Abstract: Actinomycetes (a group of filamentous bacteria) are the dominant microbial order in the Daqu (DQ) fermentation starter and in the pit mud (PM) of the Baijiu fermentation microbiome. Actinomycetes produce many of the key enzymes and flavor components, and supply important precursors, which have a major influence on its characteristic aroma components, to other microorganisms during fermentation. This paper reviews the current progress on actinomycete research related to Baijiu fermentation, including the isolation and identification, distribution, interspecies interactions, systems biology, and main metabolites. The main metabolites and applications of the actinomycetes during Baijiu fermentation are also discussed.

Keywords: actinomycete; Baijiu; flavor compound; interspecies interactions; pit mud

1. Introduction

Baijiu is one of the six major distilled liquors in the world and has been produced for centuries in China [1,2]. Baijiu is colorless, clear, and has a unique flavor, which mainly arises from the co-fermentation of microorganisms naturally inoculated. This method results in a very wide range of fermenting organisms, from both the Daqu (DQ) saccharification starter, the pit mud (PM), and the fermented grains (FGs) [3–5]. Depending on its flavor characteristics caused by the different production processes, raw materials, and microbial communities, Baijiu can be classified into the four basic Baijiu aroma types—jiangxiangxing (JXXB), nongxiangxing (NXXB), qingxiangxing (QXXB), and mixiangxing (MXXB)—and eight Baijiu aroma types derived from the above four aroma types [1]. Baijiu production consists of four successive stages: (i) saccharification of the grain starch using DQ or Xiaoqu (XQ) as the starter culture; (ii) open solid-state fermentation; (iii) distillation to produce the final liquor product; and (iv) storage aging. The open saccharification fermentation results in a highly complex microbiome, with many interactions between species [6,7]. This huge microbial diversity is responsible for the unique flavor of Baijiu, which is distinct from those of other distilled liquors, such as whisky, vodka, and tequila, which are made by submerged fermentation [8]. In essence, the diversity and stability of microbial communities associated with high acid tolerance are directly influenced by factors of the natural environmental conditions (geographical limitations, temperature, humidity, pH, and climate), raw materials (sorghum or a mixture of wheat, barley, corn, rice, and sorghum), and complex production processes [9,10]. The high complexity of the naturally selected microbiome has the potential to produce distinct flavors containing different trace components and alcohol contents (35–60%), caused by their underlying metabolism and interactions.

Actinomycetes in Baijiu fermentation derive from the DQ or XQ starter, the PM, and the fermenting grains (FGs) [11,12]. They have diverse metabolic activities, including the hydrolysis of starch, cellulose, protein, and pectin in the raw material grains, and they produce various secondary metabolites, including flavor esters (ethyl caproate, ethyl butyrate, and ethyl lactate), and other flavor compounds (3-hydroxyl-2-butanone, 2,3-butanediol, and...
pyrazine), polypeptides, and amino acids [13]. In DQ-initiated fermentation, actinomycetes produce a large amount and diversity of antibiotics, such as heptaene macrolide antibiotics and streptomycin, which can inhibit the growth of fungi and pathogenic bacteria [14,15]; in particular, Streptomyces spp., which produces geosmin that can spoil the flavor of the Baijiu in the early stages of saccharification and fermentation [16,17]. Several reports have focused on the application of actinomycete topromotecaproic acid bacteria to produce ethyl caproate, the main contributor to the flavor of nongxiangxing Baijiu [18,19]. In addition, actinomycetes reportedly help to maintain the stability of the PM and accelerate the maturation of new PM [20,21]. This review focuses on the recent research progress on actinomycetes in the Baijiu microbiome, including the distribution and abundance and species of actinomycetes in DQ and PM, ‘omics studies, and interactions between actinomycetes. The functions of actinomycetes isolated from Baijiu fermentations are also discussed.

2. Isolation and Identification of Actinomycetes from Different Stages of Baijiu Production

In the 1980s, actinomycetes were initially isolated from DQ and fermented grains from JXXB, and subsequently, isolation and identification of actinomycetes focused on the PM and DQ used for making NXXB [22,23]. A total of 86 species of actinomycetes have been isolated from five types of Baijiu (JXXB, NXXB, QXXB, ZMXXB, and FXXB), from different regions, and from the DQ, PM, and FGs. The major genera of actinomycetes isolated from Baijiu include Thermoactinomyces, Streptomyces, Nocardiosis, Massilia, Shimazuella, Kroppenstedtia, Laceyella, Micromonospora, and Arthrobacter. Summary information on the previously isolated and identified actinomycetes from different stages of Baijiu production is shown in Table 1, and more detailed information on the growth media in Table S1 (Supplementary Information).

Table 1. Actinomycete species isolated and identified from Baijiu.

| Samples               | Places                  | Types       | Species                                                                 | Media                                      | References |
|-----------------------|-------------------------|-------------|-------------------------------------------------------------------------|--------------------------------------------|------------|
| High-temperature DQ   | Maotai, Guizhou         | JXXB        | Thermoactinomyces vulgaris                                              | GTY medium                                 | [24]       |
| High-temperature DQ   | Sichuan                 | JXXB        | Streptomyces rochei                                                     | Casein medium                              | [25]       |
| High-temperature DQ   | Guizhou                 | JXXB        | Streptomyces cacaoi, Streptomyces zaomyceticus                          | Gause No. 1 medium, ISP2 medium            | [26]       |
| High-temperature DQ   | Maotai, Guizhou         | JXXB        | Laceyella sacchari                                                      | Modified Gause No. 2 Medium, ISP2 medium   | [27]       |
| High-temperature DQ   | Guizhou                 | JXXB        | Streptomyces griseus, Streptomyces albus                               | Gause No. 1 medium                        | [28]       |
| High-temperature DQ   | Maotai, Guizhou         | JXXB        | Streptomycetes sp. FBKL4.005                                            | ISP2 medium                                | [29]       |
| High-temperature DQ   | Maotai, Guizhou         | JXXB        | Streptomyces bangaladesiens                                             | GTY medium                                 | [30]       |
| FG ²                  | Gulin, Sichuan          | JXXB        | Aggregatibacter actinomycetemcomitans                                  | Beef extract peptone medium                | [31]       |
| Alcoholic fermentative| Huaihua, Guizhou        | JXXB        | Streptomyces flocculus                                                  | Gause No. 1 medium                        | [32]       |
| material              |                         |             |                                                                          |                                             |            |
| Soil of baijiu        | Huaihua, Guizhou        | JXXB        | Streptomyces sp. R11-21                                                 | Gause No. 1 medium                        | [33]       |
| production            |                         |             |                                                                          |                                             |            |
| environment           | Huaihua, Guizhou        | JXXB        | Thermostaphylospora chromogenana                                         | Gause No. 1 medium                        | [34]       |
| Samples | Places         | Types  | Species                                                                 | Media                                      | References |
|---------|---------------|--------|--------------------------------------------------------------------------|--------------------------------------------|------------|
| DQ      | Yibin, Sichuan | NXXB   | *Streptomyces althioticus*, *Streptomyces coelicoflavus*, *Streptomyces diastaticus* subsp. *ardesiacus*, *Streptomyces ghanaensis*, *Streptomyces mutabilis*, *Streptomyces rubiginosohelvolus*, *Streptomyces somaliensis*, *Streptomyces thermocarboxydus*, *Streptomyces vinaceusdrappus*, *Streptomyces violascens*, *Streptomyces virdobrunneus* | Modified Gause No. 1 Medium | [35]       |
| FG      | Yibin, Sichuan | NXXB   | *Streptomyces coerulescens*, *Streptomyces somaliensis*, *Streptomyces ghanaensis*, *Streptomyces violascens*, *Massilia timonae*, *Nocardiopsis prasina*, *Streptomyces albofaciens*, *Streptomyces althioticus*, *Streptomyces celluloflavus*, *Streptomyces cinereoruber* subsp. *cinereoruber*, *Streptomyces coelicoflavus*, *Streptomyces griseorubroviolaceus*, *Streptomyces cyanofuscatus*, *Streptomyces diastaticus* subsp. *ardesiacus*, *Streptomyces fimicarius*, *Streptomyces flavovirens*, *Streptomyces globisporus* subsp. *globisporus*, *Streptomyces griseopl anus*, *Streptomyces halstedii*, *Streptomyces matsushinii*, *Streptomyces olivaceus*, *Streptomyces pactum*, *Streptomyces rubiginosohelvolus*, *Streptomyces sclerotialus*, *Streptomyces sindenensis*, *Streptomyces somaliensis*, *Streptomyces thermocarboxydus*, *Streptomyces vinaceusdrappus*, *Streptomyces violascens* | Gause No. 1 medium | [36]       |
| PM ^3   | Yibin, Sichuan | NXXB   | *Streptomyces albofaciens*, *Streptomyces althioticus*, *Streptomyces celluloflavus*, *Streptomyces cinereoruber* subsp. *cinereoruber*, *Streptomyces coelicoflavus*, *Streptomyces flavovirens*, *Streptomyces globisporus* subsp. *globisporus*, *Streptomyces griseopl anus*, *Streptomyces halstedii*, *Streptomyces matsushinii*, *Streptomyces olivaceus*, *Streptomyces pactum*, *Streptomyces rubiginosohelvolus*, *Streptomyces sclerotialus*, *Streptomyces sindenensis*, *Streptomyces somaliensis*, *Streptomyces thermocarboxydus*, *Streptomyces vinaceusdrappus*, *Streptomyces violascens* | Gause No. 1 medium | [36]       |
| Mature medial-temperature DQ | Henan | NXXB | *Streptomyces albus*, *Streptomyces aureus*, *Streptomyces virdobrunneus*, *Streptomyces xiangenensis*, *Streptomyces cacaoi* subsp. *Cacaoi* | Gause No. 1 medium | [36] |
| Sealing mud | Yibin, Sichuan | NXXB | *Streptomyces sp.* JP12, *Streptomyces sp.* RZ1 | Gause No. 1 medium | [37] |
| FG      | Yibin, Sichuan | NXXB   | *Streptomyces sp.* JP12, *Streptomyces sp.* RZ1 | Gause No. 1 medium | [37] |
| PM      | Yibin, Sichuan | NXXB   | *Micromonospora sp.* JD3 | Gause No. 1 medium | [37] |
| The air of fermentation pit | Yibin, Sichuan | NXXB | *Streptomyces vinaceusdrappus*, *Arthrobacter protophormiae* | enriched medium and Inorganic salt medium | [38] |
| PM (20 years) | Yibin, Sichuan | NXXB | *Streptomyces albus* | Gause No. 1 medium | [39] |
| PM | Yibin, Sichuan | NXXB | *Streptomyces albus*, *Streptomyces roseosporus*, *Streptomyces griseorubroviolaceus*, *Streptomyces aureus* | Gause No. 1 medium and complete Inorganic Basal Medium | [40] |
| PM | Luzhou, Sichuan | NXXB | *Thermophilic bacteria gallinarum* | R2A medium | [41] |
| PM (50 years) | Southern of Sichuan | NXXB | *Streptomyces sampsonii*, *Streptomyces rutgersensis* | Situ-medium | [42] |
| PM | Hubei | NXXB | *Streptomyces avicenniae* | Gause No. 1 medium | [43] |
#### Table 1. Cont.

| Samples          | Places               | Types      | Species                                                                 | Media                   | References   |
|------------------|----------------------|------------|-------------------------------------------------------------------------|-------------------------|--------------|
| PM (50 years)    | Anhui                | NXXB       | Actinomyces israelii, Actinomyces meyeri, Bifidobacterium lactis,       | Isolation medium        | [44]         |
|                  |                      |            | Bifidobacterium magnum, Bifidobacterium breve, Arthrobacter nicotianae,  |                         |              |
|                  |                      |            | Nocardia africana, Nocardia altamirensis, Nocardia carnea, Nocardia     |                         |              |
|                  |                      |            |cerradoensis, Nocardia flavines, Nocardia nova, Nocardia xishanensis      |                         |              |
| DQ               | Zibo, Shandong       | ZMXXB      | Thermoactinomyces daquis                                               | R2A medium              | [45]         |
|                  |                      |            | Thermoactinomyces vulgaris                                             | R2A medium              | [46]         |
|                  |                      |            | Thermoactinomyces intermedii, Laceyella tengchongensis, Laceyella       | ISP2 medium             | [47]         |
|                  |                      |            | sediminis, Laceyella sacchari, Laceyella putida                        |                         |              |
| High-temperature| Shandong             | ZMXXB      | Thermoactinomyces vulgaris, Streptomyces thermoviolaceus               | R2A medium              | [48]         |
| DQ               | Xinghuacun, Shanxi   | QXXB       | Streptomyces sp. ZYP3, Streptomyces sp. ZYP6, Streptomyces sp. ZYP7,    | GS medium               | [15]         |
|                  |                      |            | Streptomyces sp. ZYP10, Streptomyces sp. ZYP12, Streptomyces sp. ZYP13, |                         |              |
|                  |                      |            | Streptomyces sp. ZYP15, Streptomyces sp. ZYP16, Streptomyces sp. ZYP17, |                         |              |
|                  |                      |            | Streptomyces sp. ZYP18                                                  |                         |              |
| DQ               | Xinghuacun, Shanxi   | QXXB       | Streptomyces sp. ZYP11                                                 | GW1 medium              | [51]         |
|                  |                      |            | Streptomyces sp. ZYP9                                                   | R2A medium              |              |
| DQ               | Xinghuacun, Shanxi   | QXXB       | Streptomyces sp. ZYP8                                                   | GMKA medium             |              |
| DQ               | Xinghuacun, Shanxi   | QXXB       | Streptomyces sp. ZYP14                                                  | HV medium               | [52]         |
| DQ               | Shanxi               | QXXB       | Bacillus renginii                                                       | LSA medium              | [49]         |
| DQ               | Beijing              | QXXB       | Streptomyces albus, Streptomyces cacaoi                                 | ISP2 medium             | [50]         |
| Out part of DQ   | Shanxi Xinghuacun    | QXXB       | Brevibacterium sp. Micrococcus lutens                                   | MRSA medium             | [51]         |
|                  |                      |            |                                                                          |                         |              |
| DQ, FG           | Beijing              | QXXB       | Shimazuella kribbensis, Koenenstedia sanguinis, Koenenstedia eburnea     | Modified Gause No. 2    | [52]         |
| DQ               | Shaanxi              | FXXB       | Arthrobacter aresens                                                    | Gause No. 1 medium      | [53]         |
| DQ               | Shaanxi              | FXXB       | Streptomyces albus                                                       | PDA medium              | [54]         |
| FG               | Shaanxi              | FXXB       | Arthrobacter aresens                                                    | Gause No. 1 medium      | [55]         |

1 Daqu; 2 fermented grain; 3 pit mud.

*Streptomyces albus* was detected in a cellar where JXXB is made, the PM used for NXXB, and the DQ used in FXXB and QXXB [28,39,50,54]. *Streptomyces cacaoi* was isolated from JXXB, NXXB, and QXXB [26,36,50]. *Thermoactinomyces vulgaris*, *Laceyella sacchari*, and *Thermoactinomyces intermedius* were isolated from the high-temperature DQ used for JXXB and ZMXXB [24,48]. *Streptomyces griseus*, *Streptomyces zaoymeticus*, *Thermoactinomyces thalpohillus*, and *Streptomyces flocculus* were isolated from JXXB DQ, using Gao’s No. 1 medium [26,28,32]. *Aggregatibacter actinomycetemcomitans*, *Thermostaphylospora chromogena*, *Streptomyces flocculus*, and *Streptomyces sp*. R11-21 were isolated from FG [31–34]. *Streptomyces bangladesensis* and *Streptomyces rochei* were isolated from DQ, using GTY medium and casein medium, respectively [25,30].

Gao’s No. 1 is a commonly used medium for isolating actinomycetes from NXXB fermentations. Seven, two, and twelve species were isolated from DQ, FGs, and PM, respectively [36,43]. *Arthrobacter protophormiae* was isolated using inorganic salt medium from 20-year-old PM [38]. *Streptomyces sampsonii* and *Streptomyces rutgersensis* were sep-
arated from the in situ medium and the Thermophilobacter gallinarum R2A medium from the PM [41,42]. Three genera (Streptomyces, Nocardiopsis, and Massilia) and 26 species were isolated from the fermentations using modified Gao’s No.1 medium [35]. Ten species of Streptomyces were isolated using Gao’s No.1 medium and two using HV medium from the DQ and FG of QXXB; Streptomyces ZYP11, Streptomyces ZYP9, Streptomyces ZYP8, and Brevibacterium renqinigii were also isolated from QXXB using GW1, R2A, GMKA, and LSA media, respectively [15,49]. Shimazuella kribbensis was only found in the FG from QXXB fermentation [52]. Thermoactinomyces daqus H-18 and Streptomyces thermoviolaceus were isolated using R2A medium from ZMXXB fermentation [48,56]. Arthrobacter aresens was only found in the DQ and FG of FXXB [53,55]. Using BiologEcoPlates, 13 actinomycetes were isolated from 50-year-old PM used for NXXB [44].

3. Methods for Identification of New Species of Microorganisms from Baijiu Production

Culture-independent methods, such as polymerase chain reaction denaturing gradient gel electrophoresis (PCR-DGGE) and sequencing technology, have been developed for identification of actinomycetes (Table 2). The microbiomes of four different types of Baijiu were analyzed by these methods. Thermactinomyces sanguinis could only be detected in the DQ and FG of JXXB, NXXB, QXXB, and JXXB by culture-independent methods [57–60]. Thermactinomyces vulgaris, Olsenella ului, Olsenella profusa, Lancefieldella parvula, Corynebacterium tuberculostearicum, Corynebacterium minutissimum, Streptomyces coerulorubidus, Streptomyces hainanensis, and Arthrobacter volwaeensis were identified in NXXB fermentations by PCR-DGGE [61]. Arthrobacter stackebrandii, Kocuria carniphila, Glutamicibacter creatinolyticus, Brevibacterium aurantiacum, Cellulosimicrobium junkei, Microbacterium oxydans, Corynebacterium glutamicum, Gordonia terrae, Dietzia maris, Acidipropionibacterium acidipropionici, Microbacterium hydrocarbonoxydans, Microbacterium schleiferi, and Gulosibacter molinatovorax were first identified in the PM of NXXB by 16S rRNA gene sequencing [62]. Streptomyces albus, Kroppenstedtia eburnea, Saccharopolyspora rectivirgula, Brevibacterium celere, and Thermoactinomyces vulgaris were identified as the dominant microorganisms in the DQ of QXXB, according to a similar analysis of 16S rRNA [60]. In ZMXXB, Saccharopolyspora rectivirgula, Saccharopolyspora hordei, Saccharopolyspora rectivirgula, and Rothiakristinae were identified using 16S rDNA analysis [63]. Thermactinomyces vulgaris, Thermactinomyces intermedius, and Thermactinomyces daqus were detected using ARDRA and each type represents an OTU (operational taxonomic unit) [64]. In addition, Laceyellatengchongensis, Laceyellasediminis, Laceyellasacchari, and Laceyella putidus were identified by a specific PCR assay using a new specific primer (109F/801R) [47].

| Samples          | Types | Places           | Methods           | Species                                                                 | References                          |
|------------------|-------|------------------|-------------------|-------------------------------------------------------------------------|-------------------------------------|
| High-temperature DQ | JXXB | Sichuan          | PCR-DGGE          | Thermactinomyces sanguinis                                             | [57]                                |
| DQ               | JXXB | Jiangsu          | PCR-DGGE          | Thermactinomyces sanguinis                                             | [65]                                |
| FG               | JXXB | Guizhou          | PCR-DGGE          | Thermactinomyces sanguinis                                             | [58]                                |
| FG               | JXXB | Renhuai, Guizhou | PCR-DGGE          | Uncultured Actinomycete colone 4-306, Corynebacterium sp. DNF00584     | [66]                                |
| FG               | JXXB | Renhuai, Guizhou | PCR-DGGE          | Streptomyces sp. MC21, Actinomycetales sp. JB111, Thermactinomyces sanguinis | [66]                                |
| DQ               | NXXB | South            | PCR-DGGE          | Thermactinomyces vulgaris                                              | [67]                                |
| Baobaoqu         | NXXB | Sichuan          | LC-MS/MS          | Microbacterium hominis, Thermactinomyces vulgaris                       | [68]                                |
| High-temperature DQ | NXXB | Anhui            | 16S rDNA          | Thermactinomyces sanguinis                                             | [59]                                |
| PM               | NXXB | Sichuan          | PCR-DGGE          | Olsenella ului, Olsenella profusa, Lancefieldella parvula, Corynebacterium tuberculostearicum, Corynebacterium minutissimum, Streptomyces coerulorubidus, Streptomyces hainanensis | [61]                                |

Table 2. Actinomycete species identified by culture-independent methods.
### Table 2. Cont.

| Samples                        | Types                     | Places                      | Methods                  | Species                                                                                                                                  | References |
|-------------------------------|---------------------------|-----------------------------|--------------------------|------------------------------------------------------------------------------------------------------------------------------------------|------------|
| PM                            | NXXB                      | Sichuan                     | 16S rRNA                 | *Arthrobacter stackebrandtii, Kocuria carnifila, Glutamicibacter creatinolyticus, Brevibacterium aurantiacum, Cellulosimicrobium funkei, Microbacterium oxiyans, Corinebacterium glutamicum, Gordonia terrae, Dietzia maris, Acidopropionibacterium acidopropionicum, Microbacterium hydrocarbonoxidans, Microbacterium schleiferi, Gulobacter molitiliocrux* | [62]       |
| FG Alcoholic fermentative      | NXXB                      | Sichuan                     | PCR-DGGE                 | *Arthrobacter woluwensis*                                                                                                                | [69]       |
| materials                     |                           |                             |                          | *Thermoactinomyces sanguinis*, *Streptomyces albus, Brevibacterium linens, Brachybacterium paraconglomeratum, Rothia koreensis*          | [70]       |
| Low-temperature DQ FG          | QXXB                      | Beijing, Shanxi, Taiwan, Heilongjiang, Hebei | 16S rDNA | *Streptomyces albus*, *Kroppenstedtia eburnea*                                                                                          | [71]       |
| Mature DQ                     | QXXB                      | Shanxi                       | 16SrRNA                  | *Streptomyces sanguinis*, *Streptomyces albus, Brevibacterium linens, Brachybacterium paraconglomeratum, Rothia koreensis*            | [60]       |
| DQ High-temperature DQ         | QXXB                      | Xiangyang, Hubei             | WGS                      | *Streptomyces albus, Streptomyces NHF165, Saccharopolyspora erythraea*                                                                   | [72]       |
| DQ (8 days of fermentation)    | ZMXXB                     | Shandong                     | 16S rDNA                 | *Thermoactinomyces vulgaris*, *Saccharopolyspora rectivirgula, Brevibacterium celere*                                                | [73]       |
| DQ (24 days of fermentation)   | ZMXXB                     | Shandong                     | 16S rDNA                 | *Saccharopolyspora hordei, Saccharopolyspora rectivirgula, Rothiakristina, Marmoricola aurantiacus*                                    | [63]       |
| DQ (49 days of fermentation)   | ZMXXB                     | Shandong                     | 16S rDNA                 | *Thermoactinomycesintermedius, Thermoactinomyces vulgaris, Lacyella patula, Kroppenstedtia eburnea, Saccharopolyspora hordei, Saccharopolyspora rectivirgula, Streptomyces hindustanus, Rubrobacter radiotolerans, Streptomyces coeruleopurpureus, Aciditerrimonasferrireducens, Nesterenkonia Rana, Modestobacter versicolor, Orlithinimicrobium pekingense, Cutiobacterium acnes* | [74]       |
| Northern and southernwestern DQ| ZMXXB                     | Shandong                     | 16S rDNA and 26S rDNA    | *Saccharopolyspora rosea, Saccharopolyspora rectivirgula, Saccharopolyspora hordei, Saccharopolyspora spinosa, Streptomyces albus, Streptomyces cacaois, Thermoactinomyces sanguinis, Thermoactinomyces vulgaris, Thermopolysporabyspora, Thermostaphylospora chromogena, Actinopolyspora erythraea* | [74]       |

1 Daqu; 2 fermented grain; 3 pit mud.

A comparison of actinomycetes identified by culture and culture-independent methods is shown in Table S2. *Thermoactinomyces vulgaris, Streptomyces albus, Thermoactinomyces intermedius, Thermostaphylospora chromogena, Kroppenstedtia eburnea, and Streptomyces cacaois* were identified by both methods. Eighty species were detected and identified by culture-independent methods, of which 55 species were detected without isolation. There are four major differences between the two methods: (i) the analyzed samples were from many different locations and sampling times; (ii) the isolation medium of actinomycetes were limited by traditional culture methods; (iii) metagenomics analysis of most samples by the cultured-independent methods could only assign the taxonomic classification of actinomycetes to genera; and (iv) low-abundance actinomycetes cannot be detected by targeted metagenomics such as 16S rRNA amplicon sequencing. To understand the diversity of actinomycetes within the Baijiu microbiome of a limited time, multi-omics analysis and more separation methods should be applied [75,76]. Further, combined with innovative techniques (high-throughput culture), uncultured actinomycetes should be targeted for isolation according to their special functional characteristics [77]. With the help of high-throughput analysis results, selective nutrient media, selective physicochemical...
conditions, density-based separation, inhibitors, and specific growth factors could be found to isolate the uncultured actinomycetes from the DQ, FGs, and PM of the different Baijiu ecosystems [77].

4. Distribution of Actinomycete Species from the Major Types of Baijiu

The distribution of actinomycete species from the major types of Baijiu, and from the DQ, PM, and FGs, are shown in Figure 1, and a more detailed distribution of *Thermoactinomyces* and actinomycetes in DQ is shown in Figure 2. The variation in the profile of the actinomycetes was unraveled among the niches of the different types of Baijiu. *Thermoactinomyces*, a thermophilic actinomycete, was found in the DQ and FG of JXXB from three Baijiu factories, and accounted for 34.4–66.1% of the microbiome during the DQ production process [78–80]. Actinomycetes, including the *Actinopolysporaceae*, *Brevibacteriaceae*, and *Streptomycetaceae* families, make up 3.3–9.1% of the DQ microbiome [81]. Actinomycetes were one of the main phyla (7.7%) and *Thermoactinomyces* was the dominant genus in white and yellow DQ [82]. Three types of high-temperature DQ contained four genera of actinomycetes, namely, *Saccharopolyspora*, *Brevibacterium*, *Streptomyces*, and *Thermoactinomyces*, which comprised 4.7, 1.2, 1.5, and 26.4% of the total sequences, respectively [83]. *Thermoactinomyces* and *Saccharopolyspora* accounted for 16.7 and 22.1%, respectively, of the genera in Northern JXXB DQ, under high-temperature conditions [84]. The abundance of actinomycetes in manually and mechanically produced high-temperature DQ was 1.94 and 3.08%, respectively, and increased to 14.19 and 5.06% during fermentation [85]. JXXB goes through multiple rounds of fermentation, where one round includes three distinct phases: stacking fermentation, anaerobic fermentation, and distillation. *Thermoactinomyces* and *Streptomyces* have very low abundances at the early stage of fermentation, from the first to the seventh rounds, but they are dominant at the middle stage of the seventh round [66,86]. Fermented grains undergo three processes: cooling, stacking, and cellar fermentation. In the early stage of stacking fermentation, the FG microbiome contained 11.5% *Thermoactinomyces* [6].

The relative abundance of actinomycetes increased in NXXB DQ from Day 5 to Day 20 of fermentation, then decreased over the next few weeks during fermentation and maturation [87]. *Kroppenstedtia* and *Thermoactinomyces* were dominant in medium- and high-temperature DQ, accounting for 45.1% and 12.3%, respectively [88]. *Thermoactinomyces* was dominant during storage of DQ, whereas *Saccharopolyspora* and *Micromonospora* increased in abundance during the subsequent fermentation [89,90]. *Saccharopolyspora* and *Thermoactinomyces* were the dominant genera after 18 days of DQ fermentation, reaching maximum abundances of 33.8% and 17.8%, respectively. The relative abundance at the phylum level for actinomycetes was 16.4% and that of *Thermoactinomyces* in mature DQ was 16.3% (Yibin) and 13.2% (Luzhou) [91]. The relative abundance of *Thermoactinomyces* reached 78% for special-grade DQ and 33% for first-grade DQ during summer production [92].

Dynamic changes in actinomycete relative abundance were studied in the DQ, PM, and FGs of NXXB [93]. During the fermentation and maturation of DQ, the relative abundance of actinomycetes initially increased, then decreased, and the relative abundance of the different species also changed, including *Thermoactinomyces*, *Saccharopolyspora*, and *Micromonospora*. *Kroppenstedtia* and *Thermoactinomyces* were dominant in medium- and high-temperature DQ, accounting for 45.1% and 12.3%, respectively [88]. Two genera of actinomycetes, *Kroppenstedtia* and *Thermoactinomyces*, dominated the DQ at a medium and high temperature, accounting for 45.11% and 12.29%, respectively. *Saccharopolyspora* and *Thermoactinomyces* were the dominant genera after 18 days of DQ fermentation, reaching maximum abundances of 33.8% and 17.8%, respectively [94]. *Thermoactinomyces* in mature DQ from different locations accounted for 16.26% (Yibin) and 13.21% (Luzhou) [91]. Among the different grades of DQ, the proportion of *Thermoactinomyces* in special-grade DQ reached 78% and that of first-grade DQ reached 33% [92].
Figure 1. Actinomycete species distribution in the DQ (Daqu), FGs (fermented grains), and PM (pit mud) from different types of Baijiu—jiangxiangxing (JXXB), nongxiangxing (NXXB), qingxiangxing (QXXB), zhimaxiangxingbaijiu (ZMXXB), and andmixiangxing (MXXB).

In the PM of NXXB, the relative content of actinomycetes initially decreased and then tended towards stability with increased cellar age [95,96]. The relative abundance of actinomycete genera, such as *Atopobium* and *Olsenella*, gradually increased by more than 1% during aging of PM and then stabilized in mature PM [97–100]. Moreover, the abundance of actinomycetes in mature PM (1.68 × 10^{10} copies per g) was 29 times that of aging PM (0.58 × 10^{9} copies per g) [101], and the matured PM (2.23 × 10^{9}) was 24 times that of degraded PM (9.25 × 10^{7} cells/g) [102]. In the same cellar, the diversity of the microbiome in mature pit mud was superior to that in degraded pit mud; the relative abundance of the core actinomycete species, such as *Frankia casuarinae*, *Brachybacterium faecium*, and *Mycobacterium sinense* increased, because of the long-term anaerobic conditions in PM [103].
A study of actinomycetes in different layers of a Baijiu cellar detected actinomycetes at a relative abundance of >1% in the microbiome of the middle and upper layers [100,104], whereas the relative abundance of the actinomycetes was up to 4.81% in the bottom layer [105].

In FGs, the abundance of actinomycetes gradually decreases during fermentation. During the first week, *Actinobacter* and *Saccharopolyspora* were the dominant genera, at >2% [106]. Subsequently, the dominant actinomycetes were *Thermoactinomyces*, *Arthrobacter*, and *Corynebacterium*, accounting for more than 1% [107]. The relative abundance of actinomycetes was 1.78, 1.16, and 0.31% in the FGs after 3, 15, and 45 days, respectively [90].

In qingxiangxing Baijiu (QXXB), Daqu is classified into low temperature, medium temperature, and high temperature, according to the fermentation temperature used [108]. For a medium temperature (50–60 °C) and high temperature (60–70 °C) DQ, *Thermoactinomyces* was the dominant bacterium [109]. The low-temperature DQ of QXXB is further classified into three types, namely, QingCha (QC), HongXin (HX), and HouHuo (HH), each having a distinct production process [110]. Actinomycetes account for 73% in QC, 19% in HX, and 1% in HH [110]. *Thermoactinomyces* and *Streptomyces* reached a 19.5 and 14.1% relative abundance in HX, respectively, and the *Streptomyces* of QC reached 13.1% [110]. At the center and surface of the QC, HX, and HH DQ blocks, the actinomycete relative abundance was 7.6, 8.5, and 8.4% at the center and 6.9, 7.8, and 7.1% at the surface, respectively [111]. Metagenomics analysis showed that the relative abundance of actinomycetes in low-temperature Daqu (LTD) samples accounted for 24.25%, mainly *Streptomyces albus* (6.53%), *Streptomyces* sp. NHF165 (5.15%), and *Saccharopolyspora erythraea* (1.55%) [72]. There is also variation in actinomycete abundance during different storage periods of LTD. When LTD was stored for 6 months, actinomycetes accounted for 23.9, 17.9, and 1.1% in QC, HX, and HH, respectively, of which the dominant families included *Thermoactinomyces* (19.6% in HX, 2.1% in QC, and 1.8% in HH), and *Streptomyces* (14.1% in HX, 13.1% in QC, and 0.8% in HH) [110,112]. Comparing the interior and surface of LTD stored for two months, the dominant actinomycetes were *Thermoactinomyces vulgaris* in the interior and *Saccharopolyspora cebuensis*, *Brevibacterium* sp. D2, *Actinomyces* sp. 152R-3, and *Brachybacterium* sp. PB10 at the surface [113].

The process for making zhimaxiangxing Baijiu (ZMXXB) DQ consists of four stages: initial fermentation, ripening fermentation, drying, and storage [114]. Actinomycetes gradually increased up to a maximum of 8% during the initial fermentation, and then decreased during ripening and drying [114]. In mature DQ, the main actinomycete genera were represented by *Thermoactinomyces*, *Kroppenstedtia*, and *Saccharopolyspora*, accounting for 52, 17.3, and 17.3%, respectively [46,73]. In DQ matured for three months, *Actinopolyspora* and *Thermoactinomyces* accounted for 5.1 and 15.7%, respectively [115]. High-temperature ZMXXB DQ is classified into three types, depending on the storage location, namely, white for the upper layer (35–45 °C), yellow for the middle layer (45–55 °C), and black for the lower layer (55–65 °C) [116]. The dominant actinomycetes were *Thermoactinomyces* (58.6%) in white DQ, *Kroppenstedtia* (16.9%) in yellow DQ, and *Saccharopolyspora* (17.60%) in black DQ [116]. In ZMXXB FG during the early stage of fermentation, the content of actinomycetes was >5% [117].

In fengxiangxing Baijiu (FXXB) FGs, the actinomycete concentrations were, 440, 259, and 261 cells/g in the upper, middle, and lower layers [118], respectively, during two weeks of fermentation; actinomycetes exceeded 4% in the first three days, slowly decreased to 0.5% in the second week, and then dropped sharply and stabilized at 0.2% [119]. As discussed above, actinomycetes are a major constituent of the microbiomes of DQ, FGs, and PM; *Thermoactinomyces* and *Saccharopolyspora* are the dominant genera in mature DQ in the major types of Baijiu [112,116,120,121]. Actinomycetes are vital for Baijiu production, contributing to the quality of the final product by producing important flavor compounds, including four esters and five alcohols [7,119]; actinomycetes in the FG are derived from the DQ and PM, making a major contribution to starch saccharification. The niche adaptation and distribution of actinomycetes in brewage environments changes with some environmental
factors such as temperature, moisture, and nutrient availability. Baijiu product quality and safety are associated with the brewing microbial community, which also depends on the actinomycete species. An improved understanding of the dynamic changes in actinomycete relative abundance under different fermentation conditions will require further research.

Figure 2. Relative abundance heatmap of *Thermoactinomyces* and actinomycetes in DQ samples obtained from high-temperature Daqu (HTD), white Daqu (WDQ), yellow Daqu (YDQ), black Daqu (BDQ), low-temperature Daqu (LTD), Taiwanese Daqu (TWDQ), the Daqu-making process (DQMP), Yibin Daqu (YBDQ), 1-year-old pit mud (1aPM), first-grade Daqu (FGDQ), special-grade DQ (SGDQ), 0-day fermented grain (0DFG), Hongtudi distillery Daqu (HDQ), 5th fermentation round FG (5BDQ), M-type Daqu (MDQ), H-type Daqu (HDQ), Zhongxin Daqu (ZXDQ), Zhenjiu Daqu (ZJDQ), and Maotai DQ (MTDQ) [6,63,71–73,79,80,82–85,88,91,92,95,107,110,112,114,116,122].

5. Interspecies Interactions of Actinomycetes and Other Microorganisms in Baijiu Fermentation

Baijiu flavor compounds are products of co-fermentation by multiple microorganisms. The interspecific interactions between actinomycetes and other microorganisms are closely related to the major flavor compounds in DQ, FGs, and PM [123,124]. Interspecies interactions between actinomycetes fall into four main categories (Figure 3). Actinomycetes produce various enzymes, such as cellulase, amylase, pectinase, and protease, which mediate these interactions, and the enzymolysis products can be assimilated by other microorganisms in the Baijiu fermentation microbiome [125]. For example, *Streptomyces avicenniae* hydrolyzes starch and produces melanin that scavenges free radicals from the cell surface of *C. butyricum*, promoting growth and caproic acid production [19,126] (Figure 3A). Some actinomycete metabolites are precursors for flavor component production by the key
microorganisms Bacillus and caproic acid-producing bacteria (CPB) [18,37]. Acetic acid and lactic acid produced by Streptomyces and Micromonospora are precursors for yeast or Bacillus to produce ethyl acetate and ethyl lactate [37] (Figure 3B). Actinomycetes inoculated into CPB fermentation medium promote production of caproic acid and ethyl caproate [127]. Co-culture of actinomycetes with lactic acid-producing bacteria (LPB) or acetic acid-producing bacteria (APB) promote the growth of the latter and production of ethyl lactate and ethyl acetate, which improves the Baijiu quality [18]. Actinomycetes produce antibiotics that inhibit pathogenic and functional bacteria, for example, 15 strains of Streptomyces could inhibit human pathogenic bacteria during DQ production [15]. These strains of Streptomyces both produce heptaene macrolide antibiotics, which inhibit the growth of yeasts, and degrade alcohols (3-octanol and 3-methyl butanol) and esters (ethyl octanoate and ethyl decanoate) [128] (Figure 3C). Non-protein and non-peptide antibiotics, or quinomycinA produced by actinomycetes, inhibit the biological activity of Bacillus subtilis [129,130]. In DQ production, Bacillus strains inhibit the growth of Streptomyces and degrade the geosmin produced by Streptomyces (Figure 3D) [131]. Therefore, Bacillus amyloliquefaciens reduces the concentration of geosmin and the growth of Streptomyces strains, which relieves the inhibition of pyrazine compound production by Streptomyces and inhibits the formation of off-odors [132]. With further research, Bacillus subtilis may be able to downregulate the gene expression of the streptomycin Streptomyces griseus, which reduces the inhibiting effect of the latter [133].

![Figure 3](image_url)

Figure 3. Interspecies interactions of actinomycetes. (A) Actinomycetes produce diastase to convert starch into melanin that scavenges free radicals around C. butyricum. (B) Acetic acid and lactic acid produced by actinomycetes promote ethyl caproate and ethyl lactate production by yeasts and Bacillus. (C) Antibiotics produced by actinomycetes inhibit yeasts, promoting alcohol and pyrazine production by Bacillus. (D) Bacillus produces lipopeptides that inhibit the growth of Streptomyces and reduce geosmin production.

The interaction mechanism between different actinomycetes and with other microorganisms is still poorly understood, but there is great potential for improving our under-
standing of this using ‘omics technology [75,134]. Moreover, genome-scale metabolic models (GSMMs), which can analyze and visualize the interaction mechanisms between actinomycetes and functional microorganisms in the Baijiu, should be constructed and applied [135].

6. Actinomycete ‘Omic’ Research

The important metabolic pathways and functions of actinomycetes isolated from Baijiu fermentations have been analyzed by sequencing and annotation of the genomes of several actinomycete species (Table 3). Annotation of the *Thermoactinomyces daquis* H-18 genome revealed 1184 enzymatic reactions, 264 transporters, 2361 transcription units, and 6 coding sequences (CDSs) of heat-shock proteins, which confer tolerance of high temperatures [45]. During growth at 60 °C in high-temperature DQ, actinomycete gene expression related to fatty acid biosynthesis increased six-fold [136]. The genes Clp, groEL, and pstB in thermophilic actinomycetes increase their survivability at a high temperature, allowing them to become dominant when increasing the DQ temperature [64]. Genome annotation of *Streptomyces* sp. FBKL4.005 revealed the genes coding for metabolic pathways associated with characteristic Baijiu flavors, sugar degradation, and streptomycin and neomycin production [29].

| Species                      | Strain   | NCBI Access No. | Size (Mb) | GC%  | Proteins | rRNA Operons | tRNA Genes | References |
|------------------------------|----------|-----------------|-----------|------|----------|--------------|------------|------------|
| *Thermoactinomyces daquis* H-18 | NZ_JPST01000000 | 3.44           | 48.8      | 3440 | 5        | 58           | [45]       |
| *Streptomyces mutabilis* Z9A-32 | HQ238326 | 7.83           | 71.4      | 6711 | 19       | 82           | [35]       |
| *Streptomyces vinaceoussporus* W8A-43 | HQ238406 | 8.46           | 72.5      | 7332 | 5        | 67           | [35]       |
| *Streptomyces violaceus* S11A-6 | HQ238298 | 8.92           | 70.5      | 7754 | 24       | 71           | [35]       |
| *Streptomyces griseus* A2 | JX007982 | 8.55           | 72.2      | 6968 | 18       | 67           | [28]       |
| *Streptomyces albus* NRRLB-2365 | DQ026669.1 | 7.59           | 72.7      | 6166 | 4        | 59           | [28]       |
| *Thermoactinomyces vulgaris* ATCC15734 | AF089892 | 2.62           | 48        | 2590 | 21       | 72           | [24]       |
| *Thermophilicactinomyces gallinarum* LZ4J-2T | NZ_JADCJZ000000000000.1 | 1.85         | 65.2      | 1599 | 6        | 49           | [41]       |
| *Streptomyces cocaoi* NBRC12748 | NR041061 | 8.57           | 73.4      | 6679 | 8        | 61           | [50]       |
| *Arthrobacter stackebrandii* NG3 | MT269547.1 | 4.43           | 65.6      | 3683 | 15       | 54           | [62]       |

Comparative genomics has revealed the wide diversity of gene clusters in actinomycetes [137]. Genes coding for the geosmin biosynthetic pathway were all found in the core genome of *Streptomyces* [138]. In addition, metaproteomics and metabolomics were also used to investigate the functional changes in actinomycetes [68,139,140]. Actinomycete abundance had a negative correlation with lactic acid and a positive correlation with pH, determined by transcriptomic sequencing [141]. Actinomycete transcriptomic analysis revealed that aged PM has a higher content of seven key enzymes than degraded PM [103].

The combination or comparison of multiple ‘omics studies has not yet been applied to actinomycetes from the Baijiu microbiome to analyze and amplify their genetic elements and metabolic pathway. The GSMMs of Baijiu actinomycetes have not yet been constructed and analyzed. ‘Omic’ analysis, combined with the GSMMs of actinomycetes, should be performed to attain a comprehensive understanding of actinomycetes in future research. Gene engineering could be used to regulate and produce natural products from Baijiu actinomycetes.
7. Enzymes and Metabolites Produced by Baijiu Actinomycetes

It was found that actinomycetes are characterized by metabolic diversity in the following. Actinomycetes have been found to produce cellulase, amylase, pectinase, protease, endoglucanase, and beta-glucosidase, which can contribute to the saccharification and fermentation of Baijiu [15,19,123,142]. During fermentation, the lipase and phosphatase produced by *Thermoactinomyces* can reduce the ethyl lactate production [116]. *Thermoactinomyces vulgaris* also produces protease, which can hydrolyse protein into amino acids [46]. Aside from enzymes, actinomycetes also produce many metabolites, including aroma compounds, antibiotics, and off-odor compounds (Table 4). *Thermophilicabacter gallinarum* can convert glucose into lactic acid and acetic acid [41]. Actinomycetes also have the potential to produce butyric acid, thereby providing the precursor for ethyl butyrate and enriching the flavor of the Baijiu [143]. *Thermoactinomyces* can use a wide variety of carbon and nitrogen sources and synthesize important flavor components, such as ethyl caproate, furfuryl alcohol, phenethyl alcohol, pyrazine, butanoate, and acetic acid [143]. *Streptomyces* species synthesize some flavor compounds, such as 3-hydroxy-2-butanone, 2,3-butanediol, ethanol and ethyl acetate, butanol, acetone, 3-methyl-3-buten-1-ol, and dimethyl disulfide [39,42,144]. *Thermoactinomyces* and *Actinomycetales* produce 5 pyrazines (trimethylpyrazine, tetramethylpyrazine, 2,3,5-trimethyl-6-ethylpyrazine, 2,5-dimethyl-3-butylpyrazine and 2,5-dimethyl-3-(3-methylbutyl)pyrazine), 2 aromatics (4-ethenyl-1,2-dimethoxy-benzene and (1-pentylhexyl)-benzene), and 1 alcohol (1-octen-3-ol) [145]. *Streptomyces* sp. R11-21 growing on wheat can produce 2-methyl isobornyl alcohol and terpenoid compounds, and 3-hydroxy-2-butanoate and terpenes when growing on sorghum [33]. *Streptomyces bangladeshensis* is capable of producing terpenes and pyrazine [30]. *Streptomyces* in NXXB fermentations can produce esters (ethyl butyrate, ethyl lactate, and ethyl caproate), acids (butyric acid and caproic acid), and aldehydes (acetaldehyde and furfural) [146]. More meaningfully, the main actinomycetes strains were capable of producing antibiotics [26,27,147]. *Streptomyces aureus* and *Streptomyces albus* can produce the brown pigments salinomycin and polylysine, respectively, which inhibit the growth of functional bacteria and form the main aroma compounds [148–150]. Four strains of *Streptomyces* secrete heptane macrolide antibiotics, which inhibit fungal growth [128]. Actinomycetes can produce antibiotics that inhibit harmful microorganisms [151]; for example, *Streptomyces* strains that produce geosmin, which are regarded as serious microbial contaminants of the PM [16].

Table 4. Secondary metabolites produced by the actinomycetes isolated from Baijiu.

| Microorganisms                | Substrate          | Product                                      | References |
|-------------------------------|--------------------|----------------------------------------------|------------|
| *Streptomyces* sp. R11-21     | Flour              | 2-Methyl isobornyl alcohol and terpenes      | [33]       |
| *Streptomyces* bangladeshensis| Wheat or sorghum   | 3-Hydroxy-2-butanoate and terpenes            | [30]       |
| *Streptomyces albus*          | Glucose            | Terpenes and pyrazine                         |            |
| *Streptomyces sampsonii*      | Wheat bran         | 3-Hydroxy-2-butanoate, 2,3-butanediol, ethanol and ethyl acetate | [39]       |
| *Streptomyces rutgersensis*   | Glucose            | Butyric acid, hexanoic acid, ethyl butyrate, ethyl hexanoate, ethyl lactate and furfural | [152]      |
| *Streptomyces mutabilis*      | Glucose            | Furfuryl alcohol, phenethyl alcohol, 2,6-dimethylpyrazine, and 2,3,5,6-tetramethylpyrazine |            |
| *Thermoactinomyces* FBKL4.010 | Wheat              |                                              |            |
| *Streptomyces* sp. A22        | Wheat bran         | Ethyl hexanoate and phenethyl alcohol         | [132]      |
| *Streptomyces aureus*         | Tyrosine           | Brown-pigment                                | [149]      |
| *Streptomyces albus* S5       | Glucose            | Salinomycin                                  | [148]      |
| *Streptomyces cacow*          | Sorghum            | Lipids                                       | [26]       |
| *Streptomyces zaomyceticus*   | Sorghum            | Tetramethylpyrazine                           | [27]       |
| *Laceyellasacchari*           | Sorghum            |                                              |            |
Table 4. Cont.

| Microorganisms                        | Substrate | Product                                      | References |
|---------------------------------------|-----------|----------------------------------------------|------------|
| *Streptomyces sampsonii*              | Oat       | 3-Hydroxy-2-butanone and 2,3-butanediol      | [42]       |
| *Streptomyces rutgersensis*           | Glucose   | Ethyl caproate, and geosmin                  |            |
| *Streptomyces radiopugnans, Streptomyces sampsonii* | Starch    | Geosmin                                      | [16]       |
| *Streptomyces fradiae*                | Starch    | Ethyl lactate and caproic acid               | [146]      |
| *Streptomyces sampsonii*              | Starch    | Butanoate, Aceticacid, hexyl ester           | [143]      |
| *Thermoactinomyces sp.*               | Starch    | Heptaene macrolide antibiotics               | [128]      |
| *Streptomyces albus*                  | Starch    | Bultanol, acetone, 3-methyl-3-buten-1-ol, dimethyl disulfide | [144] |
| *Thermoactinomyces griseus*           | Cellulose | Pyrazines, aromatics and and alcohol         | [145]      |
| *Actinomyces ramosus*                 | Starch    | Lactic acid and acetic acid                  | [41]       |
| *Actinomyces albus*                   | Glucose   | Poly-lysine                                  | [150]      |
| *Thermoactinomyces sp.*               | DQ        | Enzymes, pyrazine and aromatic substances    | [123]      |
| *Actinomyces*                         | FG        | Salinomycin and terpenes                     | [123]      |
|                                       | PM        | Acids, esters and terpenes                   |            |

8. Potential Applications of Actinomycetes in Baijiu Fermentation

Actinomycetes have useful regulatory functions in Baijiu fermentation, as discussed below. Actinomycetes produce highly active hydrolytic enzymes that enable full utilization of all the components of baijiu FGs [15,153], particularly cellulase, which degrades the abundant cellulose to produce short-chain fatty acids in FGs and distiller’s grains [154]. Undesirable isopropanol and lactic acid produced in Baijiu fermentation are degraded by *Arthrobacter protophormiae* [38,155], and actinomycetes produce antibiotics that inhibit the growth of human pathogenic bacteria [15]. Geosmin produced by *Streptomyces* ameliorates the effect of excess acidity during fermentation and since actinomycetes are relatively heat tolerant, they can maintain their metabolic activity in high-temperature DQ and PM [128,156]. The hyphae of *Thermoactinomyces* facilitate the evaporation of water from DQ and help to soften the grains, which aids their starter function [128]. Actinomycetes, as dominant strains in PM, are regarded as indicators of PM aging, and are studied to distinguish between the PM of different maturities [4,96]. Actinomycetes can facilitate denitrification of the PM using sulfur and sulfides and inhibit degradation of the PM [157]. New DQ and PM inoculated with selected actinomycetes reach maturity relatively quickly and old PM can be maintained in good condition, thereby maintaining Baijiu quality [102]. As stated above, actinomycetes are important for DQ biocontrol, PM maintenance, the formation of Baijiu flavor, and resource utilization of distiller’s grains. However, for the future practical application of actinomycetes, some progress needs to be made to promote caproic acid production, inhibit the growth of pathogenic bacteria, and degrade distiller’s grains. Hence, actinomycetes has the potential to improve the safety and quality of Baijiu, which provide a direction for applied value research.

9. Conclusions

Actinomycetes hydrolyze starch, protein, and cellulose to supply precursors for other microorganisms to produce flavor components during fermentation, as well as producing important Baijiu flavor compounds, such as ethyl caproate and ethyl butyrate. Actinomycete relative abundance and species distribution are used as an indicator of PM quality and are important microorganisms for inhibition of PM degradation. However, the metabolic mechanism, isolation methods, and underlying interactions between actinomycetes are poorly understood, and in-depth research on the multi-omics analysis of actinomycetes has not yet been reported. Therefore, innovative separation methods are
needed to efficiently isolate unculturable actinomycetes from complex microbiomes. The omics-based approaches enhanced our understanding of the diversity and functional dynamics of actinomycetes. Future studies should also consider the potential application of actinomycetes to improve the food safety of Baijiu during fermentation, by regulating harmful microorganisms, which would improve Baijiu quality. Future research should include multi-omics studies and construction of actinomycete GSMMs, by combining bioinformatics tools, high-throughput culture methods, and genetic engineering. From the fundamental basis and new insights into actinomycetes that were provided here, through an in-depth theoretical study of Baijiu microbial populations, future studies can help improve the Baijiu product safety, sustainability, and brewage standards.

**Supplementary Materials:** The following supporting information can be downloaded at: [https://www.mdpi.com/article/10.3390/foods11223551/s1](https://www.mdpi.com/article/10.3390/foods11223551/s1), Table S1: Culture media used for isolation of actinomycetes, Table S2: Actinomycete species identified by culture and/or culture-independent methods.

**Author Contributions:** Conceptualization, C.C., H.L. and W.Z.; writing—original draft preparation, C.C. and W.Z.; writing—review and editing, C.C., H.Y. and W.Z.; visualization, C.C. and J.L. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded by grants from the National Natural Science Foundation of China (31801522).

**Data Availability Statement:** Not applicable.

**Conflicts of Interest:** The authors declare no conflict of interest. The company had no role in study design data collection and analysis, decision to publish, or preparation of the manuscript and did not affect the results and the conclusions. There are no potential conflicts of interest.

**Abbreviations**

Daqu (DQ), Pit mud (PM), Xiaoqu (XQ), Baobaoqu (BBQ), fermented grains (FG), Jiangxiangxing baijiu (JXXB), Nongxiangxing baijiu (NXXB), Qingxiangxing baijiu (QXXB), Zhimaixiangxing baijiu (ZMXXB), Fengxiangxing baijiu (FXXB), Caproic acid producing bacteria (CPB), Lactic acid producing bacteria (LPB), Acetic acid producing bacteria (APB), Genome-scale metabolic model (GSMM), Coding sequence (CDS), Operational taxonomic unit (OTU), Three kinds of Daqu (Qingcha (QC), Hongxin (HX), Houhuo (HH)), Whole-genome shotgun (WGS), Polymerase chain reaction denaturing gradient gel electrophoresis (PCR-DGGE), Liquid Chromatography-Mass Spectrometry/Mass Spectrometry (LC-MS/MS), Amplified rDNA restriction analysis (ARDRA), BiologEcoPlates (Biolog-ECO).

**References**

1. Zheng, X.W.; Han, B.Z. Baijiu, Chinese liquor: History, classification and manufacture. *J. Ethn. Foods* 2016, 3, 19–25. [CrossRef]
2. Xu, Y.R.; Wang, D.; Fan, W.L.; Mu, X.Q.; Chen, J. Traditional Chinese biotechnology. In *Biotechnology in China II: Chemicals, Energy and Environment*; Tsao, T.G., Ouyang, P., Chen, J., Eds.; Springer: Berlin/Heidelberg, Germany, 2010; pp. 189–233.
3. Ding, X.F.; Wu, C.; Zhang, L.Q.; Zheng, J.; Zhou, R.Q. Characterization of eubacterial and archaeal community diversity in the pit mud of Chinese Luzhou-flavor liquor by nested PCR DGGE. *World J. Microbiol. Biotechnol.* 2014, 30, 605–612. [CrossRef] [PubMed]
4. Zhao, J.S.; Zheng, J.; Zhou, R.Q.; Shi, B. Microbial community structure of pit mud in a Chinese strong aromatic liquor fermentation pit. *J. Inst. Brew.* 2012, 118, 356–360. [CrossRef]
5. Zou, W.; Ye, G.B.; Zhang, K.Z. Diversity, Function, and Application of Clostridium in Chinese Strong Flavor Baijiu Ecosystem: A Review. *J. Food Sci.* 2018, 83, 1193–1199. [CrossRef]
6. Zhao, L.; Mo, X.L.; Zhang, C.L.; Yang, L.; Wang, X.Y. Community diversity and succession in fermented grains during the stacking fermentation of Chinese moutai-flavored liquor making. *Food Sci. Technol.* 2021, 42, e61521. [CrossRef]
7. Ma, S.Y.; Luo, H.B.; Zhao, D.; Qiao, Z.W.; Zheng, J.; An, M.Z.; Huang, D. Environmental factors and interactions among microorganisms drive microbial community succession during fermentation of Nongxiangxing daqu. *Bioreour. Technol.* 2021, 345, 126549. [CrossRef]
8. Hong, J.X.; Wang, J.S.; Zhang, C.S.; Zhao, Z.G.; Tian, W.J.; Wu, Y.S.; Chen, H.; Zhao, D.R.; Sun, J.Y. Unraveling variation on the profile aroma compounds of strong aroma type of Baijiu in different regions by molecular matrix analysis and olfactory analysis. *RSC Adv.* 2021, 11, 33511–33521. [CrossRef]
9. Tan, Y.; Du, H.; Zhang, H.; Fang, C.; Jin, G.; Chen, S.; Wu, Q.; Zhang, Y.; Zhang, M.; Xu, Y. Geographically associated fungus-bacterium interactions contribute to the formation of geography-dependent flavor during high-complexity spontaneous fermentation. *Microbiol. Spectr.* 2022, 22, e01844. [CrossRef]

10. Wang, L. Research trends in Jiang-flavor baijiu fermentation: From fermentation microecology to environmental ecology. *J. Food Sci.* 2022, 87, 1362–1374. [CrossRef]

11. Sun, W.N.; Xiao, H.Z.; Feng, Q.; Zhang, Q.G.; Li, X.X.; Han, Y. Analysis of bacterial diversity of Chinese Luzhou-flavor liquor brewed in different seasons by illumina miseq sequencing. *Ann. Microbiol.* 2016, 66, 1293–1301. [CrossRef]

12. Wang, T.; Jiang, D.; Zijuan, C.; Ruiping, Z.; Wen, T.; Xinghai, H. Isolation method of actinomycetes from pit mud. *Liquor Mak. Sci. Technol.* 2009, 26–28.

13. Zhou, J.B.; Xu, Y.X.; Guo, W.; Zhang, M.C.; Xiong, X.M.; Fang, S.L. Research of Actinomycetes Enzyme Production Capacity in the Liquor Brewing. *Liquor Mak.* 2015, 42, 44–47.

14. Pullen, C.B.; Schmitz, P.; Meurer, K.; Bamberg, D.D.v.; Lohmann, S.; de Castro França, S.; Groth, I.; Schlegel, B.; Möllmann, U.; Gollmick, F.; et al. New and bioactive compounds from Streptomyces strains residing in the wood of Celastraceae. *Planta* 2002, 216, 162–167. [CrossRef]

15. Zhang, L.H.; An, Q.; Zhang, Y.P.; Zhang, X.H.; Lv, P.J.; Li, X.T.; Hu, Q.P. Evaluation of The Potential of Daqu-Derived Actinobacteria for Light-Flavour Chinese Liquor. *Eur. J. Food Sci. Technol.* 2019, 7, 1–9.

16. Du, H.; Lu, H.M.; Xu, Y.; Du, X.W. Community of environmental streptomyces related to geosmin development in Chinese liquors. *J. Agric. Food. Chem.* 2013, 61, 1343–1348. [CrossRef]

17. Hu, D.; Fan, W.L.; Xu, Y. Characterization of geosmin as source of earthy odor in different aroma type Chinese liquors. *J. Agric. Food. Chem.* 2011, 59, 8331–8337. [CrossRef]

18. Ren, Y.M.; Dai, S.; Fan, L.; Wei, M.; Shang, L.H.; Xie, W.; Zhuang, M.Y.; Hou, M.Z. Study on the isolation of actinomycetes and its application in the production of Lu-type liquor. *Liquor Mak. Sci. Technol.* 1997, 3, 13–15. [CrossRef]

19. Guo, W.; Guan, J.; Chen, M.B.; Sang, S.L. Research on the Relationship between Actinomycetes Enzyme-producing Abilities and Its Ability to Promoting Caproic Acid Bacteria Producing Caproic Acid. *Liquor Mak.* 2016, 43, 62–65.

20. Kou, M. Discussion on actinomycetes in solid-state fermentation of traditional liquor. *Food Ind.* 2020, 93–94.

21. Zhang, J.M.; Huang Yong Guang Zhou, W.M.; Cheng, L.X.; Zhao, C.L. Research Advance in Actinobacterial in Traditional Liquor Solid Fermentation Process. *Liquor Mak. Sci. Technol.* 2013, 232, 73–79. [CrossRef]

22. Cui, F.L.; Wang, Z.Y.; Wang, F.; Ping, Y.Z.Q.Z.S.; Hua, S.L. Report on the separation of fermented grains and Daqu microorganisms. *J. Microbiol.* 1981, 13–19.

23. Sun, H.L. Isolation of actinomycetes from pit mud. *China Brew.* 1987, 33–35.

24. Wang, F.R.; Zeng, H.; Xu, Z.X.; Xi, D.Z.; Wang, H.; Cao, W.T. Isolation and Identification of a Thermoactinomyces sp. Strain from High-temperature Jiangxiang Daqu. *Liquor Mak. Sci. Technol.* 2017, 4, 42–45. [CrossRef]

25. Yu, H.; Huang, D.; Chen, Z.; Tang, J.; Mao, X.; Deng, L.; Liu, D.; Lu, K.B. Isolation of protease-producing actinomycetes from sauce-flavor Daqu and its protease-producing conditions. *China Brew.* 2017, 36, 64–68.

26. Luo, X.Y.; Wang, X.D.; Yi, Q.S. Isolation, screening and aroma component analysis of 3 strains of actinomycetes from Moutai-flavor Daqu. *China Brew.* 2018, 37, 62–67.

27. Li, D.N.; Huang, W.; Wang, X.D.; Luo, X.Y.; Qiu, S.Y. Identification and Flavor Profile of a Thermoactinomycetaceae Strain Separated from Moutai-Flavor Daqu. *Food Sci.* 2018, 39, 171–176.

28. Zhang, J.M.; Huang, Y.G.; Zhou, W.M.; You, X.L.; Zhao, C.L.; Zhou, J.T. Identification of 2 Streptococcus Strains and Their Tolerance of the Liquor-making Environment of Jiangxiang Baijiu(Liquor). *Liquor Mak. Sci. Technol.* 2014, 12, 8–12. [CrossRef]

29. Li, D.N.; Wang, X.D.; Luo, X.Y.; Huang, W.; Qiu, S.Y. Whole Genome Sequencing and Sequence Analysis of Streptomyces sp.FBKL4.005 from Moutai-Flavor Daqu. *Food Sci.* 2018, 39, 206–212.

30. Wang, X.D.; Luo, X.Y.; Qiu, S.Y. Isolation and screening of a thermophilic actinomycete from Moutai-flavor Daqu and its characterization. *China Brew.* 2018, 37, 51–56.

31. Huang, Z.G.; Deng, J.; Wei, C.H.; Zhao, B.; Liu, Y.M. Separation and Identification of Bacteria Strains from Fermented Grains of Jiang-xiang Liquor. *Liquor Mak. Sci. Technol.* 2014, 6, 27–29. [CrossRef]

32. Zhang, J.M.; Huang, Y.G.Z.; Wen, M.; Cheng, L.X.; Zhao, C.L.; You, X.L.; Zhou, J.T. Identification of a Streptomyces sp.Strain Separated from Stacking Fermented Grains of Jiangxiang Baijiu(Liquor). *Liquor Mak. Sci. Technol.* 2014, 6, 16–19. [CrossRef]

33. Yang, F.; Chen, L.Q.; Lin, L.; Wang, H.Y.; Wang, L. Isolation & Identification of an Actinomycetes Strain and Analysis of Its Metabolites. *Liquor Mak. Sci. Technol.* 2014, 9, 42–44. [CrossRef]

34. Bai, C.S.; Chen, L.; Lu, H.M.; Zhou, L.; Ren, X.K. Isolation and identification of thermophilic actinomycetes from Moutai-flavor vinasse in Moutai region. *Sci. Technol. Food Ind.* 2017, 38, 199–202. [CrossRef]

35. Zhang, C.; Zhao, D.; Wang, T.; You, L.; Feng, R.Z.; Wang, S.; He, J.R. Diversity of Actinomycetes in the Brewing Process of Luzhou-flavor Multiple-grains Liquor. *Food Sci.* 2011, 32, 192–196.

36. Hou, X.G.; Sun, Z.K.; Li, X.S.; Chu, C.W.; Pan, Q.Q.; Chen, H.; Chen, Y.L.; Yuan, J.W. Isolation, identification and enzyme-production of culturable Actinomycetes from Daqu applied in making strong-flavor liquor. *Food Sci. Technol.* 2019, 44, 28–35. [CrossRef]

37. Shi, S.; Zhang, X.; Yang, K.Z.; Liao, Q.J.; Qiao, Z.W.; Zheng, J.; Liu, D.T. Preliminary Study on the Regulation Effect of Actinomycetes on Brewing Microorganisms. *Liquor Mak. Sci. Technol.* 2021, 2, 17–20. [CrossRef]
38. Luo, Q.C.; Zhao, D.; Qiao, Z.W.; Jia, Z. Isolation and Identification of an N-Propanol Degrading Actinomycete Strain. *Liquor Mak. Sci. Technol.* 2018, 12, 74–77. [CrossRef]

39. Yao, Y.L.; Zheng, R.X.; Cheng, T.Y.; Deng, J.; Ren, Z.Q.; Wei, C.H.; Huang, Z.G. Study on the Fermentation Characteristics of Actinomycetes in Pit Mud of Luzhou-flavor Liquor. *Food Res. Devel.* 2020, 41, 191–197.

40. Luan, X.S.; Hu, J.J.; Zhang, H.Y. Study on Facultatively Autotrophic Streptomyces in Cellar Mud. *Shandong Sci.* 1991, 2, 9–15.

41. Lu, L.F.; Yang, Y.; Zheng, L.; Zhang, R.; Liu, G.Q.; Tu, Y.Y.; Xu, T.; Luo, X.Z.; Ren, M.F.; Zhang, L.Q.; et al. Reclassification of Olsenella gallinarum as Thermophilobacter gallinarum comb. nov. and description of Thermophilobacter immobilis sp. nov., isolated from the mud in a fermentation cellar used for the production of Chinese Luzhou-flavour Baijiu. *Int. J. Syst. Evol. Microbiol.* 2021, 71, 5192. [CrossRef]

42. Luo, B.X.; Zheng, R.X.; Cheng, T.Y.; Ren, Z.Q.; Wei, C.H.; Deng, J.; Huang, Z.G. In situ isolation and metabolic characteristics of actinomycetes from strong-flavor Baijiu pit mud. *Food Ferment. Ind.* 2021, 47, 75–83. [CrossRef]

43. Guo, W.; Huang, Y.; Xie, Y.Q.; Fang, S.L.; Chen, M.B. Screening of Fine Actinomycetes that Promoting Caproic Acid Bacteria Producing Caproic Acid. *Liquor Mak.* 2016, 43, 47–51.

44. Tang, Y.H.; Wu, W.R. Isolation of pit mud bacteria based on Biolog ECO technology. *China Brew.* 2014, 33, 121–125.

45. Yao, S.; Xu, Y.Q.; Xin, C.H.; Xu, L.; Liu, Y.; Li, H.; Li, J.X.; Zhao, J.W.; Cheng, C.W. Genome Sequence of Thermoactinomyces daqus H-18, a Novel Thermophilic Species Isolated from High-Temperature Daqu. *Genome Announc.* 2015, 3, e01394–14. [CrossRef]

46. Liu, Y.; Zhao, T.; Yao, S.; Ge, Y.Y.; Xin, C.H.; Xu, L.; Cheng, C. Identification on a *Thermoactinomyces* sp. Separated from High Temperature Daqu of Sesame Flavor Liquor. *Biotechnol. Bull.* 2012, 10, 210–216. [CrossRef]

47. Zhang, M.; Yao, S.; Li, H.; Liu, Y.; Xin, C.H.; Xu, L.; Cheng, C. A specific PCR assay for rapid identifying *Thermoactinomyces vulgaris*. *Food Ferment. Ind.* 2014, 40, 64–66. [CrossRef]

48. Ge, Y.Y.; Yao, S.; Liu, Y.; Cao, Y.H.; Zhang, F.G.; Xin, C.H.; Xu, L.; Cheng, C. Analysis on Thermophilic Bacterial Communities in High Temperature Daqu of Sesame Flavor Liquor. *Food Ferment. Ind.* 2012, 38, 16–19. [CrossRef]

49. Yan, Y.; Xing, X.; Sun, Z.B.; Li, J.; Yao, S.Y.; Xu, J.L. *Brevibacterium renqingii* sp. nov., isolated from the Daqu of Baijiu. *Arch. Microbiol.* 2021, 203, 2291–2296. [CrossRef]

50. Zhu, T.T. Analysis of Cultivable Microbe Diversity in Niu Lanshan Daqu. *Liquor Mak. Sci. Technol.* 2018, 5, 75–79. [CrossRef]

51. Zheng, X.W.; Yan, Z.; Han, B.Z.; Zwietering, M.H.; Samson, R.A.; Boekhout, T.; Robert Nout, M.J. Complex microbiota of a Chinese “Fen” liquor fermentation starter (Fen-Daqu), revealed by culture-dependent and culture-independent methods. *Food Microbiol.* 2012, 31, 293–300. [CrossRef]

52. Wei, J.W. Isolation & Identification of Cultivable Thermoactinomycetaceae in the Production of Qingxiang Baijiu. *Liquor Mak. Sci. Technol.* 2019, 1, 56–59. [CrossRef]

53. Hu, J.X.; Yang, T.; Cai, G.L.; Wu, L.W.; Zhuang, M.Y.; Xu, W. Study on Microbial Communities in Feng & Composite-flavor Taibai Liquor (I). Microflora in Daqu. *Liquor Mak. Sci. Technol.* 2012, 5, 55–57.

54. Fang, H.Z.; Yan, Z.K.; Fu, W.X.; Zhang, Y.L. The research on Bad Flavor Substances of Geosmin in Traditional Feng-flavor DaQu. *Liquor Mak.* 2016, 43, 56–60.

55. Yang, T.; Hu, J.X.; Wu, L.W.; Cai, G.L.; Zhuang, M.Y.; Xu, W. Study on Microbial Communities during the Fermentation Process of Feng & Composite-flavor Taibai Daqu (II): Microbial Communities in Fermented grains. *Liquor Mak. Sci. Technol.* 2012, 6, 44–46.

56. Yao, S.; Liu, Y.; Zhang, M.J.; Zhang, X.; Li, H.; Zhao, T.; Xin, C.H.; Xu, L.; Zhang, B.L.; Cheng, C. *Thermoactinomyces daqus* sp. nov., a thermophilic bacterium isolated from high-temperature Daqu. *Int. J. Syst. Evol. Microbiol.* 2014, 64, 206–210. [CrossRef]

57. Ye, G.B.; Wang, C.H.; Qiao, X.Y.; Luo, H.B.; Zhao, Y.C.; Bian, M.H. Study on the Structure of Bacterial Communities of Ultra-high-temperature Daqu. *Liquor Mak. Sci. Technol.* 2014, 4, 5–8. [CrossRef]

58. Shan, Q.; Liang, H.Z.; Zhang, C.X.; Zhang, L.Q.; Tan, X.; Liang, L.Q.; Li, C.W. Changes of Microbial Diversity in Stacked Fermentation for the Production of Moultai Flavor Liquor. *J. Food Sci. Biotechnol.* 2016, 35, 330–335.

59. Zhang, H.M.; Shu, Y.; Zhou, Q.W.; Li, A.J.; He, H.K.; Zhang, Z.Z. Analysis of the Microbial Community Structure of Gujinggong Liquor Starter through Culture-free Approach. *Mod. Food Sci. Technol.* 2014, 30, 44–49. [CrossRef]

60. Ye, G.B.; Wang, C.H.; Wang, Y.; Zhen, P.; Wang, Y.; Luo, H. Comparative analysis of bacterial community structure of Chinese Fen-Daqu. *Food Mach.* 2015, 31, 11–15. [CrossRef]

61. Liu, M.K.; Tang, Y.M.; Zhao, K.; Ren, D.Q.; Yao, W.C.; Tian, X.H. Analysis of actinobacteria community and diversity in the pit mud of chinese luzhou-flavour liquor. *Acta Ecol. Sin.* 2015, 35, 858–864.

62. Xu, J.L.; Sun, L.P.; Xing, X.; Sun, Z.B.; Gu, H.Y.; Lu, X.; Li, Z.P.; Ren, Q. Culturing Bacteria From Fermentation Pit Mud of Baijiu With Culturomics and Amplicon-Based Metagenomic Approaches. *Front. Microbiol.* 2020, 11, 1223. [CrossRef] [PubMed]

63. Su, Y.; Yang, L.; Hui, L.C.; Yuan, Y.G.; Ming, Juan, Z.; Chun Hui, X.; Ling, X.; Chi, C. Bacterial communities during the process of high-temperature Daqu production of roasted sesame-like flavour liquor. *J. Inst. Brew.* 2015, 121, 440–448. [CrossRef]

64. Yu, X.J.; Feng, H.J.; Zhai, L.; Bai, X.B.; Xu, L.; Yu, P.P.; Cheng, C.; Yao, S. Dynamic changes of *Thermoactinomyces* and their functional genes in high temperature Daqu of Sesame-flavored Baijiu. *Food Ferment. Ind.* 2019, 45, 71–77. [CrossRef]

65. Gao, Y.B.; Wang, H.Y.; Yu, Y. PCR-DGGE Analysis of the Bacterial Community of Chinese Liquor High and Medium Temperature Daqu. *Microbiol. China* 2010, 37, 999–1004. [CrossRef]

66. Cheng, C.Y.; Liu, X.F.; Yuan, Y.X.; Yan, Z.Y.; Liao, Y.Z.; Fu, S. Bacterial community structure in distiller’s yeast and accumulated fermented grains of Maotai-flavor liquor. *Chin. J. Appl. Environ. Biol.* 2014, 20, 825–831.

67. Huang, X.H.J.; Li, Z.; Han, B. Microbial diversity analysis in strong-flavor and sauce-flavor Daqu. *China Brew.* 2016, 35, 33–37.
68. Fan, W.Y.; Zhao, X.R.; Du, G.C.; Chen, J.; Li, J.H.; Zheng, J.; Qiao, Z.W.; Zhao, D. Metaproteomic analysis of enzymatic composition in Baobaoqu fermentation starter for Wuliangye baijiu. *Int. J. Food Sci. Technol.* 2021, 56, 4170–4181. [CrossRef]

69. Zhan, W.X.; Qiao, Z.W.; Hu, C.; Wang, Z.Y. Analysis of Bacterial Community in Fermented Grains During the Production of Chinese Strong Aromatic Spirits by PCR Technique. *J. Sichuan. Univ. (Eng. Sci. Ed.)* 2005, 5, 82–87.

70. Li, D.; Suyi, Z.; Zhenyu, M.; Zonghua, A.; Songtao, W.; Liangyang, S.; Yan, Y.; Zhang, B. PCR-DGGE analysis of microbial community structure in fermented grains of Luzhou-flavor liquor. *Liquor Mak. Sci. Technol.* 2014, 25–27,31. [CrossRef]

71. Hou, Q.C.; Wang, Y.R.; Cai, W.C.; Ni, H.J.; Zhao, H.J.; Zhang, Z.D.; Liu, Z.J.; Liu, J.M.; Zhong, J.A.; Guo, Z. Metagenomic and physicochemical analyses reveal microbial community and functional differences between three types of low-temperature Daqu. *Food Res. Int.* 2022, 156, 111167. [CrossRef] [PubMed]

72. Yao, S.; Ge, Y.; Li, H.; Liu, Y.; Zhao, J.W.; Zhang, F.G.; Xin, C.H.; Cheng, C. Analysis on Bacterial Communities in High Temperature Daqu of Sesame Flavor Liquor through Culture-free Approach. *Food Ferment. Ind.* 2012, 38, 1–6. [CrossRef]

73. Zheng, X.; Yan, Z.; Robert Nout, M.J.; Boekhout, T.; Han, B.; Zwietering, M.H.; Smid, E.J. Characterization of the microbial community in different types of Daqu samples as revealed by 16S rRNA and 26S rRNA gene clone libraries. *World J. Microbiol. Biotechnol.* 2015, 31, 199–208. [CrossRef] [PubMed]

74. Pal, S.; Jana, A.; Mondal, K.C.; Halder, S.K. Omics Approach to Understanding Microbial Diversity. *Biotechnol. Adv. Microbiol. Mol. Biol. Nanotechnol.* 2022, 26,–36.

75. Kumar, R.R.; Jadeja, V.J.; Shree, M.; Virani, N.A. Isolation of Actinomycetes: A Complete Approach. *Int. J. Curr. Microbiol. Appl. Sci.* 2016, 5, 606–618. [CrossRef]

76. Lewis, W.H.; Tahon, G.; Geesink, P.; Sousa, D.Z.; Ettema, T.E.G. Innovations to culturing the uncultured microbial majority. *Nat. Rev. Microbiol.* 2020, 19, 225–240. [CrossRef]

77. Gou, M.; Wang, H.Z.; Yuan, H.W.; Zhang, W.X.; Tang, Y.Q.; Kida, K. Characterization of the microbial community in three types of fermentation starters used for Chinese liquor production. *J. Inst. Brew.* 2015, 121, 620–627. [CrossRef]

78. Wang, X.D.; Ban, S.D.; Zhou, H.X.; Hu, B.D.; Qiu, S.Y. Comparative Analysis of Bacterial Populations of Three Maotai-Flavored Daqus in Zunyi, Guizhou. *Food Sci. Food Res.* 2016, 37, 110–116.

79. Wang, X.D.; Ban, S.D.; Hu, B.L.; Qu, S.Y.; Zhou, H.X. Bacterial diversity of Moutai-flavour Daqu based on high-throughput sequencing method. *J. Inst. Brew.* 2017, 123, 138–143. [CrossRef]

80. Wang, X.D.; Lei, A.L.; Ban, S.D.; Qiu, S.Y. Research on bacterial diversity of Maotai-flavour Daqu. *Food Ferment. Ind.* 2017, 43, 70–75. [CrossRef]

81. Hou, Q.C.; Wang, Y.R.; Wang, W.P.; Tian, L.X.; Zhao, H.J.; Guo, Z. Difference of bacterial community structure and functional prediction in high-temperature Daqu of Maotai and Yaozhai. *Food Ferment. Ind.* 2022, 48, 36–44. [CrossRef]

82. Wang, Y.R.; Cai, W.C.; Wang, W.P.; Shu, N.; Zhang, Z.D.; Hou, Q.C.; Shan, C.H.; Guo, Z. Analysis of microbial diversity and functional differences in different types of high-temperature Daqu. *Food Sci. Nutr.* 2021, 9, 1003–1016. [CrossRef] [PubMed]

83. Jiang, Q.; Wu, X.; Xu, Y.; Zhang, Y.; Wang, Z.; Shen, L.; Yang, W.; Sun, J.; Liu, Y. Microbial composition and dynamic succession during the Daqu production process of Northern Jiang-flavored liquor in China. *J. Biotech.* 2021, 11, 224. [CrossRef] [PubMed]

84. Zuo, Q.C.; Huang, Y.G.; Min, G. Evaluation of bacterial diversity during fermentation process: A comparison between handmade and machine-made high-temperature Daqu of Maotai-flavor liquor. *Ann. Microbiol.* 2020, 70, 57. [CrossRef]

85. Wang, L.C.; Zhong, K.; Luo, A.M.; Chen, J.; Shen, Y.; Wang, X.; He, Q.; Gao, H. Dynamic changes of volatile compounds and bacterial diversity during fourth to seventh rounds of Chinese soy sauce aroma liquor. *Food Sci. Nutr.* 2021, 9, 3500–3511. [CrossRef]

86. Mao, J.J.; Liu, X.L.; Gao, T.; Gu, S.B.; Wu, Y.; Zhao, L.N.; Ma, J.L.; Li, X.; Zhang, J. Unraveling the correlations between bacterial diversity, physicochemical properties and bacterial community succession during the fermentation of traditional Chinese strong-flavor Daqu. *LWT 2021, 154, 112764. [CrossRef]

87. Liu, Y.B.; Zhao, Z.J.; Chen, H.F.; Sun, X.Y.; Pan, C.M. Analysis of Bacterial Community Structure in Medium Temperature Daqu and High Temperature Daqu of Luzhou-flavor Liqiu by High-throughput Sequencing. *Mod. Food Sci. Technol.* 2018, 34, 229–235. [CrossRef]

88. He, M.W.; Jin, Y.; Zhou, R.Q.; Zhao, D.; Zheng, J.; Wu, C.D. Dynamic succession of microbial community in Nongxiangxing daqu and microbial roles involved in flavor formation. *Food Res. Int.* 2022, 159, 111559. [CrossRef]

89. Wang, X.S.; Du, H.; Hu, Y. Source tracking of prokaryotic communities in fermented grain of Chinese strong-flavor liquor. *Int. J. Food Microbiol.* 2017, 244, 27–35. [CrossRef]

90. Wu, S.K.; Xie, J.; Wei, C.H.; Liu, Y.M.; Huang, Z.G.; Wan, S.L.; Deng, J. Comparison of Microbial Community Structure of Starter Cultures (Daqu) for Luzhou-Flavor Liquor in Different Regions of Sichuan. *Food Sci. 2019, 40, 144–152.

91. Su, G.; Wang, X.H.; Dong, D.W.; Ma, W.; Yang, J.M.; Ye, H. Application of High-Throughput Sequencing Technology in the Quality Grade Determination of Yanghe Daqu. *Liquor Mak. Sci. Technol.* 2019, 86–90. [CrossRef]

92. Xu, Y.Q.; Zhao, J.R.; Liu, X.; Zhang, C.S.; Zhao, Z.G.; Li, X.T.; Sun, B.G. Flavor mystery of Chinese traditional fermented baijiu: The great contribution of ester compounds. *Food Chem.* 2021, 369, 130920. [CrossRef] [PubMed]

93. Zheng, Y.L.; Zhao, T.; Wang, J.S.; Cai, K.Y.; Chen, P.; Deng, J.S.F.; Shang, L.; Cao, J.H.; Chen, M.B. Changes in the Microbial Community Structure during the Digitally Managed Fermentation of High-temperature Daqu. *Food Sci.* 2022, 43, 171–178.
95. Tao, Y. Microbial community compositions and diversity in pit mud of Chinese Luzhou-flavor liquor. CIESC J. 2014, 65, 1800–1807.
96. Zhang, Q.Y.; Yuan, Y.J.; Liao, Z.M.; Zhang, W.X. Use of microbial indicators combined with environmental factors coupled with metrology tools for discrimination and classification of Luzhou flavoured pit muds. J. Appl. Microbiol. 2017, 123, 933–943. [CrossRef]
97. Tao, Y.; Li, J.B.; Rui, J.P.; Xu, Z.C.; Zhou, Y.; Hu, X.H.; Wang, X.; Liu, M.H.; Li, D.P.; Li, X.Z. Prokaryotic Communities in Pit Mud from Different-Aged Cellars Used for the Production of Chinese Strong-Flavored Liquor. Appl. Environ. Microbiol. 2014, 80, 2254–2260. [CrossRef]
98. Hu, X.L.; Du, H.; Ren, C.; Xu, Y. Illuminating Anaerobic Microbial Community and Cooccurrence Patterns across a Quality Gradient in Chinese Liquor Fermentation Pit Muds. Appl. Environ. Microbiol. 2016, 82, 2506–2515. [CrossRef]
99. Tao, Y.; Wang, X.; Li, X.Z.; Wei, N.; Jin, H.; Xu, Z.C.; Tang, Q.L.; Zhu, X.Y. The functional potential and active populations of the pit mud microbiome for the production of Chinese strong-flavour liquor. Microb. Biotechnol. 2017, 10, 1603–1615. [CrossRef]
100. Liu, M.K.; Tang, Y.M.; Guo, X.J.; Zhao, K.; Tian, X.H.; Liu, Y.; Yao, W.C.; Deng, B.; Ren, D.Q.; Zhang, X.P. Deep sequencing reveals high bacterial diversity and phylogenetic novelty in pit mud from Luzhou Laojiao cellars for Chinese strong-flavor Baijiu. Food Res. Int. 2017, 102, 68–76. [CrossRef]
101. Luo, Q.C.; Liu, C.L.; Li, W.F.; Wu, Z.Y.; Zhang, W.X. Comparison between Bacterial Diversity of Aged and Aging Pit Mud from Luzhou-flavor Liquor Distillery. Food Sci. Technol. Res. 2014, 20, 867–873. [CrossRef]
102. Liang, H.P.; Luo, Q.C.; Zhang, A.Y.; Wu, Z.Y.; Zhang, W.X. Comparison of bacterial community in matured and degenerated pit mud from Chinese Luzho flavour liquor distillery in different regions. J. Inst. Brew. 2016, 122, 48–54. [CrossRef]
103. Zhou, W.G.; Liao, Z.M.; Wu, Z.Y.; Suyama, T.K.; Zhang, W.X. Analysis of the difference between aged and degenerated pit mud microbiome in fermentation cellars for Chinese Luzhou-flavor baijiu by metatranscriptomics. J. Sci. Food Agric. 2021, 101, 4621–4631. [CrossRef] [PubMed]
104. Chen, L.; Li, Y.Z.; Jin, L.; He, L.; Ao, X.L.; Liu, S.L.; Yang, Y.; Liu, A.P.; Chen, S.J.; Zou, L.K. Analyzing bacterial community in pit mud of Yibin Baijiu in China using high throughput sequencing. PeerJ 2020, 8, e9122. [CrossRef] [PubMed]
105. Zhang, H.M.; Meng, Y.J.; Wang, Y.L.; Zhou, Q.W.; Li, A.J.; Liu, G.Y.; Li, J.X.; Xing, X.H. Prokaryotic communities in multidimensional bottom-pit-mud from old and young pits used for the production of Chinese Strong-Flavor Baijiu. Food Chem. 2019, 312, 126084. [CrossRef]
106. Hu, X.L.; Tian, R.J.; Wang, K.L.; Cao, Z.H.; Yan, P.X.; Li, F.Q.; Li, X.S.; Li, S.L.; He, P.X. The prokaryotic community, physicochemical properties and flavors dynamics and their correlations in fermented grains for Chinese strong-flavor Baijiu production. Food Res. Int. 2021, 148, 110626. [CrossRef]
107. Xiao, C.; Yang, Y.; Lu, Z.M.; Chai, L.J.; Zhang, X.J.; Wang, S.T.; Shen, C.H.; Shi, J.S.; Xu, Z.H. Daqu microbiota exhibits species-specific and periodic succession features in Chinese baijiu fermentation process. Food Microbiol. 2021, 98, 103766. [CrossRef]
108. Feng, J.T.; Lu, Z.M.; Shi, W.; Xiao, C.; Zhang, X.J.; Chai, L.J.; Wang, S.T.; Shen, C.H.; Shi, J.S.; Xu, Z.H. Effects of different culture temperatures on microbial community structure, enzyme activity, and volatile compounds in Daqu. Chin. J. Appl. Environ. Biol. 2021, 27, 760–767. [CrossRef]
109. Li, Z.J.; Fan, Y.H.; Huang, X.N.; Han, B.Z. Microbial Diversity and Metabolites Dynamic of Light-Flavor Baijiu with Stacking Process. Ferment 2022, 8, 67. [CrossRef]
110. Zhang, X.Y.; Zhao, J.; Du, X.Q. Barcoded pyrosequencing analysis of the bacterial community of Daqu for light flavour Chinese liquor. Lett. Appl. Microbiol. 2014, 58, 549–555. [CrossRef]
111. Li, C.; Mu, L.; Wang, J.Y.; Lei, Z.H.; Chen, J.Y.; Han, B.Z. Physicochemical and microbiological analysis of Fen-type Daqu. China Brew. 2009, 140–142.
112. Cai, W.C.; Wang, Y.R.; Ni, H.; Liu, Z.J.; Liu, J.M.; Zhong, J.A.; Hou, Q.C.; Shan, C.H.; Yang, X.Q.; Guo, Z. Diversity of microbiota, microbial functions, and flavor in different types of low-temperature Daqu. Food Res. Int. 2021, 150, 110734. [CrossRef] [PubMed]
113. Shi, J.; Xiao, Y.W.; Li, X.R.; Ma, E.B.; Du, X.S.; Quan, Z.X. Analyses of microbial consortia in the starter of Fen Liquor. Lett. Appl. Microbiol. 2009, 48, 478–485. [CrossRef] [PubMed]
114. Xie, M.W.; Lv, F.X.; Ma, G.D.; Farooq, A.; Li, H.H.; Du, Y.; Liu, Y. High throughput sequencing of the bacterial composition and dynamic succession in Daqu for Chinese sesame flavour liquor. J. Inst. Brew. 2019, 126, 98–104. [CrossRef]
115. Fan, G.S.; Du, Y.H.; Fu, Z.L.; Chen, M.; Wang, Z.; Liu, P.X.; Li, X.T. Characterisation of physicochemical properties, flavour components and microbial community in Chinese Guojing roasted sesame-like flavour Daqu. J. Inst. Brew. 2019, 126, 105–115. [CrossRef]
116. Wu, X.Y.; Jing, R.X.; Chen, W.H.; Geng, X.J.; Li, M.; Yang, F.Z.; Yan, Y.Z.; Liu, Y. High-throughput sequencing of the microbial diversity of roasted-sesame-like flavoured Daqu with different characteristics. 3 Biotech. 2020, 10, 502. [CrossRef]
117. Wang, H.Y.; Zhang, X.J.; Zhao, L.P.; Xu, Y. Analysis and comparison of the bacterial community in fermented grains during the fermentation for two different styles of Chinese liquor. J. Ind. Microbiol. Biotechnol. 2008, 35, 603–609. [CrossRef]
118. Yun, J.L.; Yan, X.; Zhu, B.; Ju, W.T.; Wei, G.H.; Hu, J.X.; Li, H.W.; Chen, X. Analysis of Microflora in Fermented Grains during the Fermentation of Taibai Liquor. Liquor Mak. Sci. Technol. 2006, 12, 40–42.
119. Liu, C.J.; Gong, X.W.; Zhao, G.; Soe Htet, M.N.; Jia, Z.Y.; Yan, Z.K.; Liu, L.; Zhai, Q.H.; Huang, T.; Deng, X.P.; et al. Liquor Flavour Is Associated With the Physicochemical Property and Microbial Diversity of Fermented Grains in Waxy and Non-waxy Sorghum (Sorghum bicolor) During Fermentation. Front. Microbiol. 2021, 12, 618458. [CrossRef]
120. Huang, Y.H.; Yi, Z.L.; Jin, Y.L.; Zhao, Y.G.; He, K.Z.; Liu, D.Y.; Zhao, D.; He, H.; Luo, H.B.; Zhang, W.X.; et al. New microbial resource: Microbial diversity, function and dynamics in Chinese liquor starter. *Sci. Rep.* 2017, 7, 14577. [CrossRef]

121. Tian, N.; Guo, X.; Wang, M.Z.; Chen, C.; Cui, H.H.; Zhang, L.P.; Tang, H. Bacterial community diversity of shilixiang baijiu Daqu based on metagenomics. *J. Food Biochem.* 2020, 44, e13410. [CrossRef]

122. Hu, Y.L.; Dun, Y.H.; Li, S.N.; Fu, B.; Xiong, X.M.; Peng, N.; Liang, Y.X.; Zhao, S.M. Changes in microbial community during fermentation of high temperature Daqu used in the production of Chinese Baiyinbiao liquor. *J. Inst. Brew.* 2017, 123, 594–599. [CrossRef]

123. Guo, X.W.; Fan, E.D.; Ma, B.T.; Li, Z.X.; Zhang, Y.X.; Zhang, Z.M.; Chen, Y.F.; Xiao, D.G. Research progress in functional bacteria in solid-state fermented Baijiu in China. *Food Ferment. Ind.* 2020, 46, 280–286. [CrossRef]

124. Feng, H.J.; Zhai, L.; Yu, X.J.; Cheng, K.; Liu, Y.; Yao, S. Fatty acids metabolism changes of Streptomyces Species. *Food Sci.* 2012, 50, 2615–2621. [CrossRef] [PubMed]

125. Yuan, S.Q.; Jin, Z.Y.; Ali, A.; Wang, C.J.; Liu, J. Caproic Acid-Producing Bacteria in Chinese Baijiu Brewing. *Front. Microbiol.* 2022, 13, 883142. [CrossRef] [PubMed]

126. Zou, W.; Zhao, C.; Luo, H.-b. Diversity and Function of Microbial Community in Chinese Strong-Flavor Baijiu Ecosystem: A Review. *Front. Microbiol.* 2018, 9, 671. [CrossRef] [PubMed]

127. Cao, X.Z.; Huang, C.P.; Xiong, L.; Zhou, Z.B. Effect of co-cultivation on growth and metabolism of caproic acid bacteria. *China Brew.* 2010, 11, 35–38.

128. Du, H.; Lu, H.M.; Xu, Y. Influence of geosmin-producing Streptomyces on the growth and volatile metabolites of yeasts during Chinese liquor fermentation. *J. Agric. Food. Chem.* 2015, 63, 290–296. [CrossRef]

129. You, X.L.; Huang, Y.L.; Huang, Y.G.; Zhou, W.M. Study on the biological characteristics of actinomycetes on functional bacteria producing maotai-flavor during fermentation. *Liquor. Mak. Sci. Technol.* 2015, 8, 1–5. [CrossRef]

130. Huang, B.; Liu, N.; Huang, Y.; Chen, J.C. Coculture of actinomycetes with *Bacillus subtilis* and its effect on the bioactive secondary metabolites. *Chin. J. Microbiol. Technol.* 2009, 25, 932–940.

131. Zhi, Y.; Wu, Q.; Du, H.; Xu, Y. Biocatalysis of geosmin-producing *Streptomyces* spp. by two *Bacillus* strains from Chinese liquor. *Int. J. Food Microbiol.* 2016, 231, 1–9. [CrossRef]

132. Huang, Y.L.; Zhang, J.M.; Huang Yong Guang Hu, J.F.; Hu, F.; Zhong, F.D. Flavor regulation of Moutai-flavor Baijiu brewing by *Streptomyces* sp. A22. *China Brew.* 2016, 35, 27–31.

133. Schneider, J.; Yepes, A.; García-Betancur, J.-C.; Westedt, I.; Mieliw, B.; López, D. Streptomycin-Induced Expression in *Bacillus subtilis* of Ymp, a Lactonase-Homologous Protein That Inhibits Development and Streptomycin Production in *Streptomyces griseus*. *Appl. Environ. Microbiol.* 2011, 78, 599–603. [CrossRef] [PubMed]

134. Ren, D.H.; Liu, S.P.; Zhang, S.Y.; Qin, H.; Han, X.; Mao, J. Multi-Omics Reveals Microbial Roles and Metabolic Functions at the Spatiotemporal Niche in Pit Mud. *Res. Sq.* 2022, 1–33.

135. Ye, C.; Wei, X.Y.; Shi, T.Q.; Sun, X.; Xu, N.; Gao, C.; Zou, W. Genome-scale metabolic network models: From first-generation to next-generation. *Appl. Microbiol. Biotechnol.* 2022, 106, 4907–4920. [CrossRef] [PubMed]

136. Feng, H.J.; Zhai, L.; Yu, X.J.; Cheng; K.; Liu, Y.; Yao, S. Fatty acids metabolism changes of *Thermoactinomyces daquis* CICC 10681 at different temperatures. *Food Ferment. Ind.* 2018, 44, 49–54. [CrossRef]

137. Doroghazi, J.R.; Metcalf, W.W. Comparative genomics of actinomycetes with a focus on natural product biosynthetic genes. *BMC Genom.* 2013, 14, 611. [CrossRef]

138. Kim, J.N.; Kim, Y.J.; Jeong, Y.J.; Roe, J.H.; Kim, B.G.; Cho, B.K. Comparative Genomics Reveals the Core and Accessory Genomes of *Streptomyces* Species. *J. Microbiol. Biotechnol.* 2015, 25, 1599–1605. [CrossRef]

139. Zhao, C.; Su, W.; Mu, Y.; Mu, Y.C.; Jiang, L. Integrative Metagenomic—Metabolomics for Analyzing the Relationship Between Microorganisms and Non-volatile Profiles of Traditional Xiaoao. *Front. Microbiol.* 2020, 11, 617030. [CrossRef]

140. Liu, M.K.; Tang, Y.M.; Guo, X.J.; Zhao, K.; Penttinen, P.; Tian, X.H.; Zhang, X.Y.; Ren, D.Q.; Zhang, X.P. Structural and Functional Changes in Prokaryotic Communities in Artificial Pit Mud during Chinese Baijiu Production. *mSystems* 2020, 5, e00829-19. [CrossRef]

141. Song, Z.W.; Du, H.; Zhang, Y.; Xu, Y. Unraveling Core Functional Microbiota in Traditional Solid-State Fermentation by High-Throughput Amplicons and Metatranscriptomics Sequencing. *Front. Microbiol.* 2017, 8, 1294. [CrossRef]

142. Gan, S.; Yang, F.; Sahu, S.K.; Luo, R.; Liao, S.L.; Wang, H.Y.; Jin, T.; Wang, L.; Zhang, P.F.; Liu, X.; et al. Deciphering the Composition and Functional Profile of the Microbial Communities in Chinese Moutai Liquor Starters. *Front. Microbiol.* 2019, 10, 1540. [CrossRef] [PubMed]

143. Yang, Y.; Wang, S.T.; Lu, Z.M.; Zhang, X.J.; Chai, L.J.; Shen, C.H.; Shi, J.S.; Xu, Z.H. Metagenomics unveils microbial roles involved in metabolic network of flavor development in medium-temperature daqu starter. *Food Res. Int.* 2021, 140, 110037. [CrossRef] [PubMed]

144. Schöller, C.; Gürtler, H.; Pedersen, R.; Molin, S.; Wilkins, K. Volatile metabolites from actinomycetes. *J. Agric. Food. Chem.* 2002, 50, 2615–2621. [CrossRef] [PubMed]

145. Jin, Y.; Li, D.Y.; Ai, M.; Tang, Q.X.; Huang, J.; Ding, X.F.; Wu, C.D.; Zhou, R.Q. Correlation between volatile profiles and microbial communities: A metabolomic approach to study Jiang-flavor liquor Daqu. *Food Res. Int.* 2019, 121, 422–432. [CrossRef]

146. Wang, T.; You, L.; Zhao, D.; Feng, R.Z.; Wang, S.; Feng, X.Y.; Lin, Q. Preliminary Analysis of Volatiles in Fermentation Broths of Actinomycetes Isolated from Luzhou-Flavor Liquor Brewing Environments. *Food Sci.* 2012, 33, 184–187.
147. Li, H.; Lian, B.; Ding, Y.; Nie, C.; Zhang, Q. Bacterial diversity in the central black component of Maotai Daqu and its flavor analysis. *Ann. Microbiol.* **2014**, *64*, 1659–1669. [CrossRef]

148. You, X.L.; Huang, Y.G.H.; Yun, L.; Hu, F.; Hu, J.F.; Zhong, F.D. Activity of the Metabolites of an Actinomycetes Strain from Jiangxiang Baijiu Production Process and Its Effects on Other Functional Bacteria in Liquor-Making Environment. *Liquor Mak. Sci. Technol.* **2018**, *18*, 17–23. [CrossRef]

149. Shi, S.; Hu, C.; Zhang, W.X. Preliminary study on an actinomycete producing brown-pigment and its 16S rDNA sequence analysis. *Sci. Technol. Food Ind.* **2010**, *31*, 239–240. [CrossRef]

150. Wang, X.D.; Yang, Y.H.; Li, Y.L.; Chen, H.M. Biological Characteristics and Screening and Identification of PL Producing Strain. *Food Ferment. Ind.* **2007**, *1*, 40–42.

151. Chaudhary, H.S.; Soni, B.; Shrivastava, A.; Shrivastava, S.R. Diversity and versatility of actinomycetes and its role in antibiotic production. *J. Appl. Pharm. Sci.* **2013**, *3*, 83–94.

152. You, L.; Wang, T. Volatile Products of 4 Streptomyces Strains Isolated from Strong-flavor Liquor Factories. *Food Ind.* **2012**, *33*, 118–120.

153. Bezuidt, O.; Gomri, M.A.; Pierneef, R.; Van Goethem, M.W.; Kharroub, K.; Cowan, D.A.; Makhalanyane, T.P. Draft genome sequence of Thermoactinomyces sp. strain AS95 isolated from a Sebkha in Thamelaht, Algeria. *Stand. Genom. Sci.* **2016**, *11*, 68. [CrossRef] [PubMed]

154. Zhou, X.B.; Zheng, P. Spirit-based distillers’ grain as a promising raw material for succinic acid production. *Biotechnol. Lett.* **2013**, *35*, 679–684. [CrossRef]

155. Luo, Q.C.; Qiao, Z.W.; Zheng, J.; Zhang, X.; Lei, X.J.; Shi, S.; Liu, D.T. Screening and metabolic kinetic analysis of *Arthrobacter protophormiae* for lactic acid degradation. *China Brew.* **2021**, *40*, 82–86.

156. Xiao, C.; Lu, Z.M.; Zhang, X.J.; Wang, S.T.; Ao, L.; Shen, C.H.; Shi, J.S.; Xu, Z.H. Bio-Heat Is a Key Environmental Driver Shaping the Microbial Community of Medium-Temperature Daqu. *Appl. Environ. Microbiol.* **2017**, *83*, e01550-17. [CrossRef] [PubMed]

157. Luan, X.S. Isolation and characteristics of facultative autotrophic *Streptomyces* in the fermentation tank of Qu liquor. *Food. Ferment. Ind.* **2001**, *11*, 17–20.