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Effects of Lake Erie dredged material on microbiomes in a farm soil of Northwestern Ohio

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Abstract

Dredged materials are often considered as candidates for replenishing lost topsoils in the watersheds of rivers and lakes. This study aimed to investigate the impacts of Lake Erie dredged material on the microbial community in a farm soil of Northwestern Ohio. Dredged material from the Toledo Harbor, OH was mixed with a local farm soil at ratios of 0:100, 10:90, 20:80, and 100:0 for soybean growth in a greenhouse for 123 days and was subject to 16S rRNA gene sequencing. α-Diversity analysis revealed that although the original dredged material hosted a highly diverse microbiome, soils blended with the dredged material had similar levels of bacterial diversity to 100% farm soil throughout the experiment. β-Diversity analysis demonstrated that, given the same plant status, that is, with or without soybean, blended soils had similar bacterial communities to 100% farm soil during the experiment. Furthermore, by the end of the experiment, all soils with soybeans merged into one cluster distinctive from those without the plants, indicating that the growth of plants played a dominating role in defining the structure of soil microbiomes. The majority (73.8%) of the operational taxonomy units that were unique to the original dredged material were not detected by the end of the experiment. This study demonstrates that up to 20% of the dredged material can be safely blended into the farm soil without distorting the microbial communities of the latter, implying a potential beneficial use of the dredged material for topsoil restoration.

1 | INTRODUCTION

Each year, several 100 million cubic yards of dredged material are excavated in the United States to clear navigational channels (US EPA, 2007). Situated at the mouth of the Maumee River and along the west boundary of Lake Erie, the Port of Toledo of Ohio, is one of the busiest and most dredged ports on the Great Lakes. To ensure the safety of the cargo ships, up to a million cubic yards of sediments are dredged from the Toledo Harbor each year (Hull & Associates Inc., 2018). Proper disposal of the dredged material has been an environmental challenge. Dumping them back into the lake away from the ship channels was the standard practice. However, this practice carries tremendous environmental risks because

Abbreviations: Contig, contiguous sequence; D0, Day 0; D123, Day 123; D25, Day 25; OTU, operational taxonomy unit; PCoA, principal coordinate analysis; PCR, polymerase chain reaction.

it could interrupt local ecosystems and release high levels of nutrients into the water, posing a threat to water quality (Hull & Associates Inc., 2018; W. Liu et al., 2019; Moog et al., 2018). Consequently, open-lake disposal has been banned by Ohio Laws since July 1, 2020 (Ohio Revised Code, 2015). Safe disposal of the dredged sediments becomes an urgent need.

Returning the dredged material to its original location is viewed by many as an ideal solution to two connected problems, that is, soil erosion and dredged material disposal. The dredged material and its rich nutrients, organic matters, and microbes could be a good supplement to local farms to replenish their lost topsoil, which was in fact the origin of the dredged material. However, before the practice can be widely adopted, its impacts on local soil ecosystems must be carefully evaluated. To address these concerns, we have blended dredged material into a farm soil to grow soybeans in a greenhouse and assessed the impacts of the dredged material on soil health, crop growth, and soil microbiomes. In our previous publication (Brigham et al., 2021), we reported that the dredged material improved the soil health by reducing soil bulk density and increasing soil organic matter, cation exchange capacity, and calcium content; crop biomass and yields were also improved; and phosphorus and nitrogen levels in the runoff water remained the same. Here, we would like to evaluate how the dredged material affects the structure and development of soil microbiomes using 16S rRNA gene as the phylogenetic marker.

As a key component of soil ecosystem, microbes help to maintain and improve soil structure through secretion of clay-binding polysaccharides (Nannipieri et al., 2017) and neoformation and transformation of minerals (Umar et al., 2016). In addition, microbes are essential for plant health and crop yield. They participate in a wide range of biochemical activities that are vital to plants, such as nutrient cycling and waste decomposition (Finzi et al., 2015; Jacoby et al., 2017). They also boost plant immune systems and increase plants resilience to environmental stresses and diseases (Venturi & Keel, 2016). Plants and soil microbiomes coevolve to maintain an ecological balance (Zhalnina et al., 2018), which is critical to soil functions and biomass production (C. Chen et al., 2019; Garbeva et al., 2004).

Core Ideas

- Dredged sediment from Lake Erie has high bacterial diversity.
- Up to 20% of dredged material has little effect on bacterial α- or β-diversity in farm soils.
- Plants play a dominant role in shaping the β-diversity of soil microbiomes.
- Under the same biotic and abiotic influence, different soil blends tend to have similar microbiomes over time.

2 | MATERIALS AND METHODS

2.1 | Collection of soil samples

Detailed information on the greenhouse experiment and soil sample collection has been described in detail in our previous publication (Brigham et al., 2021). Briefly, the dredged sediment was collected from an outdoor facility of the Great Lakes Dredged Material Center for Innovation (Toledo, OH). The sediment had been dewatered without any agricultural management for 2 years prior to the collection; it had a pH value of 7.9 and C:N ratio of 7.99. The farm soil was collected from a conventional farm a few miles away; the soil was Latty silty clay with a pH value of 7.5 and C:N ratio of 5.46. By the end of the experiment, the pH of the dredged material dropped to 7.6, and the pH of the farm soil remained at 7.5.

Soils from both sources were transported to a greenhouse and were mixed with the ratios of dredged material to farm soil of 0:100 (DM0 [100% farm soil]), 10:90 (DM10 [90% farm soil + 10% dredged sediment]), 20:80 (DM20 [80% farm soil + 20% dredged sediment]), and 100:0 (DM100 [100% dredged sediment]). Due to various practical constraints, including transportation and compaction of topsoil by heavy machinery during sediment dispersal, it would not be realistic to recommend more than 20% dredged sediment to a farm field. Each soil mix was used to fill eight 15-L high-density polyethylene buckets, leaving 4 cm clear from the rim. Half of the buckets were randomly chosen for soybean planting, and the other half served as blank controls. Each bucket had one plant. The buckets were randomly placed on the same rack, exposed to the same ambient environment (temperature, moisture, sunlight, and so on), and managed in the same way (such as watering frequencies and volumes). No fertilizers, pesticides, or herbicides were applied during the experiment. Weeds were manually pulled out as soon as they were visible and laid down on the top of the soil in the same bucket for natural decay. The growing season lasted for 123 days. Soil samples were collected on day 0 (D0), day 25 (D25), and day 123 (D123) from each bucket (about 6 cm away from the center and 6-cm deep) and immediately stored at −20°C until further handling. Altogether, we collected 72 soil samples representing 18 treatments: two for D0, eight for D25, and another eight for D123, with four replicates for each treatment. Samples having soybeans have their names end with the suffix "S", for example, DM0_D123S. Please also see Table S1 for sample name keys.

2.2 | Metagenomic DNA extraction and sequencing

Metagenomic DNA was extracted with the Qiagen DNeasy PowerSoil Kit according to the manufacturer's instructions. The quality of DNA was measured with a Nanodrop 1000, and its quantity was measured with a Quantus fluorometer. The DNA extracts were then loaded into a 96-well plate and subjected to 16S rRNA amplicon sequencing. The V4 hypervariable regions of the 16S rRNA genes were amplified with the forward primer GTGCCAGCMGCCGCGGTAA and reverse primer GGACTACHVGGGTWTCTAAT (Kozich et al., 2013). The amplicons were sequenced using the Illumina MiSeq platform, generating paired-end reads of ~250 bases. ZymoBIOMICS Microbial Community DNA Standard (Zymo Research) and water were used as the positive and negative controls for polymerase chain reaction (PCR) and sequencing quality assessment. The sequences are publicly available in the National Centre for Biotechnology Information Sequence Read Archive database with the accession number PRJNA1096646.

2.3 | Data processing and statistical analyses

Sequencing reads were processed using the software package Mothur v.1.46.1 (Kozich et al., 2013) by following its standard operation protocol (https://mothur.org/wiki/miseq_sop/). Briefly, paired reads were assembled into contiguous sequences (contigs), and those with ambiguous base calls, longer than the expected length, or more than eight homopolymers were removed. Unique contigs were aligned to the bacterial alignment database SILVA v.138 (Yilmaz et al., 2013). Contigs with no more than two differences were combined, and chimeras were filtered out using the VSEARCH algorithm (Rognes et al., 2016). The remaining contigs were classified into taxonomy lineages based on the Ribosome Database Project v.18 database (Q. Wang et al., 2007). Meanwhile, the contigs were clustered into operational taxonomy units (OTUs) at 3% distance level. Downstream analyses, including α- and β-diversity analyses, were performed after subsampling with the smallest sample size.

The statistical analyses in this study largely followed the instructions on https://rpubs.com/dillmcfarlan/R_microbiotaSOP. Samples were compared based on three independent factors, that is, soil type (DM0 vs. DM10 vs. DM20 vs. DM100), time (D0 vs. D25 vs. D123), and plant status (soybean vs. no-soybean). For α-diversity analyses, normality of metrics was examined with the Shapiro–Wilk test. Normally distributed metrics were subject to analysis of variance (ANOVA) tests, followed by the Tukey's honest significance tests. Non-normally distributed metrics were subject to the Kruskal–Wallis test, followed by pairwise Wilcoxon rank sum test. For β-diversity analyses, the membership and structure of the 72 samples were analyzed with principal coordinate analysis (PCoA) using Bray–Curtis distances. Permutational analysis of variance (PERMONOVA) was used, followed by pairwise comparisons if more than two samples were involved and the primary PERMONOVA result was significant. Scripts simper_pretty.r and R_krusk.r (asteinberger9, 2020) were used to identify OTUs that contributed the most to the β-diversity separation. A Co-occurrence network was generated with CoNet (Faust & Raes, 2016) and analyzed in Cytoscape (Shannon et al., 2003); clustering of nodes was assisted with CytoCluster (Li et al., 2017).

3 | RESULTS

3.1 | Overview of sequencing data

Our sequencing error rate was 0.025%, determined by comparing the assembled sequences of the mock community to their known sequences. A total of 531,667 contigs were assembled. After removing contigs with PCR errors, poor sequencing qualities, chimeric sequences, false lineages, and positive and negative controls, we ended up with 419,701 clean contigs, 78.9% of the original assembly. The number of clean contigs ranged from 8909 to 3446 in individual samples. These contigs were binned into 12,819 OTUs (≥97% sequence identity), representing a diverse pool of phylogenetic types at a subgenus level. The number of OTUs observed in each sample was plotted as a function of sequencing depth, known as the rarefaction curve (Figure S1). All rarefaction curves approached their plateau stages at the end, showing adequate sequencing depths.

The abundances of these OTUs were highly skewed in the data pool. For example, the most abundant member Otu00001 (*Acidobacteria*_Gp6) had 6482 sequences, which was ~1.5% of the total contigs. On the other hand, the bottom 4204 OTUs were singletons, that is, showed up only once. The abundance of an OTU dropped sharply when moving down the OTU rank, while the cumulative percentages of OTUs increased rapidly (Figure S2). Out of the 12,819 OTUs, the top 10 counted to more than 10% of the total sequences, and the top 2000 OTUs made up to nearly 90% of the total (Figure S2). The observed OTUs were assigned into 34 phyla, with 21.1% of the total contigs attributed to Proteobacteria and about 19.4% to Acidobacteria (Figure S3).

About 26.9% of the clean contigs were confidently assigned to a genus (i.e., without the "unclassifed" suffix). The top five genera were *Stenotrophobacter*, *Sphingomonas*, *Ohtaekwangia*, *Gaiella*, and *Flavisolibacter*. Some of the genera were known to contain species of human pathogens (Bartlett et al., 2022), but only 4.1% of the total contigs were assigned to

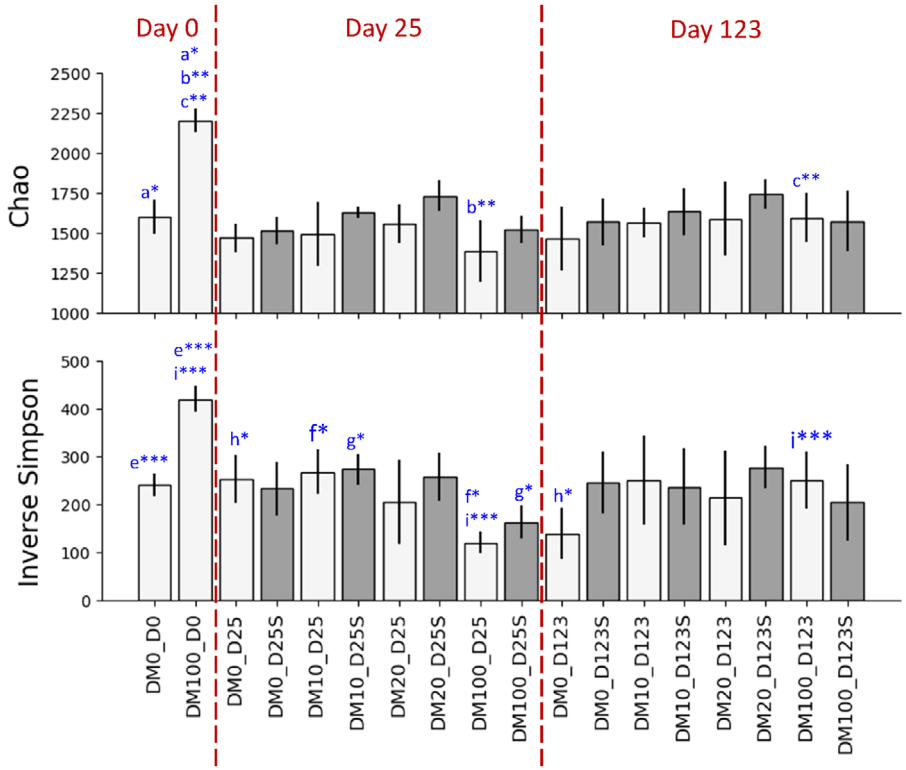

FIGURE 1 α-Diversity analysis of the samples as measured by Chao's richness (top) and Inverse Simpson's diversity (bottom) indices. Error bars are the standard deviations of each treatment. Treatments without soybeans are indicated as white bars, and those with soybeans are in gray (and their names end with the suffix "-S"). Asterisks denote significance within the bars annotated with the same letters on top; *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

these genera, and there was no evidence to suggest that these contigs belonged to any of the pathogenic species. Therefore, the microbiomes involved in this study pose little human health risks.

To compare the samples at an equal sequencing depth, a subsampling process was performed based on the smallest sample size (3446 contigs), which resulted in a total of 10,810 OTUs. The number of OTUs found in individual samples ranged from 734 to 1293 with a mean of 973, and the coverages varied between 79.2% and 90.0% with a mean of 86.0%. These metrics suggested that our subsamples were able to cover the majority members of the original bacterial communities and were then used for downstream analyses.

3.2 | α-Diversity measurements

The richness of the samples was measured by Chao's richness index (Figure 1, upper panel), which was non-normally distributed according to the Shapiro–Wilk test (p-value = 0.006605). Kruskal–Wallis and Wilcoxon tests revealed that on D0 the dredged material (DM100_D0) started with a much richer bacterial community than the farm soil (DM0_D0) (p-value = 0.02092), but the difference between the two diminished by D25. DM100_D0 also had a higher richness level than DM100_D25 or DM100_D123 (p-value = 0.0061 in both cases), while the latter two were like each other, indicating a loss of richness in the dredged material by D25.

The diversity of the samples was measured by the inverse Simpson index (Figure 1, lower panel), which was normally distributed according to the Shapiro–Wilk test (p-value = 0.5182) and was then subjected to ANOVA and Tukey's honest significance tests. On D0, the dredged material (DM100_D0) was highly diverse compared to the farm soil (DM0_D0) (p-value = 0.000143). By D123, all treatments were similar, despite the soil types and plant status. When traced across the timeline, the diversity of the dredged material dropped sharply from D0 to D25 (DM100_D0 vs. DM100_D25, p-value = 0.0000180) and then partially recovered by D123 (p-values were 0.0077600 for DM100_D25 vs. DM100_D123 and 0.0013595 for DM100_D0 vs. DM100_D123). The diversity of the farm soil remained at similar levels from D0 to D25 and then decreased by D123 (DM0_D25 vs. DM0_D123, p-value = 0.0303434). When plant status was concerned, none of the comparable plant and no-plant pairs (e.g., DM0_D25 vs. DM0_D25S) showed any difference.

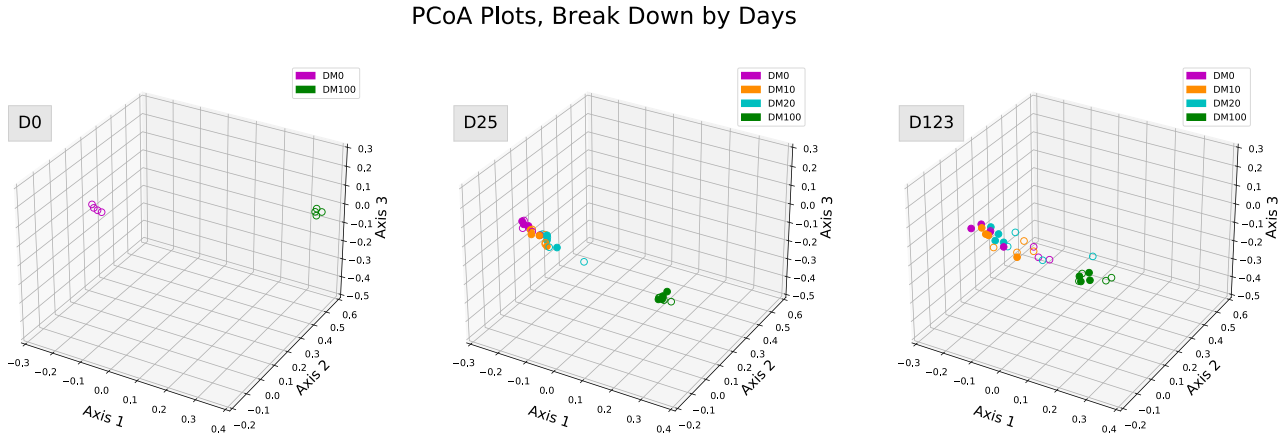

FIGURE 2 Principal coordinate analysis (PCoA) clustering on different days. Open dots refer to samples with no soybean, and filled dots represent those with soybeans.

These results suggested that although the dredged material started with a highly diverse microbiome, many of the community members were undetectable by D25. Meanwhile, microbes from the greenhouse environment (such as air and water) started to colonize the dredged material and partially compensated the lost diversity by D123. At the end of the experiment, the α-diversity levels in all treatments were similar.

3.3 | β-Diversity measurements

In PCoA analysis, the first three axes explained up to 55.6%, 74.9%, and 87.2% of the Bray–Curtis differences among all samples. Inspecting the PCoA results in the three-dimensional (3D) space revealed the dynamics of the microbial communities (Figure 2). At the beginning of the experiment (D0), the dredged material (DM100_D0) and farm soil (DM0_D0) hosted drastically different microbiomes (p-value = 0.032). By D25, the DM0 samples were mixed with the DM10 and DM20 samples, and they were clearly separated from the DM100 samples, regardless of whether there were soybeans or not (p-value < 0.001). These results suggest that at this stage, the bacteria populations in the blended samples were largely inherited from the original farm soil. By the end of the experiment (D123), samples became more dispersed, although the DM100 samples were still separated from other soil types (p-value < 0.001). Meanwhile, the samples with soybeans and those without soybeans began to separate, no matter what the soil types were (p-value = 0.002).

The same soil type from different time points was distinct from each other (p-value < 0.05), exhibiting a development trend over the time (Figure S4). These patterns reveal that dredged material has no dominating impact on microbiome structures in the blended soils. Instead, plant status and time are the determination factors.

3.4 | OTUs differed in the plant and no-plant groups on Day 123

Note that 182 OTUs that individually contributed at least 0.1% to the separation of the plants versus no-plants groups on D123 were identified, and 34 of them were statistically significant (p-value < 0.05 after correction from false discovery rate), which were further examined by plotting their fold changes against their average abundance (Figure S5). Seventeen OTUs dominated the plant group, with 14 skewed for 2× or more (green circles in Figure S5). Another 17 OTUs were prevalent in the no-plant group; all of them were skewed for at least 2×, including nine OTUs that were skewed for 10× or more (solid red dots in Figure S5). OTUs that were overrepresented in the plant group generally had high relative abundances and a narrower range of fold changes, and those overrepresented in the no-plant group tended to have high levels of skewness and lower relative abundances. These patterns highlighted the powerful regulation effects of plants on soil microbes. The growth of soybean selectively fostered a set of microbial species, imposing a biotic constraint on the structure of microbiomes. On the other hand, when there was no plant, the microbial structure became more relaxed and had greater freedom to diversify, resulting in more skewed OTUs.

The skewed OTUs were classified at the genus level and plotted according to their relative abundance. The 17 OTUs that were more prevalent in the plant group were classified into nine genera (Figure 3). The top three abundant genera belonged to the phyla Acidobacteria (Gp6_unclassified, *Stenotrophobacter*) and Verrucomicrobia (Verrucomicrobia_unclassified). The 17 OTUs that were prevalent in the no-plants group were classified into 16 genera (Figure 4), with the top three abundant genera belonging to the phyla Proteobacteria (*Hydrogenophaga, Arenimonas*) and Bacteroidetes (*Terrimonas*). *Imperialibacter* (Otu00694) and an unclassified genus in the phylum Chloroflexi (Otu00204,

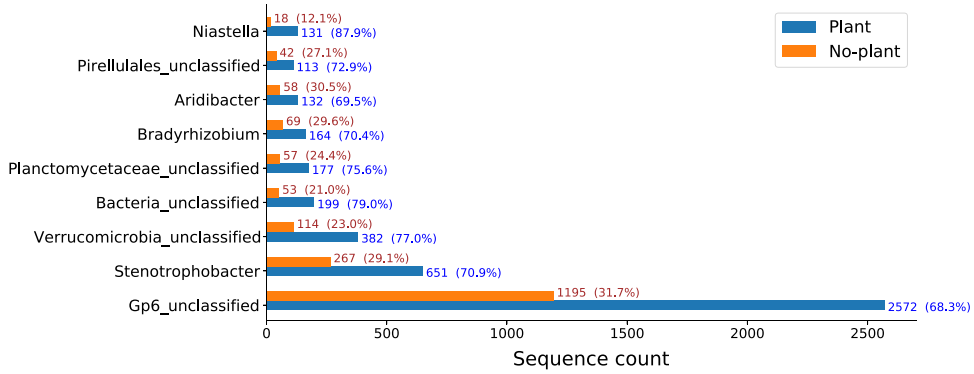

FIGURE 3 Genera dominating the plant group. Values next to each bar are the collective relative abundances for each genus. The relative percentages of each plant versus no-plant pair are included in parentheses.

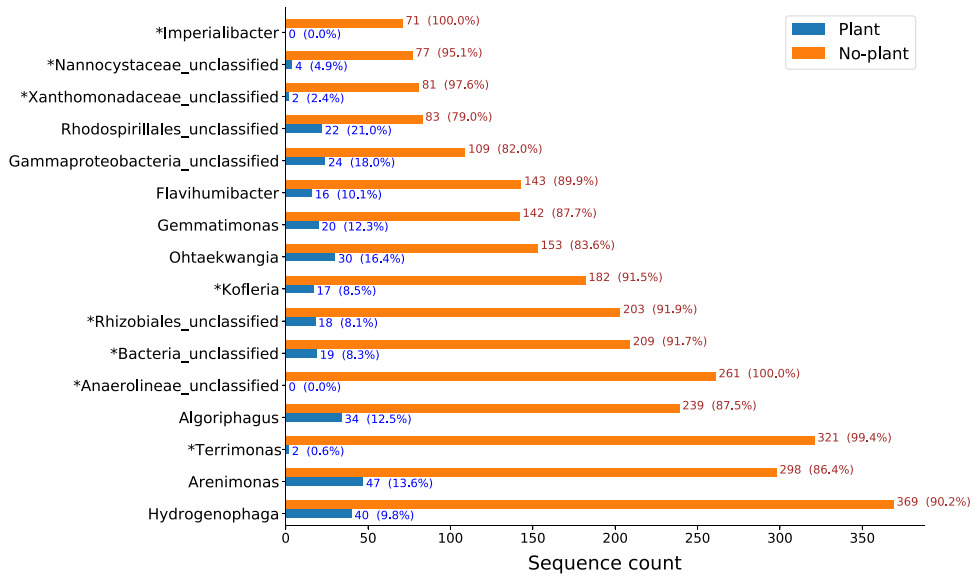

FIGURE 4 Genera dominating the no-plant group. Values next to each bar are the collective relative abundances for each genus. The relative percentages of each plant versus no-plant pair are included in parentheses. Genera that are skewed for 10× for more are marked with asterisks.

Anaerolineae_unclassified) were only found in the no-plant group.

The skewed OTUs were further analyzed through co-occurrence network analysis with CoNet (Faust & Raes, 2016). Under the same network building method and settings, no significant associations among the OTUs were identified with the plant group, that is, zero node and zero edge, whereas the OTUs in the no-plant group generated a network of 31 nodes and 136 edges (Figure 5A). This indicates that regulation of plants on these OTUs was highly complex and did not follow any simple patterns. In the no-plant group, these OTUs formed two connected components. The main component consisted of 29 nodes and 135 edges, and the minor one had two nodes and one edge. Both nodes of the minor component belonged to the order Myxococcales, but Otu00250 was in the family *Kofleriaceae* and Otu00470 in *Nannocystaceae*. The entire network had more positive edges than negative ones (96 vs. 40).

The network had a diameter of 4, a radius of 2, and a characteristic path length of 1.8, indicating a small-world topology. The network was well connected with a density of 0.33, and the average number of neighbors of each node was 9.3. In addition, the network had a heterogeneity of 0.58, suggesting a substantial tendency to contain hub nodes. Indeed, Otu00055 and Otu00057 were the top two hub nodes, both had a degree of 19 (14 positives + 5 negatives), and both belong to the order Gp6 in the phylum of Acidobacteria. They also had the highest positive degree among all nodes. Otu00202, a member of the order Chitinophagales in the phylum *Bacteroidetes*, had the highest negative degree, with five positives and 10 negative edges. Otu00207, a member of the order Cytophagales, also in the phylum *Bacteroidetes*, had the

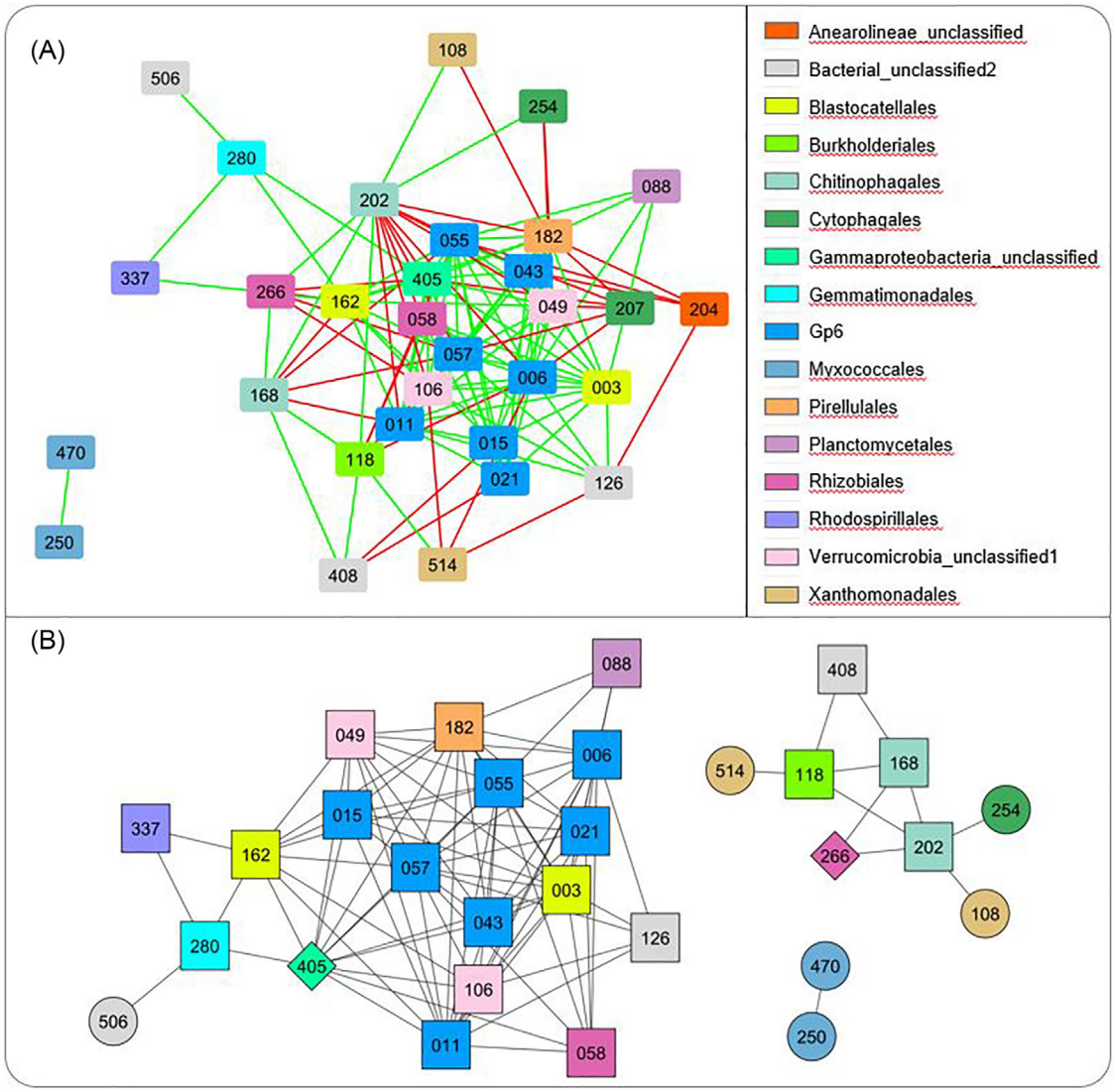

FIGURE 5 Co-occurrence network of the operational taxonomy units (OTUs) that were differentially expressed in the no-plant group on Day 123. Each node is an OTU, labeled with their IDs in the form of Otu00xxx and colored by their orders. (A) The entire network. Positive (copresence) edges are shown in green, and negative (mutual exclusion) edges are shown in red. (B) Cluster identification on the positive edges. Square nodes are members of a cluster, diamond-shaped are the seeds of their respective clusters, and round ones are unclustered. The network was generated with CoNet (Faust & Raes, 2016) and clustered with CytoCluster (Li et al., 2017).

second highest negative degree of six, with zero positive edge. Meanwhile, Otu00162 (Blastocatellales), Otu00182 (Pirellulales), and Otu00405 (Gammaproteobacteria_unclassified) had the highest betweenness centrality of 0.12, 0.10, and 0.10, respectively, indicating their bottleneck roles in the network.

The network had a clustering coefficient of 0.63. An analysis on their positive edges with CytoCluster (Li et al., 2017) identified two clusters: one with 18 nodes and 84 edges and the other with five nodes and seven edges (Figure 5B). Overall, OTUs belonging to the same orders were placed in the same cluster, indicating their shared ecological preferences and functions in the microbial community. The only exceptions were the pairs of Otu00058-Otu00266 (Rhizobiales) and Otu00126-Otu00408 (Bacteria_unclassified2). Among them, Otu00058 was in the family *Bradyrhizobiaceae*, well known for their nitrogen-fixing ability and symbiotic relationship with legumes, such as soybean; Otu00266 belonged to an unclassified family. The large cluster was dominated by Acidobacteria, including Gp6 and Blastocatellales (Otu00003 and Otu00162), but also contained members from Proteobacteria (Gammaproteobacteria_unclassified, Rhodospirillales, and Rhizobiales), Planctomycetes (Planctomycetales, Pirellulales), Gemmatimonadetes (Gemmatimonadales), and Verrucomicrobia (Verrucomicrobia_unclassified1). The smaller cluster mainly had members from Proteobacteria (Burkholderiales, Rhizobiales) and Bacteroidetes (Chitinophagales).

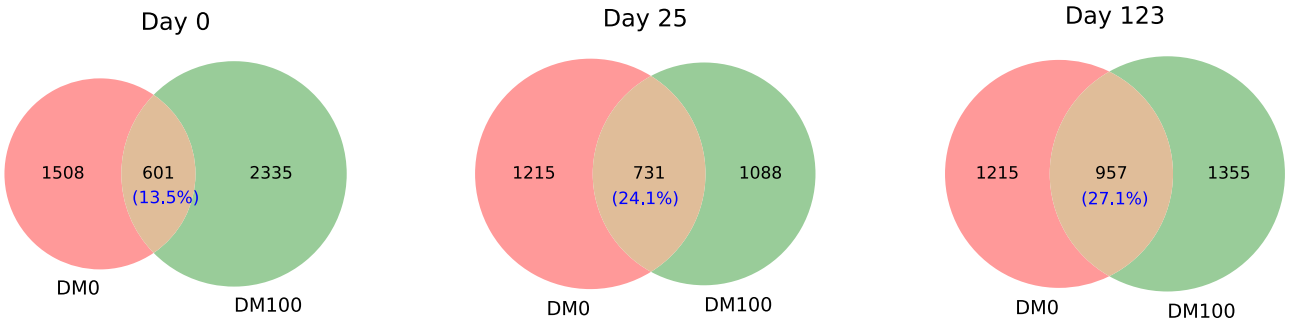

FIGURE 6 Numbers of operational taxonomy units (OTUs) in the farm soil and the dredged material without soybeans. Numbers in blue are the percentages of shared OTU compared to the union of the pairs.

3.5 | OTUs differed in the farm soil and the dredged material

At the beginning of the greenhouse experiment, the dredged material harbored a rich microbiota that was distinctive from the farm soil. In the PCoA plots (Figure 2), when there were no plants, the microbiome centroids of the two soil types had Euclidean distances of 0.74, 0.60, and 0.28 on Days 0, 25, and 123, respectively, showing a trend of convergence. When soybeans were planted, the distance between the two soils reduced from 0.58 on D25 to 0.40 on D123, which was a slower progression pace but nonetheless the same trend. This again reflected the constraint of plant growth on microbiome development.

Examination of the memberships of the microbiomes of DM0 versus DM100, no soybeans, uncovered the same trend of convergence (Figure 6). On D0, the dredged material had 2936 OTUs, and the farm soil had 2109. They shared 601 OTUs, or 13.5% of the total. That percentage increased to 24.1% by D25 and 27.1% by D123, showing that as time progressed, the two soil types resembled each other more and more.

Among the 2335 OTUs that were unique to the dredged material on D0, 2262 of them (96.9%) had less than 20 sequences (Figure S6), and 1211 of them (51.9%) were singletons. Given the high quality of our sequencing data (with an error rate of 0.025%), these singletons were most likely to be authentic. By D123, 611 of these unique OTUs (26.2%) remained in at least one of the buckets, regardless of soil type and plant status. These surviving OTUs were grouped at the phylum level, and their relative abundances in each treatment group were analyzed (Figure S7). In most cases, the survived OTUs had reduced numbers of sequences compared to the original dredge (DM100_D0). It is worthwhile to point out that although some OTUs were not detected in DM0_D0, they were found in DM0_D123 and DM0_D123S, probably seeded by the greenhouse environment during the experiment. Many of the phyla also demonstrated a plant versus no-plant pattern, another emphasis on the effects of plant growth on soil microbes.

4 | DISCUSSIONS

4.1 | The dredged material had little impact on farm soil microbiomes in the long run

In this study, we observed that up to 20% of the dredged material had no measurable impacts on soil microbiome. The lack of dredge's effect is not unique to our study; others also observed little to no change in microbiomes growing on dredged material (Mattei et al., 2017), sometimes even with 75% dredge material to 25% local soil if plants were present (Chiellini et al., 2013). Microbial systems seem to homogenize under the pressures of plant but soil selection in most cases, although synergistic effects have been observed with multiple amendment methods. For example, soil amended with 50% of dredged material and 5% of biochar resulted in an increase in α-diversity of the microbiome, while neither 50% dredge nor 5% biochar by itself was enough to cause a significant change (Huang et al., 2019).

4.2 | Impacts of soybean growth on bacterial communities—The plant effect

A persistent theme we observed in this work is the impacts of plant growth on soil microbiomes. It has long been recognized that composition and activities of rhizosphere microbiomes are regulated and constrained by the constant interaction between live roots and microbes (Venturi & Keel, 2016). Our data demonstrate that the influence of plants on microbes goes beyond rhizospheres. For instance, the PCoA plots illustrate that the growth of soybeans from seedlings on D25 to mature plants on D123 drastically shifts the soil microbial structures, causing the no-plant samples to separate from their

plant-growing counterparts, while different soil types begin to resemble each other (Figure 2). The analyses on the OTUs differentially present in the plant versus no-plant group (Figure S5) and the fates of OTUs unique to the dredged material (Figure S6) resonate the dominating roles that the soybeans play in defining microbial community structures.

Soils domesticated by crop plants are distinct from undomesticated soils in their microbial taxa (Edwards et al., 2019). Our phylogenetic analysis reveals that the soybean and non-soybean groups did harbor distinct taxa profiles. Among the genera that have been characterized and are dominating in the plant group, *Stenotrophobacter* and *Aridibacter* are Gram-negative aerobes belonging to the phylum *Acidobacteria*, and both have been isolated from savannah soils (Huber et al., 2014; Pascual et al., 2015). *Bradyrhizobium* are slow-growing *rhizobiales*, and many of them live a commensal, nodule, and nitrogen-fixating lifestyle (Jordan, 1982), even though some species have lost the nitrogen fixating genes and abandoned commensalism (Avontuur et al., 2019). *Niastella* spp. are Gram-negative and aerobic, belonging to the phylum *Bacteroidetes*; they have been found in farmland soils (Weon et al., 2006), soil crusts of deserts (B. Zhang et al., 2016), and persimmon tree rhizosphere (Akter et al., 2021).

Among the genera that were prevalent in the no-plant group, *Imperialibacter* and *Terrimonas* belong to the Bacteriodetes phylum and are Gram-negative and aerobic. The former has been isolated from groundwater (H. Wang et al., 2013), and the latter has been found in multiple rhizospheres and farm soils (Han et al., 2017; Jiang et al., 2018; Kim et al., 2017). *Arenimonas* belongs to the Proteobacteria phylum and is Gram-negative, non-motile, non-spore-forming, and rod-shaped; they have been isolated from a variety of environments, including soil (S. Zhang et al., 2015), reservoir sediment (Huy et al., 2013), active sludge (H. Liu et al., 2018), freshwater (Yuan et al., 2014), iron mine (F. Chen et al., 2012), and so on.

4.3 | Impacts of environmental conditions on bacterial communities—The time effect

When constraints from the plants are lifted, abiotic environmental factors become the main force that governs the development of soil microbiomes. This can be best illustrated by the development of the microbiomes in the dredged material. At the time of collection, the dredged material resembled a wild soil as opposed to the domesticated farm soil. Over the course of 123 days in the greenhouse, various abiotic constraints were selected for certain taxa in the soil, pushing the dredged material to resemble the farm soil more and more (Figures 2 and 5). Abiotic factors that could be affecting the microbial community include soil moisture, nutrients, pH, temperature, and so on. It has been documented in many studies that the structure of soil microbial communities is heavily affected by seasonal and climate changes (Barboza et al., 2018; Voriskova et al., 2019). In our case, it is likely that all the abovementioned forces played a role in driving the DM100 microbiome to converge with DM0. It is worth noting that sometimes even though changes in community structures are not prominent, microbes can cope with environmental variations via differential gene expression (Bei et al., 2021), which is a topic out of the scope of this study.

5 | CONCLUSIONS

Among the three factors we have investigated here, that is, soil types, time, and plant status, soil type is not significant in shaping soil microbiomes in the long run. Time and the growth of plants are two influential factors that drive the development of soil microbiomes. Our results suggest that applying dredged material to farm field should not interrupt the diversity and structure of the indigenous microbial communities. Therefore, from the microbial ecology perspective, it is safe to use the dredged material to replenish lost topsoil of farmlands.

AUTHOR CONTRIBUTIONS

Jyotshana Gautam: Investigation; methodology. **Wolfgang Ebersole**: Writing—original draft; writing—review and editing. **Russell Brigham**: Investigation; methodology. **Junfeng Shang**: Data curation; formal analysis; software; validation; writing—review and editing. **Angélica Vázquez-Ortega**: Conceptualization; funding acquisition; resources; supervision; writing—review and editing. **Zhaohui Xu**: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing—original draft; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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