ARTICLE

Profiling Lignocellulose Degraders in the Microbiome of Rice Straw from Three Selected Lowland Farms in General Santos City, Philippines Using a High-Throughput Microarray Platform

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ABSTRACT

Crop residues, such as rice straw, usually regarded as agricultural wastes recalcitrant to degradation, offer a myriad of services in the field, including reservoirs of valuable microorganisms and bioactive substances that are necessary for productive agroecosystems. However, very few studies report on the utilization of rice straw as a source of lignin-degrading microorganisms. This study probed into the taxonomic diversity of microorganisms associated with rice straw using metagenomic DNA obtained from samples collected in three lowland rice fields in General Santos City, Philippines for bioprospecting of microorganisms with ligninolytic potential and expanding the knowledge on prokaryotic lignin-degraders. Three samples collected from each site were pooled into one sample for the extraction of genomic DNA that was further subjected to the Axiom™ Microbiome Array (AMA) analysis, a relatively new high-throughput detection system, that can comprehensively identify a wide range of microorganisms at the species and strain levels. The sequences identified via AMA analysis were distributed across 3 superkingdoms, 7 phyla and 55 families. Our data showed that the samples contain a few

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Date received: October 15, 2023
Date revised: December 5, 2023
Date accepted: December 6, 2023

KEYWORDS

Axiom™ Microbiome Array; crop residue; culture-independent; lignocellulose degradation; microbiome; rice straw

fungi and some DNA viruses but are primarily composed of prokaryotic bacteria, with Actinomycetota, Bacillota, Bacteroidota, and Pseudomonadota being the dominant phyla in terms of the number of detected species. The rice straw microbiomes harbored several microbial species that have been widely reported elsewhere as lignocellulose degraders. Several noteworthy species detected by AMA were closely related to *Bacteroides thetaiotaomicron*, *Cellvibrio japonicus*, *Pseudomonas putida, Flavobacterium rivuli*, *Fusarium graminearum*, and *Streptomyces* sp. The results of this study provide molecular evidence that rice straw-associated microbiomes are rich sources of biological agents for crop residue management.

INTRODUCTION

Crop wastes left in the field after harvest are often linked to plant disease epidemics, as they can act as a source of primary inoculum for residue-borne plant pathogens (Bockus and Shroyer 1998; Suffert and Sache 2011; Vera and Murray 2016; Raveloson et al. 2018; Kerdraon et al. 2019). In low-tillage systems, leaving plant residues unburied can form "brown bridges" that may allow the survival and persistence of various phytopathogens or opportunistic saprobes (Thompson et al. 2015). Nonetheless, *in situ* retention of crop residues (coupled with zero or reduced tillage practices) is more appealing for farmers owing to the vital ecosystem services it provides to agroecosystems. Among the advantages are the prevention of erosion, increased water storage capacity of soils, and improvement of soil organic matter and nutrient recycling (Smil 1999; Derpsch et al. 2010). It is also worth noting that residue retention can enhance the microbial biomass and catabolic diversity (microflora activity) in zero tillage systems by continuously providing a source of energy to microorganisms (Govaerts et al. 2007). Despite the plethora of beneficial effects in the field, crop residues are unquestionably an underexplored ecotone existing between plant and soil microbial communities (Kerdraon et al. 2019).

A lignocellulosic resource like rice straw substantially consists of lignin (13.5%), cellulose (24%), and hemicellulose (27.8%) (Rosado et al. 2021). Among the two typical methods used to dispose of this crop waste, in-field incineration is more broadly practiced than soil incorporation due to its low cost and the resulting ease of tillage, and also to avoid issues associated with the latter method, such as the slow residue biodegradation rate and the possibility of disease carryover from the retained wastes (Dobermann and Fairhurst 2002; Domínguez-Escribá and Porcar 2010; Allen et al. 2020; Van Hung et al. 2020). The rapid decomposition of rice straws in nature is impeded by the aromatic and heteropolymer lignin component of vascular plant cell walls (Ruiz-Dueñas and Martinez 2009; Abdel-Hamid et al. 2013; Singh and Arya 2019). The extensive utilization of lignocellulose, thus, depends on the breakdown of the complex lignin polymer (Gai et al. 2014). It will be of great interest to investigate the microorganisms with lignocellulolytic capabilities present in the microbiomes of decomposing crop by-products such as rice straws to maximize their usage for environmentally sound activities in the fields of soil nutrition improvement and agricultural waste management and to support in-farm efforts.

A generally accepted theory states that only about 1% of all microorganisms existing on earth are culturable using conventional microbiological cultivation techniques (Dangar et al. 2017). This culturability paradigm is addressed using metagenomic analysis methods, which may also serve as unique avenues for exploiting microbial metabolic capabilities that cannot be simply achieved by adopting routine cultivation-dependent strategies (Healy et al. 1995; Joshi et al. 2014; Andreote et al. 2017). While cost-prohibitive (Kwong et al. 2015), whole-genome metagenomic analysis is undeniably one of the most reliable approaches for the taxonomic profiling of microbiomes because of its excellent accuracy (Ranjan et al. 2016; Brumfield et al. 2020). However, array-based methods, despite their limitation in the discovery of novel taxa, have also been utilized for microbial identification in complex sample types (Paliy et al. 2009; Gardner et al. 2010; McLoughlin 2011; Dubinsky et al. 2013). Compared to next-generation sequencing (NGS) for metagenomic sequence analyses of complex environmental samples, microarray technologies appear more advantageous as they involve less complex data processing, resistance to contaminating agents, rapid sample preparation, and output generation (Nikolaki and Tsiamis, 2013). In a single assay, the new Axiom™ Microbiome Array (AMA; Applied Biosystems, Carlsbad, CA, USA) can detect microorganisms at the species and strain levels across all kingdoms or domains of life (Thissen et al. 2019; Kao et al. 2020; Slezak et al. 2020). It can also determine the composition of mock microbiomes with absolute accuracy and even identify microorganisms at the plasmid level (Thissen et al. 2019), which cannot be achieved using other DNA microarrays with poor taxonomic resolution and limitations in their sensitivity (Carey and Kostrzynska 2010).

The Philippines produces over 11 million tons of rice straw waste from an estimated annual rice yield of 15.2 million tons. A fraction of this waste comes from Region XII (SOCCSKSARGEN), which approximately supplies about 7% of the nation's irrigated palay (rice grain) (Philippine Statistics Authority 2019). Despite extensive microbiological research being conducted on rice plants and rice production in the country, much is yet to be understood about the microbiomes of rice straw residue. To this end, we collected samples from rice fields in General Santos City within the SOCCSKSARGEN region and subjected them to exploratory microbiome analysis via AMA technology in an attempt to acquire baseline information on the associated microbial communities. Our goals were to (1) characterize the taxonomic diversity of the microbiome of rice straw samples collected from three sites at the superkingdom, phylum, and family levels using the AMA platform and (2) discuss the potential of detected species for plant cell wall-degradation applications based on a literature survey. The microbial profile presented here provides preliminary data on microbial populations that might be naturally occurring or transiently associated with rice straw. To our knowledge, this is the first study applying AMA to the microbiome of rice straw residue.

MATERIALS AND METHODS

Collection of rice straw samples

Three farm owners or managers provided verbal consent to collect samples and relevant information about the farm after being apprised about the research to be conducted. For this baseline study, a non-probability sampling method based on convenience was employed (Etikan et al. 2016). Samples were collected specifically from farms whose fields contained unburied rice straws and were located within city limits, at a short distance from the laboratory, where they were stored and processed.

Samples were collected from three selected rice fields within General Santos City, two in Barangay San Isidro (codes: IsidA and IsidB) and one in Barangay Buayan (code: Byn). The rice straws in these fields had been gathered in piles and were exposed to natural elements. The piles were one month old or less at the time of sampling. The rice farms practiced conventional and monoculture farming, with three to four

planting seasons per year (Table 1). Rice straw samples were randomly collected from one big pile of rice straw present from each farm site, and sampling was specifically done from the edges and on sections of the pile that were not in contact with the soil. This was to reduce soil contaminants and target only rice straw-associated DNA (including microbial DNA present in the samples) in the extraction. The samples from each farm were collected from two to three sampling points in every pile to achieve a certain degree of randomness and were pooled to fill polypropylene plastic bags (#02 PP 8" x 14"), which roughly weigh around 200g to 300 g with the straws. The samples were delivered promptly to the laboratory, where they were stored at 4°C until analysis.

Table 1: Sampling locations in General Santos City, Philippines for the rice straw samples obtained from rice fields and subjected to the Axiom™ Microbiome Array Technology, and related information* on planting seasons, age of pile sampled, applied pesticides and fertilizers.

Sample code	Sampling site	Planting season*	Age of pile sampled*	Applied pesticide/s*	Applied fertilizers*
IsidA	Brgy. San Isidro. 6°08'35.4"N 125°11'19.3"E	every 3 months	1 month	2,4-D (2,4-Dichlorophenoxyacetic acid)	urea
				Cleanse® 2 EC	complete fertilizer (14-14-14)
IsidB	Brgy. Isidro 6°08'35.0"N 125°11'19.6"E	every 3 months	1 month (majority already incorporated in soil)	2,4-D (2,4-Dichlorophenoxyacetic acid)	urea
				Cleanse® 2 EC	complete fertilizer (14-14-14)
Byn	Brgy. Buayan 6°07'20.5"N 125°12'50.4"E	every 4 months	<1 month	Clearout® 41 Plus	urea
				Karate® 2.5 EC	ammonium sulfate
				Lorsban™ + Lannate™	

Information provided by farm owner/manager

DNA extraction and Axiom™ Microbiome Assay (AMA)

The rice straw samples collected from each site were utilized for the subsequent procedures of the AMA (Thermo Fisher Scientific, Waltham, MA) analysis workflow. As described in Thissen et al. (2019), which was the first published study that employed this assay, the technology utilizes a chip containing probes that are specific to a "target." The target is a sequence record in the Axiom™ Microbial Detection Analysis Software (MiDAS) database. A single AMA chip is covered with up to 1.38 million probes (consisting of random control probes and target-specific probes) that can identify more than 12,000 species of microorganisms, including fungi, protozoa, viruses, archaea, and bacteria as of October 2014 (Thissen et al. 2019).

Metagenomic DNA (mgDNA) was extracted using the ZymoBIOMICS DNA Miniprep Kit (Zymo Research, Irvine, CA, USA) according to manufacturer's instructions, and the DNA was quantified using the Qubit dsDNA Assay Kit (Thermo Fisher Scientific, Waltham, MA, USA). The extracted mgDNA was subjected to AMA analysis via the Axiom™ 2.0 Assay (Affymetrix Pte Ltd, Singapore) using a DNA quantity of 50 ng per sample as the assay input. For the target preparation and array processing, the 24-array format was specifically employed for this study. Reduced EDTA TE Buffer (10 mM Tris-HCl, pH 8.0, and 0.1 mM EDTA) was used as the no-template control (NTC) and the Ref103 human genomic DNA as the positive control. The GeneTitan Multi-Channel equipment (Thermo Fisher Scientific, Waltham, MA, USA) was used to analyze the array plate. All the workflow steps were based on the standard protocols indicated by the manufacturer.

AMA data analysis

The AMA data obtained from all samples and controls were analyzed using Axiom™ MiDAS (Thermo Fisher Scientific, Waltham, MA, USA), which performs calculations based on the Composite Likelihood Maximization Method (CLIMax) algorithm created at the Lawrence Livermore National Laboratory, USA (Gardner et al. 2010; McLoughlin 2011). The algorithm comprises several stages and involves making a composite likelihood model that best explains the observed probe intensity data. Axiom™ MiDAS generates a list of "detected" microbial species or sequences belonging to microbial species that have a high probability of being present in the analyzed sample. A more detailed explanation of the algorithm can be found in the Applied Biosystems's Axiom™ Microbiome Solution User Guide (available at https://www.thermofisher.com/order/catalog/product/902903). Briefly, to identify microorganisms in a sample, Axiom™ MiDAS requires the detection of over 20% of the target-specific probes and a signal intensity exceeding the 99th percentile in the negative control (random) probes.

The raw data files (.CEL file format) generated from each array of the AMA run were uploaded into the Axiom™ MiDAS software to obtain an analysis summary, graphics, and a comprehensive list of detected species. The data were further used for descriptive analysis and visualization. A heatmap and stacked column chart were generated in Microsoft Excel (2016) to showcase the diversity and frequency distribution of the species detected in the three samples at different taxonomic levels (i.e., superkingdom, phylum, and family).

A quality control (QC) analysis using specific probes of AMA target non-polymorphic regions of the human genome was also performed. In this QC analysis, a metric called Dish QC (DQC), which is based on the intensities of the detected probe sequences, was generated for the positive control (Ref103). A low Ref103 DQC value (<0.82) denoted a potential issue in the performance of the samples on the array plate. Our assay passed the QC analysis as the DQC value of Ref103 was above the 0.83 threshold. The species richness (S), Shannon's Evenness (J'), Shannon's Diversity index (H'), and Simpson's Diversity index (D) values were also calculated to describe diversity (Simpson 1949; Shannon 2001).

RESULTS AND DISCUSSION

Utility of AMA to non-human samples

The Axiom™ MiDAS-generated graphical outputs for the log of conditional scores vs. the ratio of conditional/initial scores depict target-level data for the IsidA, IsidB, and Byn samples (Figure 1). The blue dots denote unique target sequences detected in the samples. Target sequences are entries in MiDAS database and represent microbial data from sequence databases such as the National Center for Biotechnology Information (NCBI). These graphs showcase the applicability of AMA to atypical samples such as rice straw for microbial community profiling and provide a snapshot of the complexity of each microbiome examined. The data summarized in these graphs exhibited some variability. It can be noticed that the detected targets presented different ratios below or above the default threshold value of 0.2. Axiom™ MiDAS sets the default threshold value of 0.2 to eliminate targets with minimal contribution to the model. With this setting, targets that have 80% (or more) of their initial log-likelihood score explained by prior hits on the microarray chip are "unlikely to be present as distinct targets in the sample" (Applied Biosystems's Axiom™ Microbiome Solution User Guide; Link: https://www.thermofisher.com/order/catalog/product/902903).

The current advancements in molecular technologies such as AMA have enabled the in-depth examination of composite plant microbial biomes (Rastogi et al. 2013; Jongman et al. 2020). The complexity of communities has been readily suggested by studies conducted on the root endorhizosphere and rhizospheres (Sengupta et al. 2017; Moronta-Barrios et al. 2018). Among the techniques commonly used in most rice microbiome studies are the cloning of the 16S rRNA gene, NGS, PCR-denaturing gradient gel electrophoresis, and terminal restriction fragment length polymorphism (Kim and Lee 2020). Here, we have demonstrated the utility of AMA in identifying members of the microbial communities present in environmental samples with high accuracy at the species and strain levels based on available records in the public genetic databases as of October 2014. The remarkable accuracy of AMA for species and strain-level identification is expected from our analysis owing to the numerous mock experiments using metagenomic control materials, as exemplified by Thissen et al. (2019). In contrast also to 16S rRNA sequencing, AMA targets both conserved and unique regions of microbial genomes, providing a higher level of taxonomic resolution. One of AMA's most recent applications, which was also among the few published ones, was in monitoring microbiome changes in astronauts' bodies at different time points during space flight, a type of research that was previously done using 16S rRNA-based metabarcoding and traditional culture-based analyses (Morrison et al. 2021). So far, the AMA platform has been applied only to human biological samples (Morrison et al. 2021; Pedro et al. 2023). In the present study, we underscore the utility of this new microarray-based technology for microbiome analysis of non-human environmental samples.

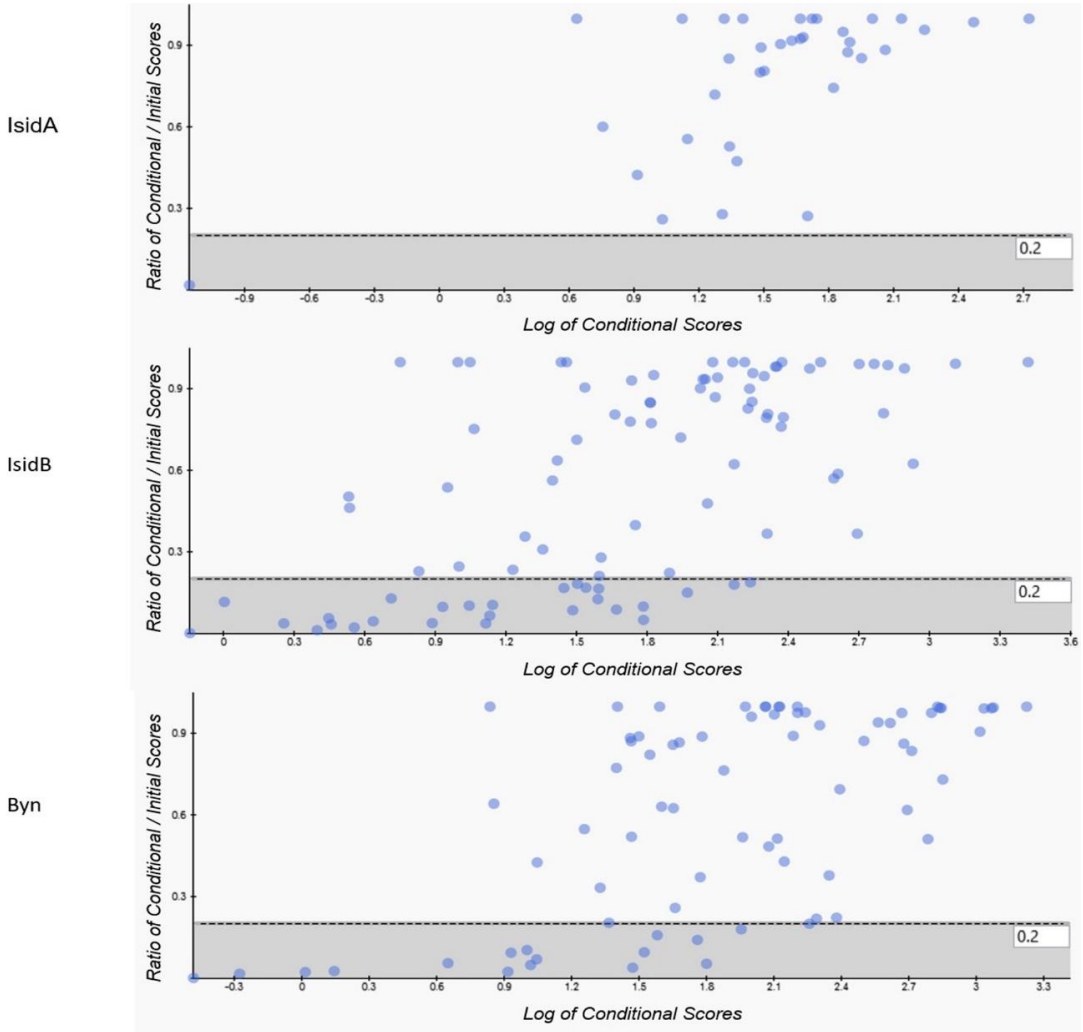

Figure 1: Axiom™ Microbial Detection Analysis Software (MiDAS)-generated graphical outputs of the log of conditional scores vs. ratio of conditional/initial scores for the three rice straw samples from rice fields in General Santos City analyzed by Axiom™ Microbiome Array Technology. Genomic targets were detected with varying ratios below or above the default threshold value of 0.2. Each dot represents one unique target sequence, which is an entry in MiDAS database and represent microbial data from public databases like NCBI.

Rice straw microbiome is diverse

Table 2 displays the total number of targets and specific taxa (family, genus, and species) detected in each sample. As shown in the Table, the number of targets (IsidA = 36, IsidB = 93 and Byn = 77), families (IsidA = 29, IsidB = 37 and Byn = 23), genera (IsidA = 34, IsidB = 57 and Byn = 29) and species (IsidA = 36, IsidB = 85 and Byn = 63) are varied across three samples. The values in this Table pertain to the unweighted diversity of the microbiomes in the samples. The total hits (IsidA = 373, IsidB = 5381, and Byn = 2435) varied among samples but are considered high in terms of the number of species detected (184 species across all samples). Nevertheless, the array identifies relatively higher microbial targets or taxa in human samples compared to our environmental samples (Morrison et al. 2021; Pedro et al. 2023). It must be noted that AMA may also detect relic DNA sequences alongside those derived from living cells. Additionally, the variation in the number of hits may have been influenced by the condition of the samples during DNA extraction and the compatibility of the extraction technique. To be specific, immediately storing the samples after collection could have stabilized their microbial composition, making them compatible for processing using the genomic DNA extraction kit, which resulted in high-quality data. Due to the nature of the amplification and the thresholding of probe intensities, the microarray is highly sensitive to low levels of target sequences in NTC samples. The detection of a target in the NTC, could be due to two factors. First, in the absence of competing template DNA, any minute amount of contaminating DNA present in the NTC may be amplified and carried through the assay until the hybridization step, where it may hybridize onto the array. Second, in the absence of high intensity signals from probes corresponding to true positive targets, even the lowest intensity signals from the NTC may be above signal thresholds as determined by background probes and may be utilized by the algorithm for determining the presence of a primary target.

Table 2: Summary of Axiom™ Microbial Detection Analysis Software (MiDAS) output for rice straw samples from three different rice fields in General Santos City, Philippines.

Sample source	Total hits	Number of targets detected	Number of species detected	Number of genera detected	Number of families detected
IsidA	373	36	36	34	29
IsidB	5,381	93	85	57	37
Byn	2,435	77	63	29	23
NTC	1	1	1	1	1
REF103	0	0	0	0	0

Legend: IsidA (Brgy, San Isidro A), IsidB (Brgy. San Isidro B), Byn (Buayan), REF103 (Axiom™ Reference Genomic DNA 103), NTC (no template control)

As shown in Table 2, our analysis detected 36 (IsidA), 93 (IsidB), and 77 (Byn) targets. It is widely understood that plant microbiome composition can be shaped by a number of internal and external factors, which may include plant genotype and tissue type (Yang et al. 2017), the depletion of available organic nutrients due to the inevitable plant senescence (Vorholt 2012; Leveau 2015), and vulnerability to extreme external stressors (Bertani et al. 2016). Anthropogenic interventions (e.g., soil and farm management practices), the presence of other antagonistic microorganisms, and climate conditions can also affect the microbial composition of both below- and above-ground plant microbiomes (Rastogi et al. 2013; Venkatachalam et al. 2016; Zhan et al. 2018; Compant et al. 2019). Overall, many factors, including human activities, location, conditions imposed by the immediate environment, and genetics, have a significant impact on the microbiome composition of plant-derived samples.

'Superkingdom' Bacteria dominates rice straw microbiome

As shown in Figure 2, Bacteria unequivocally dominated all three samples with respect to the detected targets (IsidA = 94%, IsidB = 96%, and Byn = 95%). Moreover, a few species of fungi (IsidA = 3%, Byn = 4%) and viruses (IsidA = 3%, IsidB = 4%, and Byn = 1%) were identified in our analysis. Interestingly, among the detected species (whose detailed description is further included below), some are known to participate in the degradation of plant materials as potentially saprophytic organisms. We hypothesized that these bacterial species play a role in the natural biodegradation of the rice straw under field conditions. Bacteria residing in the exposed parts of plants, for example in the phyllosphere, can be equipped with adaptations (e.g., DNA repair systems and the ability to produce extracellular polysaccharides) to tolerate extreme conditions in these regions (Lindow and Brandl 2003; Monier and Lindow 2004). These coping mechanisms or traits, if present, may allow species in rice straw to persist or thrive in the rice field environment.

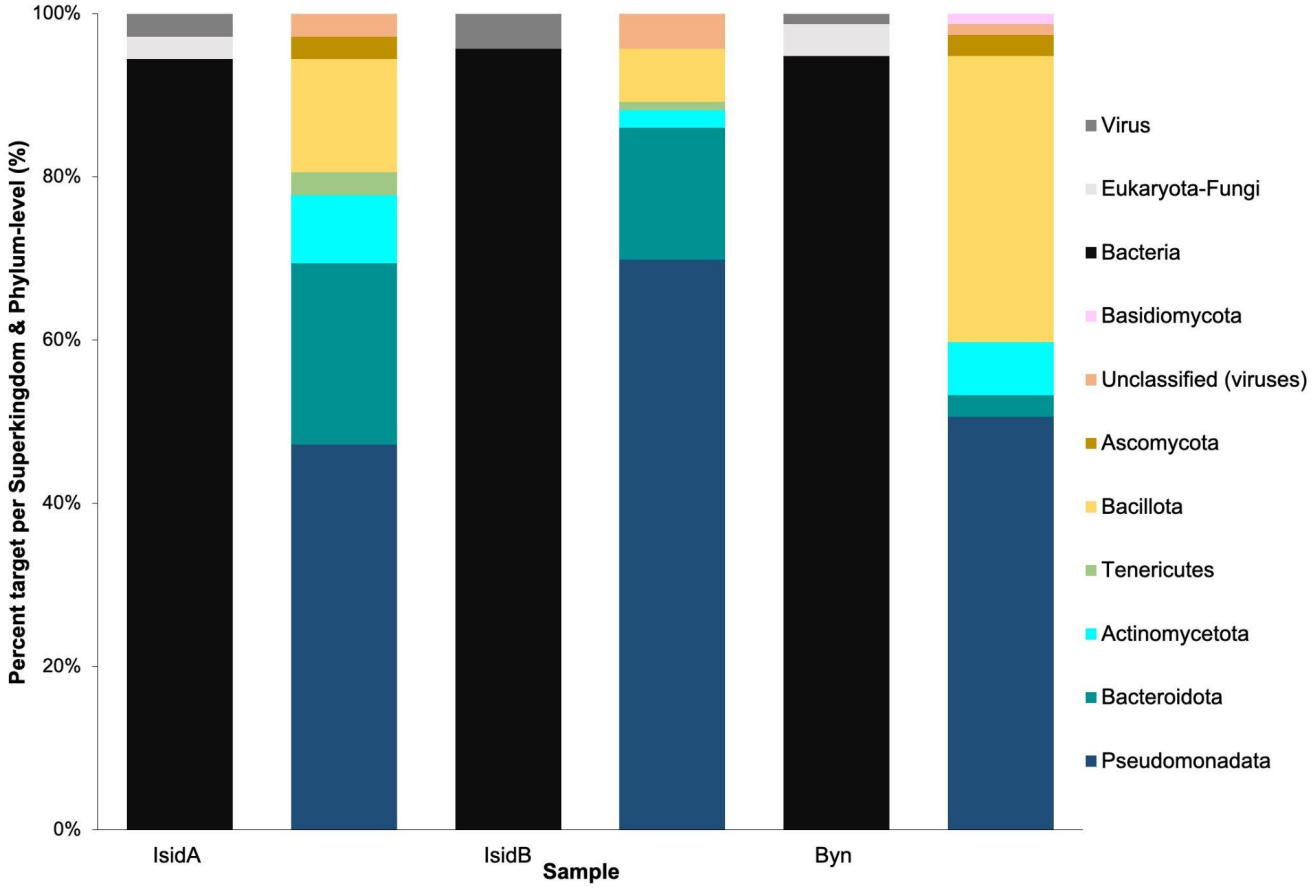

Figure 2: Superkingdom- and phylum-level percent distribution of targets in the microbiomes of rice straw samples detected by Axiom™ Microbiome Microarray Technology. The samples were collected from the following locations: IsidA, IsidB- Brgy (San Isidro A); Byn- Brgy (Buayan), General Santos City. New phyla names are as follows: Bacillota (Firmicutes), Actinomycetota (Actinobacteria), Bacteroidota (Bacteroidetes), Pseudomonadata (Proteobacteria).

Recently, revised names for the 42 phyla under Bacteria were published (Oren and Garrity 2021). The new names are incorporated in this paper in parentheses after the first mention of the original names which are used by MiDAS. Phylum Proteobacteria (Pseudomonadota corrig. phyl. nov.) (IsidA = 47%, IsidB = 70%, and Byn = 51%) was evidently the most widely detected, followed by Bacteroidetes (Bacteroidota corrig. phyl. nov.) (IsidA = 22%, IsidB = 16%, and Byn = 3%), Firmicutes (Bacillota corrig. phyl. nov.) (IsidA = 14%, IsidB = 6%, and Byn = 35%), Actinobacteria (Actinomycetota corrig. phyl. nov.) (IsidA = 8%, IsidB = 2%, and Byn = 6%), Tenericutes (Mycoplasmatota corrig. phyl. nov.) (IsidA = 3% and IsidB = 1%), Ascomycota (IsidA = 3% and Byn = 3%), and Basidiomycota (Byn = 1%) (Figure 2). All samples were shown to share some distinct similarity in terms of detected microorganisms at the superkingdom (bacteria and viruses) and phylum levels (Pseudomonadota, Bacteroidota, Bacillota, Actinobacteria) (Figure 3). Pseudomonadota, Bacteroidota, Bacillota, and Actinomycetota are all regarded as common inhabitants of the phyllosphere (Bulgarelli et al. 2013; Ding et al. 2019). Previous studies have identified these four phyla as members of the thriving microbial community in decomposing rice straw and composting maize straw (Reddy et al. 2013; Wei et al. 2018; Zhan et al. 2018). In addition, members of these phyla are also prevalent in desert and arid land soils (Soussi et al. 2016), which may support the hypothesis that the members of these taxa can withstand or tolerate dry and open environments like those farms in the Philippines where rice straws are left to decompose in the field. The occurrence of similar microorganisms at the higher taxon level (Pseudomonadota, Bacteroidota, Bacillota, and Actinomycetota) across samples from different fields may reflect commonalities in their core ecological functions in rice straw, such as their role in lignocellulose biodegradation. It is especially interesting to note that the aforementioned bacterial phyla have lignocellulolytic members. In particular, certain detected species belonging to α-Pseudomonadota and γ-Pseudomonadota, Actinomycetota, and Bacillota are some of the most widely known lignin-degrading bacteria (Fisher and Fong 2014; Janusz et al. 2017). Their detection in the rice straw samples using AMA can be indicative of their role in the breakdown of rigid components of the plant cell wall.

The microorganisms detected in the three rice straw samples examined exhibited high diversity (S = 30 ± 3.76, H'= 3.04 ± 0.23, and D = 0.05 ± 0.03) at the family level and an even distribution (0.9 ± 0.04) (Table 3). The heatmap (Figure 3) illustrates the diversity and family distribution among the samples. Twenty-seven families belonging to Pseudomonadota constituted the largest portion of all microbiomes surveyed, with species under *Enterobacteriaceae* and *Pseudomonadaceae* families being frequently detected. According to some studies, these taxa are widely observed in rice microbial community profiles (Ding et al. 2019; Reddy et al. 2013). As for the Bacteroidota phylum, six families, namely *Porphyromonadaceae, Flavobacteriaceae, Bacteroidaceae, Sphingobacteriaceae, Cyclobacteriaceae,* and *Cytophagaceae,* were detected. Among the Actinomycetota families found in the samples were *Streptomycetaceae, Microbacteriaceae, Nocardiopsaceae, Brevibacteriaceae,* and *Mycobacteriaceae*. Bacillota consisted of *Staphylococcaceae, Clostridiaceae, Enterococcaceae, Bacillaceae, Peptococcaceae, Streptococcaceae, Aerococcaceae, Peptostreptococcaceae, Oscillospiraceae,* and *Lachnospiraceae.* Only one Mycoplasmacota family (*Acholeplasmataceae*) was detected by AMA. Some of the species belonging to the above-mentioned families are associated with plant polymer degradation (Lu et al. 2014; Větrovský et al. 2014; Luis et al. 2018). The AMA

analysis also reported DNA viruses belonging to the *Siphoviridae*, *Podoviridae*, and *Myoviridae* families. These viruses, which are bacteriophages, are known to maintain the ecological balance within microbial communities through density-dependent "predation" of their host bacteria (Rodriguez-Valera 2009).

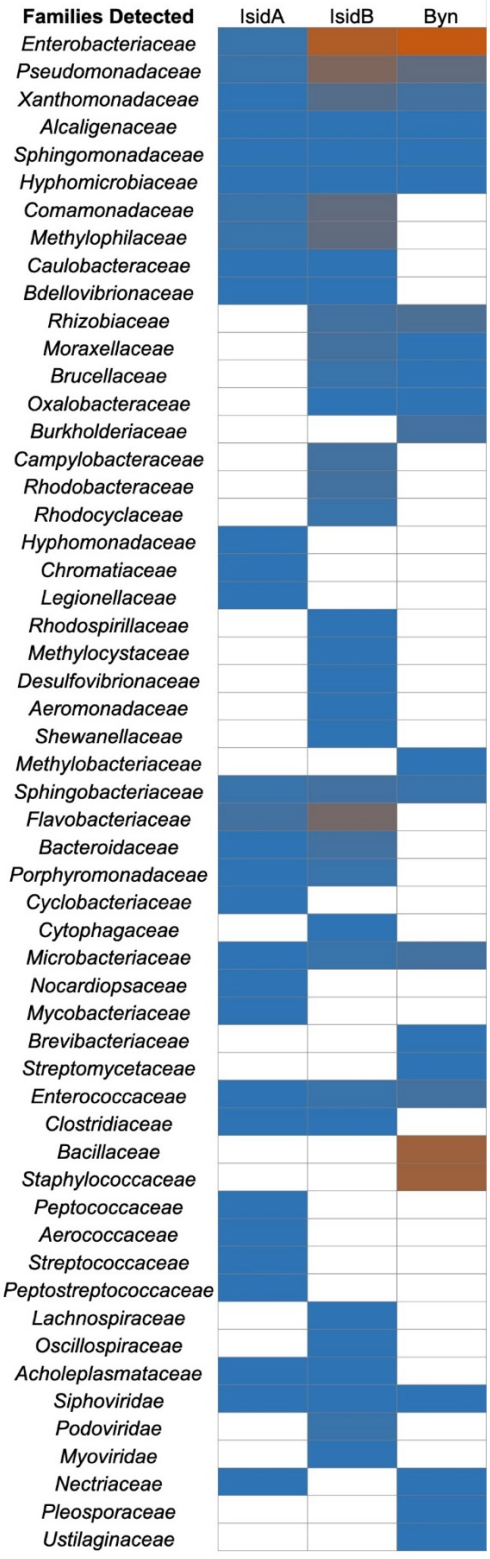

Figure 3: Relative distribution of the family composition and frequency of all phyla detected via Axiom™ Microbiome Array Technology across three microbiomes from rice straw samples obtained from rice fields in General Santos City, Philippines. The light shade of blue signifies lowest count, while darker shade of blue towards orange hue indicates higher counts. White means no targets under the family were detected.

Table 3: Diversity indices measured based on microbial families detected from rice straw samples (IsidA, IsidB, Byn) from three different low land farms in General Santos City, Philippines.

Diversity index	IsidA	IsidB	Byn	Mean ± SEM
S	30	36	23	30 ± 3.76
H'	3.33	3.2	2.59	3.04 ±. 0.23
J'	0.98	0.89	0.83	0.9 ± 0.04
D	0.01	0.05	0.1	0.05 ±. 0.03

*Species richness (S), Shannon's Diversity (H'), Shannon's Evenness (J'), Simpson's Diversity Index (D), ± standard error of the mean (SEM).

Some fungal species belonging to phyla Ascomycota (*Nectriaceae* and *Pleosporaceae*) and Basidiomycota (*Ustilaginaceae*) were also detected (Table 3). A few of these species are infamous pathogens of rice crops and have been reported to exhibit plant cell wall-degrading capabilities (Dallagnol et al. 2011; Gomes et al. 2015; Pak et al. 2017). For instance, phylum Ascomycota is a well-known fungal taxon present in the rice endosphere and whose members have been demonstrated to be reservoirs of β-glucosidase-encoding genes (Zang et al. 2017). Like most Basidiomycetes, fungal species belonging to families *Nectriaceae* and *Pleosporaceae* are known as primary lignin heteropolymer degraders (Maciel et al. 2010; Cragg et al. 2015; Fillat et al. 2017).

Rice straw microbiomes are rich in ligninolytic bacteria

A number of microbial species detected in this study are worth mentioning due to their notable ability to hydrolyze or degrade resistant plant cell wall components. Of all species identified, *Microbacterium* sp., *Devosia* sp., and *Enterobacter cloacae* were present in all three samples examined. Genes coding for the GH1 β-glucosidase were discovered by Zang et al. (2017) on operational taxonomic units closely related to *Microbacterium* sp., *Devosia* sp., and other microorganisms. The study found that genes coding for this enzyme, which catalyzes the last step of cellulose hydrolysis, persisted throughout the composting of cattle manure-rice straw. Additionally, it is critical to point out that *Devosia* sp. is frequently present during the composting process of organic wastes (Zang et al. 2017; Cai et al. 2018; Wei et al. 2018). However, cellulolytic activities have also been previously reported in *Microbacterium* sp. and *E. cloacae* (Wenzel et al. 2002; Ramin et al. 2009). In particular, different strains of *E. cloacae* have been extensively studied for their ability to transform lignin derivatives (Grbić-Galić and La Pat-Polasko 1985; Grbić-Galić 1986). The detection of these three bacterial species in all the samples analyzed in our study indicates that they are part of the rice straw's core microbiome. As described in Compant et al. (2019), plant core microbiomes intimately depend on plant genotype and consist of keystone species with crucial functional roles that directly impact host fitness.

Species found in one or two of the samples analyzed have also been implicated in biodegradation. A striking example is *Cellvibrio japonicus*, a saprophytic bacterial species that was detected in both IsidA and IsidB rice straw samples. This bacterium is widely known for its powerful capacity to degrade the highly complex molecular structures of plant cell walls and its immense potential for biomass bioconversion (Deboy et al. 2008; Gardner and Keating 2010; Gardner and Keating 2012). Another remarkable species detected in our samples was the fibrolytic *Bacteroides thetaiotaomicron,* an integral constituent of the human gut microbiota. This species was shown to contain numerous degrading enzymes that cells deploy to metabolize plant cell wall components and other carbohydrate polymers (Xu et al. 2003; Tailford et al. 2007; Luis et al. 2018). Finally, *Flavobacterium rivuli*, which was also present in our samples, is known for its CAZyme-encoding genes, which makes it an

archetypal bacterium for the study of plant polysaccharide polymer degradation (Hahnke et al. 2015).

Biocatalysts that hydrolyze carbohydrates are extremely valuable for lignocellulosic feedstock conversion initiatives, since 75% of this kind of biomass consists of polysaccharides (Marriott et al. 2016). Carbohydrate polymers (cellulose and hemicellulose) generally constitute the lignocellulosic biomass (Fisher and Fong 2014). Cellulose, which is a linear chain of (1,4)-D-glucopyranose units, confers recalcitrance to plant cell walls against chemical hydrolysis or enzymatic degradation (Santhanam et al. 2012; Anwar et al. 2014). In this context, *Streptomyces* spp. are, by far, the most well-studied actinomycetes owing to their inherent ability to produce different cellulolytic and ligninolytic enzymes (McCarthy and Broda 1984; Lu et al. 2014; Větrovský et al. 2014; Johansen 2016).

The identification of bacteria capable of producing lignin-modifying enzymes (LMEs) in rice straw samples suggests a function in the breakdown of lignin during decomposition. Lignin is an amorphous aromatic heteropolymer that represents 15–30% of lignocellulose by dry weight (Chandra et al. 2015). This molecule provides structural support, hydrophobicity, and defense to plant cells against saprophytes and pathogens (Ruiz-Dueñas and Martínez 2009; de Gonzalo et al. 2016; Bajpai 2017). The exceptional recalcitrance conferred by lignin toward degradation is attributed to: (1) non-specific or non-productive binding to hydrolytic enzymes (Li and Ragauskas 2016), (2) lack of distinct bonding patterns in its chemical architecture (Den et al. 2018), (3) properties of its three-dimensional structure (Santhanam et al. 2012), and (4) the complexes it forms with carbohydrates (Santhanam et al. 2012). *Pseudomonas putida*, which was positively identified by AMA, is among the ligninolytic bacteria that are extensively studied for their capability to synthesize the principal LMEs, i.e., laccase (Lac), manganese peroxidase (MnP), and lignin peroxidase (LiP) (Xu et al. 2018).

Over the years, efforts to biodegrade or modify the lignin polymer in plant biomasses have centered on fungal pretreatments, especially those that use species classified as white-rot Basidiomycetes, whose ligninolytic activities have been extensively elucidated (Bugg et al. 2011; Abdel-Hamid et al. 2013). Along with a few bacterial species, fungi utilize the major lignin-degrading enzymes, i.e., LiP, MnP, Lac, and versatile peroxidase (Chandel et al. 2015; Sindhu et al. 2016; Datta et al. 2017). Despite the astounding ligninolytic enzymes systems active in fungi and their ideal cultivation requirements, their practical or industrial-level applications still face numerous challenges. The lengthy delignification process, undesirable depletion of the cellulosic components, sterility issues, generation of toxic agents, problems related to the outcomes of genetic manipulation, and difficulties encountered in the large-scale production of recombinant proteins are some of the obstacles that must be overcome in pretreatments with fungal lignin-degrading enzymes (Coconi-Linares et al. 2014; Plácido and Capareda 2015; Masran et al. 2016; Lu-Chau et al. 2019). Consequently, lignin-degrading bacteria earned the spotlight for the advantages they offer over fungi, such as their ability to tolerate diverse and unfavorable environmental conditions, the reduced incubation time needed for cultivation, and highly specific enzymatic reactions (Chandel et al. 2015; Priyadarshinee et al. 2016).

Many species detected in our rice straw samples have also been reported to contain either genes or functional cellulase enzymes with promising catalytic activity in various lignocellulosic substrates or biomasses (Lee et al. 2008; Leo et al. 2016; Tan et al. 2018). Among them are species belonging to genera *Bacillus, Chryseobacterium, Enterobacter*, and *Acinetobacter*, to name a few. *Escherichia coli* and *Legionella pneumophila* are two examples of species detected in the rice straw samples that can produce endoglucanases (e.g., exoglucanase, endoglucanase, and β-glucosidase), which have been reported to randomly cleave the cellulose chain (Pearce and Cianciotto 2009; Pang et al. 2017). The potential of a wild-type strain of *E. coli* for biofuel production research was demonstrated by its ability to produce ethanol and hydrogen from corn straws (Pang et al. 2017).

AMA analysis also detected *Nocardiopsis dassonvillei* and *Aeromonas caviae*, two bacterial species that have been previously suggested to be hemicellulose producers. Specifically, Tsujibo et al. (1990) purified xylanases X-I, X-II, and X-III, which hydrolyze a primary component of hemicellulose, from the alkalophilic actinomycete *N. dassonvillei*, while the *A. caviae* strain ME-1, isolated from *Samia cynthia pryeri*, was shown to produce variations of xylanases I and V (Kubata et al. 1992; Kubata et al. 1994; Usui et al. 1999).

Our analysis also detected a number of notorious rice plant pathogens in the straw samples examined, i.e., *Agrobacterium tumefaciens, Fusarium virguliforme, F. graminearum* (Goswami and Kistler, 2005; Conejo-Saucedo et al. 2010; Kikot et al. 2010; Gomes et al. 2015; Pak et al. 2017; Kim et al. 2018) and *Xanthomas oryzae.* (Niño-Liu et al. 2006; White and Yang 2009). These phytopathogens are highly likely to be involved in the decomposition of rice straw because they produce biodegradative enzymes described in the literature. One study identified a gene coding for an endoglucanase in *X. oryzae* as a contributor to the bacterium's virulence (Hu et al. 2007). Chang et al. (2016) reported the same findings for the genome of *F. virguliforme*, which codes for a wide array of plant cell wall-degrading enzymes that were also discovered in other necrotrophic and hemibiotrophic fungal phytopathogens. Similarly, *F. graminearum* infects various crops worldwide using cell wall-degrading enzymes (Kikot et al. 2009). Overall, the major insight gleaned from these studies is that enzymes that can degrade the plant cell wall can be an advantageous factor for the pathogenicity and saprophytic activities of plant pathogens.

Characterizing the microbiome diversity of agricultural soils and composts is currently a sought-after approach to speed up the degradation of agricultural residues (Singh et al. 2019). Several studies have demonstrated that microbial species can accelerate the rice straw decomposition process or rate (Karunanandaa et al. 1995; Hatamoto et al. 2008; Kausar et al. 2010; Kumar et al. 2015; Borah et al. 2016; Ji et al. 2018). Some examples of microbial species present in agro-waste compost systems correlated to plant material biodegradation are *Bacillus* spp., *Brevibacillus* sp., *Halobacillus* sp., *Aeromicrobium*, and *Thermoactinomyces* spp. (Lu et al. 2005; Vargas-Garcia et al. 2007; Chang et al. 2009). Therefore, it seems plausible that rice straw also harbors microorganisms with biodegradation abilities that could be potentially exploited for the development of effective agro-waste management strategies. However, it remains unclear whether the microbiome members are actively functional throughout the process of rice straw decomposition. For instance, a study has revealed that the community structure of the rice straw microbiome is only stable up to the 15th day of decomposition (Weber et al. 2001). This finding, however, is in contrast to another microbiome study that maintains that more pronounced community dynamics occur after 2 weeks of decomposition (Wegner and Liesack 2016). All things considered, a complete investigation of the microbiome composition at different points in time during the rice straw composting process would be ideally required to further clarify this matter. This attempt will not only answer questions on

microbial community dynamics during decomposition but may also uncover other keystone species that are only active at particular phases of biodegradation.

The very few species of microorganisms consistently detected across the three rice straw samples analyzed could be part of the straw's core microbiome. In theory, these common microorganisms are abundant, ecologically relevant, and geographically shared (Hanski 1982; Kembel et al. 2014). The species that were detected by our AMA analysis in at least one or two samples may be part of satellite or rare taxa present in rice. Jousset et al. (2017) suggested that these taxa are in contrast to core species and may be influenced by the geographical habitat. In addition, the study argued that species rarity stems from a variety of factors, including stochastic population fluctuations and fitness trade-offs. Simply put, rare taxa can be superabundant in a specific habitat but uncommon in others. Most importantly, while usually overlooked because of their relatively low abundance in a particular environment, rare microbial taxa are sometimes actively responsible for driving ecosystem functioning (Campbell et al. 2011; Debroas et al. 2015). These organisms may have genes in their genome that could be functional only under certain conditions (Jousset et al. 2017). In a study by Liu et al. (2019), a few *Enterobacter* spp. and *Klebsiella* spp. were suggested to be part of the core microbiome of the banana plant endosphere and are considered keystone species that confer resistance against *Fusarium* wilt despite their relatively low abundance. It has also been shown that less abundant species are pivotal to soil ecosystems and that the loss of these particular taxa eventually inhibits the suppression of soil-borne pathogen (Gera Hol et al. 2015). Along this line, Wegner and Liesack (2016) suggested that task sharing occurs between the more abundant and less abundant taxa during plant polymer degradation in paddy soil slurries supplemented with rice straw.

The numerous unique targets detected in the rice straw (either from live cells or dead cells) examined in the present study are interesting since this kind of sample is regularly exposed to environmental conditions (intense light during the day and fluctuating temperature) that may be particularly harsh for microbial growth and survival. However, the detected targets may not represent the complete microbiome composition of the samples due to the following reasons: (1) a separate assay experiment based on cDNA synthesis to facilitate the analysis of RNA viruses was not conducted in our study, and (2) sequences corresponding to new species of microorganisms that were added to Axiom™ database after October 2014 were not included in the analysis. Nonetheless, we have corroborated the hypothesis that rice straws can represent a favorable niche environment for a variety of microbial life as observed in other microbiomes found in above-ground plant parts (Vorholt 2012; Rastogi et al. 2013). Schmidt et al. (2011) described a comparable case where a microbial biomass was discovered in the soils collected from the barren lands of the Himalayas. Our findings and the above-mentioned study clearly show that microbial communities in environments or geographic locations characterized by limitations in terms of available nutrients and water as well as continuous exposure to fluctuating environmental conditions are actually diverse.

CONCLUSIONS

Improvements in molecular biology techniques have broadened our understanding of the functional and taxonomic diversity of microbiomes associated with complex environmental samples and paved the way for the current breakthroughs in biotechnology and microbial ecology. In this study, we took advantage of the applicability of a new microarray technology to profile the microbiome of sun-dried rice straw collected from local rice fields at the superkingdom, phylum, and family levels. While unconventional, our study is important as crop residues like rice straws may represent an unexploited reservoir of microbe-derived biomolecules with biotechnological values, despite the theoretically low probability of microbial survival because of harsh environmental conditions. Here, we presented a simplified microbiome profile of rice straw samples and discussed the detected microbial species with potential applications in biodegradation based on relevant findings already reported in the literature. Bioprospecting microbiomes using molecular techniques with the goal of discovering plant cell wall-degrading enzymes is one approach in developing synthetic communities (De Roy et al. 2014; Roell and Zurbriggen 2020; Song et al. 2020) for crop waste management purposes. This deliberate control or engineering of plant-associated microbiomes is seen as a groundbreaking technology for sustainable agriculture (Foo et al. 2017; Mitter et al. 2017; Song et al. 2020). It should be noted that one of the key areas of interest in targeted microbiome engineering for the bioconversion of agro-waste biomass to biofuels or other useful microbial products is the recovery of microbial enzymes capable of degrading the plant cell wall. Moreover, technologies such as the more recent microarray-based technologies (e.g., PhyloChip, a 16S rRNA-based microarray, and GeoChip, a functional gene-based microarray), which have been deployed in metagenomics research (Sebat et al. 2003; Techtmann and Hazen 2016), can serve as a tool for the discovery of enzymes in mgDNA. In this study, we emphasize the enormous potential of rice straw as a reservoir of sought-after enzymes for biotechnological applications in agro-waste management as well as supporting the adoption of AMA technology as, perhaps, a less expensive and quicker alternative to sequencing-based exploratory tools in microbiome profiling.

ACKNOWLEDGMENTS

We thank Mikael Pura, Rai Anonuevo, Goi Chuan Tan, and Christopher Ng for their invaluable assistance in the AMA. We also thank the research staff of the Pathogen-Host-Environment Interactions Research Laboratory of the Institute of Biology, College of Science, University of the Philippines Diliman for their assistance in DNA extraction. The authors also acknowledge Camille Concepcion-Silvosa for the technical suggestions. This study was financially supported by the Commission on Higher Education Discovery-Applied Research and Extension for Trans/Inter-disciplinary Opportunities (CHED DARE TO) Research Grant.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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