
		61.3333	0.9245561	61.5347	3.627977	3.9264577			14.317643
Sunburst.05	61	333	5	21	36	1	0.977988	45.4297656	8
		231.823		231.577	6.244902	4.9978561			77.506253
Sunburst.06	204	529	11.04251	917	37	5	0.99154	118.20331	5
			0.4923659	33.3279	2.307691	3.2662388			6.5554321
Sunburst.07	33	33	6	766	93	2	0.956992	23.2514881	1
		1300.36	84.349896	1313.73	17.21792				849.79393
SW102.01	661	913	8	961	41	6.3621531	0.997996	499.001996	8
		2380.54	191.69492	2405.20	15.69208	6.6029326			
SW102.02	798	688	1	226	59	9	0.998492	663.129974	1832.3246
		758.794	47.138486	755.958	15.62673	5.9716331			369.39039
SW102.03	484	393	3	608	43	7	0.99687	319.488818	3
		793.045	43.863284	800.693	15.20757				
SW102.04	522	455	9	061	04	6.0783177	0.997264	365.497076	440.66336
		1037.39	72.873095	1011.43	17.55745	6.1260082			518.14414
SW102.05	557	823	3	725	61	5	0.997286	368.459838	6
		545.011	31.403449	565.668	12.82308	5.6877861			236.27209
SW102.06	391	111	6	334	41	8	0.995596	227.066303	9
			2.2303578	77.2480	4.314111	4.0450301			19.113207
SW109.01	76	77.5	1	166	34	7	0.97858	46.6853408	7
				41.2737	2.709759				8.6065827
SW109.02	41	41	0.2469324	255	07	3.4328486	0.961836	26.2027041	4
			60.039323	973.887	18.10678	6.1203808			503.93733
SW109.03	551	946	6	63	14	5	0.997308	371.471025	8
		107.857	6.3350402	104.429	4.952243	4.3188250			27.662922
SW109.04	100	143	3	098	42	3	0.984176	63.1951466	1
		144.807	1.1265561	146.463	5.203400				46.134760
SW109.05	144	692	4	757	52	4.7150251	0.989222	92.7815921	6
			2.3261795	44.7873	2.485914	3.5940011			9.4113548
SW109.06	44	45	1	431	29	9	0.968868	32.12129	7
		458.222	33.945054	435.872	9.938721	5.4450033			160.03554
SW109.07	317	222	8	385	04	3	0.994486	181.356547	6
		82.8571	1.3946665	83.3088	4.499746	4.1874380			21.150173
SW110.01	82	429	3	896	92	5	0.982186	56.1356237	3

		825.411	48.780317	772.572	14.60961	6.1071805			450.97506
SW110.02	527	765	8	416	38	1	0.997406	385.505012	8
		798.962	39.216606	830.401	15.60662	6.1457769			496.98551
SW110.03	548	264	9	116	49	6	0.997474	395.882819	9
					3.603239				14.013230
SW110.04	60	60	0	60	28	3.8856459	0.97624	42.0875421	2
		102.333	0.7585402	102.712	4.970449	4.3883292			28.423670
SW110.05	102	333	2	117	37	4	0.98537	68.3526999	5
			18.055641	293.765	7.543141	5.1113165			99.470471
SW110.06	239	296.5	1	997	39	5	0.992004	125.062531	7
					2.247805	3.4529103			7.8209646
SW112.01	38	38	0	38	95	5	0.963954	27.7423293	9
			0.4933771	38.2777	1.942205	3.4570502			7.8209646
SW112.03	38	38	9	778	17	9	0.964716	28.3414579	9
			1.2952673	57.4978	3.514503	3.7856122			13.111649
SW112.04	57	57.5	1	983	42	5	0.972816	36.7863449	3
		350.258		346.502	7.517912	5.4187040			139.50889
SW112.05	293	621	16.574448	027	2	1	0.994522	182.548375	4
		96.6666		96.1614	4.781793	4.3380314			25.793473
SW112.06	95	667	2.2045363	415	98	2	0.9846	64.9350649	8
					2.065116	3.3471525			6.8040632
SW112.07	34	34	0	34	43	7	0.960178	25.1117473	3
		998.937	55.867297	1045.23	17.58806	6.2536799			645.37092
SW114.01	604	5	2	435	44	5	0.997728	440.140845	7
		386.571	17.559381	375.829	7.422961	5.5696491			165.45875
SW114.02	323	429	7	321	37	5	0.99548	221.238938	9
		785.269	38.483632	812.478	15.36338	6.1335031			
SW114.03	542	231	2	316	57	9	0.997442	390.930414	483.37524
		2838.97	254.66957	2870.12	16.33949	6.6092716			1946.6333
SW114.04	807	222	4	007	29	9	0.998482	658.761528	9
		495.142	29.713622	473.017	10.17081	5.6495506			205.95653
SW114.05	364	857	5	313	75	8	0.995624	228.519196	8
		88.6666	4.4908603	87.4215	4.615603	4.1227654			21.844089
SW114.07	84	667	8	719	31	6	0.98023	50.5816894	3
			0.0992509	67.2028	4.068502	3.9451636			16.184541
SW114.08	67	67	3	536	12	1	0.976966	43.4140835	4
			9.6567964	311.412	5.471092	5.4390300			132.26882
SW115.01	284	311.55	4	824	91	6	0.994722	189.465707	2
		2898.46		2884.04	13.35152	6.6685517			2419.7627
SW115.02	837	61	249.31555	551	03	5	0.998622	725.689405	8
		1466.80		1517.40	18.08361	6.4207845			1004.4280
SW115.03	694	667	98.459852	599	24	8	0.998112	529.661017	4
		822.007	44.036882	824.114	15.88440	6.1353856			485.61692
SW115.04	543	092	6	014	11	3	0.997444	391.236307	7
			20.348782	328.695	8.397857	5.1688365			
SW115.06	262	333.4	6	018	74	4	0.992	125	115.55145
			126.47829	1753.29	17.03139	6.4819939			
SW116.02	728	1740.7	5	48	67	9	0.99825	571.428571	1204.2124
		2207.68	167.39303	2281.26	15.23266	6.6061864			
SW116.03	798	085	3	827	02	1	0.998506	669.344043	1832.3246
		1813.15	134.05897	1866.32	17.50813	6.4907478			1251.8622
SW116.05	735	217	7	534	57	8	0.998256	573.394495	8

			59.339305	999.748	19.75033	6.0799997			
SW116.07	542	930.128	5	134	77	7	0.997072	341.530055	483.37524
		1447.09	92.913821	1475.47	16.84388	6.4515826			1069.5348
SW116.08	706	317	4	377	07	4	0.998206	557.413601	7
		713.439	38.111760	787.171	16.89353	5.9544505			374.59615
SW116.09	487	394	3	713	21	1	0.996664	299.760192	7
		366.428	21.837920	368.981	8.768288	5.3205579			133.06144
SW122.01	285	571	2	817	86	9	0.99364	157.232704	7
			2.5842331	69.2796	4.071990				16.184541
SW122.02	67	69	3	504	03	3.8993284	0.975504	40.8229915	4
		413.838	15.307925	421.873	8.208279				195.49644
SW122.03	354	71	4	189	85	5.6665673	0.995926	245.459008	5
		131.666	8.0006549	126.221	5.170465	4.4950221			35.605862
SW122.05	120	667	2	269	05	9	0.986472	73.920757	2
		105.333	4.1251151	103.015	4.694652	4.4101508			28.423670
SW122.06	102	333	3	706	7	5	0.985426	68.6153424	5
			0.6206871	50.8760	3.353897	3.6167772			11.076870
SW123.01	50	50.2	9	602	4	8	0.968186	31.4327026	8
			0.4890096	23.5247		2.8611842			4.1993718
SW123.02	23	23	5	303	1.7591	2	0.933426	15.020879	9
		74.1111		75.6248	4.313761	3.8457485			17.467286
SW123.04	71	111	3.1006765	977	74	6	0.972622	36.5256776	6
		347.837	30.158536	331.011	8.837619	5.0507301			101.49086
SW123.05	242	838	5	052	16	8	0.991038	111.582236	4
					1.371988	3.3944481			6.8040632
SW123.06	34	34	0	34	68	7	0.96294	26.9832704	3
			4.3392619	100.045	4.810379	4.3102378			26.909539
SW123.08	98	102.2	8	873	46	8	0.98365	61.1620795	2
					2.701351	3.3406406			7.5634245
SW123.09	37	37	0	37	01	8	0.958218	23.9337514	5
			41.605091	761.943	15.29225	5.9929967			385.21207
SW124.01	493	740	3	89	28	9	0.996924	325.097529	7
		1292.58	81.263119	1335.18	17.82383	6.3785069			884.35986
SW124.02	669	599	2	265	77	6	0.998028	507.099392	2
			32.108803	498.286	10.69483	5.6405265			209.17261
SW124.03	367	514	5	973	89	3	0.99553	223.713647	1
		896.641		927.474	18.04594	6.0501102			448.89384
SW124.04	526	026	58.341897	031	61	2	0.99703	336.700337	2
		864.282	53.513328	924.436	18.47727	6.0417601			444.75983
SW124.05	524	258	7	656	51	1	0.996972	330.250991	4
		894.063	47.921104	960.870	18.78322	6.1707030			552.94865
SW124.06	571	694	1	215	19	1	0.9974	384.615385	2
		667.657	30.555908	697.271	14.53763	6.0207062			385.21207
SW127.01	493	343	3	655	25	1	0.99709	343.642612	7
		78.6666	2.2042773	78.9334	4.343880	4.0427247			19.448027
SW127.03	77	667	9	648	99	9	0.978958	47.5239996	4
					2.641022	3.5083058			8.3425609
SW127.04	40	40	0	40	53	8	0.965962	29.3789294	6
		196.111	7.8214233	194.488	5.495054	4.9072919			64.054480
SW127.05	180	111	9	214	92	7	0.990942	110.399647	1
			1.0591134	100.137	4.847002	4.3011674			27.285333
SW127.06	99	99.6	4	629	36	3	0.982466	57.032052	1

					2.770274	3.5758062			9.1409943
SW127.07	43	43	0	43	1	3	0.968068	31.3165477	4
		392.484	20.896337	394.986	8.967902	5.4558879			155.60752
SW128.01	312	375	4	534	23	1	0.99458	184.501845	3
		150.076		154.143	5.565713	4.3789688			45.673925
SW128.02	143	923	4.1280238	344	67	5	0.982148	56.0161327	4
			0.4866642	19.3706	2.048086	2.3949373			3.3283031
SW128.03	19	19	6	19	57	6	0.881198	8.41736671	1
					3.903123				15.242462
SW128.04	64	64	0	64	75	3.9237705	0.975576	40.9433344	8
					2.215646	3.2258587			6.5554321
SW128.05	33	33	0	33	84	1	0.952642	21.1157566	1
					1.309307	2.2966286			2.3044443
SW128.06	14	14	0	14	34	3	0.875366	8.02349279	1
		861.389	53.433810	830.197	15.52612	6.0907763			453.06585
SW129.01	528	831	7	982	43	3	0.997306	371.195249	4
		538.780	29.045800	537.935	11.50814	5.7503007			
SW129.02	399	22	4	175	23	1	0.996034	252.143217	245.87671
		828.436	49.952721	802.482	15.18090				438.62905
SW129.03	521	975	2	816	18	6.0772823	0.997272	366.568915	3
		911.059	54.945604	970.392	18.66920	6.1061963			
SW129.04	549	702	2	393	72	6	0.997182	354.861604	499.29176
			42.080110	641.626	14.17244	5.7986501			279.25447
SW129.05	425	646.625	5	598	85	5	0.996154	260.0104	9
		1142.28	78.015661	1180.96	19.09270	6.2106376			621.49858
SW129.06	596	347	3	226	1	2	0.997542	406.834825	1
					2.190890				5.8233357
SW31.01	30	30	0	30	23	3.0852854	0.945866	18.4726789	9
					0.963624	2.2390348			2.3044443
SW31.03	14	14	0	14	11	1	0.858202	7.05228565	1
					1.839732				4.8804419
SW31.04	26	26	0	26	42	3.0493745	0.946344	18.6372447	6
		79.3333	0.9249512	79.4706	4.431733	4.1405708			20.123282
SW31.05	79	333	5	263	96	2	0.98132	53.5331906	8
					1.322875	2.5340035			2.7047898
SW31.06	16	16	0	16	66	6	0.911206	11.2620222	6
			0.4937104	40.1868	2.684726	3.4847579			8.3425609
SW31.07	40	40	4	67	94	6	0.96575	29.1970803	6
		1083.81		1081.42	16.80824	6.2911341			696.29238
SW33.01	620	579	64.532596	018	14	2	0.997848	464.684015	7
		362.205	12.554748	362.792	6.639766				162.73204
SW33.02	320	48	6	142	2	5.5708467	0.995528	223.613596	9
		1428.79	98.343364	1366.97	16.58372	6.3986478			925.37053
SW33.03	678	286	1	366	52	9	0.998096	525.210084	6
		1639.92	112.71225	1628.25	16.21770	6.4920891			
SW33.04	729	715	2	185	83	6	0.998294	586.166471	1210.8657
		2501.04	199.10825	2617.03		6.6425969			2147.5297
SW33.05	821	511	3	967	14.67729	6	0.99857	699.300699	2
		1303.60	84.013939	1349.35	18.81321	6.3653057			862.55656
SW33.06	664	265	2	139	05	1	0.997982	495.540139	8
		1177.84	79.315215	1203.65	18.52369	6.2509562			670.28051
SW38.03	612	091	4	042	44	9	0.997674	429.922614	5

		128.230	3.5599718	127.799	4.976695	4.5357387			37.284421
SW38.05	124	769	1	801	05	8	0.986764	75.5515261	1
		183.230	10.632199	186.067	6.446704	4.6670977			53.283425
SW38.08	159	769	7	433	68	2	0.987926	82.822594	2
		11.643834	86.0334	4.512650	3.8596990				19.784719
SW40.01	78	93.6	3	614	94	8	0.97251	36.3768643	8
		1.5802298	87.1796	4.619396	4.1893661				22.545448
SW40.03	86	87	7	919	96	4	0.981636	54.4543672	7
		3.4443596	116.662	5.085906	4.4602852				33.144492
SW40.05	114	117.5	9	351	97	1	0.985974	71.2961643	1
				3.010186	3.7165490				10.794182
SW40.07	49	49	0	49	79	6	0.97272	36.6568915	1
		0.4947642	48.1610	2.873662	3.7158136				10.513519
SW40.08	48	48	5	024	47	3	0.97287	36.8595651	9
		664.853	34.724433	702.893	14.94659	5.9359553			344.33832
SW40.09	469	659	1	196	72	2	0.99674	306.748466	1
		172.75986	2170.37	17.03852	6.5359544				1462.4471
SW43.04	762	2152.04	4	263	82	4	0.998346	604.594921	6
		446.181	26.003820	434.897	9.737036	5.5506106			179.55857
SW43.05	338	818	6	751	3	6	0.99503	201.207244	6
		209.972	5.5984958	212.743	5.474219	5.0187191			74.599851
SW43.06	199	973	7	621	28	1	0.991912	123.63996	3
		763.266	41.327118	817.411	16.79084				416.84738
SW43.07	510	667	6	937	3	6.0271439	0.996988	332.005312	1
		1757.07	125.32180	1871.02	18.99345				1273.0791
SW43.08	738	534	9	408	74	6.4967984	0.99826	574.712644	4
		633.294	38.729967	644.634	13.91327	5.8080659			283.33186
SW43.09	428	737	4	653	25	5	0.996198	263.019463	7
		1410.72	94.611359	1451.75	18.50389				
SW46.01	680	109	1	494	5	6.3937451	0.998046	511.770727	934.8075
		715.722	38.512163	733.864	14.59347	5.9981188			379.86965
SW46.02	490	222	3	85	81	8	0.997004	333.778371	9
		382.166	21.991383	382.836	8.730470	5.3930006			143.63640
SW46.04	298	667	6	675	75	6	0.994236	173.490632	8
		1852.18	131.96638	1875.62	16.01166	6.5442029			1445.1947
SW46.05	760	121	9	984	99	8	0.998392	621.890547	1
		1363.33	93.472807	1397.52	18.65401	6.3482679			841.41469
SW46.06	659	813	9	822	17	6	0.997928	482.625483	2
		1147.76	69.956191	1162.16	17.26003	6.3141691			744.68150
SW49.01	634	471	6	993	7	6	0.99789	473.933649	1
		959.281	57.225214	1041.20	19.01996	6.1591322			550.38240
SW49.03	570	69	4	129	96	8	0.997394	383.729854	8
		225.028	8.3254188	225.001	5.352650	5.0574989			78.684440
SW49.04	206	571	3	183	5	5	0.992248	128.998968	2
		9.1880682	215.042	4.734906	5.1035270				76.920499
SW49.05	203	222.375	9	156	71	6	0.992956	141.964793	8
		3696.56	356.66937	3821.17	13.28291	6.7004636			2946.5009
SW49.07	861	122	6	219	27	2	0.998662	747.384156	9
		160.687	6.5400071	157.389	4.955924	4.7395828			48.940833
SW50.01	150	5	8	41	38	5	0.989294	93.405567	4
		0.4930066	36.3805	1.828162	3.3943770				7.3080809
SW50.02	36	36	5	41	46	2	0.961728	26.1287625	3

			0.4967426	77.1556	4.371533	4.1016497			19.448027
SW50.04	77	77	4	42	25	3	0.978962	47.5330355	4
		270.634	14.994995	273.208	7.329285	5.0486945			90.972487
SW50.05	226	146	6	032	65	4	0.99152	117.924528	5
		14.347272	274.058	7.230033	5.0337627				90.972487
SW50.06	226	269.4	6	509	75	1	0.991252	114.311843	5
		421.245	32.003419	422.220	10.58460	5.2786440			137.87913
SW51.04	291	283	8	328	53	6	0.993042	143.71946	6
		0.0990867	55.3411	3.295062	3.7914025				12.520377
SW51.05	55	55	4	99	38	6	0.97375	38.0952381	3
		5.3706097	78.9042	4.324772	4.0147670				19.113207
SW51.06	76	81.25	9	093	9	9	0.97785	45.1467269	7
		150.769	7.3624733	146.966	5.283612	4.6034867			43.850023
SW51.08	139	231	9	957	92	6	0.987286	78.6534529	6
		0.1234276	40.3710	2.809075	3.4342469				8.3425609
SW51.09	40	40	1	482	33	6	0.963066	27.0753236	6
		162.437	8.1461593	159.136	5.737042	4.6733323			
SW58.01	148	5	8	152	13	3	0.98829	85.3970965	47.997644
		27.463211	173.401	6.877900	4.3815745				39.425196
SW58.02	129	190.75	4	199	91	9	0.984006	62.5234463	8
		3.9161574	81.2211	4.368121					19.113207
SW58.03	76	80.5	1	229	71	3.8240742	0.971712	35.3506787	7
		1.2954545	60.5070	3.621399	3.9010984				14.013230
SW58.06	60	60.5	5	73	39	5	0.97694	43.3651344	2
				3.198557	3.7778140				11.648288
SW58.07	52	52	0	52	37	1	0.973852	38.2438427	1
				3.135249	3.6251846				10.234894
SW58.09	47	47	0	47	15	6	0.9697	33.0033003	7
		2218.63	168.30984	2254.01	14.65760	6.6111904			1856.8282
SW63.02	800	83	8	11	05	3	0.998522	676.589987	8
		55.708170	1015.40	18.56500	6.2140248				595.80752
SW63.03	587	971.2	2	894	61	8	0.997602	417.014179	1
		1402.29		1394.20	18.30181	6.3834456			902.29902
SW63.04	673	787	95.766148	466	41	8	0.998032	508.130081	9
		1151.76	70.944254	1149.66	17.10747	6.3137867			741.09718
SW63.05	633	667	4	334	1	6	0.997894	474.833808	4
		1122.24	65.186885	1154.21	17.85312				766.62362
SW63.06	640	54	4	806	42	6.329736	0.997926	482.160077	5
		516.944	23.458376	539.202	11.40023	5.7776168			253.27906
SW63.07	405	444	7	793	07	9	0.996194	262.743037	7
		0.4947642	48.1944	2.971564	3.7002456				10.513519
SW64.01	48	48	5	849	78	5	0.972234	36.0152705	9
		0.2462960	34.4562	2.009731	3.2804634				6.8040632
SW64.02	34	34	9	359	91	4	0.955036	22.2400142	3
		52.3333	0.9242565	52.7819	3.208699	3.6578331			11.648288
SW64.03	52	333	8	731	85	7	0.968262	31.5079715	1
		0.4435179	63.7052	3.955878					14.932265
SW64.04	63	63.125	9	147	82	3.6988139	0.968618	31.8654006	5
			41.2576	2.803450	3.4153709				8.6065827
SW64.06	41	41	0.2469324	295	83	2	0.95907	24.431957	4
		0.4918693	31.3759	2.176306	3.1894652				
SW64.07	31	31	8	414	75	3	0.953168	21.3529211	6.0650427

					1.629062	3.0495168			4.8804419
SW65.03	26	26	0	26	97	8	0.942742	17.4648084	6
			1.8138697	45.4161	3.142597	3.4204977			9.4113548
SW65.05	44	45	5	932	25	4	0.960964	25.6173788	7
					2.978181	3.5906407			9.9583175
SW65.06	46	46	0	46	53	7	0.966146	29.538607	9
			0.2456518	29.4444	1.666988	3.0944588			5.5839911
SW65.07	29	29	4	444	54	3	0.947566	19.0715948	2
					1.358732	2.9796503			4.8804419
SW65.08	26	26	0	26	44	4	0.936222	15.6793879	6
		1541.64	103.54737	1673.12	20.12552	6.4499819			1104.1769
SW65.09	712	286	9	092	32	9	0.99815	540.540541	9
		947.271	62.304263	958.196	18.50230	6.1037410			487.86919
SW65.10	544	186	9	283	51	2	0.997246	363.108206	8
					2.215646	3.2698721			6.5554321
SW781.03	33	33	0	33	84	7	0.956548	23.0139004	1
					2.504050	3.3988180			7.5634245
SW781.05	37	37	0	37	77	8	0.962778	26.865832	5
					1.788854				3.5419457
SW781.06	20	20	0	20	38		0.916226	11.9368778	8
					1.809068	2.7808027			
SW781.07	22	22	0	22	07	3	0.925568	13.4350817	3.9775371
					2.018433	2.9845488			5.1125109
SW781.08	27	27	0	27	57	4	0.936848	15.8348113	2
					1.658312	3.4308854			7.3080809
SW782.01	36	36	0	36	4	7	0.96345	27.3597811	3
			2.2305169	83.0866	4.500469				21.150173
SW782.02	82	83.5	4	84	05	4.2050299	0.9829	58.4795322	3
		292.108	13.706247	292.026	6.788258	5.2337778			107.68916
SW782.03	251	696	1	065	42	4	0.99333	149.925038	4
		280.576	22.286481	254.600	6.628178	5.0358842			85.327629
SW782.09	217	923	4	492	14	1	0.991516	117.86893	4
		723.038	38.663407	766.500	15.83018				385.21207
SW786.01	493	168	6	847	16	5.9810855	0.996788	311.332503	7
		735.857	35.791741	756.524	14.82240				434.58801
SW786.02	519	143	1	259	52	6.0826	0.9973	370.37037	5
		741.791	43.869913	743.850	15.16405				369.39039
SW786.03	484	304	6	712	72	5.9462728	0.996526	287.85262	3
			25.764350	467.603	10.14834	5.6409390			201.72496
SW786.06	360	471.8	9	276	56	1	0.995624	228.519196	6
				376.528	8.822307	5.3767999			143.63640
SW786.07	298	369.25	19.054615	849	66	8	0.993932	164.798945	8
		1012.78		1072.72	19.09012				612.80147
SW786.09	593	378	60.040602	665	33	6.2193803	0.997598	416.319734	3
		1499.92	99.820617	1534.39	17.08353	6.4470481			1069.5348
SW787.01	706	857	3	205	78	5	0.998186	551.267916	7
		1056.46		1114.73	18.86348	6.2232462			624.42799
SW787.02	597	154	65.253601	09	22	9	0.997602	417.014179	6
		2767.94	236.81439	2755.97	14.27855	6.6440253			2178.8469
SW787.03	823	068	3	481	99	7	0.998572	700.280112	4
		1982.06	141.77635	2026.35	15.14634	6.5868475			1673.6418
SW787.04	784	579	9	704	98	1	0.99848	657.894737	1

		646.802	29.564399	665.689	13.94684	5.9994619			365.95694
SW787.05	482	92	1	818	58	6	0.997048	338.753388	7
		297.396	11.386718	297.021	6.246260	5.3102846			117.01568
SW787.06	264	226	2	915	36	6	0.993794	161.134386	1
					3.783842	4.0028546			14.932265
SW788.01	63	63	0	63	01	7	0.979754	49.3924726	5
					1.316561	2.3543936			2.5030219
SW788.02	15	15	0	15	18	8	0.879288	8.28418053	3
			0.4841229		1.544436	2.3367279			2.7047898
SW788.04	16	16	2	16.584	71	5	0.876364	8.08825908	6
					0.953462	2.1119626			
SW788.05	11	11	0	11	59	7	0.844528	6.43202635	1.7290385
			0.4909902	28.5219	1.802994	3.0172264			5.3470387
SW788.06	28	28	5	479	8	2	0.94003	16.6750042	8
			0.2470058	42.3230	2.628861	3.5156234			8.8727322
SW788.07	42	42	8	794	97	3	0.96585	29.2825769	1
			0.4894725	25.0864	1.486409	3.0453847			4.4238312
SW788.10	24	24	1	198	51	8	0.948544	19.4340796	1
			25.114456	184.906	7.157030	4.3333098			40.732534
SW789.01	132	192.2	3	52	8	6	0.982354	56.6700669	1
			0.0710705	100.188	4.850969	4.3972881			27.662922
SW789.06	100	100	3	378	97	8	0.985366	68.3340167	1
			0.1236910	48.4451	2.997810	3.6571330			10.513519
SW789.07	48	48	6	802	7	2	0.970726	34.1600055	9
		370.131	18.441485	367.710	7.835813				147.84082
SW789.08	303	148	8	768	9	5.4550575	0.994744	190.258752	4
			13.212941	333.599	6.240322	5.4768672			141.15073
SW790.01	295	337.6	3	637	78	7	0.995088	203.583062	4
			0.2461829	33.3284	2.406633	3.1917852			6.5554321
SW790.03	33	33	8	898	31	8	0.951062	20.4340186	1
			1.8140507	47.5118	3.265108	3.4562311			9.9583175
SW790.07	46	47	6	713	18	9	0.962304	26.5280136	9
					1.328422				2.9096498
SW793.02	17	17	0	17	33	2.4908301	0.902418	10.2477916	3
					2.366431	3.2884088			7.0549535
SW793.03	35	35	0	35	91	8	0.954492	21.9741584	3
					1.581138	2.5854474			3.1175139
SW793.06	18	18	0	18	83	8	0.917158	12.0711716	4
					0.974679	2.7854278			3.5419457
SW793.09	20	20	0	20	43	4	0.930386	14.3649266	8
					0.948683	1.8878644			1.5445238
SW793.10	10	10	0	10	3	9	0.810434	5.27520758	2
					1.609630	2.8108780			
SW795.04	22	22	0	22	11	9	0.930508	14.3901456	3.9775371
			0.4931969	37.2942	2.167712	3.4277975			7.5634245
SW795.07	37	37	6	31	65	1	0.96396	27.7469478	5
					0.960768				2.1091676
SW795.09	13	13	0	13	92	2.3976174	0.898864	9.887676	9
					1.561249				2.7047898
SW795.10	16	16	0	16	5	2.4102199	0.896332	9.64617818	6
			0.2425356	17.8308	1.774503	2.5228005			2.9096498
SW796.03	17	17	3	148	65	2	0.909696	11.0737066	3

					1.358732	3.1038568			4.8804419
SW796.04	26	26	0	26	44	8	0.95008	20.0320513	6
		149.555	4.9829943	149.631	5.390597	4.6730675			45.215037
SW796.05	142	556	8	339	72	8	0.988782	89.1424496	5
					2.070196				7.0549535
SW796.06	35	35	0	35	68	3.3809776	0.96205	26.3504611	3
					3.125290	3.4371735			9.1409943
SW796.10	43	43	0	43	68	4	0.959992	24.995001	4
					1.620185	2.9123211			4.4238312
SW797.01	24	24	0	24	18	6	0.93673	15.805279	1
					3.603117	3.8380698			13.111649
SW797.02	57	57	0	57	56	1	0.974412	39.0808191	3
					1.596871	2.6838457			3.5419457
SW797.04	20	20	0	20	94	1	0.919916	12.4868888	8
					0.963624	2.2614517			2.3044443
SW797.06	14	14	0	14	11	6	0.870718	7.73502885	1
		563.082	27.427164	578.552	12.38594	5.8351822			279.25447
SW797.09	425	569	4	045	97	9	0.996424	279.642058	9
					3.195741	3.5668079			10.234894
SW798.05	47	47	0	47	85	6	0.965328	28.8417167	7
					0.982607	3.2202277			5.5839911
SW798.06	29	29	0	29	37	5	0.955364	22.4034412	2
		110.571	2.5150130	112.088	5.114972	4.3651484			30.750531
SW798.09	108	429	3	235	26	8	0.984544	64.699793	5
			0.2457980	30.4786	2.053989	3.2099464			5.8233357
SW798.10	30	30	2	994	87	8	0.955386	22.4144887	9
					1.333333	2.7259285			3.1175139
SW799.03	18	18	0	18	33	1	0.928784	14.0417884	4
					1.866513				
SW799.05	31	31	0	31	05	3.2578298	0.957222	23.3765019	6.0650427
		55.3333	0.9243672	55.5916	3.449167	3.7821489			12.520377
SW799.07	55	333	7	843	61	8	0.974084	38.5862016	3
			16.813203	209.034	6.798887	4.7630813			60.363131
SW799.09	173	216.125	6	524	43	8	0.989052	91.3408842	1
		195.791	11.029161	192.486	6.073507				59.327189
SW799.10	171	667	9	382	98	4.7611125	0.988738	88.7941751	1
			0.1647618	44.3347	2.854134	3.5303744			9.4113548
SW802.04	44	44	4	037	42	6	0.96553	29.010734	7
					3.174901	3.7404316			11.076870
SW803.03	50	50	0	50	57	7	0.972994	37.0288084	8
			0.4909902	28.4176	1.767283	3.1044229			5.3470387
SW803.04	28	28	5	955	31	3	0.948632	19.4673727	8
					1.341640	2.7913704			3.5419457
SW803.05	20	20	0	20	79	2	0.931386	14.5742851	8
		51.3333		51.7428	3.216859	3.6694280			
SW803.06	51	333	0.9242168	336	98	1	0.969834	33.1499039	11.361576
			12.108790	186.530	5.539810	4.8045816			58.812315
SW803.07	170	196.4	1	556	24	8	0.989402	94.3574259	3
					1.648863	3.3003673			6.3090836
SW803.08	32	32	0	32	25	9	0.958406	24.0419291	3
					1.888800	3.4276346			7.5634245
SW803.09	37	37	0	37	56	8	0.96211	26.3921879	5

					1.646109	3.2577012			
SW805.01	31	31	0	31	78	4	0.95692	23.2126277	6.0650427
			0.2480694	65.2219	3.869117	3.9193552			15.554577
SW805.02	65	65	7	077	21	5	0.976268	42.1371987	7
			0.2477168	55.2919	3.052005	3.8404970			12.520377
SW805.03	55	55	5	282	22	2	0.975504	40.8229915	3
		407.118	17.846479	404.106	7.986731	5.5998246			179.55857
SW805.04	338	421	7	58	12	1	0.99555	224.719101	6
					0.974679	2.8595438			3.5419457
SW805.05	20	20	0	20	43	6	0.937284	15.9448944	8
		195.387	2.6507250	197.021	4.033269	5.0639293			70.623828
SW805.06	192	097	9	517	06	9	0.99266	136.239782	2
					1.653872	3.3595380			6.8040632
SW805.07	34	34	0	34	46	4	0.9603	25.1889169	3
			1.8401708	97.7915	4.795703	4.3725341			26.535662
SW805.08	97	98.2	9	191	85	2	0.984734	65.5050439	1
		295.489	14.789478	296.018	6.956748				106.29379
SW806.01	249	796	3	045	49	5.2054738	0.99304	143.678161	2
			4.6273642	58.0724	3.499970	3.8171965			13.111649
SW806.02	57	60	6	869	53	7	0.97427	38.865138	3
					1.833030	2.9655511			4.6508688
SW806.03	25	25	0	25	28	9	0.94062	16.8406871	2
			0.4873397	21.1111	1.212469	2.8358486			3.5419457
SW806.04	20	20	2	111	61	1	0.93648	15.7430731	8
			2.3175348		1.928104	3.1881191			5.8233357
SW806.05	30	31	4	32.12	02	5	0.953784	21.6375281	9
			0.4923659	33.2941	1.999130	3.3099720			6.5554321
SW806.06	33	33	6	9	2	1	0.959222	24.5230271	1
			5.8565645	175.825	4.707394	4.9275278			58.812315
SW806.08	170	179.5	5	824	14	9	0.991544	118.259224	3
			0.6202686	86.0507	4.598278	4.1318451			22.193839
SW806.09	85	85.25	3	291	97	9	0.980432	51.103843	2
			11.998471	178.978	6.737979				45.215037
SW808.01	142	170.12	5	261	83	4.4453889	0.984218	63.3633253	5
			2.8816147	59.6076	3.647304	3.7775234			13.410226
SW808.02	58	60	7	403	05	4	0.973232	37.3580395	7
			0.1237684	51.3347	3.156760	3.7051349			
SW808.03	51	51	4	152	34	5	0.972308	36.1115124	11.361576
					1.866513	3.2341032			
SW808.04	31	31	0	31	05	9	0.95598	22.7169468	6.0650427
			0.2429563		1.362106				3.1175139
SW808.05	18	18	3	18.6	71	2.570515	0.912676	11.4516055	4
		216.562	11.718162	217.109	6.422373	4.8525849			67.849120
SW808.06	187	5	8	214	53	3	0.989662	96.7305088	5
		407.246	22.131121	408.480	9.021575	5.4834924			162.73204
SW808.07	320	154	7	747	09	8	0.99469	188.323917	9
				194.946	5.639601	4.8970522			
SW809.01	178	204.4	12.108828	914	04	1	0.99097	110.741971	62.989346
			0.4935481	39.3469	2.351994	3.4342916			
SW809.02	39	39	2	388	6	7	0.962318	26.5378695	8.0806827
			1.2941636	45.1479	2.681644	3.5009398			9.4113548
SW809.03	44	44.5	5	562	41	2	0.963256	27.2153277	7

		227.714	22.863570	213.805	7.162040	4.6610082			57.279981
SW809.04	167	286	5	3	01	8	0.98754	80.2568218	7
		304.615	28.805505	272.532	7.484375	5.0031086			85.327629
SW809.05	217	385	6	498	64	9	0.991174	113.301609	4
				41.3100	2.484734	3.4734062			8.6065827
SW809.06	41	41	0.4938648	306	86	4	0.96344	27.3522976	4
			0.4850712	18.1111	1.201914	2.5543183			2.9096498
SW809.07	17	17	5	111	86	6	0.908938	10.9815291	3
				41.2538	2.373659	3.5205353			8.6065827
SWG32.02	41	41	0.4938648	84	21	5	0.965334	28.8467086	4
		101.333	15.071557	90.1604	4.694679	4.1069418			21.496200
SWG32.03	83	333	8	386	9	9	0.980706	51.8295843	3
			9.2962342	163.648	5.377482				50.850983
SWG32.04	154	170.5	9	136	33	4.7879969	0.990256	102.627258	5
		317.285	8.8111908	322.004	5.593233	5.4785320			
SWG32.05	292	714	6	987	27	2	0.995124	205.086136	138.69251
		353.137	14.792722	345.239	6.557215	5.5101147			148.69107
SWG32.08	304	931	3	587	13	1	0.995228	209.555742	3
					0.966091	2.4866551			2.5030219
SWG39.01	15	15	0	15	78	2	0.904668	10.4896572	3
		528.135	22.387572	526.681	10.84031	5.8614962			275.22571
SWG39.02	422	135	9	273	27	3	0.996624	296.208531	7
		249.807	15.468139	235.861	6.028905	5.0531145			81.068072
SWG39.05	210	692	5	084	78	8	0.992116	126.839168	8
		546.722	26.836037	545.455	11.21525	5.8283957			267.31096
SWG39.06	416	772	2	834	23	3	0.99649	284.900285	5
			13.789171	246.842	6.033289				
SWG39.07	215	252.5	4	409	66	5.0622552	0.992004	125.062531	84.09905
					1.870828	3.2234867			6.3090836
Timber.04	32	32	0	32	69	1	0.951664	20.6885137	3
					0.963624	2.3617307			2.3044443
Timber.06	14	14	0	14	11	5	0.89116	9.1877986	1
			10.091014	206.560	5.448567	4.9804185			69.507464
Timber.07	190	212	5	338	22	1	0.991758	121.329774	7
		891.149	54.734200	954.593	19.35277	6.0832006			474.51298
WS4U.02	538	606	7	369	81	9	0.997136	349.162011	6
			19.937958	341.111	7.778163	5.3394405			129.90842
WS4U.03	281	351	3	39	45	1	0.99381	161.550889	7
		613.032		605.653	12.90464	5.8068552			277.90619
WS4U.05	424	609	36.62875	172	5	4	0.996194	262.743037	9
			138.55759	1951.51	16.95901	6.5255707			1387.0462
WS4U.06	753	1887	6	607	04	8	0.998336	600.961539	8
		619.205	35.894854	641.760	13.53377	5.7890665			283.33186
WS4U.07	428	882	9	819	11	3	0.995836	240.153698	7
		1088.04	66.696762	1137.36	18.48859				667.10792
WS4U.08	611	082	7	841	39	6.2573398	0.997706	435.919791	1
					2.738612	3.0383803			6.3090836
WS98SB.01	32	32	0	32	79	7	0.938828	16.3473485	3
		2426.93	197.63015	2484.73	15.80698	6.6025057			1844.5148
WS98SB.02	799	651	8	584	47	6	0.998486	660.501982	3
		1114.49	71.024387	1119.28	17.63597	6.2590029			663.95241
WS98SB.04	610	64	9	408	84	8	0.997732	440.917108	1

		793.105	45.941701	795.717	15.66741	6.0524142			422.68149
WS98SB.05	513	691	3	803	56	2	0.997164	352.609309	6
		603.319	25.719927	643.275	13.57448	5.9470239			337.92165
WS98SB.06	465	149	7	296	65	6	0.996834	315.85597	5
				86.3404	4.601967	4.1681999			22.193839
WS98SB.07	85	86	1.5802193	574	23	5	0.981536	54.1594454	2
					2.070196	3.3413749			7.0549535
WS98SB.09	35	35	0	35	68	1	0.959136	24.4714174	3
		148.687	6.5399460	147.014	5.396665				43.398891
WS98SB.10	138	5	5	608	83	4.5484329	0.985916	71.0025561	2

Supplemental Table 1:

Alpha Diversity Metrics: Results from the Alpha Diversity analysis for 365 switchgrass genotypes.

family	snps	h2	se	>0.9	>0.1	>0.1 (outliers)
Xanthobacteraceae		5	0.45489741	0.15006082	TRUE	TRUE
Sphingomonadaceae		31	0.25080413	0.13608337	TRUE	TRUE
Micrococcaceae		89	0.26493375	0.1376574	FALSE	TRUE
Chitinophagaceae	NA		0.25752125	0.13692033	FALSE	TRUE
Koribacteraceae		6	0.14298423	0.11619551	FALSE	TRUE
Mycobacteriaceae		15	0.06959644	0.08384037	FALSE	TRUE
Pyrinomonadaceae		8	0.0688696	0.08341623	FALSE	TRUE
Pirellulaceae	NA		0.00794786	0.13035936	FALSE	TRUE
Myxococcaceae	NA		0	0.17460424	FALSE	TRUE
Polyangiaceae	NA		0	0.1601444	FALSE	TRUE
Reyranellaceae		18	0	0.13129499	FALSE	TRUE
Bacillaceae		12	0	0.11080426	FALSE	TRUE
Chthoniobacteraceae		7	0	0.08612535	FALSE	TRUE
Nitrosomonadaceae		1	0	0.0821527	FALSE	TRUE
A21b		2	0	0.06449511	FALSE	TRUE
Haliangiaceae		80	0	0.05771382	FALSE	TRUE
Rhodanobacteraceae		11	0	0.05728122	FALSE	TRUE
Nitrospiraceae	NA		0	0.05377501	FALSE	TRUE
Solibacteraceae	NA		0	0.04764666	FALSE	TRUE
Comamonadaceae		5	0	0.04073533	FALSE	TRUE
Pedosphaeraceae	NA		0	0.04072739	FALSE	TRUE
Gaiellaceae		1	0	0.03478031	FALSE	TRUE
Bryobacteraceae		4	0	0.03154768	FALSE	TRUE
Gemmatimonadaceae		3	0	0.0254416	FALSE	TRUE
Steroidobacteraceae	NA		0	0.01622218	FALSE	TRUE
Acidothermaceae		3	-0.0067312	0.00802897	FALSE	TRUE
SC-I-84	NA	NA	NA	FALSE	TRUE	TRUE
Unknown Family_4	NA	NA	NA	FALSE	TRUE	TRUE

Hyphomicrobiaceae	NA	NA	NA	FALSE	TRUE	TRUE
Micromonosporaceae		8	0.32336921	0.14287441	FALSE	TRUE
Caulobacteraceae		2	0.2011677	0.15233479	FALSE	TRUE
Bdellovibrionaceae		12	0.19268472	0.12781354	FALSE	TRUE
Xiphinematobacteraceae		4	0.16183436	0.12038463	FALSE	TRUE
Nocardioidaceae		1	0.12583433	0.1099005	FALSE	TRUE
Oxalobacteraceae		22	0.10620934	0.10302864	FALSE	TRUE
Xanthomonadaceae		16	0.08703035	0.09431779	FALSE	TRUE
Rhizobiaceae		1	0.08088047	0.16039007	FALSE	TRUE
Intrasporangiaceae		91	0.07681519	0.08921872	FALSE	TRUE
Sphingobacteriaceae	NA		0.06792159	0.08320344	FALSE	TRUE
Thermoanaerobaculaceae		11	0.05084146	0.10051362	FALSE	TRUE
Opitutaceae	NA		0.01157036	0.0346631	FALSE	TRUE
Diplorickettsiaceae		2	0.00896882	0.03285347	FALSE	TRUE
Blastocatellaceae	NA		0	0.63004088	FALSE	TRUE
Microscillaceae	NA		0	0.35296219	FALSE	TRUE
Acetobacteraceae	NA		0	0.22778964	FALSE	TRUE
Bifidobacteriaceae	NA		0	0.08574337	FALSE	TRUE
Vermiphilaceae	NA		0	0.08323864	FALSE	TRUE
Burkholderiaceae		31	0	0.06809019	FALSE	TRUE
Vicinamibacteraceae		20	0	0.0513239	FALSE	TRUE
Frankiaceae		2	0	0.03337879	FALSE	TRUE
Microbacteriaceae		42	0	0.02255735	FALSE	TRUE
Solirubrobacteraceae		2	0	0.02232189	FALSE	TRUE
Devosiaceae		3	0	0.02229932	FALSE	TRUE
Ktedonobacteraceae		20	0	0.01184748	FALSE	TRUE
Rhizobiales Incertae Sedis	NA		NA	NA	FALSE	TRUE
X67-14	NA		NA	NA	FALSE	TRUE
TRA3-20	NA		NA	NA	FALSE	TRUE
WD2101 soil group	NA		NA	NA	FALSE	TRUE
JG30-KF-AS9	NA		NA	NA	FALSE	TRUE
Beijerinckiaceae	NA		NA	NA	FALSE	TRUE
env.OPS 17	NA		NA	NA	FALSE	TRUE
Azospirillaceae		1	0.53923556	0.15319359	FALSE	TRUE
Methylophilaceae	NA		0.39228257	0.13234329	FALSE	TRUE
Pseudonocardiaceae		3	0.34591637	0.14266118	FALSE	TRUE
Isosphaeraceae		24	0.2535165	0.13616372	FALSE	TRUE
Paenibacillaceae		11	0.23699145	0.13424919	FALSE	TRUE
Clostridiaceae		309	0.18235269	0.12480892	FALSE	TRUE
Kineosporiaceae		64	0.17626353	0.12688325	FALSE	TRUE

Flavobacteriaceae		211	0.1756527	0.12278504	FALSE	TRUE	FALSE
Iamiaceae		25	0.138249	0.11405764	FALSE	TRUE	FALSE
Geminicoccaceae		50	0.12800102	0.11102073	FALSE	TRUE	TRUE
Labraceae		7	0.11543509	0.13795443	FALSE	TRUE	TRUE
Chthonomonadaceae		33	0.06042788	0.08631568	FALSE	TRUE	FALSE
Phaselicystidaceae	NA		0.04328935	0.04395835	FALSE	TRUE	TRUE
cvE6		14	0.01969061	0.06606464	FALSE	TRUE	FALSE
Anaeromyxobacteraceae	NA		0.01845726	0.02758436	FALSE	TRUE	TRUE
Solimonadaceae		25	0.01797846	0.04217796	FALSE	TRUE	FALSE
Phycisphaeraceae		11	0.01003618	0.07399336	FALSE	TRUE	FALSE
Nakamurellaceae		56	0.00733123	0.0313196	FALSE	TRUE	TRUE
Rubritaleaceae		2	0.00299102	0.02880787	FALSE	TRUE	FALSE
Spirochaetaceae		3	0.00111513	0.0238385	FALSE	TRUE	FALSE
Alicyclobacillaceae		8	5.04E-05	0.03636558	FALSE	TRUE	TRUE
SM2D12		60	0	0.21567637	FALSE	TRUE	FALSE
Moraxellaceae		2	0	0.07885071	FALSE	TRUE	TRUE
Rhodomicrobiaceae		11	0	0.07551665	FALSE	TRUE	FALSE
A0839		1	0	0.05401663	FALSE	TRUE	FALSE
Planococcaceae		1	0	0.04551408	FALSE	TRUE	FALSE
Geodermatophilaceae	NA		0	0.03953639	FALSE	TRUE	TRUE
Hyphomonadaceae		6	0	0.02803625	FALSE	TRUE	FALSE
Streptomyetaceae		11	0	0.0244267	FALSE	TRUE	TRUE
Geobacteraceae		28	0	0.02304121	FALSE	TRUE	TRUE
Pseudomonadaceae		24	0	0.02231061	FALSE	TRUE	TRUE
URHD0088		81	-0.0028494	0.01910465	FALSE	TRUE	FALSE
Abditibacteriaceae		87	-0.005207	0.01375589	FALSE	TRUE	FALSE
Ilumatobacteraceae		3	-0.0054262	0.02290175	FALSE	TRUE	FALSE
Verrucomicrobiaceae		1	-1.8867917	79.8301507	FALSE	TRUE	FALSE
Cellulomonadaceae		15	-1.9632452	67.3985434	FALSE	TRUE	TRUE
Fibrobacteraceae	NA		-2.4936366	137.92784	FALSE	TRUE	FALSE
Thermoactinomycetaceae		23	-2.5751422	150.57728	FALSE	TRUE	FALSE
Peptostreptococcaceae		45	-3.8013187	81.2594218	FALSE	TRUE	FALSE
Parachlamydiaceae		14	-4.6415211	71.2198938	FALSE	TRUE	FALSE
Gemmataceae	NA		NA	NA	FALSE	TRUE	FALSE
Dongiaceae	NA		NA	NA	FALSE	TRUE	FALSE
CPla-3 termite group	NA		NA	NA	FALSE	TRUE	FALSE
Acidobacteriaceae (Subgroup 1)	NA		NA	NA	FALSE	TRUE	TRUE
KF-JG30-B3	NA		NA	NA	FALSE	TRUE	FALSE
X37-13	NA		NA	NA	FALSE	TRUE	FALSE
NS11-12 marine group	NA		NA	NA	FALSE	TRUE	FALSE

AKYH767	NA	NA	NA	FALSE	TRUE	TRUE	
Nostocaceae	NA	NA	NA	FALSE	TRUE	FALSE	
Caldilineaceae		88	0.76067873	0.15879238	FALSE	FALSE	FALSE
Holophagaceae		271	0.65671928	0.15669245	FALSE	FALSE	FALSE
Gallionellaceae		339	0.65416872	0.15683858	FALSE	FALSE	FALSE
Dethiobacteraceae	NA		0.62208092	0.1131101	FALSE	FALSE	FALSE
Amoebophilaceae		243	0.55321342	0.15365691	FALSE	FALSE	FALSE
Coriobacteriaceae		483	0.48429688	0.15094295	FALSE	FALSE	FALSE
Proteiniboraceae		209	0.43875513	0.1493015	FALSE	FALSE	FALSE
Aerococcaceae		231	0.42740944	0.1488965	FALSE	FALSE	FALSE
Sanguibacteraceae		470	0.37437605	0.14575336	FALSE	FALSE	FALSE
Wohlfahrtiimonadaceae		397	0.35941743	0.14514329	FALSE	FALSE	FALSE
Prevotellaceae		69	0.32828338	0.14307546	FALSE	FALSE	FALSE
Sporichthyaceae		197	0.28849102	0.14004792	FALSE	FALSE	FALSE
Alcaligenaceae		368	0.28154792	0.13934373	FALSE	FALSE	FALSE
Defluviicoccaceae		315	0.2798717	0.13911257	FALSE	FALSE	FALSE
Leptospiraceae		229	0.21808269	0.13091858	FALSE	FALSE	FALSE
Cyclobacteriaceae		521	0.20954394	0.13018992	FALSE	FALSE	FALSE
Obscuribacteraceae		219	0.18240802	0.12479559	FALSE	FALSE	FALSE
Spirosomaceae		411	0.17824146	0.12530481	FALSE	FALSE	FALSE
Erysipelotrichaceae		218	0.17748616	0.1232979	FALSE	FALSE	FALSE
Brevibacillaceae		162	0.17234433	0.12269324	FALSE	FALSE	FALSE
Omnitrophaceae		1	0.17212481	0.12300393	FALSE	FALSE	FALSE
Paludibacteraceae		221	0.16980054	0.1239147	FALSE	FALSE	FALSE
Akkermansiaceae	NA		0.16815901	0.12097812	FALSE	FALSE	FALSE
Cryomorphaceae	NA		0.16815901	0.12097812	FALSE	FALSE	FALSE
Bacteroidaceae		95	0.15706174	0.11871881	FALSE	FALSE	FALSE
Leptotrichiaceae		411	0.14468155	0.11591839	FALSE	FALSE	FALSE
Cellvibrionaceae		23	0.13897261	0.11354993	FALSE	FALSE	FALSE
Morganellaceae	NA		0.13096179	0.11149072	FALSE	FALSE	FALSE
Hydrogenophilaceae		418	0.12965953	0.11115586	FALSE	FALSE	FALSE
Terrimicrobiaceae		220	0.12007945	0.10722102	FALSE	FALSE	FALSE
WX65		60	0.11502143	0.10310093	FALSE	FALSE	FALSE
Legionellaceae		154	0.11389058	0.10533955	FALSE	FALSE	FALSE
Sumerlaeaceae		158	0.10742225	0.10392821	FALSE	FALSE	FALSE
Sandaracinaceae		243	0.10576886	0.10177004	FALSE	FALSE	FALSE
Nocardiaceae		35	0.10035008	0.09940176	FALSE	FALSE	FALSE
Halomonadaceae		200	0.08853067	0.15415457	FALSE	FALSE	FALSE
Anaerolineaceae		360	0.08144329	0.09026023	FALSE	FALSE	FALSE
Thermaceae		205	0.07620147	0.14974382	FALSE	FALSE	FALSE

Cytophagaceae	19	0.07041701	0.08371033	FALSE	FALSE	FALSE
Magnetospirillaceae	308	0.06858003	0.09539432	FALSE	FALSE	FALSE
Arcobacteraceae	217	0.06132036	0.07754565	FALSE	FALSE	FALSE
Ruminococcaceae	4	0.05736914	0.07498634	FALSE	FALSE	FALSE
Methyloigellaceae	99	0.05513853	0.07494552	FALSE	FALSE	FALSE
Bacteriovoracaceae	58	0.04963317	0.07027572	FALSE	FALSE	FALSE
Neisseriaceae	117	0.04484694	0.06957396	FALSE	FALSE	FALSE
AKIW781	65	0.04173726	0.06354817	FALSE	FALSE	FALSE
Rubinisphaeraceae	20	0.04112421	0.063642	FALSE	FALSE	FALSE
Gemellaceae	250	0.03846134	0.06204274	FALSE	FALSE	FALSE
Trueperaceae	250	0.03685005	0.06030392	FALSE	FALSE	FALSE
Saccharimonadaceae	250	0.03685005	0.06030392	FALSE	FALSE	FALSE
Oxobacteraceae	250	0.03685005	0.06030392	FALSE	FALSE	FALSE
Oligosphaeraceae	284	0.03302006	0.05765196	FALSE	FALSE	FALSE
Thermomonosporaceae	119	0.0249567	0.0495929	FALSE	FALSE	FALSE
Rhodobacteraceae	22	0.02005565	0.04473901	FALSE	FALSE	FALSE
Pasteurellaceae	302	0.01828478	0.04338533	FALSE	FALSE	FALSE
Lachnospiraceae	104	0.01781246	0.05359081	FALSE	FALSE	FALSE
Selenomonadaceae	302	0.01553585	0.04045114	FALSE	FALSE	FALSE
DEV007	369	0.01132861	0.0358079	FALSE	FALSE	FALSE
Alteromonadaceae	64	0.0105716	0.04212393	FALSE	FALSE	FALSE
Schlesneriaceae	26	0.01026488	0.03455747	FALSE	FALSE	FALSE
Saprospiraceae	199	0.00747033	0.03160117	FALSE	FALSE	FALSE
Actinospicaceae	327	0.00683266	0.03874494	FALSE	FALSE	FALSE
UBA12409	56	0.00375163	0.02858096	FALSE	FALSE	FALSE
Bifidobacteriaceae	267	0.00373363	0.02719774	FALSE	FALSE	FALSE
Sulfurimonadaceae	222	0.00269238	0.02610891	FALSE	FALSE	FALSE
Tannerellaceae	268	0.0022849	0.02572081	FALSE	FALSE	FALSE
Thermomicrobiaceae	221	0.00193853	0.02508234	FALSE	FALSE	FALSE
Vampirovibrionaceae	299	0.00166096	0.02470817	FALSE	FALSE	FALSE
Sulfurospirillaceae	512	0	1.41266348	FALSE	FALSE	FALSE
Sporomusaceae	55	0	0.53576159	FALSE	FALSE	FALSE
Rhodocyclaceae	339	0	0.46270774	FALSE	FALSE	FALSE
Veillonellaceae	NA	0	0.28029337	FALSE	FALSE	FALSE
BSV26	26	0	0.1916218	FALSE	FALSE	FALSE
Micropepsaceae	22	0	0.17047885	FALSE	FALSE	FALSE
Dysgonomonadaceae	320	0	0.10911275	FALSE	FALSE	FALSE
Eggerthellaceae	NA	0	0.10837229	FALSE	FALSE	FALSE
Leuconostocaceae	NA	0	0.10837229	FALSE	FALSE	FALSE
Streptosporangiaceae	267	0	0.09141077	FALSE	FALSE	FALSE

Crocinitomicaceae	7	0	0.08330471	FALSE	FALSE	FALSE
Chloroflexaceae	73	0	0.06733627	FALSE	FALSE	FALSE
Rhodothermaceae	NA	0	0.05466097	FALSE	FALSE	FALSE
LWQ8	240	0	0.03622526	FALSE	FALSE	FALSE
Fimbrimonadaceae	415	0	0.03347359	FALSE	FALSE	FALSE
Acidiferrobacteraceae	67	0	0.02598065	FALSE	FALSE	FALSE
Silvanigrellaceae	5	0	0.02305175	FALSE	FALSE	FALSE
Caloramatoraceae	416	0	0.02255735	FALSE	FALSE	FALSE
Chromobacteriaceae	92	0	0.02255735	FALSE	FALSE	FALSE
Haliaceae	272	0	0.02226287	FALSE	FALSE	FALSE
Weeksellaceae	26	0	0.02212612	FALSE	FALSE	FALSE
Longimicrobiaceae	57	0	0.0220318	FALSE	FALSE	FALSE
Simkaniaceae	5	0	0.02027306	FALSE	FALSE	FALSE
Carnobacteriaceae	538	0	0.0185994	FALSE	FALSE	FALSE
Blattabacteriaceae	NA	0	0.0148498	FALSE	FALSE	FALSE
Nannocystaceae	3	0	0.01281651	FALSE	FALSE	FALSE
Hymenobacteraceae	96	0	0.01103008	FALSE	FALSE	FALSE
Enterobacteriaceae	281	-0.001057	0.02115837	FALSE	FALSE	FALSE
Desulfovibrionaceae	419	-0.0016626	0.02045536	FALSE	FALSE	FALSE
Staphylococcaceae	22	-0.0459734	0.15984776	FALSE	FALSE	FALSE
S32	418	-0.17952	4.0598948	FALSE	FALSE	FALSE
Desulfobulbaceae	408	-0.9083787	105.776702	FALSE	FALSE	FALSE
Barnesiellaceae	408	-0.9083787	105.776702	FALSE	FALSE	FALSE
Psychromonadaceae	278	-1.7288246	91.5697065	FALSE	FALSE	FALSE
Vulgatibacteraceae	84	-1.7783036	1.20791225	FALSE	FALSE	FALSE
Kaistiaaceae	324	-1.8310767	83.8592642	FALSE	FALSE	FALSE
Bogoriellaceae	280	-1.8538133	80.2846575	FALSE	FALSE	FALSE
Idiomarinaceae	169	-2.4796445	131.65033	FALSE	FALSE	FALSE
Microtrichaceae	85	-2.9002719	609.137226	FALSE	FALSE	FALSE
Paracaedibacteraceae	13	-2.9232174	367.275503	FALSE	FALSE	FALSE
Prolixibacteraceae	13	-3.0826234	175.050572	FALSE	FALSE	FALSE
Woeseiaceae	73	-3.1008482	168.423304	FALSE	FALSE	FALSE
Demequinaceae	NA	-3.2695624	121.800573	FALSE	FALSE	FALSE
Caldakalibacillaceae	20	-3.3221406	114.828941	FALSE	FALSE	FALSE
Halanaerobiaceae	75	-3.5777428	90.7245235	FALSE	FALSE	FALSE
Acholeplasmataceae	111	-3.6316076	87.8364168	FALSE	FALSE	FALSE
Erysipelatoclostridiaceae	96	-3.7160219	84.1578126	FALSE	FALSE	FALSE
Alcanivoracaceae1	70	-3.7730001	82.1393022	FALSE	FALSE	FALSE
Aneurinibacillaceae	84	-3.8207342	80.6500404	FALSE	FALSE	FALSE
Streptococcaceae	56	-4.0198736	76.1528722	FALSE	FALSE	FALSE

Deinococcaceae		60	-4.0612542	75.4414778	FALSE	FALSE	FALSE
Porphyromonadaceae		23	-7.0024208	86.3138376	FALSE	FALSE	FALSE
Corynebacteriaceae		42	-14.232355	203.724539	FALSE	FALSE	FALSE
KD3-93	NA		NA	NA	FALSE	FALSE	FALSE
Lactobacillaceae	NA		NA	NA	FALSE	FALSE	FALSE
CWT CU03-E12	NA		NA	NA	FALSE	FALSE	FALSE
Desulfotobiaceae	NA		NA	NA	FALSE	FALSE	FALSE
JG30-KF-CM45	NA		NA	NA	FALSE	FALSE	FALSE
Christensenellaceae	NA		NA	NA	FALSE	FALSE	FALSE
Unknown Family	NA		NA	NA	FALSE	FALSE	FALSE
Actinomycetaceae	NA		NA	NA	FALSE	FALSE	FALSE
Amb-16S-1034	NA		NA	NA	FALSE	FALSE	FALSE
bac2nit3	NA		NA	NA	FALSE	FALSE	FALSE
27F-1492R	NA		NA	NA	FALSE	FALSE	FALSE
Caedibacteraceae	NA		NA	NA	FALSE	FALSE	FALSE
type III	NA		NA	NA	FALSE	FALSE	FALSE
Symbiobacteraceae	NA		NA	NA	FALSE	FALSE	FALSE
Bacteroidetes vadinHA17	NA		NA	NA	FALSE	FALSE	FALSE
Shewanellaceae	NA		NA	NA	FALSE	FALSE	FALSE
Parvibaculaceae	NA		NA	NA	FALSE	FALSE	FALSE
LiUU-11-161	NA		NA	NA	FALSE	FALSE	FALSE
Coxiellaceae	NA		NA	NA	FALSE	FALSE	FALSE
Catenulisporaceae	NA		NA	NA	FALSE	FALSE	FALSE
Inquilinaceae	NA		NA	NA	FALSE	FALSE	FALSE
UCG-010	NA		NA	NA	FALSE	FALSE	FALSE
Rubrobacteriaceae	NA		NA	NA	FALSE	FALSE	FALSE
[Eubacterium] coprostanoligenes group	NA		NA	NA	FALSE	FALSE	FALSE
Phormidiaceae	NA		NA	NA	FALSE	FALSE	FALSE
AB1	NA		NA	NA	FALSE	FALSE	FALSE
Streptosporangiales Incertae Sedis	NA		NA	NA	FALSE	FALSE	FALSE
Pseudanabaenaceae	NA		NA	NA	FALSE	FALSE	FALSE
Dermabacteraceae	NA		NA	NA	FALSE	FALSE	FALSE
Caldicoprobacteraceae	NA		NA	NA	FALSE	FALSE	FALSE
NS9 marine group	NA		NA	NA	FALSE	FALSE	FALSE
Puniceicoccaceae	NA		NA	NA	FALSE	FALSE	FALSE
Rickettsiaceae	NA		NA	NA	FALSE	FALSE	FALSE
Desulfotibacteraceae	NA		NA	NA	FALSE	FALSE	FALSE
Chitinibacteraceae	NA		NA	NA	FALSE	FALSE	FALSE
Desulfallus-Sporotomaculum	NA		NA	NA	FALSE	FALSE	FALSE
Syntrophomonadaceae	NA		NA	NA	FALSE	FALSE	FALSE

Supplemental Table 2:

Bacterial Family Association Data: Data represents the number of significant SNPs associated with each family, the heritability estimate and standard error, and an indicator for their presence above the occupancy thresholds 0.9 and 0.1 for the full ASV dataset and 0.1 for the outlier ASV dataset.

GO term	Ontology	Description	Number in input list	Number in BG/Ref	p-value	FDR	Family
GO:0016887	F	ATPase activity	15	698	0.0044	0.04	Xanthobacteraceae
GO:0016817	F	hydrolase activity, acting on acid anhydrides	26	1415	0.0019	0.02	Xanthobacteraceae
GO:0016818	F	hydrolase activity, acting on acid anhydrides, in phosphorus-containing anhydrides	26	1391	0.0015	0.02	Xanthobacteraceae
GO:0016874	F	ligase activity	16	600	0.0003	0.02	Xanthobacteraceae
GO:0003774	F	motor activity	6	152	0.0045	0.04	Xanthobacteraceae
GO:0017111	F	nucleoside-triphosphatase activity	26	1324	0.0007	0.02	Xanthobacteraceae
GO:0016462	F	pyrophosphatase activity	26	1357	0.0011	0.02	Xanthobacteraceae
GO:0019787	F	small conjugating protein ligase activity	6	130	0.0021	0.02	Xanthobacteraceae
GO:0004842	F	ubiquitin-protein ligase activity	6	130	0.0021	0.02	Xanthobacteraceae
GO:0005623	C	cell	103	8213	0.0085	0.03	Sphingomonadaceae
GO:0004446	C	cell part	103	8213	0.0085	0.03	Sphingomonadaceae
GO:0016021	C	integral to membrane	27	1616	0.0083	0.03	Sphingomonadaceae
GO:0003124	C	intrinsic to membrane	27	1651	0.011	0.03	Sphingomonadaceae
GO:0001602	C	membrane	58	4123	0.0063	0.01	Sphingomonadaceae
GO:0004445	C	membrane part	37	2042	0.0005	0.02	Sphingomonadaceae
GO:0004222	F	metalloendopeptidase activity	6	100	0.0007	0.02	Sphingomonadaceae
GO:0008237	F	metallopeptidase activity	8	119	0.0000	0.00	Sphingomonadaceae
GO:0007072	P	cellular macromolecule localization	10	311	0.0016	0.02	Sphingomonadaceae
GO:0004423	P	cellular metabolic process	142	11155	0.0006	0.01	Sphingomonadaceae
GO:0009987	P	cellular process	190	14248	0.0009	0.00	Sphingomonadaceae
GO:0003461	P	cellular protein localization	10	311	0.0016	0.02	Sphingomonadaceae
GO:0009719	P	response to endogenous stimulus	5	48	0.0001	0.00	Sphingomonadaceae
GO:0009725	P	response to hormone stimulus	5	48	0.0001	0.00	Sphingomonadaceae
GO:0001003	P	response to organic substance	5	48	0.0001	0.00	Sphingomonadaceae
GO:0008026	F	ATP-dependent helicase activity	5	232	0.0084	0.04	Micromonosporaceae
GO:0001687	F	ATPase activity	12	698	0.0004	0.00	Micromonosporaceae
GO:0004262	F	ATPase activity, coupled	9	422	0.0004	0.00	Micromonosporaceae
GO:0004386	F	helicase activity	8	477	0.0042	0.03	Micromonosporaceae
GO:0001678	F	hydrolase activity	43	5652	0.0075	0.04	Micromonosporaceae
GO:0001681	F	hydrolase activity, acting on acid anhydrides	19	1415	0.0002	0.00	Micromonosporaceae
GO:0001681	F	hydrolase activity, acting on acid anhydrides, in phosphorus-containing anhydrides	19	1391	0.0001	0.00	Micromonosporaceae

GO:00					0.0000	0.00	Micromonos
17111	F	nucleoside-triphosphatase activity	19	1324	9	27	poraceae
GO:00						0.04	Micromonos
70035	F	purine NTP-dependent helicase activity	5	232	0.0084	4	poraceae
GO:00					0.0001	0.00	Micromonos
16462	F	pyrophosphatase activity	19	1357	2	27	poraceae
GO:00						0.04	Micromonos
07242	P	intracellular signaling cascade	7	291	0.001	1	poraceae
GO:00						0.04	Micromonos
07264	P	small GTPase mediated signal transduction	7	289	0.001	1	poraceae

Supplemental Table 3:

GO Term Data: Data represents the Ontologies, Descriptions, Number of genes in the input list and reference genome, p-value, and FDR for GO terms associated with Xanthobacteraceae, Sphingomonadaceae, and Micromonosporaceae abundances.