UNIVERSIDADE FEDERAL DE SÃO CARLOS

CENTRO DE CIÊNCIAS E TECNOLOGIAS PARA A SUSTENTABILIDADE

PROGRAMA DE PÓS-GRADUAÇÃO EM BIOTECNOLOGIA A E MONITORAMENTO AMBIENTAL (PPGBMA)

JULIANE BRITTEZ DE MOURA

TAXONOMIC AND BIOTECHNOLOGICAL POTENTIAL ASSESSMENT OF MICROBIAL DIVERSITY ON PHOTOVOLTAIC PANELS SURFACES IN A TROPICAL ENVIRONMENT

Sorocaba,

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“Avaliação da taxonomia e do potencial biotecnológico da diversidade microbiana na superfície de painéis fotovoltaicos em ambiente tropical”

Dissertação apresentada ao Programa de Pós-Graduação em Biotecnologia e Monitoramento Ambiental para obtenção do título de Mestre em Biotecnologia e Monitoramento Ambiental.

Orientação: Prof. Dr. Iolanda Cristina Silveira Duarte

Co-orientação: Prof. Dr. Tiago Palladino Delforno

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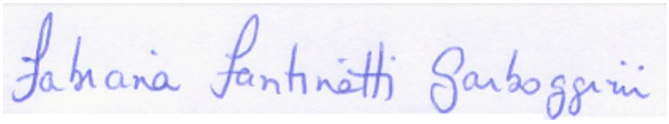

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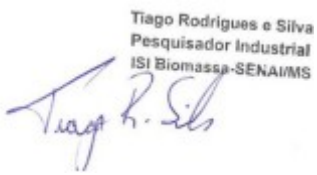
Examinador



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Dr. Tiago Rodrigues e Silva (SENAI)

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Somewhere, something incredible is waiting to be known.

Carl Sagan

ABSTRACT

Photovoltaic panels can be colonized by a highly diverse microbial diversity, despite life-threatening conditions. Although they are distributed worldwide, the microorganisms living on their surfaces have never been profiled or bioprospecting in tropical regions from an ecological point of view. In this work, photovoltaic panels from two cities in southeast Brazil, Sorocaba and Itatiba, were investigated using culture-independent, culture-dependent techniques and literature review to search for preliminary evidences of the colonization process and biotecnological potential. Results showed that, despite significant differences in microbial diversity ($p < 0.001$), the taxonomic profile was very similar for both photovoltaic panels, dominated mainly by Proteobacteria, Bacteroidota and lower amounts of Cyanobacteria phyla. A predominance of *Hymenobacter* and *Methylobacterium-Methylorubrum* was observed at the genus level. Moreover, we identified a common core composed by *Hymenobacter*, *Deinococcus*, *Sphingomonas*, *Methylobacterium-Methylorubrum, Craurococcus-Caldovatus*, *Massilia* and *Noviherbaspirillum* sharing genera. Predicted metabolisms focused on specific genes associated to radiation and desiccation resistance, and pigments, were detected in members of the common core and the most abundant genera. The photovoltaic panels surfaces displayed cultivable and pigmented colonies growing in a wide range of temperatures. We identified the isolated strains as *Arthrobacter koreensis, Dermacoccus nishinomiyaensis, Gordonia sp., Kocuria sp., Microbacterium hydrotermale, Mycolicibacterium aurum, Verrucosispora qiuiae, Pseudomonas coleopterorum, Psychrobacter sp., Serratia nematodiphila, Sphingomonas paucimobilis, Hymenobacter flocculans, Rhodotorula mucilaginosa*, *Rhodotorula sp*. In the literature documentation, most of these strains, or at least their closest relatives, were described as tolerant or resistant to UV light, desiccative conditions and biofilm capability, all being important adaptation mechanisms to thrive and engage the colonization process on photovoltaic panels surfaces. Moreover, a wide range of biotechnological applications was discussed, reinforcing the finding that photovoltaic panels are a repository of biotechnological interest.

Key-words: Bioprospecting; Microbial ecology; Solar panel; Sun-exposed environment; Stress-resistant.

RESUMO

Os painéis fotovoltaicos podem ser colonizados por uma alta diversidade microbiana apesar das condições que ameaçam o desenvolvimento da vida. Embora eles estejam distribuídos ao redor do mundo, os microrganismos que vivem em sua superfície são pouco conhecidos em região de clima tropical. No presente trabalho, painéis fotovoltaicos de duas regiões do sudeste brasileiro, Sorocaba e Itatiba, foram investigados por meio das técnicas independente e dependente de cultivo e revisão da literatura em busca de evidências preliminares que suportem hipóteses sobre o processo de colonização e potencial biotecnológico do microbioma residente. Os resultados mostraram que, apesar da diferença significativa da diversidade microbiana entre os painéis fotovoltaicos investigados ($p < 0.001$), o perfil taxonômico foi similar, dominado pelos filos Proteobacteria, Bacteroidota e quantidades menores de Cianobacteria. Em nível de gênero, foi observado uma predominância de *Hymenobacter* e *Methylobacterium-Methylorubrum.* Além disso, identificou-se um *common core* composto pelos gêneros *Hymenobacter*, *Deinococcus*, *Sphingomonas*, *Methylobacterium-Methylorubrum, Craurococcus-Caldovatus*, *Massilia, Noviherbaspirillum* e *1174-901-12*. As análises de predição funcional revelaram metabolismos envolvidos em processos de estresse. Entre eles, genes relacionados a processos de radiação, dissecação, e pigmentação foram verificados e encontrados nas amostras. As amostras dos painéis fotovoltaicos exibiram colônias cultiváveis e pigmentadas que cresceram em uma ampla faixa de temperatura. As linhagens isoladas foram identificadas como *Arthrobacter koreensis, Dermacoccus nishinomiyaensis, Gordonia sp., Kocuria sp., Microbacterium hydrotermale, Mycolicibacterium aurum, Verrucosispora qiuiae, Pseudomonas coleopterorum, Psychrobacter sp., Serratia nematodiphila, Sphingomonas paucimobilis, Hymenobacter flocculans, Rhodotorula mucilaginosa* e *Rhodotorula sp*. Baseado na revisão da literatura foi possível verificar que a maioria desses isolados, ou, pelo menos, os seus parentes mais próximos, foram descritos em relação à tolerância ou resistência à radiação UV, dissecação e com habilidade de formação de biofilmes, todos sendo mecanismos de adaptação importantes para iniciar e manter o processo de colonização na superfície de painéis fotovoltaicos. Várias aplicações biotecnológicas foram discutidas e podem ser aplicáveis por meio da obtenção de microrganismos encontrados nessas condições, reforçando a ideia de que os painéis fotovoltaicos são possíveis repositórios de interesse biotecnológico.

Palavras-chave: Bioprospecção; Ecologia microbiana; Painel solar.

CONTENTS

DISSERTATION OUTLINE

This work is composed by 4 chapters. The content in each of them is as follow:

- **Chapter 1**: Introduction
- **Chapter 2**: Extremophilic taxa predominate in a microbial community of photovoltaic panels in a tropical region
- **Chapter 3**: Biotechnological potential of pigmented microorganisms isolated from photovoltaic panels surfaces in a tropical region.
- **Chapter 4**: Conclusion: an overview and future considerations.

CHAPTER 1

INTRODUCTION

1.1 Context and Motivation

Microorganisms are vast and diverse on planet Earth (Locey and Lennon 2016). However most of them, specially members of Bacteria and Archaea domains, remain still unknown (Vitorino and Bessa 2018). This reveals a gap in microbial diversity knowledge and also in unexplored resources of relevant novel biotechnological tools. Although the investigations of microbial diversity have focused on indoor biomes for a long time (Dorado-Morales *et al.* 2016), any air-exposed surface on earth is suitable to be covered by microbial life. Glass surfaces are not an exception. Documentations reporting colonization of different microorganisms on glass are old (Mellor 1923; Perezy-Jorba *et al.* 1980; Thorseth *et al.* 1992) and yet a field to be explored in-depth, because it varies depending on the surrounding environment.

An example of a outdoor environment built with an intermediated glass material is the photovoltaic panels. Although they are distributed worldwide, the colonization process of microoganisms living on their surfaces was poorly investigated. Studies assessing the microbiome of photovoltaic panels revealed that their glass surfaces are rich in pigmented microorganisms, similar to those found in irradiated places, making them interesting and accessible sources of biotechnological interest. Previous investigation of the colonization process of these microorganisms on such surfaces suggested that to thrive, they must overcome the threatening environment by building up tolerance to irradiation and desiccation, besides the biofilm formation capability, all these being important adaptation mechanisms to these communities to cope with the environmental condition on photovoltaic panels surfaces (Dorado-Morales *et al.* 2016; Porcar *et al.* 2018; Tanner *et al.* 2018a; Tanner *et al.* 2018b; Tanner *et al.* 2020). Despite of these important findings and according to our very best knowledge, the microbial diversity living on photovoltaic panels surfaces was only widely looked into Mediterranean and Polar regions, whereas in tropics was not properly explored yet, except for research carried out in São Paulo that focused on impacts of microbial colonization in the photovoltaic energy yield.

Furthermore, the presence of cells (or biofilm matrix) and pigments on photovoltaic panels surfaces could lead to dispersion and absorption of light, reducing the energy that reaches the photovoltaic cells, and hence negatively impacting the energy production (Noack-Schönmann *et al.* 2014; Shirakawa *et al.* 2015). Additionally, microbial biofilm formation contributes to enhancing the soiling effect (dust accumulation), one of the main concerns in the power production losses field (Sarver *et al.* 2013; Noack-Schönmann et al., 2014; Cordero *et al.* 2018; Martin-Sanchez *et al.* 2018; Porcar *et al.* 2018).

The knowledge of communities living on photovoltaic panels surfaces is a very important field to investigated. In the first place this contributes to complementary documentation of microbial ecology in general, which we know has a large gap to be filled. To evaluate the microbial ecology of these communities is crucial the understanding of how this communities vary and evolve in many regions, including tropics that is considered a hotspot of biodiversity. Moreover, explore their behavior will lead us to find patterns not only in taxonomic identities, but also in functional characteristics associated with the evolutionary process, which is deeply related to the intrinsic mechanisms that force the formation of a native microbiome, especially considering the man-made structures, a relatively recent biotope. Taking into account the extreme environment that the surfaces of photovoltaic panels represent, is reasonable to think that the metabolites of the microorganisms living there have the potential to help us to improve our lives by applying it in the restoration of environments, measures of climate changes, food production, bio-engineering of chemicals and pharmaceutical products. Furthermore, this information can drive us to find better sanitizer alternatives in order to promote a more efficient cleaning process to reduce the impacts of energy losses caused by microbes colonization.

Our motivation to this work is to contribute, as complementary information, to the efforts that have been done worldwide to provide one more piece in this puzzle and fill a part of a gap, focusing in tropical regions, by the investigation of Bacteria and Archaea diversity living on surfaces of photovoltaic panels in two cities of southeast Brazil using culture-independent and culture-dependent techniques, bioinformatic approaches, as well literature retrievies to infer about the colonization process and biotechnological potential of microbial life that have originated and evolved on artificial man-made photovoltaic panels glass surfaces.

1.2 Objectives

The primary objective of this work was to investigate and compare the bacterial and archaeal diversity and explore the biotechnological potential of pigmented microorganisms living on photovoltaic panel glasses surfaces in two tropical cities in the southeast of Brazil.

To accomplish that, specific tasks were defined as secondary objectives:

- Compare the bacterial and archaeal taxonomic profile of the photovoltaic panels investigated;
- Determine the microbial common core between photovoltaic panels investigated;
- Perform prediction of the functional content of microbial communities, focusing in genes related to radiation and desiccation-resistance and pigments production.
- Isolate and identify pigmented microorganisms;
- Search in the literature reports the biotechnological potential of the identified isolates and their closest relatives;

CHAPTER 2

Extremophilic taxa predominates in a microbial community of photovoltaic panels in a tropical region

ABSTRACT

Photovoltaic panels can be colonized by a highly diverse microbial diversity, despite life-threatening conditions. Although they are distributed worldwide, the microorganisms living on their surfaces have never been profiled in tropical regions using 16S rRNA high-throughput sequencing and PICRUst metagenome prediction of functional content. In this work, we investigated photovoltaic panels from two cities in southeast Brazil, Sorocaba and Itatiba, using these bioinformatics approach. Results showed that, despite significant differences in microbial diversity ($p < 0.001$), the taxonomic profile was very similar for both photovoltaic panels, dominated mainly by Proteobacteria, Bacteroidota, and lower amounts of Cyanobacteria phyla. A predominance of *Hymenobacter* and *Methylobacterium-Methylorubrum* was observed at the genus level. Moreover, we identified a microbial common core composed of *Hymenobacter, Deinococcus, Sphingomonas, Methylobacterium-Methylorubrum, Craurococcus-Caldovatus, Massilia, Noviherbaspirillum,* and *1174-901-12* sharing genera. Predicted metabolisms focused on specific genes associated to radiation and desiccation resistance, and pigments, were detected in members of the common core and the most abundant genera. Our results suggested that taxonomic and functional profiles investigated were consistent with the harsh environment that photovoltaic panel represent and the microbes living there are a possibly source of metabolites with biotechnological interest.

Keywords: arid environment; biofouling; microbial diversity; solar panel; sun-exposed environment; stress-resistance

2.1 Introduction

Microorganisms are ubiquitous and were predicted to have upward of 10^{12} different species on planet Earth (Locey and Lennon 2016). However, most of them are still unknown,

primarily in the Bacteria and Archaea domains, which comprises underexplored microbiota (Vitorino and Bessa 2018). A gap in the knowledge of microbial diversity implies not only in poor taxonomic documentation but also in unexplored and potentially relevant novel biotechnological tools. Investigations of microbial diversity have focused on indoor biomes so far, but microorganisms living in extreme outdoor environments are possibly more attractive according to the viewpoint of the technological resource, due to their higher mutation rate that makes them a promising resource of new metabolites (Dorado-Morales *et al.* 2016; Tanner, Vilanova and Porcar 2017; Sayed *et al.* 2020).

An archetypal example of an extreme and artificial outdoor environment is the photovoltaic panel. This infra-structural element is distributed worldwide, forecasted to become the most important electrical energy source in the coming years, according to the International Energy Agency (IEA). This structure is reported to support a highly diverse microbial life on its surface, despite life-threatening conditions such as solar irradiation, desiccation, and related thermal fluctuations, besides the desiccative effects (Dorado-Morales *et al.* 2016; Porcar *et al.* 2018; Tanner *et al.* 2018a).

Previous studies assessing microbiome of the glass surface of photovoltaic panels in the Arctic and Antarctic (Tanner *et al.* 2018a), Valencia (Dorado-Morales *et al.* 2016; Tanner *et al.* 2020), and Berkeley (Porcar *et al.* 2018), revealed that their microbial colonization is similar, despite the geographical and climatic differences. These studies showed that photovoltaic panel surfaces are rich in pigmented microorganisms, with radiation and desiccation resistance, making them especially interesting for industrial and commercial applications. Carotenoids and scavenger compounds, responsible for pigmentation properties, have been suggested as one of the strategies attributed to the ability of these microorganisms to cope with oxidative species that promote DNA damage and protein oxidation in the irradiation and water loss processes (Qi et al. 2019). These mechanisms of surveillance proved to be an interesting pathway to search for biocompounds. For example, pigmented strains screened on surfaces of photovoltaic panels revealed antioxidant activity suggesting that microbes retrieved from these structures have the biotechnological potential for bioproduct prospection (Tanner *et al.* 2018b).

Additionally, the accumulation of dust and microorganisms, known as soiling, negatively affected the efficiency of photovoltaic panels in São Paulo city (Brazil). Shirakawa *et al.* (2015) reported a decrease in power production by 11% after 18 months in Brazil. In

environments where the soiling process is more intense, such as in desert conditions, losses can reach 39% (Cordero *et al.* 2018). In an even worse scenario where there are dust storms, reductions in energy yield could be greater than 50% (Adinoyi and Said 2013).

Thus, the knowledge of communities living on photovoltaic panels and their colonization process is a very important field to be investigated in-depth worldwide, especially in the tropics, which has been frequently reported as a hot spot for biodiversity (Pereira 2016; Vitorino and Bessa 2018). However, such information was only broadly investigated in the Mediterranean and, to a less extent, polar climates. In tropical regions, the microbial community on photovoltaic panels has not yet been investigated, except for the study carried out in São Paulo that aimed to clarify the impacts of soiling to reduce photovoltaic panel energy efficiency (Shirakawa *et al.* 2015).

Therefore, as a complementary contribution to the efforts made worldwide, specifically those focusing on tropical regions, we investigated the Bacteria and Archaea diversity of the photovoltaic panel glasses surfaces in two tropical cities in the southeast of Brazil. Accordingly to the best of our knowledge, this is the first report that aimed to provide complementary data in taxonomic documentation of photovoltaic panels in Brazilian tropical regions through high-throughput sequencing of gene 16S rRNA and also predicts the functional profile associated with these microorganisms.

2.2 Material and methods

2.2.1 Sampling

Sampling was carried out in winter (June 2020) from 2 photovoltaic panels located in southeast Brazil: Sorocaba (-23º28’55”, -47º22’19.9”) and Itatiba (-22º59’36.3”, -46º50’48”). Seven photovoltaic modules from Sorocaba (PSR) and four from Itatiba (PSI) were sampled, based on the method used by Dorado-Morales et al. (2016) and Porcar et al. (2018) including some modifications. The surfaces of photovoltaic panels were scrubbed with gauze bandage soaked in sterile phosphate-buffered saline (PBS) (LGC biotecnologia, Brazil) (10 X, pH = 7.2) diluted 10% (v/v). The dust collected was transferred into a glass flask containing 150 mL of sterile PBS and immediately transported to the laboratory. The glass flasks were shaken at 180 rpm for 10 minutes. The slurry obtained was transferred into 50 mL sterile polypropylene conical tubes and centrifuged at 5000 rpm for 3 minutes. The glass flasks were washed 10x with PBS and centrifuged again in order to optimize the biological material

recovery from gauze bandage. The pellets were stored at -20 ºC for taxonomic identification by 16S rRNA sequencing.

Climatological data (from June 2020) were recorded daily from the National Institute of Meteorology (INMET) network of monitoring stations. The mean temperature was 19ºC and the average relative humidity was 72% in both cities. The solar irradiance was 311.5 $W.m^{-2}$ PSR and 267.0 $W.m^{-2}$ PSI, and mean precipitation levels were 0.05 mm and 0.1 mm, respectively. The average temperature of the photovoltaic panels during the sampling process was 43 ºC PSR and 21 ºC PSI. Concerning the installation time and cleanliness of these photovoltaic panels, the PSR have been in operation for 2 years and have never been cleaned. The PSI were installed 1 year from the sampling day and were cleaned 6 months before the collection.

2.2.2 DNA isolation and 16S rRNA sequencing

The genomic DNA was extracted from pellets obtained in the sampling step using the PowerSoil® DNA isolation kit (MOBIO Laboratories, Carlsbad, USA), following the instructions of the manufacturer, with a final elution volume of 50 µL. Three replicates were sequenced for each photovoltaic panel sample (pellets), yielding a total of 6 sequencing datasets. The quality of the extracted DNA was analyzed by electrophoresis on a 0.8 % agarose gel. Extracted DNA was stored at -20 ºC until required for 16S rRNA sequencing. The 16S rRNA sequencing was performed using Illumina MiSeq platform; 2x250bp. Degeneracy primers 515FB (5'GTGYCAGCMGCCGCGGTAA3') and 806RB (5'GGACTACNVGGGTWTCTAAT3') were used for targeting Bacteria and Archaea domains (Parada et al. 2016; Apprill et al. 2015).

2.2.3 Bioinformatics and statistical analysis

The quality control of the raw data was performed using FASTQC v.011.5 (Andrews 2010). Low-quality sequences (Phred score ≤ 30) and read lengths smaller than 100 bp were trimmed using Trimmomatic v.0.39 (Bolger, Lohse and Usadel 2014). Complementary bioinformatic analysis were carried out by Quantitative Insights Into Microbial Ecology (QIIME 2, version 2019.4) (Bolyen *et al.* 2019). The 'cutadapt' plugin was used for trimming primers (Martin 2011). QIIME 2 plugin tool was used to import quality read filters, as an "artifact" file. Afterwards, the artifact files were quality-checked (denoising), the chimera

was removed and clustered into representative sequences, Amplicon Sequence Variants (ASVs), using the "dada2" plugin (Callahan *et al.* 2016). The ASVs were aligned with maffit (Katoh *et al.* 2002) and used for phylogenetic reconstruction with fasttree2 (Price, Dehal and Arkin 2010). The taxonomic assignment of ASVs was implemented using a q2-feature-classifier plugin (Bokulich *et al.* 2018) and classify-consensus-vsearch (Rognes *et al.* 2016) against SILVA ribosomal RNA gene database version 132. (Quast *et al.* 2013).

The functional profiles were predicted using the Phylogenetic Investigation of Communities of Unobserved States (PICRUSt2) software (Douglas *et al.* 2019). PiCRUSt2 can infer metagenome functional content from 16S rRNA gene sequencing data using the output ASV table from taxonomic analysis as input into the PICRUSt2 QIIME2 plugin. The prediction results were obtained from PICRUst2 output against the KEGG ortholog database (Kanehisa *et al.* 2016) to reconstruct metabolic pathways. The STAMP software package (v2.1.3) (Parks *et al.* 2014) was used to analyze metabolic profiles. The functional data that were poor or unspecific were eliminated from the analysis and used only to calculate frequency profiles. The comparison of the functional profile between the PSR and PSI was performed with a two-sided Welch's t-test combined with Welch's inverted method for confidence intervals (nominal coverage 95%). Furthermore, a false-discovery-rate (FDR) was applied as a multiple test correction. The data was graphically expressed in an extended error bar plot, where different functional profiles (KEGG level 2) were clustered by similarity. Moreover, specific KEGGs records, related to radiation-resistance, desiccation-resistance and pigments (carotenoids and flavonoids) were selected to track the functional profile previously reported in photovoltaic panel communities (Dorado-Morales *et al.* 2016; Porcar *et al.* 2018).

The R statistical environment was used for statistical analysis and graphic preparation from taxonomic and prediction of functional profile data associated with taxonomy. The taxonomic data were imported as a phyloseq object (phyloseq software) (McMurdie and Holmes 2013). Our work was limited to archaea and bacterial classification, therefore to avoid problems with misclassification of mitochondrial and chloroplast ribosomal amplification from eukaryotes, these sequences were removed (Escobar-Zepeda *et al.* 2018). To check the reproducibility of the 3 replicates, a scatter-plot visualization was used in which specific thresholds were defined. For this procedure, biological information with low abundance and low reproducibility was removed. Then, the replicates were combined using the geometric mean and shown in a rarefaction curve. Alpha diversity was described using Chao1, Simpson and

Shannon index, coverage and observed species. To evaluate dissimilarities between the samples (PSR and PSI), beta diversity was performed by Principal Coordinate Analysis (PCoA) using Bray-Curtis metric, based on abundance species. As complementary information to PCoA, the ANOSIM test, an analysis of similarity, was applied to determine if the differences among samples was significant. For this purpose, the Bray-Curtis similarity index was used as a metric based on the abundance of ASVs (Clarke and Gorley 2006). The taxonomic information was analyzed using the DESeq2 package for differential abundance comparisons. The common core was constructed using the Venn diagram package and overlapping by ASVs and genera. Sequencing reads were deposited in the European Nucleotide Archive (ENA) under project number PRJEB43933.

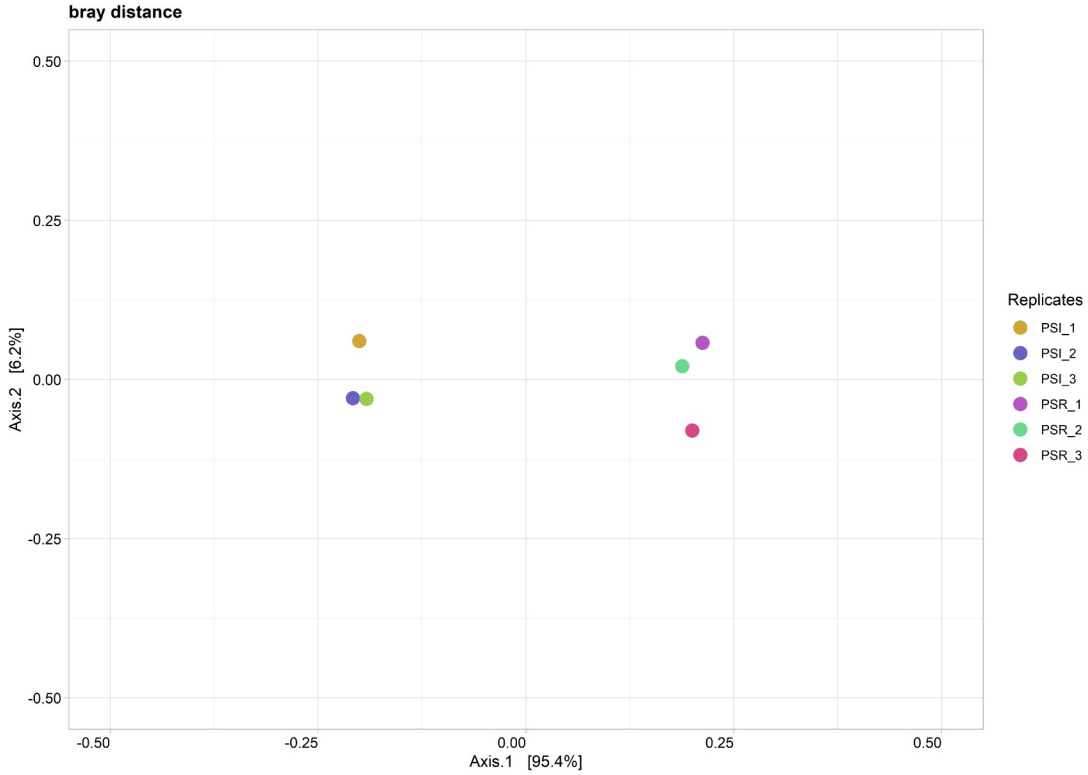
2.3 Results

Two samples (PSR and PSI) with 3 technical replicates for each of them were sequenced, yielding 6 datasets. Rarefaction curves, with 99% of similarity, showed that the depth of the samples was sufficient for assessing the microbial diversity accordingly to our objective, thus enabling us to proceed with our designed workflow. The richness estimator (Chao1) shows a higher value for PSR (50.7 ± 11.1) than the PSI (19.0 ± 5.0) sample. Observed richness showed similar values, indicating that the sample coverage observed on the rarefaction curve was effective (Fig. S1, supporting information).

To allow inferences about compositional similarities between the samples and their replicates (reproducibility), the PCoA was applied using the Bray-Curtis distance. The points of 3 replicates of each sample were grouped, indicating a high correlation between replicates. Additionally, the samples were relatively ungrouped, indicating lower correlations between samples than replicates (Fig. 1). An analysis of similarities (ANOSIM) showed that inter-group differences (samples) were greater than the intra-group differences (replicates) ($R = 1$, $p = 0.1$) and the composition differences between samples were not significant ($p > 0.05$).

Regarding the microbial diversity index between the samples, differences were detected between the PSR and PSI in the Shannon index (1.971 ± 0.08 for PSR versus 0.925 ± 0.056 for PSI) and the Simpson index (0.72 ± 0.018 for PSR versus 0.455 ± 0.022 for PSI). The results demonstrated that the differences inferred were strongly significant ($p < 0.001$), thus the microbial diversity in PSR was greater when compared to PSI.

Figure 1. Principal Coordinate Analysis (PCoA) of beta diversity using a Bray-Curtis metric derived from microbial communities of photovoltaic panels (PSR and PSI) and their technical replicates. The orange, blue and green dots (PSI_1, PSI_2, PSI_3) refer to the photovoltaic panels from Itatiba and their replicates. The purple, aqua and pink dots (PSR_1, PSR_2, PSR_3) are representative of solar panels from Sorocaba and their replicates.

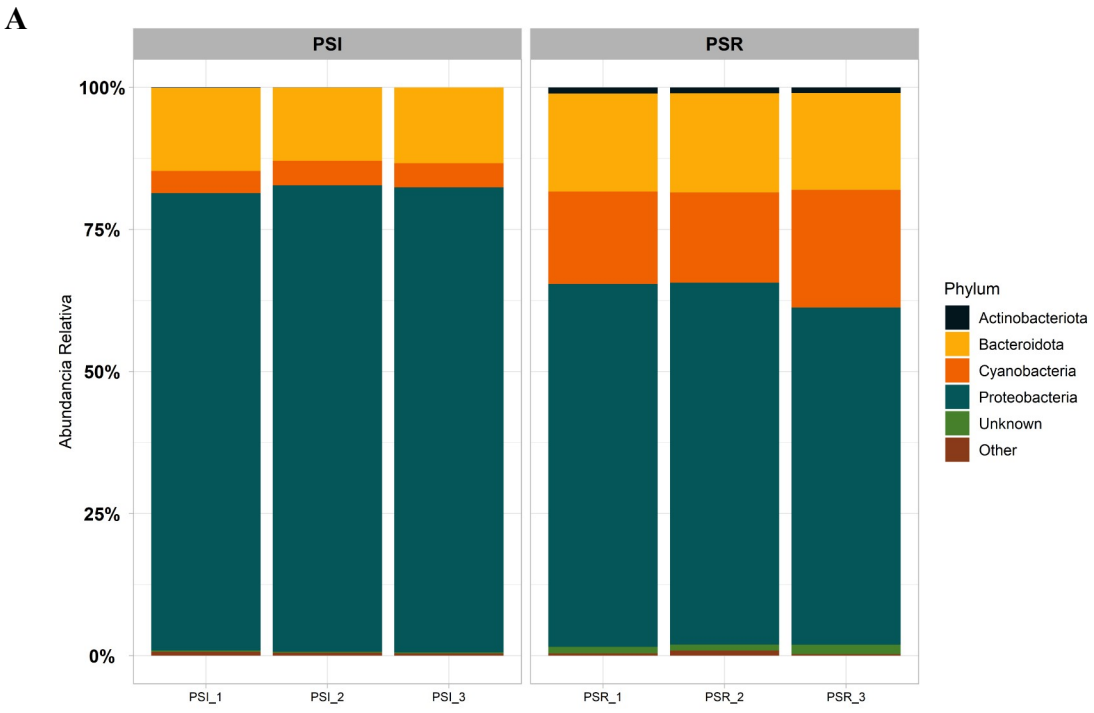


Taxonomic analyses revealed that all sequences were dominated by the Bacteria domain (100%). In the case of the PSI sample, the predominant phyla were Proteobacteria (78.7%), Bacteroidota (20.4%), and less frequently, Cyanobacteria (0.6%) and Deinococcota (0.2%). While for the PSR sample, the predominant phyla were Proteobacteria (56.6%), Bacteroidota (35.8%), and less frequently, Cyanobacteria (4.2%), Actinobacteriota (2.1%), Firmicutes (0.5%), Gemmatimonadota (0.4%) and Deinococcota (0.1%) (Fig. 2A).

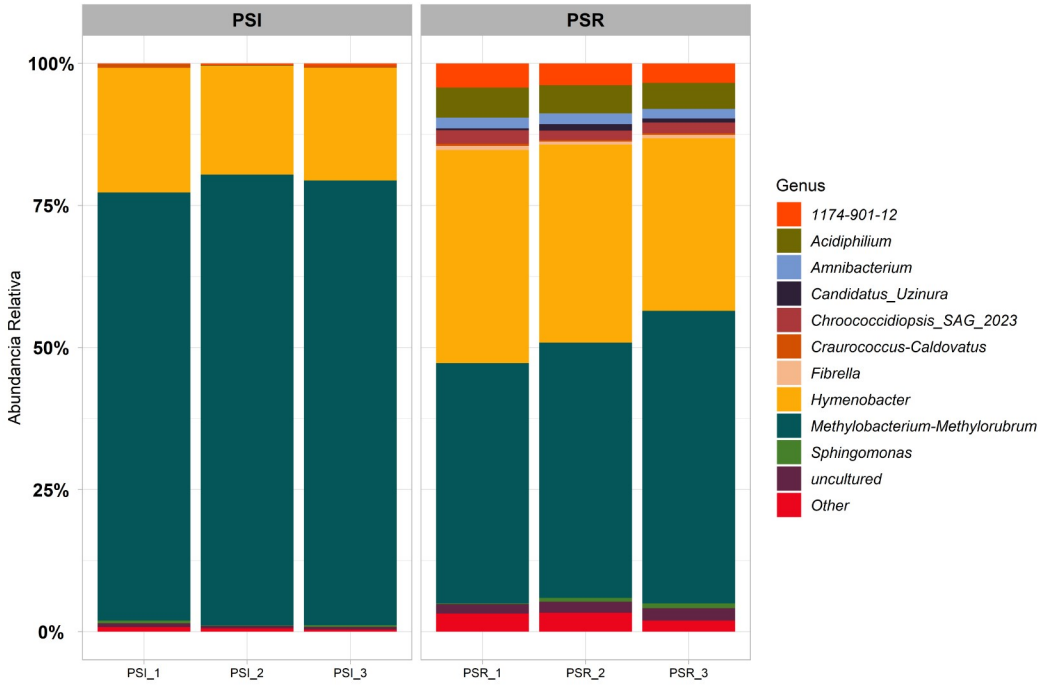
At a genus level, the PSI and PSR samples were dominated by *Methylobacterium-Methylorubrum* (77.6% and 45.8%, respectively) and *Hymenobacter* (20.3% and 34.5%, respectively) (Fig. 2B). *Methylobacterium-Methylorubrum* and *Hymenobacter* (ASV_84d0)

were statistically different in abundance and more present in PSI, while *Hymenobacter* (ASV_b846 and ASV_7eaf) were more frequently present in PSR samples (Fig. S2, supporting information). These two main genera identified in the PSI and PSR samples represent 99.1% and 92.4%, respectively, of total microbial diversity observed in this investigation. Comparatively, *Acidiphilium*, *Chroococcidiopsis, Sphingomonas, Amnibacterium, Candidatus Uzinura, Fibrella* and *Craurococcus-Caldovatus* were identified in lower proportions (Fig. 2B) and were significant associated with PSR samples (Fig. S2, supporting information).

Figure 2. Taxonomic diversity of photovoltaic panel (PSR and PSI) samples analyzed by 16S rRNA gene sequencing and visualized by relative abundance (%) histograms: **(A)** phylum level, **(B)** genus level.



B



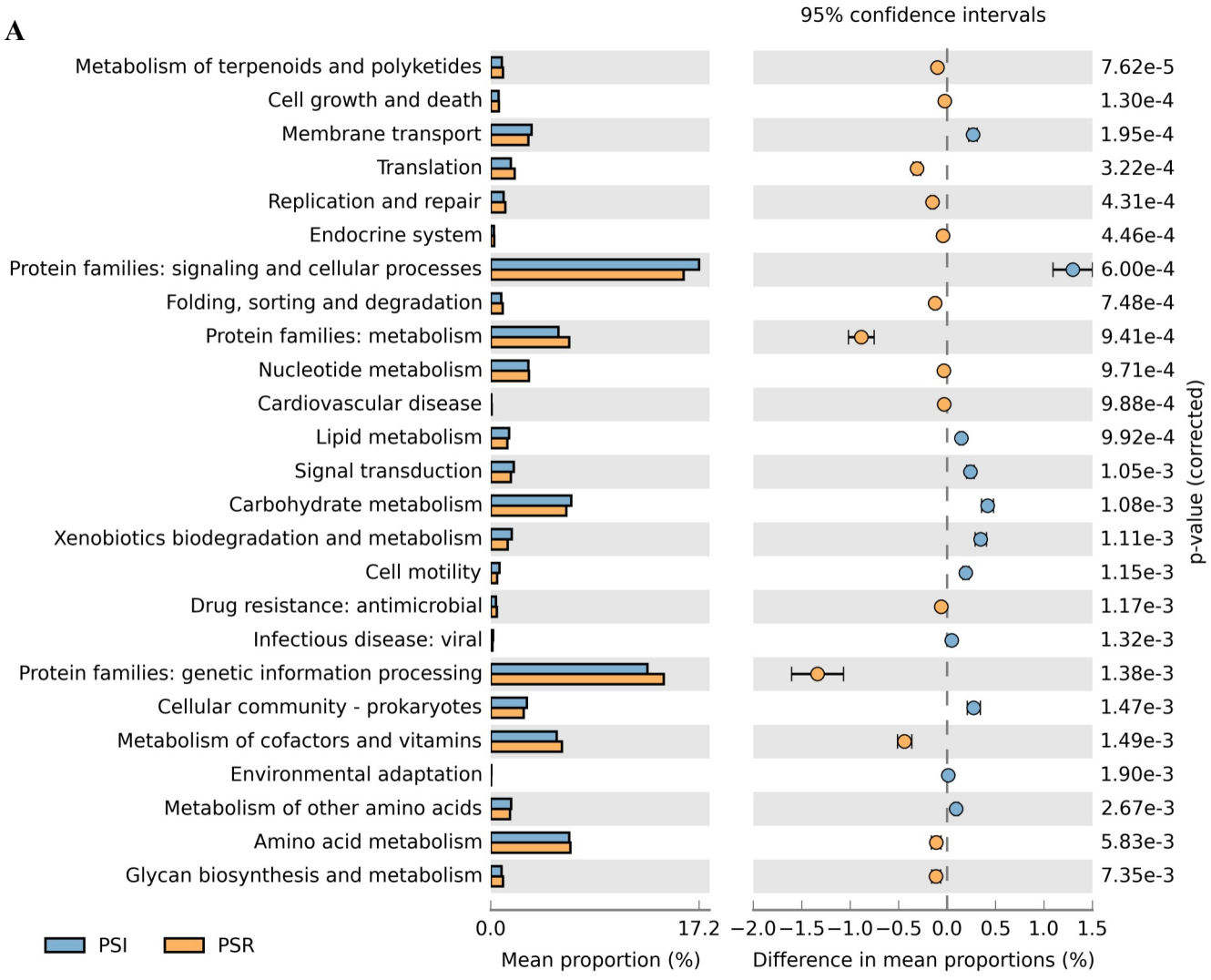
The microbial common core between the PSR and PSI photovoltaic panels comprise mainly *Hymenobacter, Deinococcus, Sphingomonas, Methylobacterium-Methylorubrum, Craurococcus-Caldovatus, Massilia, Noviherbaspirillum and 1174-901-12* (uncultured bacteria) genera (Fig. S3, supporting information).

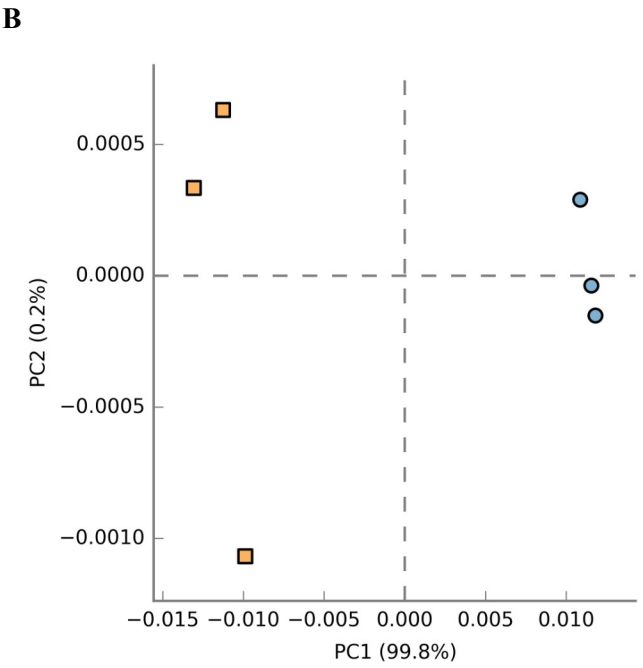
The results of the analysis of taxonomic information with DESeq2 showed that a total of 30 out of 96 ASVs were statistically different (Fig. S2, supporting information). Except for *Hymenobacter* (ASV_84d0) and *Methylobacterium-Methylorubrum*, all genera were more associated with PSR compared to PSI.

The bioinformatics workflow used to predict the functional composition from the 16S rRNA gene using PICRUSt2 software associated with the STAMP software processing revealed that the metabolic activities of PSR and PSI were associated between them in general, according to the PCA analysis (Fig. 3B) which showed that relative distances between the samples were very close to 0. The protein families responsible for signaling, the cellular process and genetic information processing were the most abundant profile in both

samples, followed by carbohydrate, protein and amino acid metabolism (Fig. 3A). Among the predicted proteins, we found some of those involved in stress response related to DNA damage (OxyR, recA, uvrA, uvrB, gyrA, gyrB, dps2), amino acid transport and metabolism (hisH, hisB, hisD, hisC, hisZ), proteases with chaperones and folding catalysts function (HflB, HsIU) and universal stress protein (YdaA) (Fig. 4, Fig. S4, supporting information).

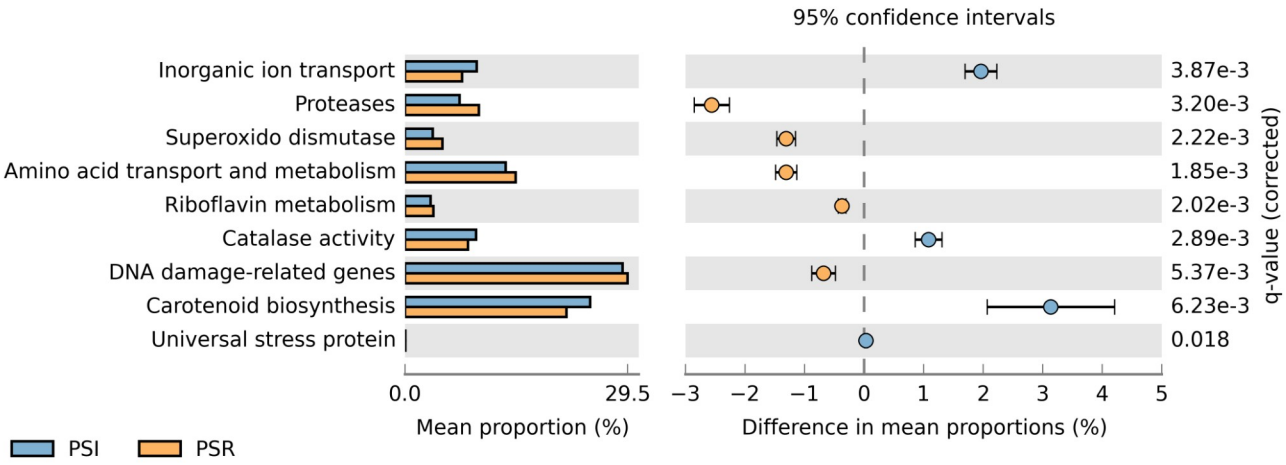
Figure 3. PICRUSt analysis to predict metagenome functional profile from 16S rRNA marker gene using STAMP software for data visualization. **(A)** General metabolic activities between predicted function profile of PSI and PSR samples, **(B)** Principal Component Analysis (PCA) between PSI and PSR predicted profile.





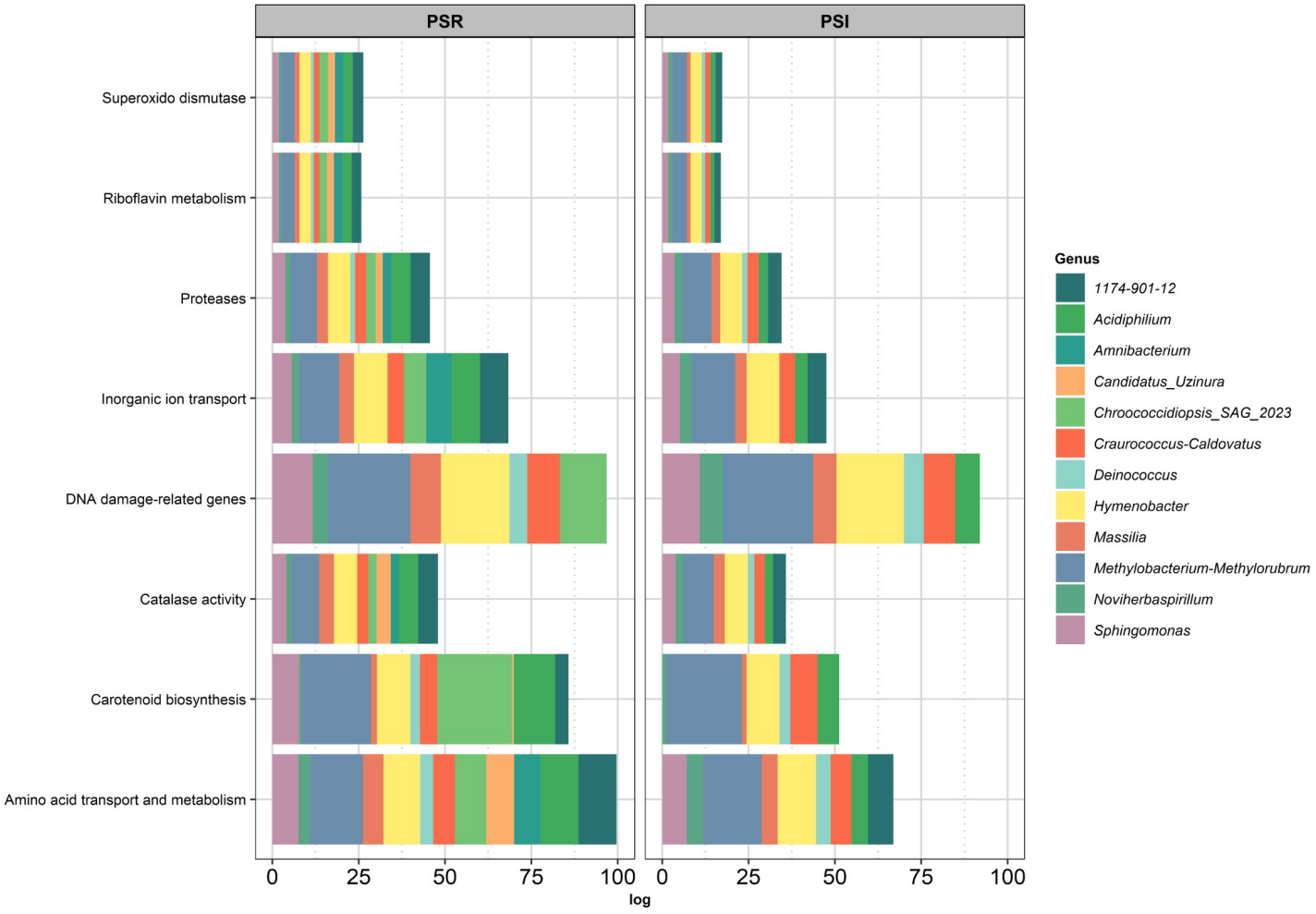
Aminoacid transport and metabolism, DNA-damage related genes, proteases, riboflavin and superoxido dismutase activities were more present in PSR. Furthermore, carotenoid biosynthesis, catalase activity, inorganic ion transport were predicted to be more influenced by PSI (Fig. 4).

Figure 4. Metabolic activities associated with specific KEGG pathways related to stress resistance (radiation, desiccation and pigments) in PSR and PSI samples.



Among the 10 most abundant genera and members of the common core, *Methylobacterium-Methylorubrum* and *Hymenobacter* were mainly involved in all metabolisms related to stress resistance (Fig. 5).

Figure 5. Metabolic activities from specific KEGG pathways related to stress resistance associated with the 10 most abundant genera and members of common core.



2.4 Discussion

Our results showed that bacterial diversity was significantly greater in the PSR than the PSI ($p < 0.001$). Concerning this difference, we propose some arguments and considerations: i) the geographic coordinates between both cities are quite similar (Itatiba is less than one degree south from Sorocaba). They have similar climates and annual doses of solar irradiance.

This suggests that the meteorological and geographic coordinates (latitude and longitude) of sampling have an insignificant or low impact on the difference of microbial diversity; ii) another point concerns cleaning, the PSI was washed in water only 6 months before sampling, while the PSR was not washed for about 2 years, except in rainfall. Tanner et al. (2020) showed that biofilm formed on photovoltaic panels surfaces cannot be destroyed by either rainfall or water cleaning and the process did not affect the taxonomic terms analyzed. Rainfalls are only able to remove large particles and have no effect on attached biofilms (Appels et al. 2013; Shirakawa et al. 2015); iii) another factor that might influence the overall microbial diversity is the seasonal behavior, in which bacterial diversity on photovoltaic panels decreases during the autumn and winter periods compared to the summer and spring months (Tanner et al. 2020); iv) another possible factor is the operation time. The PSR was installed 1 year before the PSI, however the time of exposition, as a unique and isolated factor, seems to not strongly influence the final microbial community because the biofilm formation occurs rapidly after the attachment of resistant microorganisms (Tanner et al. 2020); finally v) the surroundings of the environment in which photovoltaic panels were sampled was also a variable. The PSR sample was collected in a rural environment, surrounded by dust, trees, and wildlife while the PSI sample was carried out in an urban environment, surrounded by houses and other constructions. Anthropogenic changes and reduced forest areas have caused the reduction of contact between natural biodiversity and the urban environment. Owing to this, natural biodiversity tends to be low in urban areas (Chapin et al. 2000; Parajuli et al. 2018). Considering these arguments, it is reasonable to hypothesize that the environmental characteristics in the surroundings (where the photovoltaic panel was installed) may explain the difference between the reported microbial diversity, although it is likely that there is more than one factor behind this effect.

Despite the microbial diversity significant differences ($p < 0.001$), PCoA and ANOSIM showed that in compositional terms, PSR and PSI were similar ($p > 0.005$). Taxonomic analysis showed that PSR| and PSI shared the same most abundant phyla (Proteobacteria*,* Bacteroidota and Cyanobacteria), which represents almost all the bacterial diversity observed. A previous study of soil in extreme environments (desert and Antarctic peninsula) showed that bacterial communities were dominated by Proteobacteria*,* Bacteroidota, Firmicutes, and Actinobacteriota (An *et al.* 2013; Gaete, Mandakovic and González 2020). Cyanobacteria phyla is often associated with extremophilic microorganisms

with radiation and desiccation resistance (Varshney *et al.* 2015). The characteristics of mainly phyla, detected in this study, suggests that the bacterial community of photovoltaic panels in tropical weather might be shaped by the environmental condition based on solar radiation and desiccation conditions.

At genus level, we observed a clear dominance of *Methylobacterium-Methylorubrum* (Proteobacteria) and *Hymenobacter* (Proteobacteria) in both samples. *Methylobacterium-Methylorubrum*, phylogenetic related to *Methylobacterium* (Green and Ardley 2018), was also reported (to a less extent) in the photovoltaic panels from polar regions (0.53% and 0.48%, Arctic and Antarctic, respectively) (Tanner et al., 2017), Valencia (0.57%) (Dorado-Morales *et al.* 2016), and Berkeley (Porcar *et al.* 2018). Moreover, Porcar *et al*. (2018) showed that the *Methylobacterium* genus had a high desiccation-resistance and ability to colonize glass surfaces. Furthermore, *Methylobacterium* can adhere, form biofilm and tolerate low nutrient conditions (Yano *et al.* 2013). All these properties are consistent with photovoltaic panel surface conditions. *Hymenobacter,* whose radiation-resistant properties were previously reported (Dai *et al.* 2009; Sedláček *et al.* 2019; Maeng, Kim and Subramani 2020), was also dominant in the photovoltaic panels from Valencia (8.64%) (Dorado-Morales *et al.* 2016), polar regions (1.23% and 7.6%, Arctic and Antarctic, respectively) (Tanner *et al.* 2018a) and Berkeley (19.7%) (Porcar *et al.* 2018). After 18 months, the biofilm composition analyzed from photovoltaic panels in Brazil showed that only *Methylobacterium* and *Hymenobacter* remained in the bacterial community (Shirakawa *et al.* 2015).

Among the genera in lower proportions of presence, *Acidiphilium (Beblo-Vranesevic et al. 2018)*, *Chroococcidiopsis* (Billi *et al.* 2000) and *Sphingomonas* (Marizcurrena *et al.* 2019) were found to have radiation and desiccation resistance. *Amnibacterium, Candidatus Uzinura, Fibrella* and *Craurococcus-Caldovatus* were not related to these properties. Despite the harsh conditions, microorganisms not known to be resistant are expected to be found in lower amounts, supported and protected by biofilm formation. For example, Paulino-Lima et al. (2016) observed that *Geodermathophilus sp*., aggregated by fibrous material involved in biofilm formation, was more resistant to UV radiation than *Hymenobacter sp*. which was distributed in individual structures, suggesting that cell aggregation attenuated the UV transmission. In the biofilm formed on photovoltaic panels, taxa capable of withstanding extreme conditions, tend to grow over time, while those that are not resistant, tend to decrease

(Tanner *et al.* 2020). This might explain the predominance of extremophilic taxa concerning non-extremophilic.

Among the members of the microbial common core between PSR and PSI, *Deinococcus* genus, which includes several extremophilic species, showed a minor abundance in both samples (PSR and PSI) compared to other genera. The explanation to this might be in the ecological distribution observed in the *Deinococcus* genera species (*Deinococcus radiodurans*) as it looks as though *Deinococcus* makes an effort in the survival efficiency at the expense of reproduction (Krisko and Radman 2013). Dorado-Morales *et al.* (2016) found that the microbial common core in the photovoltaic panels of Valencia was mainly composed by *Deinococcus, Sphingomonas, Novosphingobium,* and *Hymenobacter* genera. This common core proved to be similar with PSR and PSI specifically concerning *Deinococcus, Sphingomonas* and *Hymenobacter* genera occurrence. These genera were all previously described to have UV radiation-resistance properties (Dai *et al.* 2009; Etemadifar, Gholami and Derikvand 2016; Marizcurrena *et al.* 2019). The genus *1174-901-12* related to Beijerinckiaceae and *Sphingomonas* were the most common in the early steps of tile colonization, suggesting a role of these strains in the initial biofilm formation (Romani *et al.* 2019).

Despite some differences, the main taxa detected in this work proved to be consistent with those detected on photovoltaic panels surfaces previously reported in the Mediterranean and polar conditions (Dorado-Morales *et al.* 2016; Porcar *et al.* 2018; Tanner *et al.* 2018a, 2020). More recently, Tanner *et al.* (2020) showed that after 2 years the extremophilic taxa adapted to resisting harsh desiccation and radiation environments, in the final ecological succession step, were naturally selected as preferential colonizers of the photovoltaic panel surface leading to the inference of their stable community throughout time.

Among the identified proteins to predict metagenome functional content, we found some of those involved in stress response related to DNA damage (OxyR, recA, uvrA, uvrB, gyrA, gyrB, dps2), amino acid transport and metabolism (hisH, hisB, hisD, hisC, hisZ), proteases with chaperones and folding catalyst function (HflB, HsIU) and universal stress protein (YdaA) (Fig. 4). This is consistent with extremophilic mechanisms to prevent DNA damage (Krisko and Radman 2013). Amino acid transport and metabolism, including ABC transporters (membrane transport), also present in the predicted profile, have been suggested to have a role in radiation-resistance, acting as reactive oxygen species scavenger (Daly *et al.*

2007, 2010; Krisko and Radman 2013). It was previously observed that the irradiation process could lead to an increasing in proteolytic activity, a process that is typically catalyzed by proteases, enzymes that break the peptide bonds in proteins, indicating that proteases play a role in radiation-resistance (Daly *et al.* 2010).

In general, metabolisms of specific KEGG Orthology related to stress resistance (Fig. S4, supporting information) were found in the 10 most abundant genera and members of the common core (Fig. 5). Stress metabolisms were more associated with *Hymenobacter* and *Methylobaterium-methylorubrum,* which was consistent with their abundance in both samples. This interlocks with the observation that *Hymenobacter* and *Methylobacterium* were reported to compose other photovoltaic panel microbial communities around the world.

In the viewpoint of biotechnological potential, the presence of metabolites related to stress resistance in the predicted data indicate that the microbial community investigated are possibly a supply of desired products. For example, ABC transporters, present in amino acid transport and metabolism category, have been suggested as attractive genes in plant biotechnology field (Lane *et al.* 2016). Carotenoids pigments has been highlighted as a focus of research in bioprospection (Mendes-Silva *et al.* 2020) and DNA damage proteins have been described with remarkable significance in therapeutic applications against cancer, acting as sensor proteins in the detection of DNA damage (Fernandes, Shah and Khattar *et al.* 2021).

This is the first report of microbial diversity of photovoltaic panels in a tropical region considering an ecological and biotechnological perspective. Our data showed that taxonomic analysis and predicted metabolic information were appropriated with the harsh environment on the surfaces of photovoltaic panels. Although our results provided only partial information of microbial ecology, the similarity observed in investigated communities indicates that might exist an ecological succession in the dynamic of microbial diversity on photovoltaic panels surfaces in a tropical region, primarily based on microorganisms adapted to the sun-exposed environment. Furthermore, the prediction of specific genes involved in metabolisms of stress resistance was a shred of preliminary evidence that photovoltaic panels in tropical environments might be a repository of specialized microbes that represent a source of biotechnological interest providing access to relevant metabolites, such as proteins, enzymes, and other molecules.

2.5 References

Adinoyi MJ, Said SAM. Effect of dust accumulation on the power outputs of solar photovoltaic modules. *Renew Energy* 2013;**60**:633–6.

An S, Couteau C, Luo F *et al.* Bacterial Diversity of Surface Sand Samples from the Gobi and Taklamaken Deserts. *Microb Ecol* 2013;**66**:850–60.

Andrews S, 2010. Fastqc: A Quality Control Tool For High Throughput Sequence Data. http://www.Bioinformatics.Babraham.Ac.Uk/Projects/Fastqc (22 october 2020, date last accessed)

Appels R, Lefevre B, Herteleer B *et al.* Effect of soiling on photovoltaic modules. *Sol Energy* 2013;**96**:283–91.

Apprill A, McNally S, Parsons R et al. Minor revision to V4 region SSU rRNA 806R gene primer greatly increases detection of SAR11 bacterioplankton. *Aquat Microb Ecol* 2015;**75**:129–137.

Beblo-Vranesevic K, Bohmeier M, Perras AK *et al.* Lack of correlation of desiccation and radiation tolerance in microorganisms from diverse extreme environments tested under anoxic conditions. *FEMS Microbiol Lett* 2018;**365**:1–9.

Billi D, Friedmann EI, Hofer KG *et al.* Ionizing-radiation resistance in the desiccation-tolerant cyanobacterium Chroococcidiopsis. *Appl Environ Microbiol* 2000;**66**:1489–92.

Bokulich NA, Kaehler BD, Rideout JR *et al.* Optimizing taxonomic classification of marker-gene amplicon sequences with QIIME 2's q2-feature-classifier plugin. *Microbiome* 2018;**6**:1–17.

Bolger AM, Lohse M, Usadel B. Trimmomatic: A flexible trimmer for Illumina sequence data. *Bioinformatics* 2014;**30**:2114–20.

Bolyen E, Rideout JR, Dillon MR *et al.* Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. *Nat Biotechnol* 2019;**37**:852–7.

Callahan BJ, McMurdie PJ, Rosen MJ *et al.* DADA2: High-resolution sample inference from Illumina amplicon data. *Nat Methods* 2016;**13**:581–3.

Chapin F, Zavaleta E, Eviner V *et al.* Consequences of changing biodiversity. *Nature* 2000;**405**:234–42.

Cordero RR, Damiani A, Laroze D *et al.* Effects of soiling on photovoltaic (PV) modules in the Atacama Desert. *Sci Rep* 2018;**8**:1–14.

Dai J, Wang Y, Zhang L *et al.* Hymenobacter tibetensis sp. nov., a UV-resistant bacterium isolated from Qinghai-Tibet plateau. *Syst Appl Microbiol* 2009;**32**:543–8.

Daly MJ, Gaidamakova EK, Matrosova VY *et al.* Protein oxidation implicated as the primary determinant of bacterial radioresistance. *PLoS Biol* 2007;**5**:769–79.

Daly MJ, Gaidamakova EK, Matrosova VY *et al.* Small-molecule antioxidant proteome-shields in Deinococcus radiodurans. *PLoS One* 2010;**5**:10–5.

Dorado-Morales P, Vilanova C, Peretó J *et al.* A highly diverse, desert-like microbial biocenosis on solar panels in a Mediterranean city. *Sci Rep* 2016;**6**:1–9.

Douglas G, Maffeim V, Zaneveld J *et al.* PICRUSt2: An improved and extensible approach for metagenomic inference. *bioRxiv* 2019, DOI: 10.11428/jhej1987.42.191.

Escobar-Zepeda A, Godoy-Lozano EE, Raggi L *et al.* Analysis of sequencing strategies and tools for taxonomic annotation: Defining standards for progressive metagenomics. *Sci Rep* 2018;**8**:1–13.

Etemadifar Z, Gholami M, Derikvand P. UV-Resistant Bacteria with Multiple-Stress Tolerance Isolated from Desert Areas in Iran. *Geomicrobiol J* 2016;**33**:1–7.

Fernandes SG, Shah P, Khattar E. Recent advances in therapeutic application of DNA damage response inhibitors against cancer. *Ant Canc Agen Med Chem* 2021;**21**:1871-5206

Gaete A, Mandakovic D, González M. Isolation and identification of soil bacteria from extreme environments of Chile and their plant beneficial characteristics. *Microorganisms* 2020;**8**:1–13.

Green PN, Ardley JK. Review of the genus Methylobacterium and closely related organisms: A proposal that some Methylobacterium species be reclassified into a new genus, Methylorubrum gen. nov. *Int J Syst Evol Microbiol* 2018;**68**:2727–48.

International Energy Agency (IEA). How solar energy could be the largest source of eletricity by mid-century. https://www.iea.org/news/how-solar-energy-could-be-the-largest-source-of-electricity-by-mid-century (12 march 2021, date last accessed)

Instituto Nacional de Meteorologia (INMET). https://portal.inmet.gov.br/. (30 June 2020, date last accessed)

Kanehisa M, Sato Y, Kawashima M *et al.* KEGG as a reference resource for gene and protein annotation. *Nucleic Acids Res* 2016;**44**:D457–62.

Katoh K, Misawa K, Kuma KI *et al.* MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Res* 2002;**30**:3059–66.

Krisko A, Radman M. Biology of extreme radiation resistance: The way of Deinococcus radiodurans. *Cold Spring Harb Perspect Biol* 2013;**5**, DOI: 10.1101/cshperspect.a012765.

Lane TS, Rempe CS, Davitt J *et al.* Diversity of ABC transporter genes across the plant kingdom and their potential utility in biotechnology. *BMC Biotech* 2016;**16**:16:47

Locey KJ, Lennon JT. Scaling laws predict global microbial diversity. *Proc Natl Acad Sci U S A* 2016;**113**:5970–5.

Maeng S, Kim MK, Subramani G. Hymenobacter jejuensis sp. nov., a UV radiation-tolerant bacterium isolated from Jeju Island. *Antonie van Leeuwenhoek, Int J Gen Mol Microbiol* 2020;**113**:553–61.

Marizcurrena JJ, Morales D, Smircich P *et al.* Draft Genome Sequence of the UV-Resistant Antarctic Bacterium Sphingomonas sp. Strain UV9. *Microbiol Resour Announc* 2019;**8**, DOI: 10.1128/mra.01651-18.

Martin M. Cutadapt removes adapter sequences from high-throughput sequencing reads. *Embnet J* 2011.

Mendes-Silva TC, Andrade RF, Ootani MA *et al.* Biotechnological potential of carotenoids procuced by extremophilic microorganisms and application prospects for cosmetics industry. *Sci Res Publ* 2020;**10**:397-410

McMurdie PJ, Holmes S. Phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data. *PLoS One* 2013;**8**, DOI: 10.1371/journal.pone.0061217.

Parada A, Needham D, Fuhrman J. Every base matters: assessing small subunit rRNA primers for marine microbiomes with mock communities, time series and global field samples. *Environ Microbiol* 2016;**18**:403–1414.

Parajuli A, Grönroos M, Siter N *et al.* Urbanization reduces transfer of diverse environmental microbiota indoors. *Front Microbiol* 2018;**9**:1–13.

Parks DH, Tyson GW, Hugenholtz P *et al.* STAMP: Statistical analysis of taxonomic and functional profiles. *Bioinformatics* 2014;**30**:3123–4.

Paulino-Lima IG, Fujishima K, Navarrete JU *et al.* Extremely high UV-C radiation resistant microorganisms from desert environments with different manganese concentrations. *J Photochem Photobiol B Biol* 2016;**163**:327–36.

Pereira HM. A latitudinal gradient for genetic diversity. *Science (80-)* 2016;**353**:1494–5.

Porcar M, Louie KB, Kosina SM *et al.* Microbial ecology on solar panels in Berkeley, CA, United States. *Front Microbiol* 2018;**9**:1–14.

Price MN, Dehal PS, Arkin AP. FastTree 2 - Approximately maximum-likelihood trees for large alignments. *PLoS One* 2010;**5**, DOI: 10.1371/journal.pone.0009490.

Qi H zhou, Wang W zhou, He J yan et al. Antioxidative system of Deinococcus radiodurans. Res Microbiol 2019;**171**:45–54.

Quast C, Pruesse E, Yilmaz P *et al.* The SILVA ribosomal RNA gene database project: Improved data processing and web-based tools. *Nucleic Acids Res* 2013;**41**:590–6.

Rognes T, Flouri T, Nichols B *et al.* VSEARCH: A versatile open source tool for metagenomics. *PeerJ* 2016;**2016**:1–22.

Sayed AM, Hassan MHA, Alhadrami HA *et al.* Extreme environments: microbiology leading to specialized metabolites. *J Appl Microbiol* 2020;**128**:630–57.

Sedláček I, Pantůček R, Králová S *et al.* Hymenobacter amundsenii sp. nov. resistant to ultraviolet radiation, isolated from regoliths in Antarctica. *Syst Appl Microbiol* 2019;**42**:284–90.

Shirakawa MA, Zilles R, Mocelin A *et al.* Microbial colonization affects the efficiency of photovoltaic panels in a tropical environment. *J Environ Manage* 2015;**157**:160–7.

Tanner K, Martí JM, Belliure J *et al.* Polar solar panels: Arctic and Antarctic microbiomes display similar taxonomic profiles. *Environ Microbiol Rep* 2018a;**10**:75–9.

Tanner K, Martorell P, Genovés S *et al.* Bioprospecting the solar panel microbiome: high-throughput screening for antioxidant bacteria in a Caenorhabditis elegans model. *Bioprospecting Sol panel microbiome High-throughput Screen Antioxid Bact a caenorhabditis elegansModel* 2018b:423731.

Tanner K, Molina-Menor E, Latorre-Pérez A *et al.* Extremophilic microbial communities on photovoltaic panel surfaces: a two-year study. *Microb Biotechnol* 2020;**13**:1819–30.

Tanner K, Vilanova C, Porcar M. Bioprospecting challenges in unusual environments. *Microb Biotechnol* 2017;**10**:671–3.

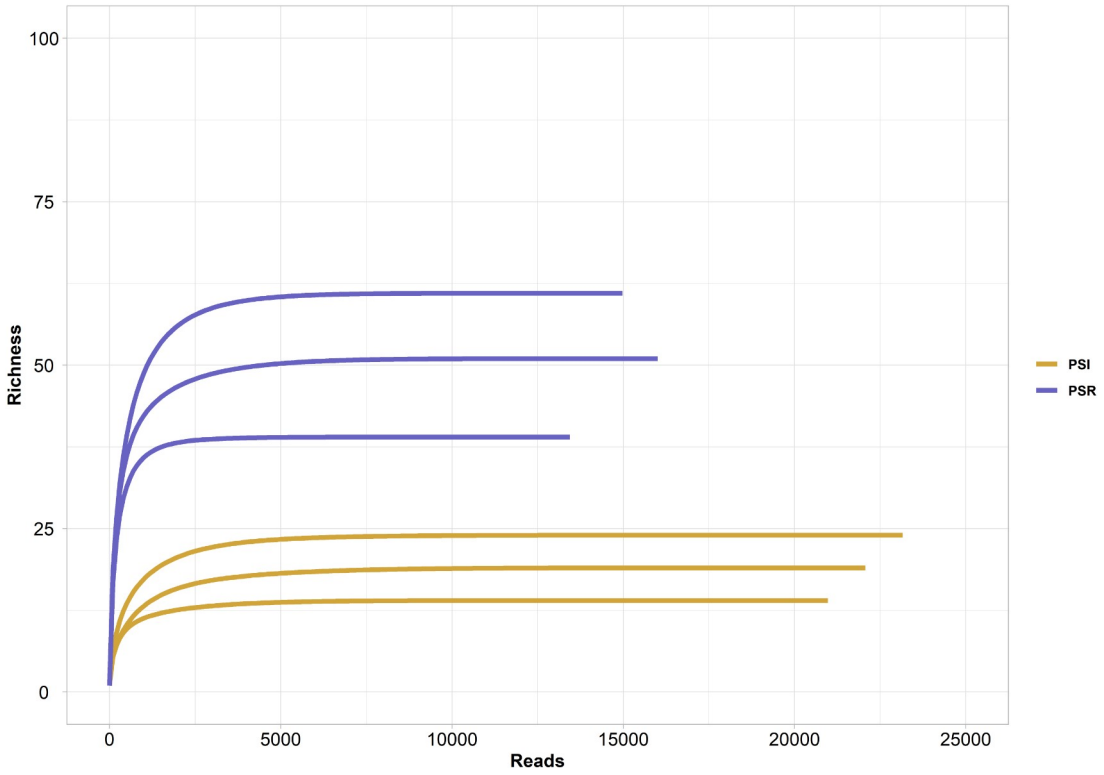
Varshney P, Mikulic P, Vonshak A *et al.* Extremophilic micro-algae and their potential contribution in biotechnology. *Bioresour Technol* 2015;**184**:363–72.

Vitorino LC, Bessa LA. Microbial diversity: The gap between the estimated and the known. *Diversity* 2018;**10**, DOI: 10.3390/D10020046.

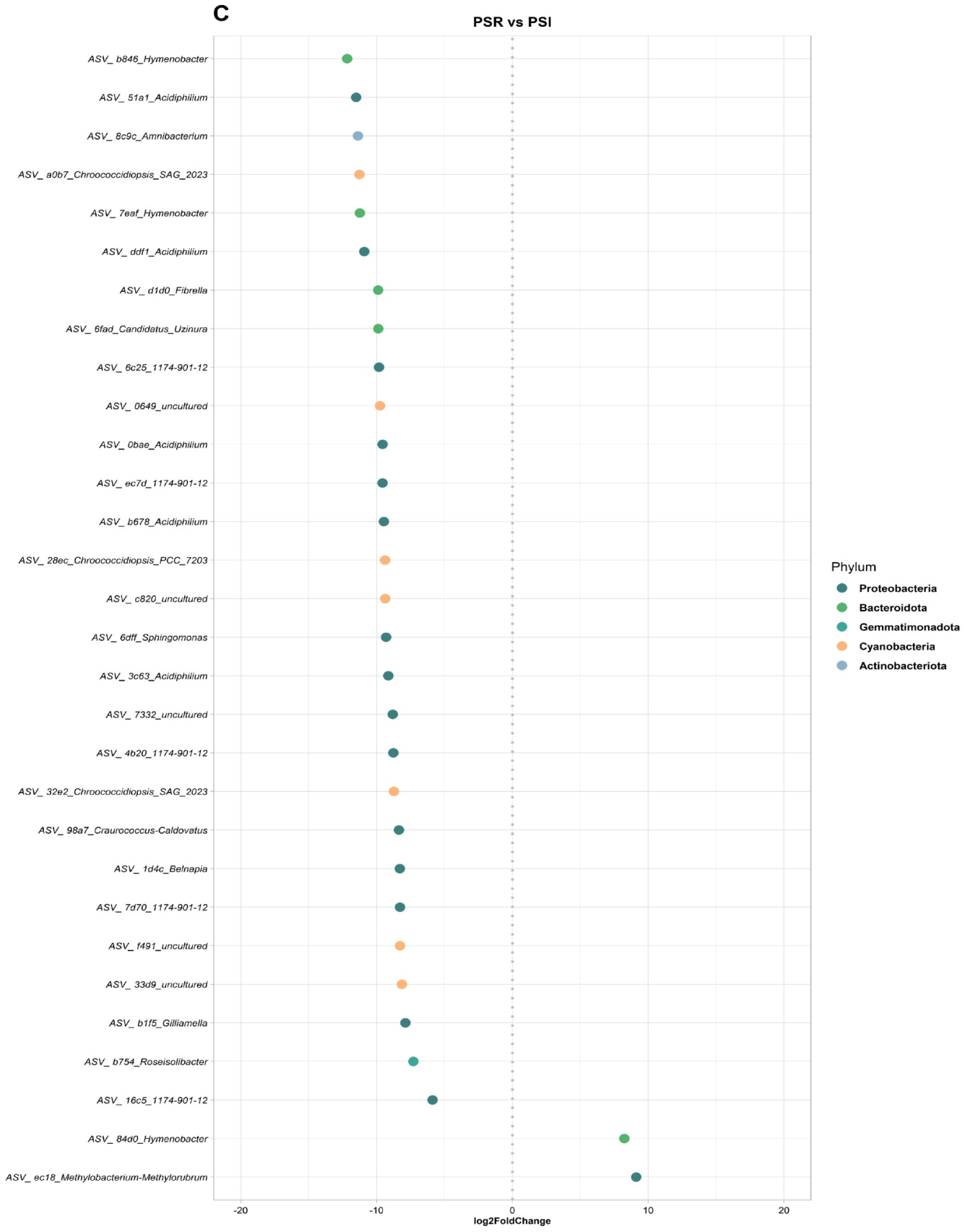
Yano T, Kubota H, Hanai J *et al.* Stress tolerance of Methylobacterium biofilms in bathrooms. *Microbes Environ* 2013;**28**:87–95.

2.6 Supplementary data

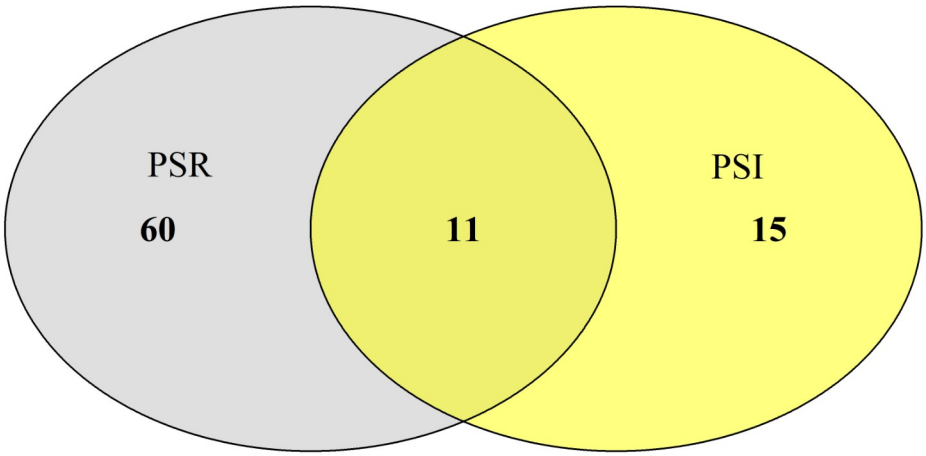
Supplementary Figure S1. Rarefaction curve of alpha diversity richness analysis (chao1) showing that the depth of 16rRNA sequencing was enough to reach total microbial diversity of photovoltaic panels from Itatiba (PSI) and Sorocaba (PSR).



Supplementary Figure S2. DESEq2 analysis of fold-change bacterial genera between PSR and PSI communities ($p < 0.005$).



Supplementary Figure S3. Venn diagram showing the exclusive and shared ASVs from photovoltaic panels (PSR and PSI).



Supplementary Figure S4. The specific KO functional orthologs and KEGG pathways used to search for genes related to radiation, desiccation and pigments in PICRUSt predicted data. Bold rows represent KOs found in the PICRUst prediction.

KO	Gene	Metabolic activity	Stress
K12347	nramp	Inorganic ion transport	Radiation
K04761	**OxyR**	**Catalase activity**	**Radiation**
K03742	cinA	DNA damage-related genes	Radiation
K22503	dps1	DNA damage-related genes	Radiation
K03553	**recA**	**DNA damage-related genes**	**Radiation**
K03701	**uvrA**	**DNA damage-related genes**	**Radiation**
K03702	**uvrB**	**DNA damage-related genes**	**Radiation**
K02469	**gyrA**	**DNA damage-related genes**	**Radiation**
K02470	**gyrB**	**DNA damage-related genes**	**Radiation**
K03781	katE	Catalase activity	Radiation
K05793	**terB**	**Catalase activity**	**Radiation**
K05791	**terZ**	**Catalase activity**	**Radiation**
K07304	**msrA**	**Catalase activity**	**Radiation**
K04047	**dps2**	**DNA damage-related genes**	**Radiation**
K03584	recO	DNA damage-related genes	Radiation
K04564	**sodA**	**Superoxido dismutase**	**Radiation**
K02501	**hisH**	**Amino acid transport and metabolism**	**Desiccation**
K01089	**hisB**	**Amino acid transport and metabolism**	**Desiccation**
K00013	**hisD**	**Amino acid transport and metabolism**	**Desiccation**
K00817	**hisC**	**Amino acid transport and metabolism**	**Desiccation**
K02502	**hisZ**	**Amino acid transport and metabolism**	**Desiccation**
K04043	dnaK	Molecular chaperone	Desiccation
K01546	**kdpA**	**Inorganic ion transport**	**Desiccation**
K01547	**kdpB**	**Inorganic ion transport**	**Desiccation**
K01548	**kdpC**	**Inorganic ion transport**	**Desiccation**
K04077	GroEL	Molecular chaperones	Desiccation
K04080	IbpA	Molecular chaperones	Desiccation
K03798	**HflB**	**Proteases**	**Desiccation**
K03667	**HslU**	**Proteases**	**Desiccation**
K14055	**YdaA**	**Universal stress protein**	**Desiccation**
K06443	**crtY**	**Carotenoid biosynthesis**	**Pigment**
K02292	**crtO**	**Carotenoid biosynthesis**	**Pigment**
K10027	**crtI**	**Carotenoid biosynthesis**	**Pigment**
K15746	crtZ	Carotenoid biosynthesis	Pigment
K00514	**crtQ**	**Carotenoid biosynthesis**	**Pigment**
K02291	**crtB**	**Carotenoid biosynthesis**	**Pigment**
K02293	**crtP**	**Carotenoid biosynthesis**	**Pigment**
K02294	**crtR**	**Carotenoid biosynthesis**	**Pigment**
K09835	**crtH**	**Carotenoid biosynthesis**	**Pigment**
K09836	**crtW**	**Carotenoid biosynthesis**	**Pigment**
K09844	**crtC**	**Carotenoid biosynthesis**	**Pigment**
K09845	**crtD**	**Carotenoid biosynthesis**	**Pigment**
K09846	**crtF**	**Carotenoid biosynthesis**	**Pigment**
K09879	**crtU**	**Carotenoid biosynthesis**	**Pigment**
K14605	**cruA**	**Carotenoid biosynthesis**	**Pigment**
K14606	**cruP**	**Carotenoid biosynthesis**	**Pigment**
K00793	**ribE**	**Riboflavin metabolism**	**Pigment**

CHAPTER 3

Biotechnological potential of pigmented microorganisms isolated from photovoltaic panels surfaces in a tropical region

ABSTRACT

Photovoltaic panels have been studied as outdoor surfaces capable to harbor specialized microbial communities with pigmented microorganisms association. Pigmentation is one of the microbial strategies to overcome a stressor environment, but is also a biological tool that brings commercial interest in many areas, such as pigment or antioxidant industries. In this work, we have investigated the pigmented microorganisms living on the surfaces of photovoltaic panels in a tropical region using Sanger sequencing approach, phylogenetic correlations and previous knowledge of literature to understand the biotechnological potential of the isolated strains and also to have a preliminary and complementary information of colonization process of this communities in association with the culture-independent technique previously employed. The samples retrieved from photovoltaic panels surfaces displayed cultivable and pigmented colonies growing in a wide range of temperatures. We identified the isolated strains as *Hymenobacter flocculans*, *Sphingomonas paucimobilis*, *Mycolicibacterium aurum*, *Serratia nematodiphila, Arthrobacter koreensis, Microbacterium hydrotermale*, *Rhodotorula mucilaginosa*, *Gordonia sp.*, *Verrucosispora qiuiae*, *Dermacoccus nishinomiyaensis*, *Kocuria sp.*, *Psychrobacter sp., Pseudomonas coleopterorum*, *Rhodotorula sp*. In the literature documentation, most of these strains, or at least their closest relatives, was described as tolerant or resistant to UV light, desiccative conditions and biofilm capability, all being important adaptation mechanisms to thrive and engage the colonization process on photovoltaic panels surfaces. Moreover, many biotechnological applications was discussed, reinforcing the finding that photovoltaic panels are a repository of biotechnological interest.

Keywords: biosprospecting; microbial ecology; solar panel.

3.1 Introduction

Biotechnology has been contributed to environmental and economic benefits, offering the possibility to industrial transformations to become more compatible with the biosphere (Gavrilescu and Chisti 2005). In this context, biological agents are suitable alternatives for the chemical industry. Microbial diversity living in an extreme environment, capable to succeed in habitats that is intolerably or even lethal for most terrestrial life, has been proved to be an attractive source of useful biological molecules with a wide commercial applications (Tanner, Vilanova and Porcar 2017; Sayed *et al.* 2020).

Microorganisms exposed to solar radiation are constantly threatened by oxidation processes that lead to direct or indirect DNA damage intermediated by either UV-light or reactive molecules capable to turn important biomolecules into dysfunctional (Qi *et al.* 2019). In order to thrive in such stress conditions, these microorganisms manufacture specialized metabolites as molecular and cellular strategies for surveillance, being a result of adaptation and evolutionary process (Rothschild and Mancinelli 2001; Rampelotto 2013). This machinery includes an efficient mechanism of DNA repair and protection against oxidative stress. For this, multiple antioxidant systems capable to scavenger oxidative species that cause cell damage, especially to proteins, is very important (Krisko and Radman 2013; Rastogi, Sonani and Madamwar 2015; Paulino-Lima *et al.* 2016). Carotenoids and scavenger compounds, responsible for pigmentation properties, are one of the strategies that can help microorganisms overcome DNA damage and protein oxidation caused by direct and indirect UV radiation products (Tian *et al.* 2009; Qi *et al.* 2019). For example, cells recovered from icy, dry, and irradiated environments have a high frequency of pigmented phenotype, suggesting that pigmentation play a role in cope with the stress associated with water loss, cryopreservation, oxidative stress and DNA damage, increasing microbial resistance to environmental stressors (Dieser, Greenwood and Foreman 2010; Ragon *et al.* 2011; Etemadifar, Gholami and Derikvand 2016).

Photovoltaic panels have been reported to harbor an adapted microbial diversity similar to those found in irradiated or sun-exposed places. (Dorado-Morales *et al.* 2016; Porcar *et al.* 2018; Tanner *et al.* 2018a). Moreover, the surface of these structures was previously screened for pigmented bacteria with antioxidant activity, suggesting that the strains living there have potential biotechnological applications (Tanner *et al.* 2018b). Even so, the potential of these strains in a tropical climate have never been studied either concerning an ecology or

biotechnological point of view. In this work, we aimed to retrieve pigmented microorganisms from photovoltaic panels surfaces and identified them through Sanger sequencing to check their identities using phylogenetic correlations. We also investigated, in the literature reports, their biotechnological potential, as well adaptation characteristics that could contribute to formulating a hypothesis about their colonization process as a complementary approach to the culture-independent technique.

3.2 Material and methods

3.2.1 Sampling

Samples were collected from two photovoltaic panels in southeast Brazil: Sorocaba (-23º28'55" S, -47º22'19.9" W) and Itatiba (-22º59'36.3" S, -46º50'48" W), counting seven photovoltaic modules in Sorocaba (PSR) and four in Itatiba (PSI). The photovoltaic panel from Soracaba has been in operation for 2 years and has never been cleaned. Regarding photovoltaic panel from Itatiba, it was installed 1 year from the sampling day and was cleaned 6 months before the collection. Sampling extraction was based on the method used by Dorado-Morales et al. (2016) and Porcar et al. (2018), with some modifications. Briefly, the surface of photovoltaic panels were strongly scrapped with gauze a bandage and sterile phosphate-buffered saline (PBS) (1 x, pH = 7.6). Dust obtained in this process was transferred into a glass flask containing 150 mL of sterile PBS and transported to the laboratory, where isolation, cultivation and identification were performed. To concentrate the slurry obtained, it was transferred to a 50 mL conical tube and centrifugated at 5000 rpm for 3 min. This process was repeated 10x, in order to optimize biological recovery from gauze bandage.

Climatological data (from June 2020) were recorded daily from the National Institute of Meteorology (INMET) network of monitoring stations. The mean temperature was 19ºC and the average relative humidity was 72% in both cities. The solar irradiance was 311.5 $W.m^{-2}$ PSR and 267.0 $W.m^{-2}$ PSI, and mean precipitation levels were 0.05 mm and 0.1 mm, respectively. The average temperature of the photovoltaic panels during the sampling process was 43ºC PSR and 21ºC PSI.

3.2.2 Cultivation and isolation of pigmented microorganisms

The pellets from PSI and PSR samples were suspended in 5 mL of PBS and serial diluted in saline solution 0.85% until 10^{-4}. Then, 100 µL of the stock solution (no dilution) and serial dilutions were plated in three replicates on Luria Bertani (LB) agar and R2A agar medium.

Plates were incubated in dark at 3ºC, room temperature (RT), 35ºC and 50ºC using spread plate technique until visible colonies has formed – observations were carried out for 1 month in a row. The growth of strains was monitored daily and pigmented microorganisms were selected based on morphology and color of colonies. Pure cultures were isolated by re-streaking on a fresh medium. Gram staining technique was performed to guarantee the purity of colonies and to characterize the isolates concerning cell wall type and morphology. The pure colonies were conserved at -80ºC in glycerol 20% until required for further analysis.

3.2.3 DNA isolation, amplification and 16S rRNA sequencing

For taxonomic identification, the genomic DNA was extracted from pure colonies using the Wizard® Genomic DNA Purification Kit (Promega Corporation, Wisconsin, EUA), following the instructions of the manufacturer, with a final elution volume of 50 µL for each isolate. Extracted DNA was subject to PCR amplification using universal primers 10F (5'-GAG TTT GAT CCT GGC TCA G-3') and 1100R (5'-AGG GTT GCG CTC GTT G-5') (Lane *et al*. 1991) for bacteria identification and for yeast identification, the primers NL1 (5′-GCA TAT CAA TAA GCG GAG GAA AAG-3′) and NL4 (5′-GGT CCG TGT TTC AAG ACG G-3′) (Kurtzman and Robnett 1997).

DNA amplification was carried out in an Eppendorf® Mastercyler® thermocycler under the following conditions: an initial step for *Taq* DNA polymerase activation at 94ºC for 2 min, followed by 30 cycles of DNA denaturation at 94ºC for 1 min, primer annealing at 55ºC for 1 minute and DNA extension at 72ºC for 3 min. After the final amplification cycle, samples were kept at 72ºC for 6 min in a final DNA extension step and immediately cooled to 4ºC. Amplicons were checked on a 0.8 % electrophoresis agarose gel and purified using Wizard® SV Gel and PCR Clean-Up System (Promega Corporation, Wisconsin, EUA) by processing PCR product amplifications, with a final elution volume of 20 µL. All 16S rRNA PCR products were sequenced by Sanger sequencing (Sanger and Coulson 1975)**.**

3.2.4 Bioinformatics and phylogenic identification

DNA sequences were edited and trimmed with the BioEdit tool (Hall 1999), in order to eliminate low-quality base sequencing. The sequences quality-checked were analyzed by their phylogenetic affiliations using the following databases: 1) EzBioCloud (Yoon *et al.* 2017), an integrated database for *Bacteria* and *Archaea* taxonomic hierarchy and 2) Nucleotide database

NCBI Basic Local Alignment Search Tool (BLAST) (Altschul *et al.* 1990) for yeast identification. The sequences together with their closest relatives, (downloaded from databases) were aligned using Clustal W multiple sequence alignment (Bioedit software) to check their matches. The phylogenetic trees were performed using MEGA v. 10.2.5 (Kumar *et al.* 2018) based on the Neighbor-joining method and reconstructed using a bootstrap analysis with 1000 replicates and Kimura-2 parameter model.

3.3 Results

Photovoltaic panel samples displayed cultivable microorganisms growing on LB and R2A medium (Fig. 1). Most of the isolates in PSI samples were observed at 3ºC, room temperature (R.T) (20-22ºC) and 35ºC (Fig. 1A). For PSR samples, a larger growth was recorded at room temperature and 35ºC (Fig. 1B). In both samples, a very few colony-forming grown was observed at higher temperatures (50ºC). Many of the isolates displayed yellow and orange pigmentation, and very few were pink. A total of 63 microorganisms were isolated and analyzed based on colony characteristics (form, color, size) and temperature condition growth (Fig. S1, supporting information). However, Gram staining and morphology analysis showed that many were similar. To selected only different phenotype strains, we delimited the further steps for colonies that were Grain staining, morphology and growth temperature distinct. Thus, 15 out of 63 colonies were finally selected for taxonomic identification through 16S rRNA sequencing (Tab. 1).

Figure 1. Cultivable microorganisms growing on LB and R2A medium at 3ºC, Room Temperature (R.T) (20-22ºC), 35ºC and 50ºC. **A)** Samples from PSI (Photovoltaic Panel from Itatiba) and **B)** Samples from PSR (Photovoltaic Panel from Sorocaba)

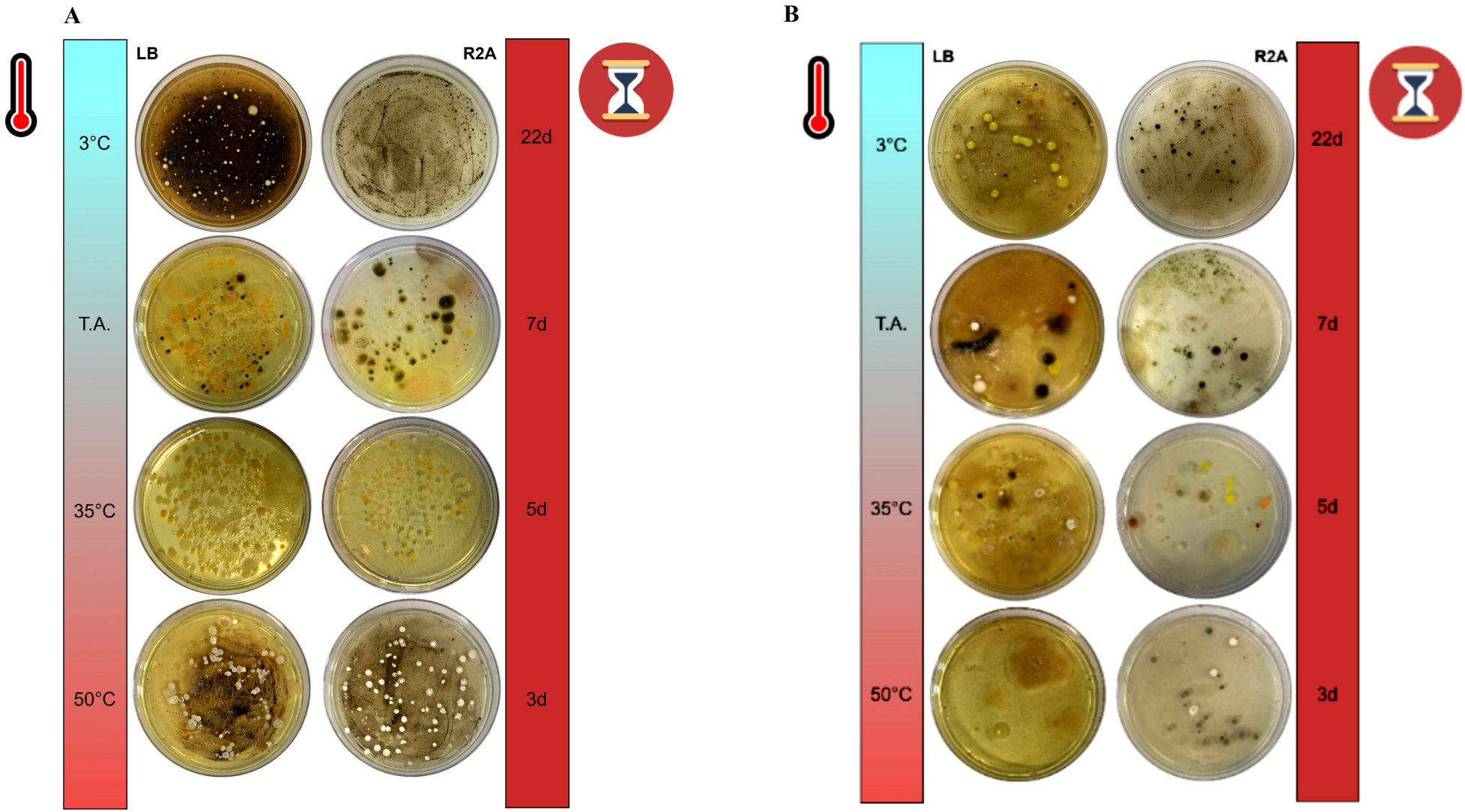


Table 1. Microorganisms selected for Sanger sequencing identification. The table contain the culture conditions, Gram staining type and microscopy analysis.

Isolate code	Media	Incubation time (h)	Incubation temperature (°C)	Gram staining	Morphology
PSI 07	R2A	72	R.T*	-	Rod
PSI 15	R2A	48	35	-	Cocci
PSI 19	R2A	48	35°C	+	Rod
PSI 26	LB	24	R.T*	-	Rod
PSI 30	LB	48	35°C	+	Rod
PSR 33	LB	72	R.T*	+	Rod
PSR 34	LB	72	R.T*	+	Cocci
PSR 37	R2A	72	R.T*	-	Cocci
PSR 46	R2A	48	35°C	+	Rod
PSR 49	R2A	120	35°C	+	Filamentous
PSR 50	LB	48	35°C	+	Cocci
PSR 51	LB	72	35°C	+	Cocci
PSI 68	LB	120	3°C	+	Cocci
PSI 70	LB	504	3°C	-	Rod
PSI 72	LB	504	3°C	+	Cocci

* R.T = Room Temperature (20-22ºC)

In total 15 isolates were identified by 16S rRNA gene sequence and assigned to the following phylogenetic groups: Actinobacteria (53%), Proteobacteria (27%), Basidiomycota (13%) e Bacteroidetes (7%) (Tab. 2). Strains with the highest similarity showed in a phylogenetic tree (see supplementary data), were identified as follow: *Mycolicibacterium aurum* (PSI 19), *Arthrobacter koreensis* (PSI 30, PSR 37), *Microbacterium hydrotermale* (PSR 33), *Gordonia sp.* (PSR 46), *Dermacoccus nishinomiyaensis* (PSR 50), *Kocuria sp.* (PSR 51), *Verrucosispora qiuiae* (PSR 49), *Sphingomonas paucimobilis* (PSI 15), *Serratia nematodiphila* (PSI 26), *Psychrobacter sp.* (PSI 68), *Pseudomonas coleopterorum* (PSI 70),

Rhodotorula sp. (PSI 72), *Rhodotorula mucilaginosa* (PSR 34), *Hymenobacter flocculans* (PSI 07).

Table 2. Taxonomic identification of isolated strains

Phylum	Isolate code	Taxonomic identification	Similarity (%) (EzBioCloud)
Actinobacteria	PSI 19	*Mycolicibacterium aurum*	98.54
	PSI 30, PSR37	*Arthrobacter koreensis*	100
	PSR 33	*Microbacterium hydrotermale*	99.05
	PSR 46	*Gordonia hongkongensis*	100
	PSR 50	*Dermacoccus nishinomiyaensis*	99.69
	PSR 51	*Kocuria arsenatis*	99.89
	PSR 49	*Verrucosispora qiuiae*	99.79
Proteobacteria	PSI 15	*Sphingomonas paucimobilis*	99.43
	PSI 26	*Serratia nematodiphila*	99.79
	PSI 68	*Psychrobacter faecalis*	100
	PSI 70	*Pseudomonas coleopterorum*	100
Basidiomycota	PSI 72	*Rhodotorula sp.*	-
	PSR 34	*Rhodotorula mucilaginosa*	-
Bacteroidetes	PSI 07	*Hymenobacter flocculans*	97.75

3.4 Discussion

The growth of pigmented microorganisms in our samples was consistent with finds of other photovoltaic panels previously investigated (Dorado-Morales *et al.* 2016; Porcar *et al.* 2018; Tanner *et al.* 2018b, 2018a). Pigmentation have been associated with a survival strategy

to withstand harsh environments, contributing to modulation of membrane fluidity, cryopreservation, desiccation, and intense solar irradiation effects (Jagannadham *et al.* 2000; Dieser, Greenwood and Foreman 2010). These strategies of microbial survival are also consistent with the thermal fluctuations, irradiation exposure and desiccation effects that occurs on surfaces of photovoltaic panels. Microorganisms living in such environment must be adapted to resist, or at least tolerate, extreme conditions to remain there throughout time (Tanner, Vilanova and Porcar 2017). Pigmented microorganisms found on solar photovoltaic surfaces might indicate that the community living there are adapted and have special mechanisms of survival, which makes them an interesting source of metabolites and biotechnological applications.

The PSI 19 strain was closest related to *Mycolicibacterium aurum,* first classified as a *Mycobacterium* genus (Oren and Garrity 2018). The genus belongs to the *Mycobacteriaceae* family, where most species are considered saprophytic microorganisms isolated from both natural environments and environments influenced by humans (Romagnoli *et al.* 2020). *Mycolicibacterium* strains were previously reported to highly stimulated the growth of fungal *Serendipita indica,* in a beneficial endophytic interaction suggesting a role in biocontrol of plant pathogen (del Barrio-Duque *et al.* 2019). Furthermore, some strains of *Mycolicibacterium* have been tested as bioinoculant and associated with a stimulatory effect in plant growth promotion (Egamberdiyeva 2007).

Arthrobacter koreensis (PSI 30, PSR 37) were previously isolated from alkaline soil (Lee *et al.* 2003) and Nerium oleander rhizosphere soil (Manzanera *et al.* 2015). Genome analysis proposed presence of plant hormones pathways, indicating a role in plant growth promotion. Moreover, the strain was described as desiccation-tolerant bacteria (Manzanera *et al.* 2015). *Arthrobacter* genus isolated from Andean Lakes, showed polyextremophilic characteristics with ability to cope in a multiple stress condition (Rasuk *et al.* 2017). Pigment production (Kuhlman *et al.* 2005) and xeroprotectants molecules (García-Fontana *et al.* 2016), such as trehalose, were investigated to contribute to their UV-radiation resistance and desiccation-tolerance and should be considered as potential biotechnological applications including astrobiological model, trehalose biosynthesis, and even in anti-biofilm activity (Li *et al.* 2015).

Microbacterium hydrotermale (PSR 33) was first isolated from hydrothermal sediment of Indian Ocean (Zhang, Ren and Zhang 2014). Until now, little is known about this strain. However, the genus comprises species UV-resistant, such as *Microbacterium radiodurans* (Zhang *et al.* 2010) and *Microbacterium sp* (Reis-Mansur *et al.* 2019). Moreover, some

species are endophytic, such as *Microbacterium testaceum* (Morohoshi *et al.* 2011) and *Microbacterium zeae* (Gao *et al.* 2017).

Gordonia sp. (PSR 46) was identified as *Gordonia lacunae, Gordonia insulae, Gordonia terrae and Gordonia hongkongensis*. *Gordonia* species have ability to degrade rubber (Linos *et al.* 1997), hydrocarbon (Xue *et al.* 2003) and phenol (Kim *et al.* 2009), indicating a possible role in bioremediation and pollution biodegradation. *Gordonia* species isolated from a drinking water system, was identified as disinfectant-resistant bacteria, bringing an emergence concern to safety (Lu *et al.* 2020). *Gordonia* is not considered UV-resistant (Lu *et al.* 2020), however *Gordonia polyisoprenivorans* showed viability after a long time of desiccation exposition, indicating possibility to survival at stress environment.

Dermacoccus nishinomiyaensis (PSR 50) originally called *Micrococcus nishinomiyaensis (Kocur, Schleifer and Kloos 1975),* and reclassified later (Stackebrandt *et al.* 1995). Although *Dermacoccus nishinomiyaensis* is known as part of the skin microbiome, it was already detected in areas of human-built environment, such as indoor track facility (Williams and MacLea 2019) and now on the photovoltaic panel surface. *Dermacoccus* is not usually considered as human pathogen, however colonization of catheter by skin flora have been reported (Joron *et al.* 2019; Tanaka *et al.* 2019), suggesting that the genus might have biofilm colonization capability. Recently, a studied observed *Dermacoccus profundi,* isolated from the Antarctic, could survive 15 minutes under UV-C exposure (Gladka *et al.* 2021), indicating that there are species in the genus *Dermacoccus* capable to thrive in irradiation conditions.

PSR 51 was identified as both *Kocuria rhizophila*, first isolated from rizoplane (Kovács *et al.* 1999), and *Kocuria arsenatis,* first isolated from a vegetal root tissue in an arsenic-polluted mine (Román-Ponce *et al.* 2016). The last one was described as arsenic-resistant and endophytic bacteria and might have a role in plant growth or bioremediation purpose. *Kocuria rhizophila* strain isolated from root plant in Sahara Desert showed resistance to gamma-radiation, desiccation and high H_2O_2 concentration (Guesmi *et al.* 2021). Strain of *K. sp*. Isolated from radioactive mines also showed resistance to UV and gamma-radiation (Asgarani *et al.* 2012). Moreover, *Kocuria flava*, the outgroup of a phylogenetic tree (Fig. S8, supporting information), showed multiple stress tolerance, such as irradiation, desiccation and salinity (Etemadifar, Gholami and Derikvand 2016). Species of *Kocuria* were reported to cause catheter-related bacteremia (Altuntas *et al.* 2004; Moissenet *et al.* 2012), suggesting the ability of biofilm formation.

Verrucosispora qiuiae (PSR 49), a micromonospora-like genus (Xi *et al.* 2012). The genus *Verrucosispora* has been recognized as a source of potential biotechnological applications in the biomedicine field, in the manufacturer of antitumors compounds (Bister *et al.* 2004). Additionally, *Micromonospora* genus is an important source of antibiotics and therapeutic drugs (Hirsch and Valdés 2010; Hifnawy *et al.* 2020) and has species reported to support extreme environments (Rasuk *et al.* 2017). *Verrucosispora sonchi*, which shares a high phylogenetic similarity with *Verrucosispora qiuiae* (Fig. S6, supporting information), is an endophytic bacteria (Ma *et al.* 2016). Interestingly, other strains phylogenetic-related, such as *Verrucosispora endophytica (Ngaemthao et al. 2017)* and *Micromonospora radicis (Kuncharoen et al. 2019),* also have the same characteristics.

Pseudomonas coleopterorum (PSI 70) was first isolated from bark beetle and showed cellulase activity, suggesting that this strain is a cellulase producing bacteria (Menéndez *et al.* 2015). In general, *Pseudomonas* genus are spread in nature thanks to their capability to adapt in a diverse environmental conditions. *Pseudomonas auriginosa* is one of the most studied *Pseudomonas* strains, because it is considered an opportunist pathogen and have biofilm colonization properties (Rasamiravaka *et al.* 2015). Furthermore, the antibiotics and antimicrobial resistance increase their capability of biofilm formation, leading to problem when it turns to remove this structure from surfaces (Drenkard and Ausubel 2002; Kamali *et al.* 2020). The colonization process of *Pseudomonas auriginosa* begins with the adhesion on a surface, which triggers the production of alginate matrix allowing the adhesion of more cells arriving from the environment (Hoyle, Williams and Costerton 1993). Although planktonic cells of *Pseudomonas auriginosa* are not well adapted to either dried and irradiated environments (Skaliy and Eagon 1972; Pazos-Rojas *et al.* 2019), cells living on biofilm matrix showed resistance to both conditions, suggesting that biofilm might represent a strategy to support the survival of *Pseudomonas* strains on desiccative and irradiated environments, being an important step in the colonization process (Roberson and Firestone 1992; Elasri and Miller 1999; Liaqat *et al.* 2020).

The strain PSI 68 was identified as both *Psychrobacter faecalis (Kämpfer et al. 2002)* and *Psychrobacter pulmonis (Vela et al. 2003),* isolated from pigeon faeces and lung of lambs, respectively. Despite the double identity, pigeon faeces are more suitable to reach the surface of the photovoltaic panel than is the lung of lambs. *Psychrobacter* genus are considered psychrophiles, able to tolerate cold temperature variations, which is consistent with the isolation temperature growth (3ºC) of PSI 68 (Bendia *et al.* 2018). This genus comprises species with biofilm formation capability (Wagner *et al.* 2020) and UV-resistance.

For example, La Duc et al. (2007) reported that *Psychrobacter sp.,* phylogenetic-related to *P. faecalis* and *P. pulmonis,* were able to survive to a dose of 1,000 J/m² of UV-C irradiation. Furthermore, *Pseudomonas* and *Psychrobacter* was observed to be tellurite-resistant and tellurite-reducing bacteria, suitable for bioabsorption, bioremediation and nanoparticle applications (Arenas *et al.* 2014)

Sphingomonas paucimobilis (PSI 15) is a soil bacteria, adapted to contaminated environments able to degrade a variety of PAH compounds (Mueller *et al.* 1990; Weissenfels, Beyer and Klein 1990; Story *et al.* 2004; Zhou *et al.* 2016). *Sphingomonas* is well known for biofilm formation capability (Leys *et al.* 2005; Mustafa, Maulud and Hamad 2018) and was reported having resistance to sanitizers chloride based (Gulati and Ghosh 2017). *Sphingomonas adhaesiva*, phylogenetic-related to *Sphingomonas paucimobilis*, was first isolated from irradiated water (Yabuuchi *et al.* 1990). *Sphingomonas* strains colonize a wide extreme environments, including the Antarctic, volcano lakes, contaminated soils and light UV-irradiated places (Marizcurrena *et al.* 2019).

Serratia nematodiphila (PSI 26) was originally isolated from an entomopathogenic nematode and reported as essential for its growth and survival. Symbiotic characteristics are rare in *Serratia* species, and have been considered as a distinguishing feature of this strain (Zhang *et al.* 2009; Kwak *et al.* 2015). Moreover, genome sequencing of the strain revealed genes encoding relevant enzymes to heavy metal resistance, antimicrobial activity, and insecticidal activity (Kwak *et al.* 2015), suggesting a role in various biotechnological applications. Furthermore, *Serratia* species were also isolated from the Antarctic environment and described as both psychrotolerant and UV-C resistant, with a thermoactived and thermostable catalase enzyme, making these microorganisms a promising source of biocompounds (Monsalves *et al.* 2020).

Rhodotorula sp. (PSI 72) and *Rhodotorula mucilaginosa* (PSR 34) have moderate (*R. mucilaginosa*) to low (*R. sp.*) capability for biofilm formation. *Rhodotorula mucilaginosa* is considered psychrotolerant and thermotolerant (Zajc *et al.* 2019). *Rhodotorula mucilaginosa* was also reported to have UV-tolerance, surviving 10% after 40 minutes of UV-C exposition, and this effect was correlated with their high carotenoid content (Villarreal et al. 2016). Additionally, UV-A and UV-B resistance were also reported (Moliné *et al.* 2010). Interestingly, beyond the carotenoid content detected, *in silico* analysis revealed enzymes with H_2O_2 scavenger role (Zajc *et al.* 2019), which is possibly another reason for the observed stress tolerance. Tanner *et al.* (2018a) cultivated *Rhodotorula mucilaginosa* from polar photovoltaic panels, and the strain was also UV and desiccation tolerant. The

Exopolysaccharides (EPS) responsible for biofilm formation of *Rhodotorula mucilaginosa* has been studied by their biotechnological implications. Research in antimicrobial and antibiofilm properties of EPS suggested a role in antibiofouling or antiadhesive agent to prevent bacterial biofilm (Vazquez-Rodriguez *et al.* 2018) or as a capping agent in the synthesis of nanoparticle biocomposites (Garza-Cervantes *et al.* 2019).

PSI 07 strain was affiliated to *Hymenobacter flocculans,* first described by (Chung *et al.* 2010) isolated from an uranium mine waste water treatment. The genus comprises species isolated from various ecological niches (Zhang *et al.* 2009; Chang *et al.* 2014; Kang *et al.* 2016). Many species were previously associated with radiation-resistance properties: *H. tibetensis (Dai et al. 2009), H. amundsenii (Sedláček et al. 2019), H. jejuensis (Maeng, Kim and Subramani 2020), H. sedentarius (Kim et al. 2017b)*. Others was described as psychrophilics (Zhang *et al.* 2011; Sedláček *et al.* 2019) or psychrotolerant (Kojima *et al.* 2016; Kim *et al.* 2017a). Furthermore, the genus *Hymenobacter* was present on photovoltaic panels surfaces already investigated so far (Dorado-Morales *et al.* 2016; Porcar *et al.* 2018; Tanner *et al.* 2018a). In Brazil, Shirakawa *et al.* (2015) identified the same species (*H. flocculans*) colonizing the surface of the photovoltaic panel in São Paulo city.

In general, the genus *Arthrobacter, Kocuria, Microbacterium, Pseudomonas, Sphingomonas, Rhodotorula* and *Hymenobacter* were also isolated from the surfaces of others photovoltaic panels in the Mediterranean city (Dorado-Morales *et al.* 2016; Porcar *et al.* 2018; Tanner *et al.* 2018b) and Polar climates (Tanner *et al.* 2018a). *Hymenobacter, Sphingomonas* and *Pseudomonas* being the most abundant between them.

Most of the isolates that we identified were described in the literature as UV-resistant, desiccation-resistant and capable to form a biofilm matrix, at least at a genus level. This is consistent with the environmental conditions that the microorganisms were isolated from. The presence of common genus of our samples in comparison to other photovoltaic panels around the world and our previous research of microbial diversity (not published yet, chapter 2) together with the description in the literature, suggests that the microorganisms living there at the moment of collecting, were possibly a result of selection pressure, that lead to a stable shaped community, able to establish a native microbiome.

Despite possibilities of being a source of commercial interest, microorganisms colonizing photovoltaic panels surfaces are also a concern to energy yield, although this is still an underestimated question (Noack-Schönmann *et al.* 2014; Shirakawa *et al.* 2015; Martin-Sanchez *et al.* 2018). Solar energy covers all electromagnetic spectrum; however, the energy distribution has a maximum in the range of visible light. For this reason, photovoltaic

panels are more influenced in the visible wavelength range, than other regions of the solar spectrum (Ogherohwo, Barnabas and Alafiatayo 2015) Pigmented microorganisms capable to absorb and scatter visible light change the incoming radiation in the photovoltaic cells and decrease its intensity (Noack-Schönmann *et al.* 2014), affecting negatively the efficiency of energy conversion. Moreover, some biofilms were reported to have sanitizers and antimicrobial resistance, which could lead to issues when using the conventional cleaning process.

3.5 References

Altschul SF, Gish W, Miller W *et al.* Basic local alignment search tool. *J Mol Biol* 1990;**215**:403–10.

Altuntas F, Yildiz O, Eser B *et al.* Catheter-related bacteremia due to Kocuria rosea in a patient undergoing peripheral blood stem cell transplantation. *BMC Infect Dis* 2004;**4**:3–5.

Arenas FA, Pugin B, Henríquez NA *et al.* Isolation, identification and characterization of highly tellurite-resistant, tellurite-reducing bacteria from Antarctica. *Polar Sci* 2014;**8**:40–52.

Asgarani E, Soudi MR, Borzooee F *et al.* Radio-resistance in psychrotrophic Kocuria sp. ASB 107 isolated from Ab-e-Siah radioactive spring. *J Environ Radioact* 2012;**113**:171–6.

Bendia AG, Araujo GG, Pulschen AA *et al.* Surviving in hot and cold: psychrophiles and thermophiles from Deception Island volcano, Antarctica. *Extremophiles* 2018;**22**:917–29.

Bister B, Bischoff D, Ströbele M *et al.* Abyssomicin C - A polycyclic antibiotic from a marine Verrucosispora strain as an inhibitor of the p-aminobenzoic acid/tetrahydrofolate biosynthesis pathway. *Angew Chemie - Int Ed* 2004;**43**:2574–6.

Chang X, Zheng J, Jiang F *et al.* Hymenobacter arcticus sp. nov., isolated from glacial till. *Int J Syst Evol Microbiol* 2014;**64**:2113–8.

Chung AP, Lopes A, Nobre MF *et al.* Hymenobacter perfusus sp. nov., Hymenobacter flocculans sp. nov. and Hymenobacter metalli sp. nov. three new species isolated from an uranium mine waste water treatment system. *Syst Appl Microbiol* 2010;**33**:436–43.

Dai J, Wang Y, Zhang L *et al.* Hymenobacter tibetensis sp. nov., a UV-resistant bacterium isolated from Qinghai-Tibet plateau. *Syst Appl Microbiol* 2009;**32**:543–8.

del Barrio-Duque A, Ley J, Samad A *et al.* Beneficial Endophytic Bacteria-Serendipita indica Interaction for Crop Enhancement and Resistance to Phytopathogens. *Front Microbiol* 2019;**10**:1–24.

Dieser M, Greenwood M, Foreman CM. Carotenoid pigmentation in Antarctic heterotrophic bacteria as a strategy to withstand environmental stresses. *Arctic, Antarct Alp Res* 2010;**42**:396–405.

Dorado-Morales P, Vilanova C, Peretó J *et al.* A highly diverse, desert-like microbial biocenosis on solar panels in a Mediterranean city. *Sci Rep* 2016;**6**:1–9.

Drenkard E, Ausubel FM. Pseudomonas biofilm formation and antibiotic resistance are linked to phenotypic variation. *Nature* 2002;**416**:740–3.

Egamberdiyeva D. The effect of plant growth promoting bacteria on growth and nutrient uptake of maize in two different soils. *Appl Soil Ecol* 2007;**36**:184–9.

Elasri MO, Miller R V. Study of the response of a biofilm bacterial community to UV radiation. *Appl Environ Microbiol* 1999;**65**:2025–31.

Etemadifar Z, Gholami M, Derikvand P. UV-Resistant Bacteria with Multiple-Stress Tolerance Isolated from Desert Areas in Iran. *Geomicrobiol J* 2016;**33**:1–7.

Gao J lian, Sun P, Wang X ming *et al.* Microbacterium zeae sp. nov., an endophytic bacterium isolated from maize stem. *Antonie van Leeuwenhoek, Int J Gen Mol Microbiol* 2017;**110**:697–704.

García-Fontana C, Narváez-Reinaldo JJ, Castillo F *et al.* A new physiological role for the DNA molecule as a protector against drying stress in desiccation-tolerant microorganisms. *Front Microbiol* 2016;**7**:1–12.

Garza-Cervantes JA, Escárcega-González CE, Díaz Barriga Castro E *et al.* Antimicrobial and antibiofilm activity of biopolymer-Ni, Zn nanoparticle biocomposites synthesized using R. mucilaginosa UANL-001L exopolysaccharide as a capping agent. *Int J Nanomedicine* 2019;**14**:2557–71.

Gavrilescu M, Chisti Y. Biotechnology - A sustainable alternative for chemical industry. *Biotechnol Adv* 2005;**23**:471–99.

Gladka G, Hovorukha V, Romanovskaya V *et al.* Correlation Between Resistance to UV Irradiation and the Taxonomic Position of Microorganisms. *Environ Res Eng Manag* 2021;**77**:67–75.

Guesmi S, Pujic P, Nouioui I *et al.* Ionizing-radiation-resistant Kocuria rhizophila PT10 isolated from the Tunisian Sahara xerophyte Panicum turgidum: Polyphasic characterization and proteogenomic arsenal. *Genomics* 2021;**113**:317–30.

Gulati P, Ghosh M. Biofilm forming ability of Sphingomonas paucimobilis isolated from community drinking water systems on plumbing materials used in water distribution. *J Water Health* 2017;**15**:942–54.

Hall TA. Hall 1999_bioedit.pdf. *Nucleic Acid Symp Ser* 1999:95–8.

Hifnawy MS, Fouda MM, Sayed AM *et al.* The genusMicromonosporaas a model microorganism for bioactive natural product discovery. *RSC Adv* 2020;**10**:20939–59.

Hirsch AM, Valdés M. Micromonospora: An important microbe for biomedicine and potentially for biocontrol and biofuels. *Soil Biol Biochem* 2010;**42**:536–42.

Hoyle BD, Williams LJ, Costerton JW. Production of mucoid exopolysaccharide during development of Pseudomonas aeruginosa biofilms. *Infect Immun* 1993;**61**:777–80.

Jagannadham M V., Chattopadhyay MK, Subbalakshmi C *et al.* Carotenoids of an Antarctic psychrotolerant bacterium, Sphingobacterium antarcticus, and a mesophilic bacterium, Sphingobacterium multivorum. *Arch Microbiol* 2000;**173**:418–24.

Joron C, Roméo B, Le Flèche-Matéos A *et al.* Dermacoccus nishinomiyaensis as a cause of persistent paediatric catheter-related bacteraemia. *Clin Microbiol Infect* 2019;**25**:1054–5.

Kamali E, Jamali A, Ardebili A *et al.* Evaluation of antimicrobial resistance, biofilm forming potential, and the presence of biofilm-related genes among clinical isolates of Pseudomonas aeruginosa. *BMC Res Notes* 2020;**13**:4–9.

Kämpfer P, Albrecht A, Buczolits S *et al.* Psychrobacter faecalis sp. nov., a new species from a bioaerosol originating from pigeon faeces. *Syst Appl Microbiol* 2002;**25**:31–6.

Kang H, Kim H, Joung Y *et al.* Hymenobacter marinus sp. nov., isolated from coastal seawater. *Int J Syst Evol Microbiol* 2016;**66**:2212–7.

Kim KK, Lee KC, Klenk HP *et al.* Gordonia kroppenstedtii sp. nov., a phenol-degrading actinomycete isolated from a polluted stream. *Int J Syst Evol Microbiol* 2009;**59**:1992–6.

Kim MC, Kim CM, Kang OC *et al.* Hymenobacter rutilus sp. nov., isolated from marine sediment in the Arctic. *Int J Syst Evol Microbiol* 2017a;**67**:856–61.

Kim MK, Kang MS, Srinivasan S *et al.* Complete genome sequence of Hymenobacter sedentarius DG5BT, a bacterium resistant to gamma radiation. *Mol Cell Toxicol* 2017b;**13**:199–205.

Kocur M, Schleifer KH, Kloos WE. Taxonomic status of Micrococcus nishinomiyaensis Oda 1935. *Int J Syst Bacteriol* 1975;**25**:290–3.

Kojima H, Watanabe M, Tokizawa R *et al.* Hymenobacter nivis sp. Nov., isolated from red snow in Antarctica. *Int J Syst Evol Microbiol* 2016;**66**:4821–5.

Kovács G, Burghardt J, Pradella S *et al.* Kocuria rhizophila sp . nov ., isolated from the rhizoplane of the narrow-leaved cattail. *Int J Syst Bacteriol* 1999:167–73.

Krisko A, Radman M. Biology of extreme radiation resistance: The way of Deinococcus radiodurans. *Cold Spring Harb Perspect Biol* 2013;**5**, DOI: 10.1101/cshperspect.a012765.

Kuhlman KR, Allenbach LB, Ball CL *et al.* Enumeration, isolation, and characterization of ultraviolet (UV-C) resistant bacteria from rock varnish in the Whipple Mountains, California. *Icarus* 2005;**174**:585–95.

Kumar S, Stecher G, Li M *et al.* MEGA X: Molecular evolutionary genetics analysis across computing platforms. *Mol Biol Evol* 2018;**35**:1547–9.

Kuncharoen N, Kudo T, Yuki M *et al.* Micromonospora radicis sp. Nov., isolated from roots of Azadirachta indica var. siamensis Valenton, and reclassification of Jishengella zingiberis as Micromonospora zingiberis comb. nov. *Int J Syst Evol Microbiol* 2019;**69**:2884–91.

Kurtzman CP, Robnett CJ. Identification of clinically important ascomycetous yeasts based on nucleotide divergence in the 5' end of the large-subunit (26S) ribosomal DNA gene. *J Clin Microbiol* 1997;**35**:1216–23.

Kwak Y, Khan AR, Shin JH. Genome sequence of *Serratia nematodophila* DSM 21420^{T}, a symbiotic bacterium from entomopathogenic nematode. *J of Microbiol* 2015;**193**;1-2.

La Duc MT, Benardini JN, Kempf MJ *et al.* Microbial diversity of indian ocean hydrothermal vent plumes: Microbes tolerant of desiccation, peroxide exposure, and ultraviolet and γ-irradiation. *Astrobiology* 2007;**7**:416–31.

Lane DJ. 16S/23S rRNA sequencing. In: Goodfellow, M. & Stackebrandt, E. (eds), *Nucleic acid techn in bact syst* 1991;115-147.

Lee JS, Lee KC, Pyun YR *et al.* Arthrobacter koreensis sp. nov., a novel alkalitolerant bacterium from soil. *Int J Syst Evol Microbiol* 2003;**53**:1277–80.

Leys NM, Ryngaert A, Bastiaens L *et al.* Culture independent detection of Sphingomonas sp. EPA 505 related strains in soils contaminated with polycyclic aromatic hydrocarbons (PAHs). *Microb Ecol* 2005;**49**:443–50.

Li Y, Li Q, Hao D *et al.* Production, purification, and antibiofilm activity of a novel exopolysaccharide from Arthrobacter sp. B4. *Prep Biochem Biotechnol* 2015;**45**:192–204.

Liaqat I, Ali NM, Mirza SA *et al.* Study of biofilm response of olea europaea to uv radiations: An in vitro approach. *J Anim Plant Sci* 2020;**30**:1273–82.

Linos A, Steinbuchel A, Sproer C *et al.* Rubber-Degrading Actinomycete Isolated From an Automobile Tyre. *Int J Syst Bacteriol* 1997;**49**:1785–91.

Lu N, Sun S, Chu F *et al.* Identification and inactivation of Gordonia, a new chlorine-resistant bacterium isolated from a drinking water distribution system. *J Water Health* 2020;**18**:995–1008.

Ma Z, Zhao S, Cao T *et al.* Verrucosispora sonchi sp. Nov., a novel endophytic actinobacterium isolated from the leaves of common sowthistle (Sonchus oleraceus L.). *Int J Syst Evol Microbiol* 2016;**66**:5430–6.

Maeng S, Kim MK, Subramani G. Hymenobacter jejuensis sp. nov., a UV radiation-tolerant bacterium isolated from Jeju Island. *Antonie van Leeuwenhoek, Int J Gen Mol Microbiol* 2020;**113**:553–61.

Manzanera M, Narváez-Reinaldo JJ, García-Fontana C *et al.* Genome sequence of Arthrobacter koreensis 5J12A, a plant growth-promoting and desiccation-tolerant strain. *Genome Announc* 2015;**3**:5–6.

Marizcurrena JJ, Morales D, Smircich P *et al.* Draft Genome Sequence of the UV-Resistant Antarctic Bacterium Sphingomonas sp. Strain UV9. *Microbiol Resour Announc* 2019;**8**, DOI: 10.1128/mra.01651-18.

Martin-Sanchez PM, Gebhardt C, Toepel J *et al.* Monitoring microbial soiling in photovoltaic systems: A qPCR-based approach. *Int Biodeterior Biodegrad* 2018;**129**:13–22.

Menéndez E, Ramírez-Bahena MH, Fabryová A *et al.* Pseudomonas coleopterorum sp. nov., a cellulaseproducing bacterium isolated from the bark beetle Hylesinus fraxini. *Int J Syst Evol Microbiol* 2015;**65**:2852–8.

Moissenet D, Becker K, Mérens A *et al.* Persistent bloodstream infection with Kocuria rhizophila related to a damaged central catheter. *J Clin Microbiol* 2012;**50**:1495–8.

Moliné M, Flores MR, Libkind D *et al.* Photoprotection by carotenoid pigments in the yeast Rhodotorula mucilaginosa: The role of torularhodin. *Photochem Photobiol Sci* 2010;**9**:1145–51.

Monsalves M, Ollivet-Besson G, Amenabar M *et al.* Isolation of a psychrotolerant and UV-C resistant bacterium from elephant island, Antarctica with a highly thermoactive and thermostable catalase 2020;**8**;95.

Morohoshi T, Wang WZ, Someya N *et al.* Genome sequence of Microbacterium testaceum StLB037, an N-acylhomoserine lactone-degrading bacterium isolated from potato leaves. *J Bacteriol* 2011;**193**:2072–3.

Mueller JG, Chapman PJ, Blattmann BO *et al.* Isolation and characterization of a fluoranthene-utilizing strain of Pseudomonas paucimobilis. *Appl Environ Microbiol* 1990;**56**:1079–86.

Mustafa K kh, Maulud SQ, Hamad PA. Detection of Sphingomonas paucimobilis and antibacterial activity of Prosopis farcta extracts on it. *Karbala Int J Mod Sci* 2018;**4**:100–6.

Ngaemthao W, Pujchakarn T, Chunhametha S *et al.* Verrucosispora endophytica sp. Nov., isolated from the root of wild orchid (Grosourdya appendiculata (Blume) Rchb.f.). *Int J Syst Evol Microbiol* 2017;**67**:5114–9.

Noack-Schönmann S, Spagin O, Gründer KP *et al.* Sub-aerial biofilms as blockers of solar radiation: Spectral properties as tools to characterise material-relevant microbial growth. *Int Biodeterior Biodegrad* 2014;**86**:286–93.

Ogherohwo EP, Barnabas B, Alafiatayo AO. Investigating the Wavelength of Light and Its Effects on the Performance of a Solar Photovoltaic Module. *Int J Innov Res Comput Sci Technol* 2015;**3**:61–5.

Oren A, Garrity G. List of new names and new combinations previously effectively, but not validly, published. *Int J Syst Evol Microbiol* 2018;**68**:1411–7.

Paulino-Lima IG, Fujishima K, Navarrete JU *et al.* Extremely high UV-C radiation resistant microorganisms from desert environments with different manganese concentrations. *J Photochem Photobiol B Biol* 2016;**163**:327–36.

Pazos-Rojas LA, Muñoz-Arenas LC, Rodríguez-Andrade O *et al. Desiccation-Induced Viable but Nonculturable State in Pseudomonas Putida KT2440, a Survival Strategy*., 2019.

Porcar M, Louie KB, Kosina SM *et al.* Microbial ecology on solar panels in Berkeley, CA, United States. *Front Microbiol* 2018;**9**:1–14.

Qi H zhou, Wang W zhou, He J yan *et al.* Antioxidative system of Deinococcus radiodurans. *Res Microbiol* 2019;**171**:45–54.

Ragon M, Restoux G, Moreira D *et al.* Sunlight-exposed biofilm microbial communities are naturally resistant to chernobyl ionizing-radiation levels. *PLoS One* 2011;**6**, DOI: 10.1371/journal.pone.0021764.

Rampelotto PH. Extremophiles and extreme environments. *Life* 2013;**3**:482–5.

Rasamiravaka T, Labtani Q, Duez P *et al.* The Formation of Biofilms by. *Biomed Res Int* 2015;**2015**:1–17.

Rastogi RP, Sonani RR, Madamwar D. Cyanobacterial Sunscreen Scytonemin: Role in Photoprotection and Biomedical Research. *Appl Biochem Biotechnol* 2015;**176**:1551–63.

Rasuk MC, Ferrer GM, Kurth D *et al.* UV-Resistant Actinobacteria from High-Altitude Andean Lakes: Isolation, Characterization and Antagonistic Activities. *Photochem Photobiol* 2017;**93**:865–80.

Reis-Mansur MCPP, Cardoso-Rurr JS, Silva JVMA *et al.* Carotenoids from UV-resistant Antarctic Microbacterium sp. LEMMJ01. *Sci Rep* 2019;**9**:1–14.

Roberson EB, Firestone MK. Relationship between desiccation and exopolysaccharide production in a soil Pseudomonas sp. *Appl Environ Microbiol* 1992;**58**:1284–91.

Romagnoli CL, Pellegrino KCM, Silva NM *et al.* Diversity of Mycobacteriaceae from aquatic environment at the São Paulo Zoological Park Foundation in Brazil. *PLoS One* 2020;**15**:1–14.

Román-Ponce B, Wang D, Soledad Vásquez-Murrieta M *et al.* Kocuria arsenatis sp. Nov., An arsenic-resistant endophytic actinobacterium associated with Prosopis laegivata grown on high-arsenic-polluted mine tailing. *Int J Syst Evol Microbiol* 2016;**66**:1027–33.

Romani M, Carrion C, Fernandez F *et al.* High bacterial diversity in piooner biofilms colonizing ceramic roof tiles. *Int Biodet & Biodeg* 2019;**144**:1047-45

Rothschild LJ., Mancinelli RL. Life in extreme environments. *Nature* 2001;**409**, DOI: 10.1038/npg.els.0000391.

Sanger F, Coulson AR. A rapid method for determining sequences in DNA by primed synthesis with DNA polymerase. *J Mol Biol* 1975;**94**:441–8.

Sayed AM, Hassan MHA, Alhadrami HA *et al.* Extreme environments: microbiology leading to specialized metabolites. *J Appl Microbiol* 2020;**128**:630–57.

Sedláček I, Pantůček R, Králová S *et al.* Hymenobacter amundsenii sp. nov. resistant to ultraviolet radiation, isolated from regoliths in Antarctica. *Syst Appl Microbiol* 2019;**42**:284–90.

Shirakawa MA, Zilles R, Mocelin A *et al.* Microbial colonization affects the efficiency of photovoltaic panels in a tropical environment. *J Environ Manage* 2015;**157**:160–7.

Skaliy P, Eagon RG. Effect of physiological age and state on survival of desiccated Pseudomonas aeruginosa. *Appl Microbiol* 1972;**24**:763–7.

Stackebrandt E, Koch C, Gvozdiak O *et al.* Taxonomic dissection of the genus Micrococcus: Kocuria gen. nov., Nesterenkonia gen. nov., Kytococcus gen. nov., Dermacoccus gen. nov., and Micrococcus cohn 1872 gen. emend. *Int J Syst Bacteriol* 1995;**45**:682–92.

Story SP, Kline EL, Hughes TA *et al.* Degradation of aromatic hydrocarbons by Sphingomonas paucimobilis strain EPA505. *Arch Environ Contam Toxicol* 2004;**47**:168–76.

Tanaka A, Watanabe Y, Ito C *et al.* Successful treatment of peritoneal dialysis-related peritonitis caused by Dermacoccus nishinomiyaensis. *CEN case reports* 2019;**8**:183–7.

Tanner K, Martí JM, Belliure J *et al.* Polar solar panels: Arctic and Antarctic microbiomes display similar taxonomic profiles. *Environ Microbiol Rep* 2018a;**10**:75–9.

Tanner K, Martorell P, Genovés S *et al.* Bioprospecting the solar panel microbiome: high-throughput screening for antioxidant bacteria in a Caenorhabditis elegans model. *Bioprospecting Sol panel microbiome High-throughput Screen Antioxid Bact a caenorhabditis elegansModel* 2018b:423731.

Tanner K, Vilanova C, Porcar M. Bioprospecting challenges in unusual environments. *Microb Biotechnol* 2017;**10**:671–3.

Tian B, Sun Z, Shen S *et al.* Effects of carotenoids from Deinococcus radiodurans on protein oxidation. *Lett Appl Microbiol* 2009;**49**:689–94.

Vazquez-Rodriguez A, Vasto-Anzaldo XG, Barboza Perez D *et al.* Microbial Competition of Rhodotorula mucilaginosa UANL-001L and E. Coli increase biosynthesis of Non-Toxic Exopolysaccharide with Applications as a Wide-Spectrum Antimicrobial. *Sci Rep* 2018;**8**:1–14.

Vela AI, Collins MD, Latre M V. *et al.* Psychrobacter pulmonis sp. nov., isolated from the lungs of lambs. *Int J Syst Evol Microbiol* 2003;**53**:415–9.

Villarreal P, Carrasco M, Barahona S *et al.* Tolerance to Ultraviolet Radiation of Psychrotolerant Yeasts and Analysis of Their Carotenoid, Mycosporine, and Ergosterol Content. *Curr Microbiol* 2016;**72**:94–101.

Wagner EM, Pracser N, Thalguter S *et al.* Identification of biofilm hotspots in a meat processing environment: Detection of spoilage bacteria in multi-species biofilms. *Int J Food Microbiol* 2020;**328**, DOI: 10.1016/j.ijfoodmicro.2020.108668.

Weissenfels WD, Beyer M, Klein J. Degradation of phenanthrene, fluorene and fluoranthene by pure bacterial cultures. *Appl Microbiol Biotechnol* 1990;**32**:479–84.

Williams A, MacLea K. Draft Genome Sequence of Dermacoccus nishinomiyaensis TSA37, Isolates from Wood Ash. *Microbiol Resour Announc* 2019;**8**:1–2.

Xi L, Zhang L, Ruan J *et al.* Description of Verrucosispora qiuiae sp. nov., isolated from mangrove swamp sediment, and emended description of the genus Verrucosispora. *Int J Syst Evol Microbiol* 2012;**62**:1564–9.Xue Y, Sun X, Zhou P *et al.* Gordonia paraffinivorans sp. nov., a hydrocarbon-degrading actinomycete isolated from an oil-producing well. *Int J Syst Evol Microbiol* 2003;**53**:1643–6.

Yabuuchi E, Yano I, Oyaizu H *et al.* Proposals of *Sphingomonas paucimobilis* gen. nov. and comb. nov., *Sphingomonas parapaucimobilis* sp. nov., *Sphingomonas yanoikuyae* sp. nov., *Sphingomonas adhaesiva* sp. nov., *Sphingomonas capsulata* comb. nov., and Two Geno. *Microbiol Immunol* 1990;**34**:99–119.

Yoon SH, Ha SM, Kwon S *et al.* Introducing EzBioCloud: A taxonomically united database of 16S rRNA gene sequences and whole-genome assemblies. *Int J Syst Evol Microbiol* 2017;**67**:1613–7.

Zajc J, Gostinčar C, Černoša A *et al.* Stress-tolerant yeasts: Opportunistic pathogenicity versus biocontrol potential. *Genes (Basel)* 2019;**10**, DOI: 10.3390/genes10010042.

Zhang CX, Yang SY, Xu MX *et al. Serratia nematodiphila* sp. Nov., associated symbiotically with the entomopathogenic nematode *Heterorhabditidoides chongmingensis* (Rhabditida:Rhabditidae). *Int J Syst Evolv Microbiol* 2009;**59**;1603-1608.

Zhang DC, Busse HJ, Liu HC *et al.* Hymenobacter psychrophilus sp. nov., a psychrophilic bacterium isolated from soil. *Int J Syst Evol Microbiol* 2011;**61**:859–63.

Zhang L, Dai J, Tang Y *et al.* Hymenobacter deserti sp. nov., isolated from the desert of Xinjiang, China. *Int J Syst Evol Microbiol* 2009;**59**:77–82.

Zhang W, Zhu HH, Yuan M *et al.* Microbacterium radiodurans sp. nov., a UV radiation-resistant bacterium isolated from soil. *Int J Syst Evol Microbiol* 2010;**60**:2665–70.

Zhang Y, Ren H, Zhang G. Microbacterium hydrothermale sp. nov., an actinobacterium isolated from hydrothermal sediment. *Int J Syst Evol Microbiol* 2014;**64**:3508–12.

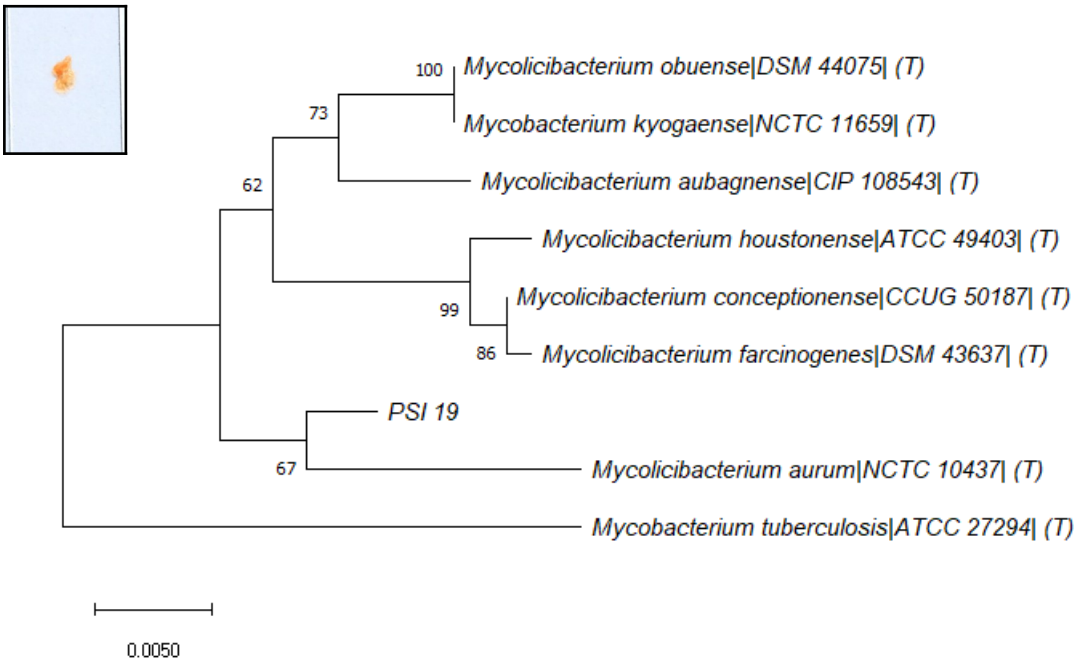
Zhou L, Li H, Zhang Y *et al.* Sphingomonas from petroleum-contaminated soils in Shenfu, China and their PAHs degradation abilities. *Brazilian J Microbiol* 2016;**47**:271–8.

3.6 Supplementary data

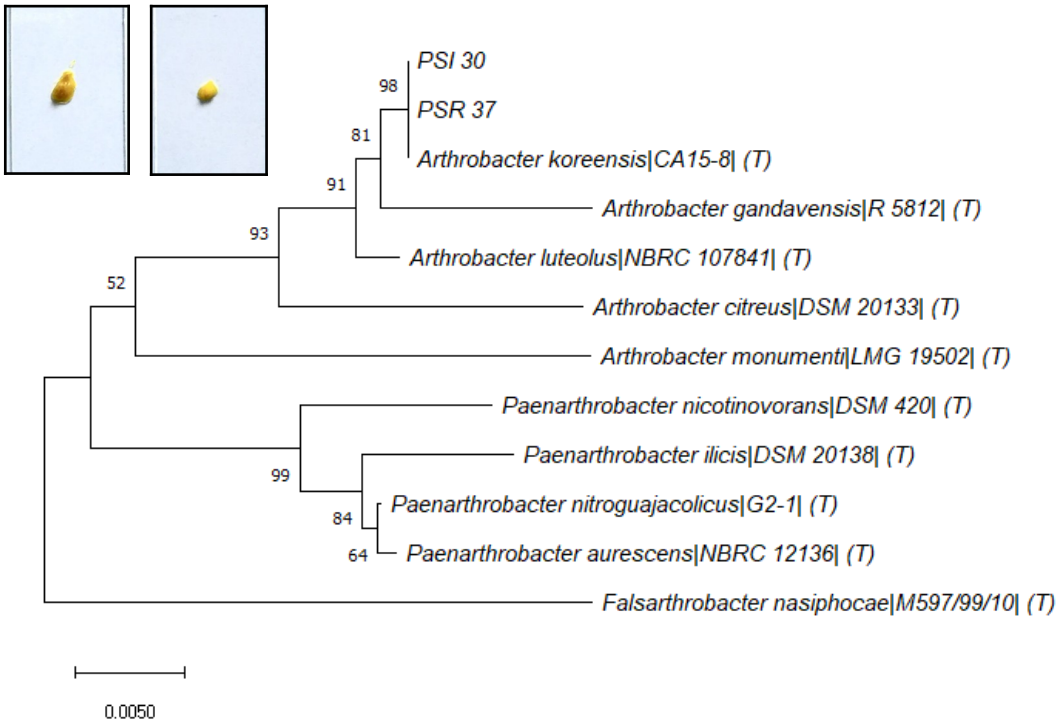
Supplementary Figure S1. Culture conditions and analyses from strains isolated from photovoltaic panel surface samples (PSR and PSI).

Isolate code	Photovoltaic panel	Media	Incubation time (h)	Incubation temperature (ºC)	Gram	Morphology
PSI01	PSI	LB	24	50°C	+	Filamentous
PSI02	PSI	LB	24	50°C	+	Filamentous
PSI05	PSI	LB	24	50°C	+	Rod
PSI06	PSI	R2A	24	50°C	+	Filamentous
PSI07	PSI	R2A	72	RT	-	Rod
PSI08	PSI	R2A	24	RT	-	Cocci
PSI10	PSI	R2A	48	RT	+	Cocci
PSI11	PSI	R2A	24	RT	+	Cocci
PSI14	PSI	R2A	48	35°C	+	Cocci
PSI15	PSI	R2A	48	35°C	-	Cocci
PSI16	PSI	R2A	48	35°C	+	Cocci
PSI17	PSI	R2A	24	35°C	-	Cocci
PSI18	PSI	R2A	24	35°C	-	Cocci
PSI19	PSI	R2A	48	35°C	+	Rod
PSI20	PSI	R2A	48	35°C	-	Cocci
PSI23	PSI	LB	24	RT	-	Cocci
PSI24	PSI	LB	48	RT	+	Cocci
PSI25	PSI	LB	24	RT	-	Cocci
PSI26	PSI	LB	24	RT	-	Cocci
PSI27	PSI	LB	48	RT	+	Cocci
PSI28	PSI	LB	24	35°C	+	Rod
PSI29	PSI	LB	48	35°C	+	Cocci
PSI30	PSI	LB	24	35°C	+	Rod
PSI31	PSI	LB	24	35°C	-	Cocci
PSR33	PSR	LB	72	RT	+	Rod
PSR34	PSR	LB	72	RT	+	Cocci
PSR35	PSR	LB	72	RT	+	Cocci
PSR37	PSR	R2A	72	RT	-	Cocci
PSR40	PSR	R2A	72	RT	+	Rod
PSR41	PSR	R2A	72	RT	+	Cocci
PSR42	PSR	R2A	72	RT	+	Cocci
PSR43	PSR	R2A	48	35°C	+	Filamentous
PSR44	PSR	R2A	48	35°C	-	Cocci
PSR45	PSR	R2A	48	35°C	+	Cocci
PSR46	PSR	R2A	48	35°C	+	Rod
PSR47	PSR	R2A	48	35°C	+	Rod
PSR48	PSR	R2A	48	35°C	-	Filamentous
PSR49	PSR	R2A	120	35°C	+	Filamentous
PSR50	PSR	LB	48	35°C	+	Cocci
PSR51	PSR	LB	48	35°C	+	Cocci
PSR52	PSR	LB	48	35°C	+	Cocci
PSR53	PSR	R2A	48	50°C	+	Filamentous
PSR56	PSR	LB	48	50°C	+	Filamentous
PSR57	PSR	LB	48	50°C	+	Filamentous
PSR58	PSR	LB	48	50°C	+	Filamentous
PSR59	PSR	LB	24	50°C	+	Filamentous
PSR60	PSR	LB	48	50°C	+	Rod
PSI 66	PSI	LB	504	3°C	+	Cocci
PSI 67	PSI	LB	504	3°C	+	Cocci
PSI 68	PSI	LB	504	3°C	+	Cocci
PSI 70	PSI	LB	504	3°C	-	Rod
PSI 71	PSI	LB	504	3°C	+	Cocci
PSR 72	PSI	LB	504	3°C	+	Cocci

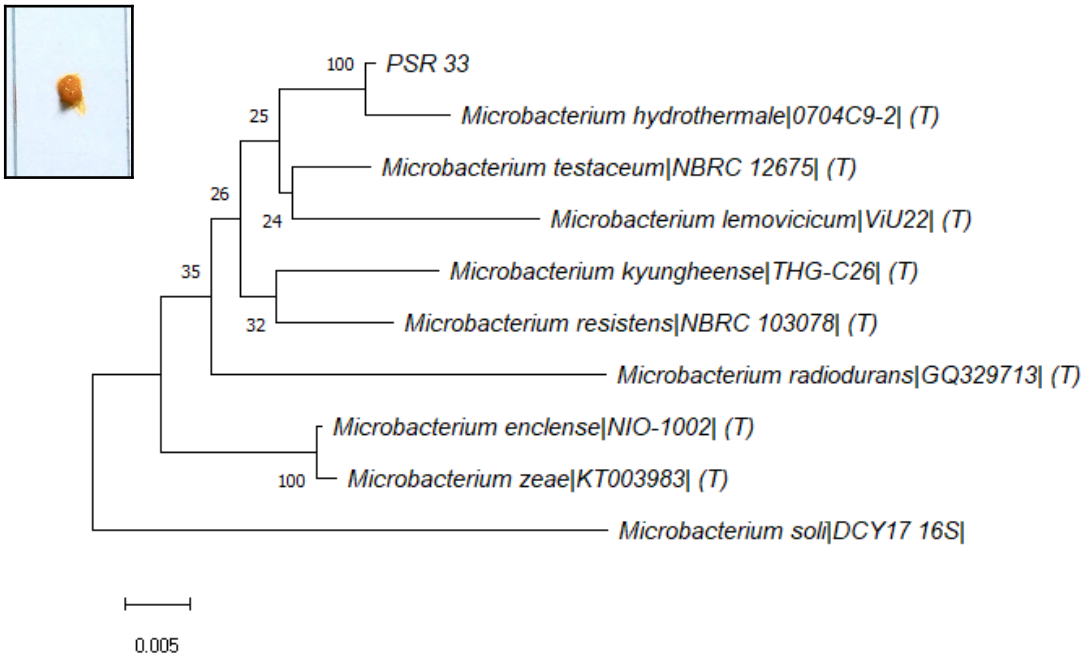
Supplementary Figure S2. Phylogenetic analysis of 16S rRNA gene sequence of PSI 19 strain isolated from photovoltaic panels surfaces samples (PSR and PSI) and their closest relatives retrieved from EzBioCloud database. Evolutionary distance calculated with Kimura 2 parameters and phylogenetic tree reconstructed with Neighbor-joining method using 1000 replicates bootstrap values.



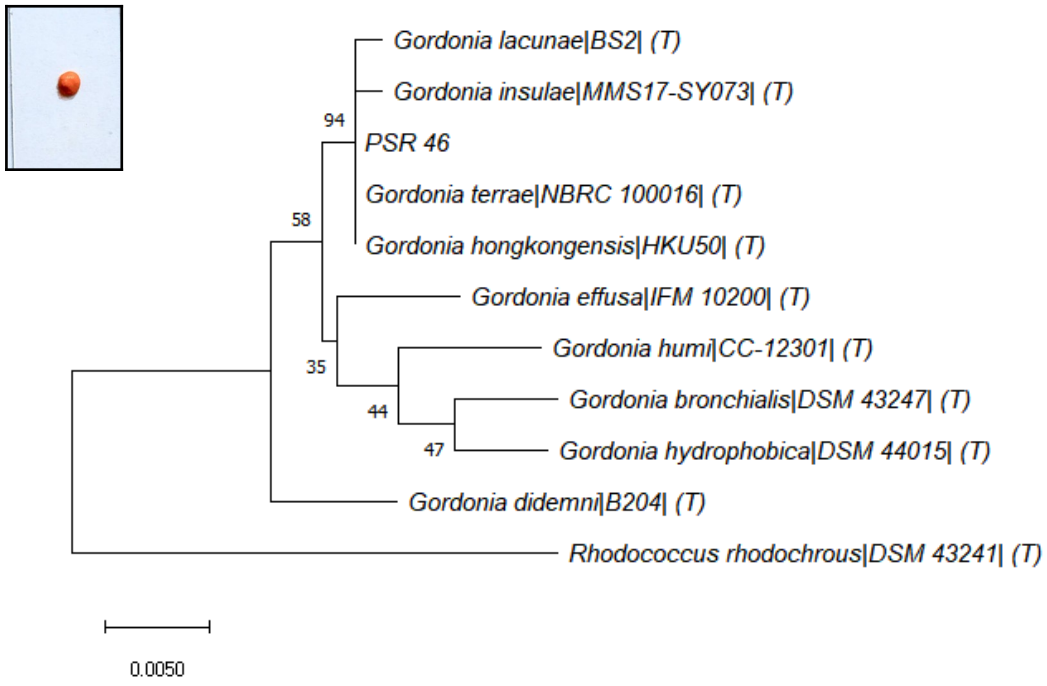
Supplementary Figure S3. Phylogenetic analysis of 16S rRNA gene sequence of PSI 30 and PSR 37 strain isolated from photovoltaic panels surfaces samples (PSR and PSI) and their closest relatives retrieved from EzBioCloud database. Evolutionary distance calculated with Kimura 2 parameters and phylogenetic tree reconstructed with Neighbor-joining method using 1000 replicates bootstrap values.



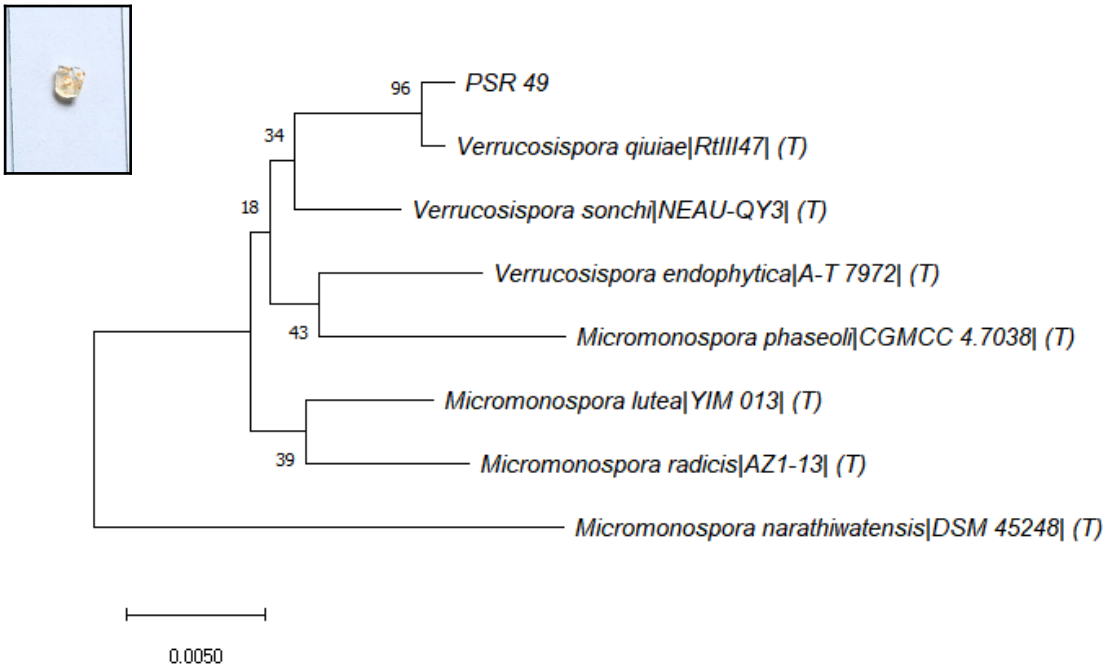
Supplementary Figure S4. Phylogenetic analysis of 16S rRNA gene sequence of PSR 33 strain isolated from photovoltaic panels surfaces samples (PSR and PSI) and their closest relatives retrieved from EzBioCloud database. Evolutionary distance calculated with Kimura 2 parameters and phylogenetic tree reconstructed with Neighbor-joining method using 1000 replicates bootstrap values.



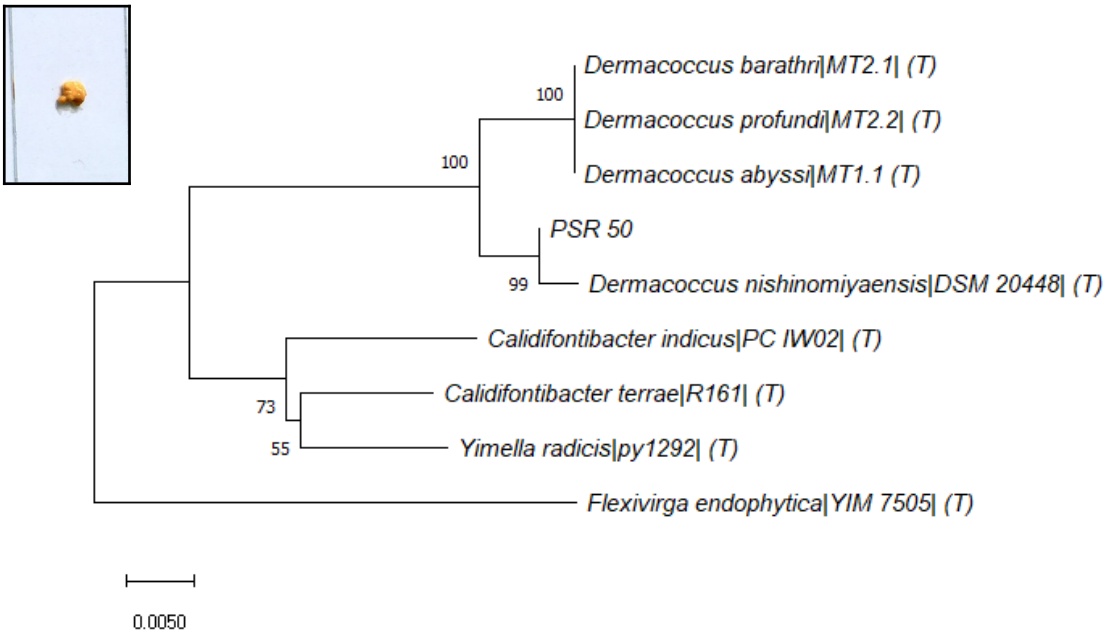
Supplementary Figure S5. Phylogenetic analysis of 16S rRNA gene sequence of PSR 46 strain isolated from photovoltaic panels surfaces samples (PSR and PSI) and their closest relatives retrieved from EzBioCloud database. Evolutionary distance calculated with Kimura 2 parameters and phylogenetic tree reconstructed with Neighbor-joining method using 1000 replicates bootstrap values.



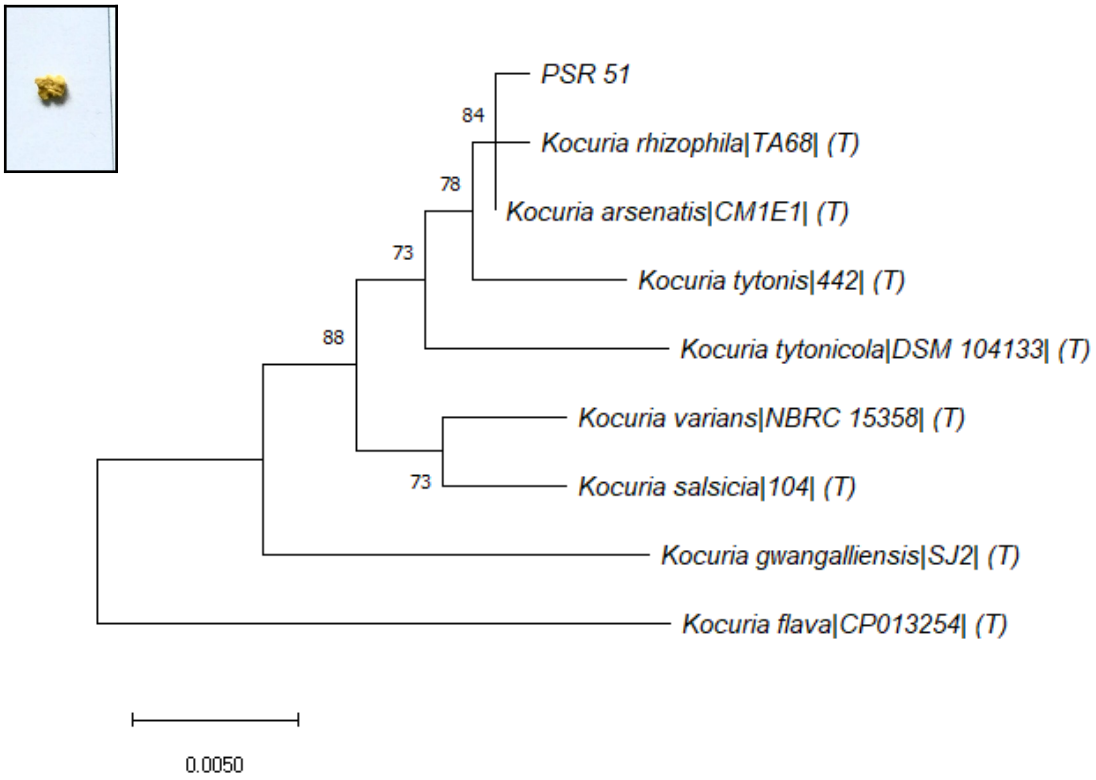
Supplementary Figure S6. Phylogenetic analysis of 16S rRNA gene sequence of PSR 49 strain isolated from photovoltaic panels surfaces samples (PSR and PSI) and their closest relatives retrieved from EzBioCloud database. Evolutionary distance calculated with Kimura 2 parameters and phylogenetic tree reconstructed with Neighbor-joining method using 1000 replicates bootstrap values.



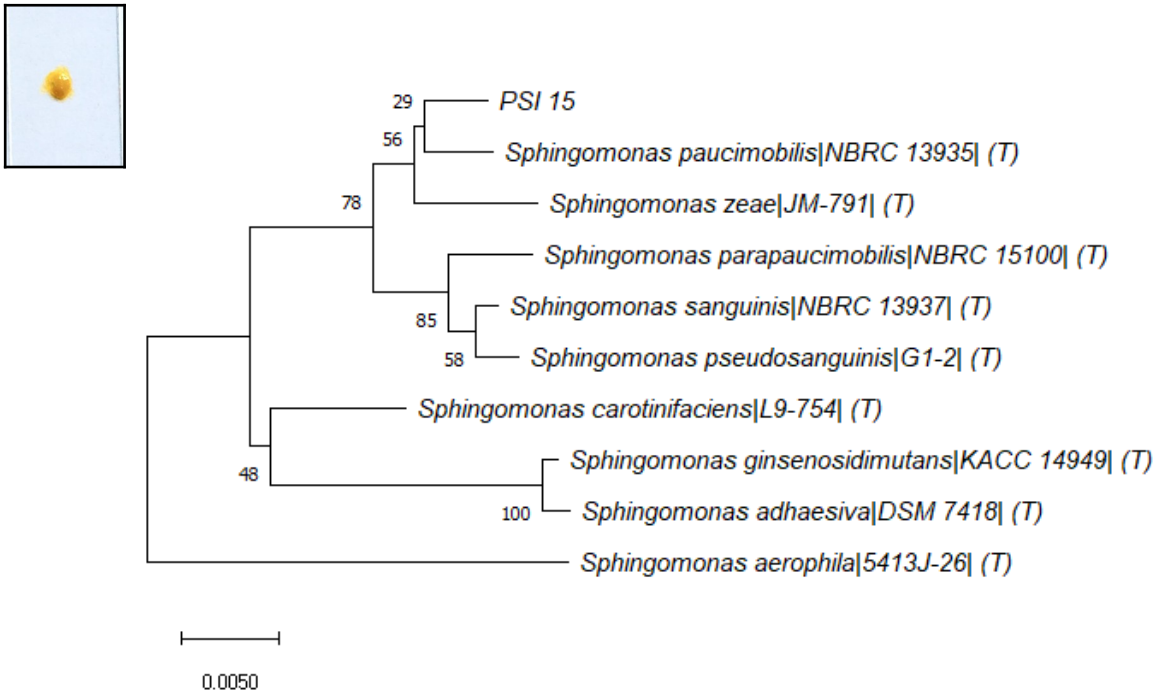
Supplementary Figure S7. Phylogenetic analysis of 16S rRNA gene sequence of PSR 50 strain isolated from photovoltaic panels surfaces samples (PSR and PSI) and their closest relatives retrieved from EzBioCloud database. Evolutionary distance calculated with Kimura 2 parameters and phylogenetic tree reconstructed with Neighbor-joining method using 1000 replicates bootstrap values.



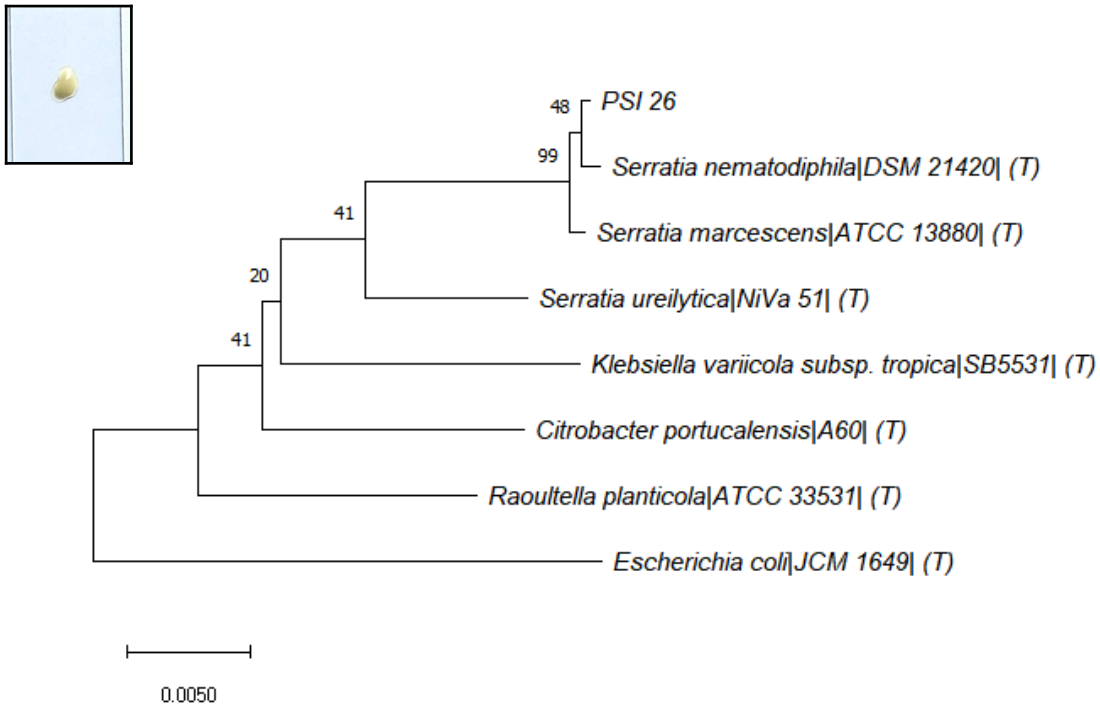
Supplementary Figure S8. Phylogenetic analysis of 16S rRNA gene sequence of PSR 51 strain isolated from photovoltaic panels surfaces samples (PSR and PSI) and their closest relatives retrieved from EzBioCloud database. Evolutionary distance calculated with Kimura 2 parameters and phylogenetic tree reconstructed with Neighbor-joining method using 1000 replicates bootstrap values.



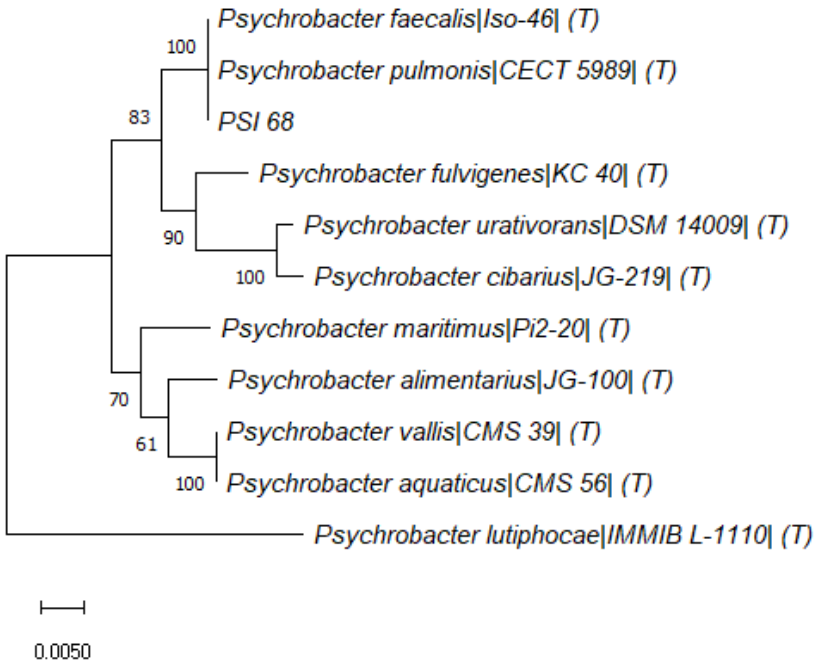
Supplementary Figure S9. Phylogenetic analysis of 16S rRNA gene sequence of PSI 15 strain isolated from photovoltaic panels surfaces samples (PSR and PSI) and their closest relatives retrieved from EzBioCloud database. Evolutionary distance calculated with Kimura 2 parameters and phylogenetic tree reconstructed with Neighbor-joining method using 1000 replicates bootstrap values.



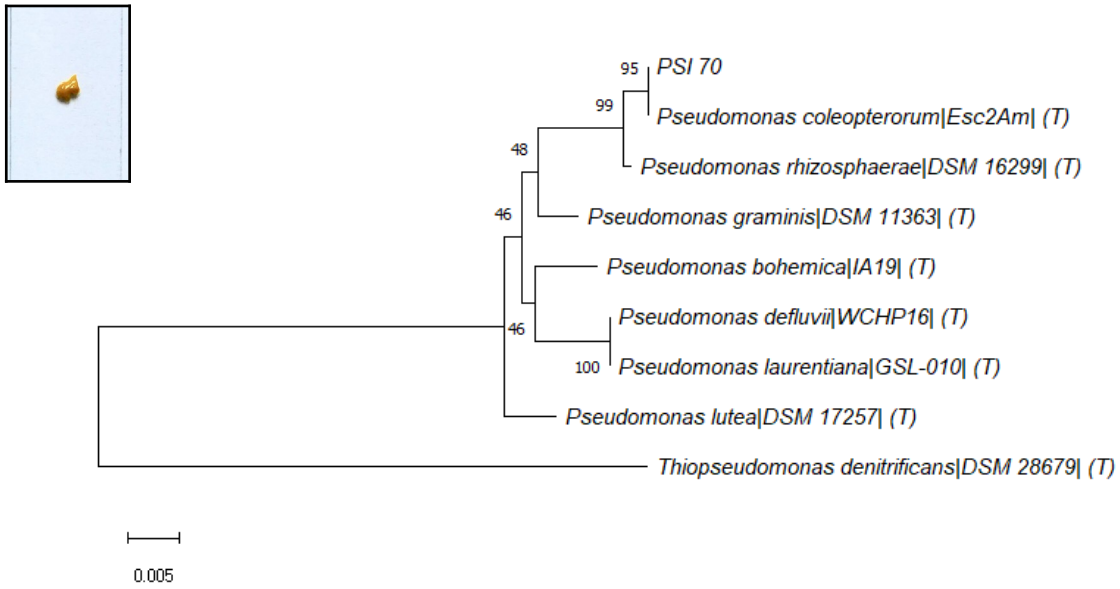
Supplementary Figure S10. Phylogenetic analysis of 16S rRNA gene sequence of PSI 26 strain isolated from photovoltaic panels surfaces samples (PSR and PSI) and their closest relatives retrieved from EzBioCloud database. Evolutionary distance calculated with Kimura 2 parameters and phylogenetic tree reconstructed with Neighbor-joining method using 1000 replicates bootstrap values.



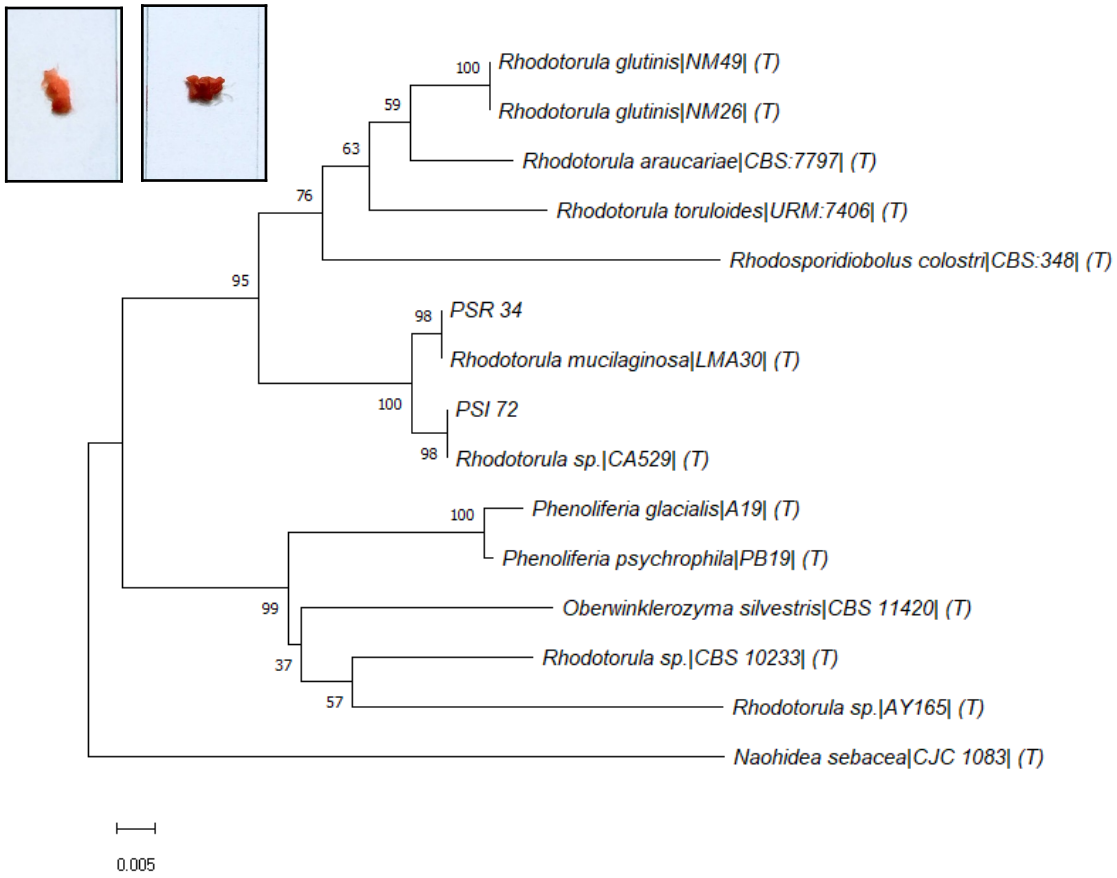
Supplementary Figure S11. Phylogenetic analysis of 16S rRNA gene sequence of PSI 68 strain isolated from photovoltaic panels surfaces samples (PSR and PSI) and their closest relatives retrieved from EzBioCloud database. Evolutionary distance calculated with Kimura 2 parameters and phylogenetic tree reconstructed with Neighbor-joining method using 1000 replicates bootstrap values.



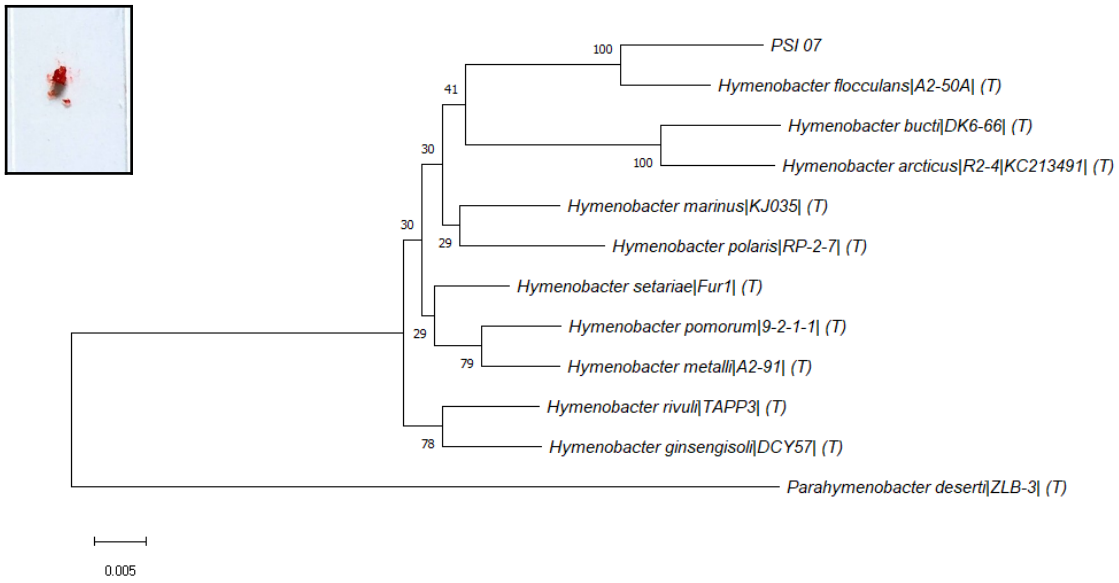
Supplementary Figure S12. Phylogenetic analysis of 16S rRNA gene sequence of PSI 70 strain isolated from photovoltaic panels surfaces samples (PSR and PSI) and their closest relatives retrieved from EzBioCloud database. Evolutionary distance calculated with Kimura 2 parameters and phylogenetic tree reconstructed with Neighbor-joining method using 1000 replicates bootstrap values.



Supplementary Figure S13. Phylogenetic analysis of 16S rRNA gene sequence of PSR 34 and PSI 72 strains isolated from photovoltaic panels surfaces samples (PSR and PSI) and their closest relatives retrieved from NCBI database. Evolutionary distance calculated with Kimura 2 parameters and phylogenetic tree reconstructed with Neighbor-joining method using 1000 replicates bootstrap values.



Supplementary Figure S14. Phylogenetic analysis of 16S rRNA gene sequence of PSI 07 strain isolated from photovoltaic panels surfaces samples (PSR and PSI) and their closest relatives retrieved from EzBioCloud database. Evolutionary distance calculated with Kimura 2 parameters and phylogenetic tree reconstructed with Neighbor-joining method using 1000 replicates bootstrap values.



CHAPTER 4

CONCLUSION

4.1 Overview and future investigations

The primary objective of this work was investigate the microbial diversity living on photovoltaic panels surfaces in Brazilian tropics and also explore the biotechnological potential of pigmented microorganisms isolated from these structures. The motivation behind this work was based on: i) the gap in microbial diversity knowledge; ii) the absence of reports related to microbial diversity on photovoltaic panels surfaces in tropical regions; iii) the biotechnological potential and; iv) the investigation of photovoltaic panels surfaces microbial profile in comparison to each other and those in Mediterranean and Polar climates.

In Chapter 2 of this work, we found that photovoltaic panels investigated showed similar taxonomic profile, dominated mainly by two genera: *Hymenobacter* and *Methylobacterium-Methylorubrum*. These microorganisms were previously reported to have important mechanisms to initiate and engage the colonization process on photovoltaic panels, such as adhesion, biofilm formation, UV and desiccation tolerance. The common core association between photovoltaic panels investigated was composed mainly by microorganisms known as extremophilic, and some of them were also identified in other photovoltaic panels around the world. The functional prediction indicate pathways and specific KEGG orthology related to genes encoding important biomolecules in the UV-resistance, desiccation-resistance, and pigmentation, all being typical adaptation process to succeed in a sun-exposed environment. These findings suggested that microbial communities living on photovoltaic panels surfaces in a tropical region are probably adapted to a harsh environmental conditon, being consistent from ecological point of view.

In Chapter 3 of this work, we observed cultivable and pigmented microorganisms growth retrieved from photovoltaic panels samples, which was consistent with previous reports. The identification of these strains revealed that, at least their closest relatives, were described as UV-resistant, desiccation-resistant, biofilm formation capability and with biotechnological potential representing relevant applications to industrial interest.

In general, this study suggested, as a hypothesis, that the microbial diversity living on photovoltaic panels surfaces, in the moment of collecting, might be a result of a final step in ecological succession, shaped by adapted communities capable of withstand extreme

conditions and settle a native microbiome, intrinsic of that region. Moreover, the biotechnological applications discussed, relative to microorganisms prospected, reinforces the possibility of photovoltaic panels surfaces being an interesting resource for biotechnological purposes.

As future investigations that can be derived from our studies, we propose a deeper investigation of microbial ecology, using metagenomics analyses and statistical tools to compare all studies done so far in a metadata analysis context, focusing on patterns in the colonization process of these microbial communities to promote a more broad and secure ecological information. Moreover, we also propose a study to observe the biofilm formation and microbial coverage over time as a suggestion to determine the steps of colonization. As complementary data to profile these communities, we propose the isolation and identification of various cultivable phenotypes. Finally, to a better understanding of biotechnological potential, a bioprospection approach is interesting, which could guide us into a myriad of possibilities.

REFERENCES

Cordero RR, Damiani A, Laroze D *et al.* Effects of soiling on photovoltaic (PV) modules in the Atacama Desert. *Sci Rep* 2018;**8**:1–14.

Dorado-Morales P, Vilanova C, Peretó J *et al.* A highly diverse, desert-like microbial biocenosis on solar panels in a Mediterranean city. *Sci Rep* 2016;**6**:1–9.Locey KJ, Lennon JT. Scaling laws predict global microbial diversity. *Proc Natl Acad Sci U S A* 2016;**113**:5970–5.

Martin-Sanchez PM, Gebhardt C, Toepel J *et al.* Monitoring microbial soiling in photovoltaic systems: A qPCR-based approach. *Int Biodeterior Biodegrad* 2018;**129**:13–22.

Mellor E. Lichens and their action on the glass and leading of church windows. *Nature* 1923;**112**;299-300.

Noack-Schönmann S, Spagin O, Gründer KP *et al.* Sub-aerial biofilms as blockers of solar radiation: Spectral properties as tools to characterise material-relevant microbial growth. *Int Biodeterior Biodegrad* 2014;**86**:286–93.

Perez-Jorba M, Dallas JP, Bauer C *et al.* Deterioration of stained glass by atmospheric corrosion and micro-organisms. *J Material Science* 1980;**15**;1640-1647

Porcar M, Louie KB, Kosina SM *et al.* Microbial ecology on solar panels in Berkeley, CA, United States. *Front Microbiol* 2018;**9**:1–14.

Sarver T, Al-Qaraghuli A, Kazmerski LL. A comprehensive review of the impact of dust on the use of solar energy: History, investigations, results, literature, and mitigation approaches. *Renewable and Sustainable Energy Reviews* 2013;**22**;698-733.

Shirakawa MA, Zilles R, Mocelin A *et al.* Microbial colonization affects the efficiency of photovoltaic panels in a tropical environment. *J Environ Manage* 2015;**157**:160–7.

Tanner K, Martí JM, Belliure J *et al.* Polar solar panels: Arctic and Antarctic microbiomes display similar taxonomic profiles. *Environ Microbiol Rep* 2018a;**10**:75–9.

Tanner K, Martorell P, Genovés S *et al.* Bioprospecting the solar panel microbiome: high-throughput screening for antioxidant bacteria in a Caenorhabditis elegans model. *Bioprospecting Sol panel microbiome High-throughput Screen Antioxid Bact a caenorhabditis elegansModel* 2018b:423731.

Tanner K, Vilanova C, Porcar M. Bioprospecting challenges in unusual environments. *Microb Biotechnol* 2017;**10**:671–3.

Thorseth IH, Furnes H, Heldal M. The importance of microbiological activity in the alteration of natural basaltic glass. *Geochemica et Cosmochimica Acta* 1992;**56**;845-850.

Vitorino LC, Bessa LA. Microbial diversity: The gap between the estimated and the known. *Diversity* 2018;**10**, DOI: 10.3390/D10020046.