



Diversity and Dynamics of Marine Arenicolous Fungi in Three Seasides of the Korean Peninsula

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Abstract

Various arenicolous fungal species have been detected from the beach sand in the coastal area. However, little has been revealed regarding their distribution and dynamics. To investigate the overall diversity of marine arenicolous fungi (MAFs) in Korea and whether the composition of MAFs is affected by ocean currents, we isolated and analyzed the fungal community from the western, southern, and eastern seashores of the Korean Peninsula. In total, 603 strains were isolated and identified as 259 species based on appropriate molecular markers for each genus (ITS, *BenA*, *CaM*, *tef1*, and *act*). The composition of MAFs showed differences among the seashores. Our results indicate that many MAFs inhabit the beach sand on the Korean Peninsula, and the composition of MAFs is also affected by ocean currents flowing along each coast.

Keywords Arenicolous fungi · Culture-dependent · Fungal composition · Fungal diversity · Beach sand

Introduction

Marine fungi are broadly defined as fungi that grow and sporulate in marine environments, build symbiotic relationships with other marine organisms. (Pang et al., 2016). Marine fungi inhabit various marine niches, including algae, corals, sponges, mangrove forests, marine snow, mudflats, and sand beaches ranging from the arctic sea to the tropical ocean (Bugni & Ireland, 2004; Hyde et al., 1998; Jones, 2000; Jones & Pang, 2012; Kohlmeyer & Kohlmeyer, 1979; Pham et al., 2021; Rămă et al., 2017; Rédou et al., 2015). They are the key components of the marine ecosystem and represent a considerable proportion of microbial diversity. Marine fungi are found in wide and diverse lineages (Hyde et al., 1998; Richards et al., 2012). Based on a broad ecological definition, they may be categorized into obligate and facultative marine fungi (Kohlmeyer & Kohlmeyer, 1979). Although obligate marine fungi grow and sporulate only in marine habitats, facultative marine fungi normally inhabit freshwater or terrestrial environments but may adapt to the marine environment. The diversity of marine fungi is

underestimated compared to that of terrestrial fungi. To date, 1857 species are known to be associated with the marine environment (www.marinefungi.org, accessed on 19 August 2022), but the number is estimated to be higher than 10,000 (Jones, 2011).

The intertidal zone of beach sands harbors unique and specialized biotic assemblages (Defeo & McLachlan, 2005). Various fungal taxa were detected in this habitat, including yeast and filamentous fungi (Ghinsberg et al., 1994; Vogel et al., 2007; Yee et al., 2016). The fungi in coastal beach sands are called marine arenicolous fungi (MAFs), which are introduced from both terrestrial and marine environments (Velez et al., 2022). MAFs have various roles and contribute to nutrient cycling as decomposers and food sources (Newell & Porter, 2000; Velez et al., 2021). Many studies on MAFs have reported on the pathogens causing water contamination and human diseases (Sabino et al., 2011; Frenkel et al., 2020; Brandão et al., 2021). However, these fungi have different functions in beach sand and are promising targets for novel compounds, such as antibacterial or anticancer agents (Overy et al., 2014; Park et al., 2018). MAFs can adapt to extreme conditions, such as salt stress and high temperature (Velez et al., 2022). Their diversity may be closely related to their habitat environment such as an ocean current.

The Korean Peninsula consists of three seashores: the western, southern, and eastern seashores. All three seashores are influenced by the branches of the Kuroshio Current. The

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maximum depth of the West Sea and South Sea are approximately 100 m and less than 200 m, respectively (Koh & Khim, 2014). Conversely, the depth of the East Sea is more than 3500 m (Chang et al., 2016). Due to such differences in the ocean current and environment, each seaside harbors different marine biodiversity (Baek, 2012; Park et al., 2019; Seo et al., 2018; Sohn et al., 2012). Fungal compositions are expected to be distinctive according to the ocean currents. However, the overall diversity of MAFs has not been studied intensively, except for some limited taxa (Lee et al., 2016; Park et al., 2019). The results from our previous metabarcoding study imply high diversity in the beach sand habitat (Park et al., 2019). Therefore, we aimed to (1) investigate the overall diversity of MAFs in Korean seashores and (2) evaluate whether the composition of MAFs is affected by the ocean currents.

Materials and Methods

Study Sites and Sample Collection

The West Korea Coastal Current flows in the West Sea toward the north, whereas the Jeju Warm Current affects the southern coast and turns clockwise around Jeju Island. The East Korea Warm Current occurs in the East Sea and flows along the coast toward the north (Park et al., 2017; Fig. 1). Considering the ocean currents along the seashores, we isolated fungi from six sites: Ganghwa (GH) and Muan (MA) from the western seaside, Jeju (JJ) and Suncheon (SC) from the southern seaside, and Goseong (GS) and Ulsan (US) from the eastern seaside (Fig. 1). At each site, sampling was performed in October 2016 and in January, April, and July of 2017 to reduce seasonal bias. Each beach sand sample was collected after removing the surface of the sand to avoid contamination, and the collection was repeated five times every 20 m at each site. Samples were transported to the laboratory in a 4 °C icebox and kept in a 4 °C refrigerator before isolation.

Fungal Isolation and Morphological Grouping

For fungal isolation, 5 g of sand samples were diluted ten-fold using artificial seawater (ASW) containing 26.518 g/L NaCl, 2.447 g/L MgCl₂, 3.305 g/L MgSO₄, 1.141 g/L CaCl₂, 0.725 g/L KCl, 0.202 g/L NaHCO₃, and 0.083 g/L NaBr (Huang et al., 2011). For each sample, 100 µL of the dilution was streaked onto three different culture media plates: glucose yeast extract agar (GYA; 1 g/L glucose, 0.1 g/L yeast extract, 0.5 g/L peptone, and 15 g/L agar), dichloran rose bengal chloramphenicol agar (DRBC; Difco, Becton Dickinson), and Sabouraud dextrose agar (SDA; Difco, Becton Dickinson) supplemented with ASW. The plates were

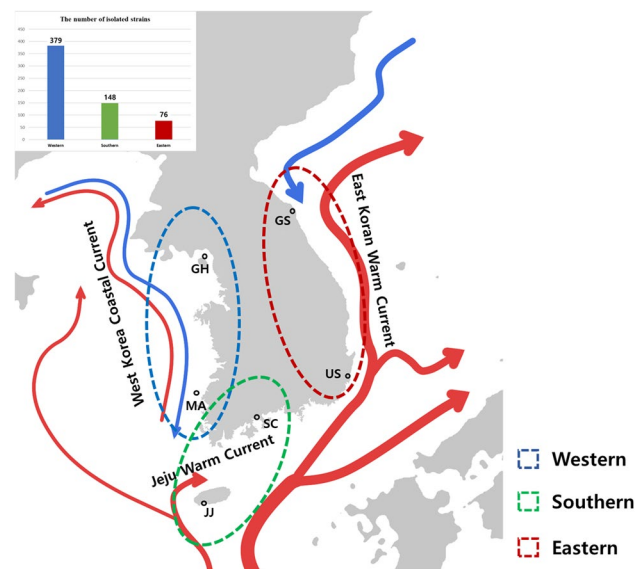


Fig. 1 Map showing the location of six sampling sites and the number of strains isolated from each site: Ganghwa (GH), Muan (MA), Jeju (JJ), Suncheon (SC), Ulsan (US), and Goseong (GS). The colored arrows indicate annual ocean currents around the Korean Peninsula (red line, warm currents; blue line, cold currents)

incubated at 25 °C for 7–14 days, and then each strain was transferred onto a potato dextrose agar (PDA; Difco, Becton Dickinson) plate with ASW. After 7–14 days, fungal strains were morphologically grouped and identified at the genus level based on their cultural characteristics on PDA (color margin, shape of the colony, and diffusible pigment production) and microscopic characteristics (shape of conidiophores and conidia). The isolated strains were stocked in 20% glycerol with ASW and stored at – 80 °C.

DNA Extraction and PCR Amplification

The genomic DNA was extracted from representative strains of each morphological group using the modified cetyltrimethylammonium bromide extraction protocol (Rogers & Bendich, 1994). The internal transcribed spacer (ITS) region and other protein-coding regions were amplified using the appropriate set of primers for each genus. The primer sets used for each genetic region were ACT-512F/ACT-783R (5'-ATGTGCAAGGCCGGT TTCG-3'/5'-TACGAGTCCTTCTGGCCCAT-3') (Carbone & Kohn, 1999) for actin (*act*), Bt2a/Bt2b (5'-GGT AACCAAATCGGTGCTGCTTTC-3'/5'-ACCCTCAGT GTAGTGACCCTTGGC-3') (Glass & Donaldson, 1995) for β-tubulin (*BenA*), CF1/CF4 (5'-GCCGACTCTTTG ACYGARGAR-3'/5'-TTTYTGCATCATRAGYTGGAC-3') (Peterson et al., 2005) for calmodulin (*CaM*), EF1 or EF1-728/EF2 (5'-ATGGGTAAGGARGACAAGAC-3' or 5'-CATCGAGAAGTTCGAGAAGG-3'/5'-GGARGT

ACCAGTRATCATGTT-3') (Carbone & Kohn, 1999; O'Donnell et al., 1998) for translation elongation factor 1- α (*tef1*), and ITS1F/ITS4 (5'-CTTGGTCATTAGAGGAAGTAA-3'/5'-TCCTCCGCTTATTGATATGC-3') (Gardes & Bruns, 1993; White et al., 1990) for the ITS region. PCR was performed in a C1000 Thermal Cycler (Bio-Rad) using previously described methods (Park et al., 2015a). The PCR products were purified with the ExpinTM PCR Purification Kit (GeneAll Biotechnology) according to the manufacturer's instructions. DNA sequencing was performed at Macrogen, using an ABI PRISM 3700 Genetic Analyzer (Life Technologies) with respective PCR primers.

Molecular Identification

The sequences were assembled and proofread using MEGA7 (Kumar et al., 2016). Each sequence was manually checked and revised. Thereafter, ITS sequences of all representative strains were identified to the species level using BLAST with UNITE database (<https://unite.ut.ee/>), according to matching reference sequences with over 97% similarity. Other protein-coding gene sequences were assigned to species using maximum likelihood (ML) phylogenetic analysis conducted via an in-house pipeline (<https://github.com/Changwanseo/FunID>). Sequences that showed less than 97% similarity to any reference sequences or those phylogenetically unidentified were identified up to the genus level (numbered with sp.). Taxonomic placements for each species were referenced from the UNITE database and manually confirmed. All sequences were deposited in GenBank (Table 1).

Statistical Analysis

Statistical analysis was conducted using R version 4.1.3 (R Core Team, 2022) to calculate alpha diversity indices and community dissimilarities, perform statistical tests, and visualize data. Alpha diversity indices (Chao1 richness and Shannon's diversity) were calculated using the R package *vegan* (Oksanen et al., 2020). The differences in alpha diversity indices between seashores were analyzed using one-way ANOVA, followed by post-hoc test adjusted with Benjamini and Hochberg method (Benjamini & Hochberg, 1995). The differences in fungal communities were visualized with Constrained Analysis of Principal Coordinates (CAP) based on Jaccard dissimilarity distance, using ordinate function implemented in the *phyloseq* package (Anderson & Willis, 2003; McMurdie & Holmes, 2013). To evaluate the effect of the seashore on fungal community composition, a permutational multivariate analysis of variance (PERMANOVA)

was conducted using the *adonis* function in *vegan* package based on Jaccard dissimilarity index with 999 permutations.

Results

Identification of Fungal Strains

A total of 603 fungal strains were isolated from the three seashores: 379 strains from the West Sea (GH and MA), 148 strains from the South Sea (SC and JJ), and 76 strains from the East Sea (GS and US) (Table 1; Fig. 1). They were initially grouped using morphological characteristics. Certain taxonomic groups were further identified to the species level based on the phylogenetic analysis of ITS or protein-coding genes. *Cladosporium* was identified with *act. Diaporthe*, *Didymella*, *Ectophoma*, *Epicoccum*, *Penicillium*, and *Talaromyces* were identified with *BenA*. *Aspergillus* species were identified using *BenA* and *CaM*. *Fusarium* and *Trichoderma* were identified using *tef1*. The rest of the species were identified with ITS sequences.

Consequently, 259 species were identified and classified into three phyla, ten classes, 26 orders, 78 families, and 121 genera. Most isolated species were taxonomically assigned to Ascomycota (236 spp., 91%), followed by Basidiomycota (18 spp., 7%), and Mucoromycota (5 spp., 2%) (Table 1; Fig. 2A). In the Ascomycota phylum, *Penicillium* (40 spp.), *Cladosporium* (34 spp.), *Aspergillus* (11 spp.), and *Trichoderma* (10 spp.) were the most diverse genera (Fig. 2A); these were dispersed across the studied seashores (Fig. 2B). In Basidiomycota and Mucoromycota, wood decay fungi and soil fungi were primarily isolated.

Fungal Composition of Each Seaside

The largest number of species were detected from the western seashore, with 165 species, followed by the southern (98 spp.) and eastern (51 spp.) seashores (Fig. 3A). The fungal community composition also varied by seashores. Only nine species were present in all three seashores: *Alternaria angustiovoidea*, *Cladosporium anthropophilum*, *C. crousii*, *C. pseudocladosporioides*, *C. rectoides*, *C. tenuissimum*, *Cladosporium* sp. 1, *Paraconiothyrium* sp. 1, and *Penicillium fructuariae-cellae*. In the western seashore, *Penicillium* (29 spp., 17.6%) was the most diverse genus, followed by *Cladosporium* (28 spp., 17.0%), *Aspergillus* (8 spp., 4.8%), and *Talaromyces* (6 spp., 3.0%). In the southern seashore, 98 species were discovered, including *Cladosporium* (14 spp., 14.3%), *Penicillium* (11 spp., 11.2%), *Trichoderma* (4 spp., 4.1%), and *Didymella* (4 spp., 4.1%). Moreover, in the eastern seashore, 51 species were identified, including *Penicillium* (14 spp., 27.5%), *Cladosporium* (9 spp., 17.6%), and *Acremonium* (2 spp., 3.9%) (Figs. 2B, 3B).

Table 1 Strains with sampling sties and their GenBank accession numbers used for phylogenetic analyses in this study

Species	Strain name	Sample site	PCR region	Accession number
Ascomycota				
<i>Acaulium album</i>	SFC20220920-G157	Muan	ITS	OP597822
<i>Achroistachys levigata</i>	SFC20220920-C024	Ganghwa	ITS	OP597823
<i>Acremonium exuviarum</i>	SFC20220920-G013	Muan	ITS	OP597824
<i>Acremonium polychromum</i>	SFC20220920-C180	Jeju	ITS	OP597825
<i>Acremonium</i> sp. 1	SFC20220920-B504	Ulsan	ITS	OP597826
<i>Acremonium</i> sp. 2	SFC20220920-G030	Suncheon	ITS	OP597827
<i>Acremonium</i> sp. 3	SFC20220920-G110	Goseong	ITS	OP597828
<i>Acremonium vitellinum</i>	SFC20220920-B095	Ganghwa	ITS	OP597829
	SFC20220920-B352	Ganghwa	ITS	OP597830
<i>Acrocalymma</i> sp. 1	SFC20220920-G302	Ganghwa	ITS	OP597831
<i>Adisciso kaki</i>	SFC20220920-C174	Suncheon	ITS	OP597833
<i>Albifimbria verrucaria</i>	SFC20220920-G012	Muan	ITS	OP597834
<i>Albifimbria verrucaria</i>	SFC20220920-G176	Muan	ITS	OP597835
<i>Alfaria</i> sp. 1	SFC20220920-B121	Ganghwa	ITS	OP597836
<i>Alternaria angustiovoidea</i>	SFC20220920-C139	Jeju	ITS	OP597837
	SFC20220920-C140	Jeju	ITS	OP597838
	SFC20220920-D024	Jeju	ITS	OP597839
	SFC20220920-D025	Jeju	ITS	OP597840
	SFC20220920-D029	Jeju	ITS	OP597841
	SFC20220920-D030	Jeju	ITS	OP597842
	SFC20220920-D031	Jeju	ITS	OP597843
	SFC20220920-D053	Jeju	ITS	OP597844
	SFC20220920-D217	Jeju	ITS	OP597845
	SFC20220920-D364	Jeju	ITS	OP597846
	SFC20220920-D372	Jeju	ITS	OP597847
	SFC20220920-D385	Jeju	ITS	OP597848
	SFC20220920-D423	Jeju	ITS	OP597849
	SFC20220920-G091	Jeju	ITS	OP597850
	SFC20220920-G148	Jeju	ITS	OP597851
	SFC20220920-G195	Jeju	ITS	OP597852
	SFC20220920-G275	Jeju	ITS	OP597853
	SFC20220920-G366	Jeju	ITS	OP597854
	SFC20220920-G393	Jeju	ITS	OP597855
<i>Alternaria subcucurbitae</i>	SFC20190612-M11	Ganghwa	ITS	OP597856
<i>Angustimassarina</i> sp. 1	SFC20220920-C375	Suncheon	ITS	OP597857
<i>Annulohypoxylon archeri</i>	SFC20220920-G065	Jeju	ITS	OP597858
<i>Apiospora serenensis</i>	SFC20220920-B248	Muan	ITS	OP597860
<i>Apiospora</i> sp. 1	SFC20220920-G128	Suncheon	ITS	OP597861
<i>Articulospora</i> sp. 1	SFC20220920-C012	Suncheon	ITS	OP597862
<i>Aspergillus citrinoterreus</i>	SFC20220920-G303	Ganghwa	<i>BenA</i>	OP584170
<i>Aspergillus clavatus</i>	SFC20220920-G527	Suncheon	<i>BenA</i>	OP584175
<i>Aspergillus flavus</i>	SFC20170919-M04	Jeju	<i>CaM</i>	OP584134
<i>Aspergillus fumigatus</i>	SFC20220920-G402	Ganghwa	<i>BenA</i>	OP584172
	SFC20220920-G492	Ganghwa	<i>BenA</i>	OP584174
	SFC20220920-G530	Ganghwa	<i>BenA</i>	OP584173
<i>Aspergillus lentulus</i>	SFC20190312-M06	Suncheon	<i>CaM</i>	OP584135
<i>Aspergillus niveus</i>	SFC20220920-G346	Muan	<i>BenA</i>	OP584171
<i>Aspergillus pseudoviridinutans</i>	SFC20220920-G251	Muan	<i>CaM</i>	OP584140
<i>Aspergillus quadrilineatus</i>	SFC20190612-M21	Ganghwa	<i>CaM</i>	OP584136

Table 1 (continued)

Species	Strain name	Sample site	PCR region	Accession number
<i>Aspergillus terreus</i>	SFC20220920-C355	Muan	<i>CaM</i>	OP584138
<i>Aspergillus venenatus</i>	SFC20220920-B315	Muan	<i>CaM</i>	OP584137
<i>Aspergillus welwitschiae</i>	SFC20220920-G002	Muan	<i>CaM</i>	OP584139
	SFC20220920-G336	Muan	<i>BenA</i>	OP584168
	SFC20220920-G396	Muan	<i>BenA</i>	OP584169
<i>Atrocalyx krabiensis</i>	SFC20220920-D326	Muan	ITS	OP597863
<i>Beauveria bassiana</i>	SFC20180817-M26	Muan	ITS	OP597864
	SFC20170919-M02	Muan	ITS	OP597865
	SFC20220920-G050	Muan	ITS	OP597866
	SFC20220920-G118	Muan	ITS	OP597867
<i>Berkeleyomyces basicola</i>	SFC20190612-M23	Ganghwa	ITS	OP597868
<i>Biatriospora</i> sp. 1	SFC20220920-B470	Suncheon	ITS	OP597869
<i>Bimuria novae-zelandiae</i>	SFC20220920-G008	Muan	ITS	OP597870
<i>Bispora</i> sp. 1	SFC20220920-C383	Suncheon	ITS	OP597871
<i>Boeremia exigua</i>	SFC20220920-B531	Jeju	ITS	OP597873
<i>Cadophora luteo-olivacea</i>	SFC20220920-G261	Ganghwa	ITS	OP597874
<i>Caliciopsis</i> sp. 1	SFC20220920-D392	Muan	ITS	OP597875
<i>Chaetocapnodium placitae</i>	SFC20220920-B139	Ganghwa	ITS	OP597878
	SFC20220920-C196	Ganghwa	ITS	OP597879
	SFC20220920-G040	Ganghwa	ITS	OP597880
<i>Chaetomium</i> sp. 1	SFC20220920-D382	Ganghwa	ITS	OP597881
<i>Chrysosporium carmichaelii</i>	SFC20220920-C380	Muan	ITS	OP597882
<i>Cladosporium allicinum</i>	SFC20190612-M05	Ganghwa	<i>act</i>	OP583970
	SFC20220920-D070	Ganghwa	<i>act</i>	OP583972
	SFC20220920-D076	Ganghwa	<i>act</i>	OP583978
	SFC20220920-D077	Ganghwa	<i>act</i>	OP583987
	SFC20220920-D078	Ganghwa	<i>act</i>	OP583979
	SFC20220920-D093	Ganghwa	<i>act</i>	OP583974
	SFC20220920-D110	Ganghwa	<i>act</i>	OP583950
	SFC20220920-D111	Ganghwa	<i>act</i>	OP583980
	SFC20220920-D112	Ganghwa	<i>act</i>	OP583982
	SFC20220920-D113	Ganghwa	<i>act</i>	OP583983
	SFC20220920-D148	Ganghwa	<i>act</i>	OP583973
	SFC20220920-D149	Ganghwa	<i>act</i>	OP583981
	SFC20220920-D159	Ganghwa	<i>act</i>	OP583985
	SFC20220920-D160	Ganghwa	<i>act</i>	OP583975
	SFC20220920-D209	Ganghwa	<i>act</i>	OP584106
	SFC20220920-D215	Ganghwa	<i>act</i>	OP584005
	SFC20220920-D222	Ganghwa	<i>act</i>	OP583993
	SFC20220920-D226	Ganghwa	<i>act</i>	OP583986
	SFC20220920-D227	Ganghwa	<i>act</i>	OP584007
	SFC20190612-M09	Ganghwa	<i>act</i>	OP583994
	SFC20220920-D287	Ganghwa	<i>act</i>	OP583971
	SFC20220920-D297	Ganghwa	<i>act</i>	OP583990
	SFC20220920-D299	Ganghwa	<i>act</i>	OP583992
	SFC20220920-D300	Ganghwa	<i>act</i>	OP584006
	SFC20220920-D301	Ganghwa	<i>act</i>	OP583976
	SFC20220920-D338	Ganghwa	<i>act</i>	OP583977
	SFC20220920-D346	Ganghwa	<i>act</i>	OP584107
	SFC20220920-D347	Ganghwa	<i>act</i>	OP583999

Table 1 (continued)

Species	Strain name	Sample site	PCR region	Accession number
<i>Cladosporium anthropophilum</i>	SFC20220920-D373	Ganghwa	<i>act</i>	OP584108
	SFC20220920-D378	Ganghwa	<i>act</i>	OP584109
	SFC20220920-D379	Ganghwa	<i>act</i>	OP583991
	SFC20220920-D386	Ganghwa	<i>act</i>	OP583989
	SFC20220920-D387	Ganghwa	<i>act</i>	OP583984
	SFC20220920-D395	Ganghwa	<i>act</i>	OP583988
	SFC20220920-D407	Ganghwa	<i>act</i>	OP584112
	SFC20180917-M01	Ganghwa	<i>act</i>	OP584110
	SFC20181014-M01	Ganghwa	<i>act</i>	OP584013
	SFC20180817-M19	Ganghwa	<i>act</i>	OP584014
	SFC20220920-B117	Ganghwa	<i>act</i>	OP584015
	SFC20220920-B265	Ganghwa	<i>act</i>	OP584022
	SFC20220920-B290	Ganghwa	<i>act</i>	OP584037
	SFC20220920-B294	Ganghwa	<i>act</i>	OP584114
	SFC20220920-B312	Ganghwa	<i>act</i>	OP584073
	SFC20220920-B508	Ganghwa	<i>act</i>	OP584053
	SFC20220920-D205	Ganghwa	<i>act</i>	OP584117
	SFC20220920-D381	Ganghwa	<i>act</i>	OP584038
	SFC20220920-D389	Ganghwa	<i>act</i>	OP584118
	SFC20220920-D421	Ganghwa	<i>act</i>	OP584101
	SFC20220920-D422	Ganghwa	<i>act</i>	OP584052
	SFC20220920-G022	Ganghwa	<i>act</i>	OP584033
	SFC20220920-G066	Ganghwa	<i>act</i>	OP584026
	SFC20220920-G067	Ganghwa	<i>act</i>	OP584020
	SFC20220920-G090	Ganghwa	<i>act</i>	OP584030
	SFC20220920-G103	Ganghwa	<i>act</i>	OP584027
	SFC20220920-G112	Ganghwa	<i>act</i>	OP584034
	SFC20220920-G123	Ganghwa	<i>act</i>	OP584016
	SFC20220920-G129	Ganghwa	<i>act</i>	OP584021
	SFC20220920-G132	Ganghwa	<i>act</i>	OP584025
	SFC20220920-G147	Ganghwa	<i>act</i>	OP584035
	SFC20220920-G155	Ganghwa	<i>act</i>	OP584017
	SFC20220920-G167	Ganghwa	<i>act</i>	OP584018
	SFC20220920-G183	Ganghwa	<i>act</i>	OP584028
	SFC20220920-G211	Ganghwa	<i>act</i>	OP584036
	SFC20220920-G241	Ganghwa	<i>act</i>	OP584029
	SFC20220920-G257	Ganghwa	<i>act</i>	OP584072
	SFC20220920-G311	Ganghwa	<i>act</i>	OP584019
	SFC20220920-G319	Ganghwa	<i>act</i>	OP584032
	SFC20220920-G342	Ganghwa	<i>act</i>	OP584031
<i>Cladosporium crousii</i>	SFC20220920-B076	Ganghwa	<i>act</i>	OP584088
	SFC20220920-D198	Ganghwa	<i>act</i>	OP584096
	SFC20220920-D200	Ganghwa	<i>act</i>	OP584120
	SFC20220920-D391	Ganghwa	<i>act</i>	OP584097
	SFC20220920-G209	Ganghwa	<i>act</i>	OP584131
<i>Cladosporium devikae</i>	SFC20220920-G286	Ganghwa	<i>act</i>	OP584089
	SFC20220920-G291	Ganghwa	<i>act</i>	OP584090
	SFC20170718-M12	Goseong	<i>act</i>	OP583956
	SFC20220920-D207	Goseong	<i>act</i>	OP584115
	SFC20220920-D244	Goseong	<i>act</i>	OP584103

Table 1 (continued)

Species	Strain name	Sample site	PCR region	Accession number
<i>Cladosporium dominicanum</i>	SFC20220920-D245	Goseong	<i>act</i>	OP584104
	SFC20220920-D285	Goseong	<i>act</i>	OP584023
	SFC20220920-D340	Goseong	<i>act</i>	OP584024
	SFC20220920-D380	Goseong	<i>act</i>	OP584116
<i>Cladosporium endoviticola</i>	SFC20190312-M02	Muan	<i>act</i>	OP583967
<i>Cladosporium floccosum</i>	SFC20220920-D254	Ganghwa	<i>act</i>	OP584098
	SFC20190612-M06	Ganghwa	<i>act</i>	OP583995
	SFC20220920-D349	Ganghwa	<i>act</i>	OP583998
	SFC20180917-M04	Ganghwa	<i>act</i>	OP583997
<i>Cladosporium halotolerans</i>	SFC20190612-M10	Ganghwa	<i>act</i>	OP583996
	SFC20220920-B130	Ganghwa	<i>act</i>	OP584121
	SFC20220920-C163	Ganghwa	<i>act</i>	OP583960
	SFC20220920-C164	Ganghwa	<i>act</i>	OP584122
<i>Cladosporium lentulum</i>	SFC20220920-B140	Ganghwa	<i>act</i>	OP583962
<i>Cladosporium macadamiae</i>	SFC20220920-D336	Ulsan	<i>act</i>	OP584095
	SFC20220920-D365	Ulsan	<i>act</i>	OP584094
	SFC20220920-B108	Ganghwa	<i>act</i>	OP584093
	SFC20220920-B135	Ganghwa	<i>act</i>	OP584091
<i>Cladosporium pseudocladosporioides</i>	SFC20170718-M11	Ganghwa	<i>act</i>	OP583969
	SFC20220920-D377	Ganghwa	<i>act</i>	OP584092
	SFC20220920-B441	Suncheon	<i>act</i>	OP584045
	SFC20220920-C176	Suncheon	<i>act</i>	OP584049
<i>Cladosporium puris</i>	SFC20220920-D142	Suncheon	<i>act</i>	OP584046
	SFC20220920-D295	Suncheon	<i>act</i>	OP584050
	SFC20220920-D315	Suncheon	<i>act</i>	OP584047
	SFC20220920-D335	Suncheon	<i>act</i>	OP584048
<i>Cladosporium ramotenellum</i>	SFC20220920-D358	Suncheon	<i>act</i>	OP584071
	SFC20220920-D374	Suncheon	<i>act</i>	OP584105
	SFC20180817-M20	Ganghwa	<i>act</i>	OP583954
	SFC20181014-M02	Ganghwa	<i>act</i>	OP584008
<i>Cladosporium rectoides</i>	SFC20190416-M09	Ganghwa	<i>act</i>	OP584011
	SFC20220920-D351	Ganghwa	<i>act</i>	OP584010
	SFC20220920-D415	Ganghwa	<i>act</i>	OP584009
	SFC20220920-B118	Ganghwa	<i>act</i>	OP583963
<i>Cladosporium sinense</i>	SFC20220920-B136	Ganghwa	<i>act</i>	OP584084
	SFC20220920-B137	Ganghwa	<i>act</i>	OP584075
	SFC20171120-M05	Ganghwa	<i>act</i>	OP584076
	SFC20220920-B466	Ganghwa	<i>act</i>	OP584079
<i>Cladosporium sp. 1</i>	SFC20220920-D073	Ganghwa	<i>act</i>	OP584081
	SFC20220920-D136	Ganghwa	<i>act</i>	OP584083
	SFC20220920-D266	Ganghwa	<i>act</i>	OP584086
	SFC20220920-D319	Ganghwa	<i>act</i>	OP584080
<i>Cladosporium sp. 1</i>	SFC20220920-D320	Ganghwa	<i>act</i>	OP584074
	SFC20220920-D321	Ganghwa	<i>act</i>	OP584085
	SFC20220920-D404	Ganghwa	<i>act</i>	OP584078
	SFC20220920-G085	Ganghwa	<i>act</i>	OP584077
<i>Cladosporium sp. 1</i>	SFC20220920-G087	Ganghwa	<i>act</i>	OP584087
	SFC20220920-G190	Ganghwa	<i>act</i>	OP584082
	SFC20180817-M16	Ganghwa	<i>act</i>	OP583955
	SFC20220920-B316	Muan	<i>act</i>	OP584039

Table 1 (continued)

Species	Strain name	Sample site	PCR region	Accession number
<i>Cladosporium</i> sp. 2	SFC20220920-B336	Muan	<i>act</i>	OP584040
	SFC20220920-B518	Muan	<i>act</i>	OP584042
	SFC20220920-C185	Muan	<i>act</i>	OP583957
	SFC20220920-D271	Muan	<i>act</i>	OP584043
	SFC20220920-D324	Muan	<i>act</i>	OP584051
	SFC20220920-D375	Muan	<i>act</i>	OP584044
	SFC20220920-D390	Muan	<i>act</i>	OP584102
	SFC20220920-D403	Muan	<i>act</i>	OP584113
	SFC20220920-B349	Muan	<i>act</i>	OP584068
	SFC20220920-G028	Muan	<i>act</i>	OP584069
	SFC20220920-G146	Muan	<i>act</i>	OP584070
<i>Cladosporium</i> sp. 3	SFC20220920-C167	Jeju	<i>act</i>	OP583965
<i>Cladosporium</i> sp. 4	SFC20190612-M07	Ganghwa	<i>act</i>	OP583959
<i>Cladosporium</i> sp. 5	SFC20220920-D363	Ganghwa	<i>act</i>	OP584133
<i>Cladosporium</i> sp. 6	SFC20190612-M20	Ganghwa	<i>act</i>	OP583953
<i>Cladosporium</i> sp. 7	SFC20220920-D039	Ganghwa	<i>act</i>	OP583951
	SFC20220920-D155	Ganghwa	<i>act</i>	OP584004
<i>Cladosporium</i> sp. 8	SFC20190612-M08	Muan	<i>act</i>	OP583952
<i>Cladosporium</i> sp. 9	SFC20220920-D345	Ganghwa	<i>act</i>	OP584111
<i>Cladosporium</i> sp. 10	SFC20220920-D211	Ganghwa	<i>act</i>	OP584132
<i>Cladosporium</i> sp. 11	SFC20220920-D213	Jeju	<i>act</i>	OP584123
	SFC20220920-D384	Jeju	<i>act</i>	OP584125
	SFC20220920-G272	Jeju	<i>act</i>	OP584124
<i>Cladosporium</i> sp. 12	SFC20171120-M08	Suncheon	<i>act</i>	OP583968
<i>Cladosporium</i> sp. 13	SFC20220920-B091	Ganghwa	<i>act</i>	OP584126
	SFC20181014-M03	Ganghwa	<i>act</i>	OP584127
	SFC20220920-G255	Ganghwa	<i>act</i>	OP584128
	SFC20220920-G365	Ganghwa	<i>act</i>	OP584129
<i>Cladosporium</i> sp. 14	SFC20180917-M02	Suncheon	<i>act</i>	OP583966
<i>Cladosporium sphaerospermum</i>	SFC20220920-G287	Suncheon	<i>act</i>	OP583961
<i>Cladosporium subtilissimum</i>	SFC20220920-D188	Ganghwa	<i>act</i>	OP584000
	SFC20220920-D189	Ganghwa	<i>act</i>	OP584001
	SFC20220920-D396	Ganghwa	<i>act</i>	OP584002
	SFC20220920-D406	Ganghwa	<i>act</i>	OP584003
<i>Cladosporium tenuissimum</i>	SFC20220920-B304	Muan	<i>act</i>	OP584119
	SFC20220920-B333	Muan	<i>act</i>	OP584054
	SFC20220920-B337	Muan	<i>act</i>	OP584055
	SFC20190514-M08	Muan	<i>act</i>	OP584041
	SFC20220920-C169	Muan	<i>act</i>	OP584060
	SFC20220920-C173	Muan	<i>act</i>	OP584065
	SFC20220920-C188	Muan	<i>act</i>	OP584067
	SFC20220920-C190	Muan	<i>act</i>	OP584062
	SFC20220920-C316	Muan	<i>act</i>	OP584063
	SFC20220920-C317	Muan	<i>act</i>	OP584056
	SFC20220920-D257	Muan	<i>act</i>	OP583958
	SFC20220920-D261	Muan	<i>act</i>	OP584064
	SFC20220920-D265	Muan	<i>act</i>	OP584057
	SFC20220920-D409	Muan	<i>act</i>	OP584066
	SFC20220920-G135	Muan	<i>act</i>	OP584061
	SFC20220920-G168	Muan	<i>act</i>	OP584058

Table 1 (continued)

Species	Strain name	Sample site	PCR region	Accession number
<i>Cladosporium xanthochromaticum</i>	SFC20220920-G337	Muan	<i>act</i>	OP584059
	SFC20180817-M01	Muan	<i>act</i>	OP584130
<i>Cladosporium xylophilum</i>	SFC20170919-M03	Jeju	<i>act</i>	OP583964
	SFC20220920-D327	Jeju	<i>act</i>	OP584099
	SFC20220920-D383	Jeju	<i>act</i>	OP584100
	SFC20220920-D413	Jeju	<i>act</i>	OP584012
<i>Clohesyomyces</i> sp. 1	SFC20220920-B432	Suncheon	ITS	OP597883
<i>Clonostachys miodochialis</i>	SFC20220920-B112	Ganghwa	ITS	OP597884
	SFC20220920-B267	Ganghwa	ITS	OP597885
	SFC20220920-B273	Ganghwa	ITS	OP597886
	SFC20220920-B538	Ganghwa	ITS	OP597887
	SFC20220920-B540	Ganghwa	ITS	OP597888
<i>Clonostachys</i> sp. 1	SFC20220920-G007	Muan	ITS	OP597889
<i>Clonostachys</i> sp. 2	SFC20220920-G131	Ganghwa	ITS	OP597890
<i>Coniothyrium</i> sp. 1	SFC20220920-C366	Suncheon	ITS	OP597892
<i>Cordana</i> sp. 1	SFC20220920-D408	Ulsan	ITS	OP597894
<i>Corollospora gracilis</i>	SFC20181014-M04	Goseong	ITS	OP597895
<i>Curvularia fallax</i>	SFC20220920-G399	Muan	ITS	OP597896
<i>Curvularia sorghina</i>	SFC20220920-G189	Ulsan	ITS	OP597897
<i>Curvularia spicifera</i>	SFC20170919-M10	Jeju	ITS	OP597898
<i>Cytospora predappioensis</i>	SFC20170919-M09	Jeju	ITS	OP597899
<i>Diaporthe</i> sp. 1	SFC20220920-G137	Ganghwa	<i>BenA</i>	OP589763
	SFC20220920-G210	Ganghwa	<i>BenA</i>	OP589764
	SFC20220920-G357	Ganghwa	<i>BenA</i>	OP589765
	SFC20180817-M21	Ganghwa	<i>BenA</i>	OP584187
	SFC20220920-C031	Suncheon	<i>BenA</i>	OP584189
<i>Didymella</i> sp. 2	SFC20181014-M07	Jeju	<i>BenA</i>	OP584188
<i>Didymella</i> sp. 3	SFC20190312-M08	Jeju	<i>BenA</i>	OP584190
<i>Didymella</i> sp. 4	SFC20220920-B507	Jeju	<i>BenA</i>	OP584191
<i>Didymosphaeria</i> sp. 1	SFC20171120-M06	Suncheon	ITS	OP597901
	SFC20220920-C103	Suncheon	ITS	OP597902
	SFC20220920-D051	Suncheon	ITS	OP597903
	SFC20220920-G139	Suncheon	ITS	OP597904
	SFC20220920-G029	Muan	ITS	OP597905
<i>Didymosphaeria</i> sp. 3	SFC20220920-G340	Ganghwa	ITS	OP597906
<i>Ectophoma</i> sp. 1	SFC20220920-B297	Muan	<i>BenA</i>	OP584177
	SFC20220920-B450	Muan	<i>BenA</i>	OP584178
<i>Epicoccum duchesneae</i>	SFC20190612-M01	Jeju	<i>BenA</i>	OP584186
<i>Epicoccum latiscollum</i>	SFC20220920-C130	Jeju	<i>BenA</i>	OP584179
	SFC20220920-C131	Jeju	<i>BenA</i>	OP584180
	SFC20220920-C132	Jeju	<i>BenA</i>	OP584185
	SFC20220920-C133	Jeju	<i>BenA</i>	OP584184
	SFC20220920-C134	Jeju	<i>BenA</i>	OP584182
	SFC20220920-C135	Jeju	<i>BenA</i>	OP584183
	SFC20220920-C138	Jeju	<i>BenA</i>	OP584181
	SFC20220920-D353	Ganghwa	<i>BenA</i>	OP584176
<i>Epicoccum layuense</i>	SFC20220920-G150	Muan	ITS	OP597907
<i>Exophiala</i> sp. 1	SFC20220920-G150	Muan	ITS	OP597907
<i>Furcaterigmium furcatum</i>	SFC20220920-C384	Suncheon	ITS	OP597908
<i>Fusarium fujikuroi</i>	SFC20220920-G038	Ganghwa	<i>tef1</i>	OP589767
<i>Fusarium incarnatum</i>	SFC20220920-C086	Jeju	<i>tef1</i>	OP589769

Table 1 (continued)

Species	Strain name	Sample site	PCR region	Accession number
<i>Fusarium oxysporum</i>	SFC20220920-G116	Jeju	<i>tef1</i>	OP584144
	SFC20220920-G356	Jeju	<i>tef1</i>	OP584145
	SFC20220920-G122	Muan	<i>tef1</i>	OP584141
	SFC20220920-G269	Muan	<i>tef1</i>	OP584143
	SFC20220920-G335	Muan	<i>tef1</i>	OP584142
<i>Fusarium proliferatum</i>	SFC20171120-M02	Muan	<i>tef1</i>	OP589768
<i>Fusarium solani</i>	SFC20220920-G361	Muan	<i>tef1</i>	OP589766
<i>Gibellulopsis piscis</i>	SFC20220920-B258	Muan	ITS	OP597909
	SFC20220920-B272	Muan	ITS	OP597910
	SFC20220920-B298	Muan	ITS	OP597911
	SFC20220920-C018	Muan	ITS	OP597912
	SFC20220920-G304	Muan	ITS	OP597913
<i>Gliomastix roseogrisea</i>	SFC20220920-B264	Muan	ITS	OP597914
<i>Hansfordia pulvinata</i>	SFC20220920-G156	Muan	ITS	OP597916
<i>Humicola olivacea</i>	SFC20220920-G006	Muan	ITS	OP597917
	SFC20220920-G245	Muan	ITS	OP597918
	SFC20220920-G312	Muan	ITS	OP597919
	SFC20220920-G334	Muan	ITS	OP597920
	SFC20220920-B537	Goseong	ITS	OP597921
<i>Humicola sardiniae</i>	SFC20220920-B543	Goseong	ITS	OP597922
	SFC20220920-G124	Goseong	ITS	OP597923
	SFC20220920-G411	Goseong	ITS	OP597924
	SFC20170919-M06	Jeju	ITS	OP597925
	SFC20170919-M08	Jeju	ITS	OP597926
<i>Ilyonectria liriodendri</i>	SFC20170919-M08	Jeju	ITS	OP597926
<i>Ilyonectria robusta</i>	SFC20170919-M08	Jeju	ITS	OP597926
<i>Lanzia</i> sp. 1	SFC20220920-B451	Suncheon	ITS	OP597928
<i>Lectera capsici</i>	SFC20220920-G347	Muan	ITS	OP597929
<i>Lophiostoma</i> sp. 1	SFC20220920-B326	Muan	ITS	OP597930
	SFC20220920-G011	Muan	ITS	OP597931
	SFC20190514-M03	Jeju	ITS	OP597932
	SFC20220920-B521	Jeju	ITS	OP597933
	SFC20220920-G141	Muan	ITS	OP597938
<i>Multiseptospora</i> sp. 1	SFC20220920-G141	Muan	ITS	OP597938
<i>Myrmecridium schulzeri</i>	SFC20220920-G326	Muan	ITS	OP597939
<i>Nemania diffusa</i>	SFC20190416-M14	Muan	ITS	OP597940
	SFC20220920-G154	Muan	ITS	OP597941
	SFC20220920-B245	Muan	ITS	OP597942
	SFC20220920-D291	Jeju	ITS	OP597943
	SFC20220920-B516	Jeju	ITS	OP597944
<i>Neocamarosporium</i> sp. 1	SFC20220920-B515	Jeju	ITS	OP597945
	SFC20220920-C048	Jeju	ITS	OP597946
	SFC20220920-D357	Ganghwa	ITS	OP597947
	SFC20220920-B295	Muan	ITS	OP597948
	SFC20220920-C337	Muan	ITS	OP597949
<i>Neostagonospora</i> sp. 1	SFC20220920-C339	Muan	ITS	OP597950
	SFC20220920-B573	Goseong	ITS	OP597951
	SFC20220920-B240	Muan	ITS	OP597952
	SFC20220920-B314	Muan	ITS	OP597953
	SFC20171120-M03	Muan	ITS	OP597954
<i>Neurospora terricola</i>	SFC20220920-G127	Suncheon	ITS	OP597955
<i>Niesslia tenuis</i>	SFC20220920-G321	Muan	ITS	OP597956
<i>Nigrospora</i> sp. 1	SFC20220920-G321	Muan	ITS	OP597956
<i>Ovatospora mollicella</i>	SFC20220920-G321	Muan	ITS	OP597956
<i>Paraconiothyrium</i> sp. 1	SFC20220920-B465	Suncheon	ITS	OP597957

Table 1 (continued)

Species	Strain name	Sample site	PCR region	Accession number
	SFC20170718-M09	Suncheon	ITS	OP597958
	SFC20220920-D313	Suncheon	ITS	OP597959
	SFC20220920-G375	Suncheon	ITS	OP597960
<i>Paraphaeosphaeria angularis</i>	SFC20190416-M15	Jeju	ITS	OP597961
<i>Paraphaeosphaeria sardoa</i>	SFC20220920-G061	Ganghwa	ITS	OP597962
<i>Paraphaeosphaeria</i> sp. 1	SFC20220920-G281	Ganghwa	ITS	OP597963
<i>Paraphoma radicina</i>	SFC20220920-B310	Muan	ITS	OP597964
	SFC20220920-C194	Muan	ITS	OP597965
	SFC20190416-M07	Muan	ITS	OP597966
<i>Paraphoma</i> sp. 1	SFC20220920-B079	Ganghwa	ITS	OP597967
	SFC20220920-B082	Ganghwa	ITS	OP597968
<i>Parasarocladium gamsii</i>	SFC20220920-B330	Muan	ITS	OP597969
	SFC20220920-C092	Muan	ITS	OP597970
	SFC20220920-C093	Muan	ITS	OP597971
	SFC20220920-C340	Muan	ITS	OP597972
<i>Parasarocladium</i> sp. 1	SFC20220920-G159	Muan	ITS	OP597973
<i>Parathyridaria</i> sp. 1	SFC20220920-B436	Suncheon	ITS	OP597974
<i>Penicillium acidum</i>	SFC102936	Suncheon	<i>BenA</i>	OP611710
	SFC20220920-B546	Suncheon	<i>BenA</i>	OP611711
<i>Penicillium allii</i>	SFC20220920-D001	Ulsan	<i>BenA</i>	OP611717
	SFC20220920-D002	Ulsan	<i>BenA</i>	OP611719
	SFC20220920-D410	Ulsan	<i>BenA</i>	OP611718
<i>Penicillium allsoppiae</i>	SFC20220920-B332	Muan	<i>BenA</i>	MK134666
	SFC20220920-B334	Muan	<i>BenA</i>	OP611749
<i>Penicillium aurantioviolaceum</i>	SFC20220920-B084	Ganghwa	<i>BenA</i>	OP611706
	SFC20220920-B099	Ganghwa	<i>BenA</i>	OP611707
	SFC20220920-B101	Ganghwa	<i>BenA</i>	OP611708
	SFC20220920-B463	Ganghwa	<i>BenA</i>	OP611709
<i>Penicillium bialowiezense</i>	SFC20220920-D005	Goseong	<i>BenA</i>	OP611728
	SFC20220920-D006	Goseong	<i>BenA</i>	OP611730
	SFC20220920-D337	Goseong	<i>BenA</i>	OP611729
	SFC20220920-D342	Goseong	<i>BenA</i>	OP611731
<i>Penicillium brasilianum</i>	SFC20220920-G459	Muan	<i>BenA</i>	OP611753
	SFC20220920-G460	Muan	<i>BenA</i>	OP611754
	SFC20220920-G461	Muan	<i>BenA</i>	OP611756
	SFC20220920-G510	Muan	<i>BenA</i>	OP611755
	SFC20220920-G534	Muan	<i>BenA</i>	OP611758
	SFC20220920-G559	Muan	<i>BenA</i>	OP611757
<i>Penicillium bussumense</i>	SFC20220920-B284	Muan	<i>BenA</i>	OP611698
<i>Penicillium citreosulfuratum</i>	SFC20170821-M07	Muan	<i>BenA</i>	OP611803
	SFC20200821-M02	Muan	<i>BenA</i>	OP611805
	SFC20200821-M03	Muan	<i>BenA</i>	OP611804
<i>Penicillium citrinum</i>	SFC20171019-M08	Muan	<i>BenA</i>	OP611784
	SFC20220920-B262	Muan	<i>BenA</i>	OP611785
	SFC20220920-B541	Muan	<i>BenA</i>	OP611789
	SFC20220920-C244	Muan	<i>BenA</i>	OP611787
	SFC20220920-C265	Muan	<i>BenA</i>	OP611788
	SFC20220920-C342	Muan	<i>BenA</i>	OP611786
<i>Penicillium corylophilum</i>	SFC20220920-B469	Suncheon	<i>BenA</i>	OP611806
	SFC20170718-M14	Suncheon	<i>BenA</i>	OP611807

Table 1 (continued)

Species	Strain name	Sample site	PCR region	Accession number
<i>Penicillium cremeogriseum</i>	SFC20200506-M19	Muan	<i>BenA</i>	OP611760
	SFC20220920-G039	Muan	<i>BenA</i>	OP611761
<i>Penicillium crustosum</i>	SFC20220920-B122	Ganghwa	<i>BenA</i>	OP611720
<i>Penicillium daejeonium</i>	SFC20220920-B252	Muan	<i>BenA</i>	OP611715
	SFC20220920-G491	Muan	<i>BenA</i>	OP611716
<i>Penicillium decaturense</i>	SFC20220920-C271	Ganghwa	<i>BenA</i>	OP611791
	SFC20190612-M03	Ganghwa	<i>BenA</i>	OP611792
	SFC20220920-D010	Ganghwa	<i>BenA</i>	OP611794
	SFC20220920-D065	Ganghwa	<i>BenA</i>	OP611793
	SFC20220920-D393	Ganghwa	<i>BenA</i>	OP611795
<i>Penicillium digitatum</i>	SFC20220920-C245	Jeju	<i>BenA</i>	OP611727
<i>Penicillium exsudans</i>	SFC20220920-B254	Muan	<i>BenA</i>	OP611713
	SFC20220920-B256	Muan	<i>BenA</i>	OP611714
	SFC20220920-B492	Muan	<i>BenA</i>	OP611712
<i>Penicillium fructuariae-cellae</i>	SFC20220920-B107	Ganghwa	<i>BenA</i>	OP611699
	SFC20220920-G436	Ganghwa	<i>BenA</i>	OP611700
	SFC20220920-G438	Ganghwa	<i>BenA</i>	OP611702
	SFC20220920-G454	Ganghwa	<i>BenA</i>	OP611705
	SFC20220920-G500	Ganghwa	<i>BenA</i>	OP611703
	SFC20220920-G521	Ganghwa	<i>BenA</i>	OP611701
	SFC20220920-G531	Ganghwa	<i>BenA</i>	OP611704
	SFC20220920-G177	Ganghwa	<i>BenA</i>	OP611759
<i>Penicillium globosum</i>	SFC20220920-B343	Muan	<i>BenA</i>	OP611790
<i>Penicillium hetheringtonii</i>	SFC20170718-M08	Ulsan	<i>BenA</i>	OP611752
<i>Penicillium janczewskii</i>	SFC20190514-M09	Ulsan	<i>BenA</i>	OP611750
	SFC20220920-G462	Muan	<i>BenA</i>	OP611777
<i>Penicillium javanicum</i>	SFC20220920-G233	Jeju	<i>BenA</i>	OP611697
<i>Penicillium jejuense</i>	SFC20220920-G505	Jeju	<i>BenA</i>	OP611695
	SFC20220920-G547	Jeju	<i>BenA</i>	OP611696
	SFC20220920-B445	Suncheon	<i>BenA</i>	OP611763
	SFC20220920-B473	Suncheon	<i>BenA</i>	OP611767
<i>Penicillium koreense</i>	SFC20220920-B475	Suncheon	<i>BenA</i>	OP611764
	SFC20220920-B477	Suncheon	<i>BenA</i>	OP611765
	SFC20220920-B479	Suncheon	<i>BenA</i>	OP611766
	SFC20220920-B490	Suncheon	<i>BenA</i>	OP611768
	SFC20220920-D289	Ganghwa	<i>BenA</i>	OP611733
<i>Penicillium madriti</i>	SFC20220920-G126	Suncheon	<i>BenA</i>	OP611748
<i>Penicillium malodoratum</i>	SFC20200821-M04	Muan	<i>BenA</i>	OP611808
<i>Penicillium menonorum</i>	SFC20220920-D344	Muan	<i>BenA</i>	OP611809
	SFC20170718-M07	Ulsan	<i>BenA</i>	OP611778
<i>Penicillium ochrochloron</i>	SFC20220920-B497	Ulsan	<i>BenA</i>	OP611779
	SFC20220920-G001	Muan	<i>BenA</i>	OP611734
<i>Penicillium olsonii</i>	SFC20220920-G004	Muan	<i>BenA</i>	OP611735
	SFC20220920-G005	Muan	<i>BenA</i>	OP611743
	SFC20220920-G225	Muan	<i>BenA</i>	OP611739
	SFC20220920-G246	Muan	<i>BenA</i>	OP611746
	SFC20220920-G247	Muan	<i>BenA</i>	OP611744
	SFC20220920-G259	Muan	<i>BenA</i>	OP611740
	SFC20220920-G382	Muan	<i>BenA</i>	OP611736
	SFC20220920-G383	Muan	<i>BenA</i>	OP611747

Table 1 (continued)

Species	Strain name	Sample site	PCR region	Accession number
	SFC20220920-G384	Muan	<i>BenA</i>	OP611737
	SFC20220920-G433	Muan	<i>BenA</i>	OP611745
	SFC20220920-G477	Muan	<i>BenA</i>	OP611738
	SFC20220920-G519	Muan	<i>BenA</i>	OP611741
	SFC20220920-G526	Muan	<i>BenA</i>	OP611742
<i>Penicillium ortum</i>	SFC20200506-M55	Goseong	<i>BenA</i>	OP611762
<i>Penicillium oxalicum</i>	SFC20220920-B109	Ganghwa	<i>BenA</i>	OP611780
	SFC20220920-B239	Ganghwa	<i>BenA</i>	OP611781
	SFC20220920-G149	Ganghwa	<i>BenA</i>	OP611783
	SFC20220920-G175	Ganghwa	<i>BenA</i>	OP611782
<i>Penicillium paneum</i>	SFC20220920-G558	Ganghwa	<i>BenA</i>	OP611725
<i>Penicillium raperi</i>	SFC20220920-B308	Muan	<i>BenA</i>	OP611769
	SFC20220920-B317	Muan	<i>BenA</i>	OP611770
	SFC20220920-G348	Muan	<i>BenA</i>	OP611772
	SFC20220920-G389	Muan	<i>BenA</i>	OP611773
	SFC20220920-G414	Muan	<i>BenA</i>	OP611774
	SFC20220920-G432	Muan	<i>BenA</i>	OP611771
<i>Penicillium roqueforti</i>	SFC20180817-M15	Ganghwa	<i>BenA</i>	OP611726
<i>Penicillium rubens</i>	SFC20171218-M02	Goseong	<i>BenA</i>	OP611721
	SFC20220920-B560	Goseong	<i>BenA</i>	OP611723
	SFC20220920-B569	Goseong	<i>BenA</i>	OP611724
	SFC20220920-D331	Goseong	<i>BenA</i>	OP611722
<i>Penicillium vallebormidaense</i>	SFC20220920-G026	Ganghwa	<i>BenA</i>	OP611810
<i>Penicillium</i> sp. 1	SFC20171120-M01	Muan	<i>BenA</i>	OP611751
<i>Penicillium sumatraense</i>	SFC20220920-B115	Ganghwa	<i>BenA</i>	OP611796
	SFC20220920-B287	Ganghwa	<i>BenA</i>	OP611801
	SFC20220920-G196	Ganghwa	<i>BenA</i>	OP611797
	SFC20220920-G415	Ganghwa	<i>BenA</i>	OP611798
	SFC20220920-G447	Ganghwa	<i>BenA</i>	OP611800
	SFC20220920-G472	Ganghwa	<i>BenA</i>	OP611799
<i>Penicillium terrigenum</i>	SFC20220920-B318	Muan	<i>BenA</i>	OP611802
<i>Penicillium virgatum</i>	SFC20190514-M07	Suncheon	<i>BenA</i>	OP611732
<i>Penicillium yunnanense</i>	SFC20220920-B544	Goseong	<i>BenA</i>	OP611775
	SFC20220920-G010	Goseong	<i>BenA</i>	OP611776
<i>Periconia</i> sp. 1	SFC20220920-B088	Ganghwa	ITS	OP597980
<i>Periconia</i> sp. 2	SFC20220920-B527	Jeju	ITS	OP597981
<i>Peroneutypa</i> sp. 1	SFC20180817-M25	Muan	ITS	OP597982
	SFC20190416-M05	Muan	ITS	OP597983
	SFC20220920-G205	Muan	ITS	OP597984
<i>Phaeoacremonium</i> sp. 1	SFC20220920-C385	Jeju	ITS	OP597985
<i>Phaeosphaeria</i> sp. 1	SFC20220920-B338	Muan	ITS	OP597986
<i>Phaeosphaeria</i> sp. 2	SFC20220920-D293	Ulsan	ITS	OP597987
	SFC20220920-D388	Ulsan	ITS	OP597988
	SFC20220920-D412	Ulsan	ITS	OP597989
<i>Phaeosphaeria</i> sp. 3	SFC20220920-C099	Jeju	ITS	OP597990
<i>Phaeosphaeria</i> sp. 4	SFC20220920-C179	Suncheon	ITS	OP597991
<i>Phaeosphaeria spartinae</i>	SFC20220920-B080	Ganghwa	ITS	OP597992
<i>Phialemoniopsis curvata</i>	SFC20220920-G140	Ganghwa	ITS	OP597998
	SFC20220920-G362	Ganghwa	ITS	OP597999
<i>Phialocephala dimorphospora</i>	SFC20170821-M09	Suncheon	ITS	OP598000

Table 1 (continued)

Species	Strain name	Sample site	PCR region	Accession number
<i>Pichia membranifaciens</i>	SFC20190612-M22	Ulsan	ITS	OP598001
<i>Plectosphaerella oratosquillae</i>	SFC20220920-D401	Ulsan	ITS	OP598002
	SFC20220920-G024	Ulsan	ITS	OP598003
	SFC20220920-G130	Ulsan	ITS	OP598004
	SFC20220920-G133	Ulsan	ITS	OP598005
	SFC20220920-G282	Ulsan	ITS	OP598006
<i>Preussia terricola</i>	SFC20220920-G242	Suncheon	ITS	OP598007
<i>Pringsheimia</i> sp. 1	SFC20220920-B081	Ganghwa	ITS	OP598008
	SFC20220920-G263	Ganghwa	ITS	OP598009
<i>Pseudocercospora adansoniae</i>	SFC20220920-G068	Ganghwa	ITS	OP598010
<i>Pseudogymnoascus roseus</i>	SFC20220920-G207	Ganghwa	ITS	OP598011
	SFC20220920-G289	Ganghwa	ITS	OP598012
<i>Pseudopithomyces rosae</i>	SFC20220920-C046	Jeju	ITS	OP598013
<i>Purpureocillium lilacinum</i>	SFC20171218-M01	Goseong	ITS	OP598014
<i>Pyrenochaetopsis leptospora</i>	SFC20220920-B078	Ganghwa	ITS	OP598015
	SFC20220920-B104	Ganghwa	ITS	OP598016
	SFC20220920-B498	Ganghwa	ITS	OP598017
	SFC20220920-G063	Ganghwa	ITS	OP598018
<i>Pyrenochaetopsis</i> sp. 1	SFC20220920-B280	Muan	ITS	OP598019
	SFC20220920-B345	Muan	ITS	OP598020
	SFC20220920-B348	Muan	ITS	OP598021
<i>Roussoella solani</i>	SFC20220920-B513	Jeju	ITS	OP598023
	SFC20220920-G107	Jeju	ITS	OP598024
<i>Roussoella</i> sp. 1	SFC20190312-M03	Suncheon	ITS	OP598025
	SFC20190312-M05	Suncheon	ITS	OP598026
	SFC20220920-B514	Suncheon	ITS	OP598027
	SFC20190612-M24	Suncheon	ITS	OP598028
<i>Sarocladium implicatum</i>	SFC20170821-M10	Suncheon	ITS	OP598029
	SFC20220920-G099	Suncheon	ITS	OP598030
	SFC20220920-G341	Suncheon	ITS	OP598031
<i>Sarocladium kiliense</i>	SFC20190612-M13	Jeju	ITS	OP598032
<i>Sarocladium</i> sp. 1	SFC20220920-B529	Jeju	ITS	OP598033
<i>Sarocladium strictum</i>	SFC20220920-B096	Ganghwa	ITS	OP598034
<i>Scolecofusarium ciliatum</i>	SFC20220920-G003	Muan	ITS	OP598036
<i>Scytalidium</i> sp. 1	SFC20220920-G153	Ganghwa	ITS	OP598037
<i>Setophaeosphaeria</i> sp. 1	SFC20220920-B435	Suncheon	ITS	OP598038
<i>Stachybotrys chartarum</i>	SFC20220920-D419	Ganghwa	ITS	OP598039
<i>Stagonosporopsis crystalliniformis</i>	SFC20220920-C195	Suncheon	ITS	OP598040
<i>Stemphylium vesicarium</i>	SFC20220920-B517	Jeju	ITS	OP598041
<i>Stephanonectria keithii</i>	SFC20220920-B434	Suncheon	ITS	OP598042
	SFC20220920-C042	Suncheon	ITS	OP598043
<i>Talaromyces aculeatus</i>	SFC20220920-G017	Muan	<i>BenA</i>	OP584164
<i>Talaromyces adpressus</i>	SFC20220920-G458	Ganghwa	<i>BenA</i>	OP584165
<i>Talaromyces amestolkiae</i>	SFC20220920-G498	Muan	<i>BenA</i>	OP584166
<i>Talaromyces aurantiacus</i>	SFC20220920-B123	Ganghwa	<i>BenA</i>	OP584162
	SFC20180817-M18	Ganghwa	<i>BenA</i>	OP584163
<i>Talaromyces diversiformis</i>	SFC20220920-G525	Muan	<i>BenA</i>	OP584167
<i>Teichospora</i> sp. 1	SFC20220920-G102	Muan	ITS	OP598044
	SFC20220920-B522	Jeju	ITS	OP598045
	SFC20190612-M18	Jeju	ITS	OP598046

Table 1 (continued)

Species	Strain name	Sample site	PCR region	Accession number
<i>Trichoderma afroharzianum</i>	SFC20220920-G019	Ganghwa	<i>tef1</i>	OP584149
	SFC20220920-G062	Ganghwa	<i>tef1</i>	OP584150
<i>Trichoderma asperellum</i>	SFC20180619-M24	Suncheon	<i>tef1</i>	OP584155
	SFC20220920-B480	Suncheon	<i>tef1</i>	OP584156
	SFC20220920-B481	Suncheon	<i>tef1</i>	OP584157
	SFC20220920-B484	Suncheon	<i>tef1</i>	OP584159
	SFC20220920-B491	Suncheon	<i>tef1</i>	OP584158
<i>Trichoderma guizhouense</i>	SFC20170919-M01	Jeju	<i>tef1</i>	OP584151
	SFC20190312-M12	Jeju	<i>tef1</i>	OP584152
<i>Trichoderma paratroviride</i>	SFC20220920-B462	Suncheon	<i>tef1</i>	OP584153
<i>Trichoderma simmonsii</i>	SFC20200604-M14	Ganghwa	<i>tef1</i>	OP584147
<i>Trichoderma songyi</i>	SFC20171120-M04	Muan	<i>tef1</i>	OP584161
<i>Trichoderma</i> sp. 1	SFC20220920-G109	Ganghwa	<i>tef1</i>	OP584154
<i>Trichoderma</i> sp. 2	SFC20220920-G258	Muan	<i>tef1</i>	OP584146
<i>Trichoderma</i> sp. 3	SFC20220920-G093	Suncheon	<i>tef1</i>	OP584148
<i>Trichoderma virens</i>	SFC20220920-G397	Muan	<i>tef1</i>	OP584160
<i>Trichothecium roseum</i>	SFC20220920-G158	Muan	ITS	OP598051
	SFC20220920-G256	Muan	ITS	OP598052
<i>Unguicularia</i> sp. 1	SFC20220920-B438	Suncheon	ITS	OP598054
<i>Verticillium klebahnii</i>	SFC20220920-C049	Suncheon	ITS	OP598055
<i>Zymoseptoria verkleyi</i>	SFC20220920-D398	Ulsan	ITS	OP598057
Basidiomycota				
<i>Antrodia sinuosa</i>	SFC20220920-D361	Ganghwa	ITS	OP597859
<i>Bjerkandera adusta</i>	SFC20220920-B500	Ulsan	ITS	OP597872
<i>Ceriporia lacerata</i>	SFC20220920-G027	Muan	ITS	OP597876
	SFC20220920-G182	Muan	ITS	OP597877
<i>Collybiopsis confluens</i>	SFC20220920-B098	Ganghwa	ITS	OP597891
<i>Coprinopsis urticicola</i>	SFC20220920-G073	Muan	ITS	OP597893
<i>Daedaleopsis confragosa</i>	SFC20220920-D318	Ganghwa	ITS	OP597900
<i>Gymnopus</i> sp. 1	SFC20220920-B501	Ulsan	ITS	OP597915
<i>Inocybe</i> sp. 1	SFC20220920-B534	Goseong	ITS	OP597927
<i>Peniophora bicornis</i>	SFC20220920-G032	Suncheon	ITS	OP597975
<i>Peniophora pseudoversicolor</i>	SFC20220920-B329	Muan	ITS	OP597976
<i>Peniophora</i> sp. 1	SFC20220920-B073	Ganghwa	ITS	OP597977
	SFC20220920-B325	Ganghwa	ITS	OP597978
	SFC20220920-G152	Ganghwa	ITS	OP597979
<i>Phanerochaete livescens</i>	SFC20220920-G217	Ulsan	ITS	OP597993
	SFC20220920-G231	Ulsan	ITS	OP597994
	SFC20220920-G232	Ulsan	ITS	OP597995
	SFC20220920-G367	Ulsan	ITS	OP597996
<i>Phanerochaete</i> sp. 1	SFC20220920-C369	Suncheon	ITS	OP597997
<i>Rhodotorula mucilaginosa</i>	SFC20220920-B138	Ganghwa	ITS	OP598022
<i>Schizophyllum commune</i>	SFC20220920-G338	Muan	ITS	OP598035
<i>Trametes versicolor</i>	SFC20220920-B511	Jeju	ITS	OP598047
<i>Trichosporon ovoides</i>	SFC20220920-C004	Muan	ITS	OP598048
	SFC20220920-G320	Muan	ITS	OP598049
	SFC20220920-G333	Muan	ITS	OP598050
<i>Xeromphalina cauticinalis</i>	SFC20220920-B505	Ulsan	ITS	OP598056
Mucoromycota				
<i>Absidia cuneospora</i>	SFC20170718-M10	Goseong	ITS	OP597821

Table 1 (continued)

Species	Strain name	Sample site	PCR region	Accession number
<i>Actinomucor elegans</i>	SFC20220920-G143	Ulsan	ITS	OP597832
<i>Mucor circinelloides</i>	SFC20220920-B266	Muan	ITS	OP597934
	SFC20190312-M04	Muan	ITS	OP597935
	SFC20220920-C088	Muan	ITS	OP597936
<i>Mucor</i> sp. 1	SFC20220920-G288	Suncheon	ITS	OP597937
<i>Umbelopsis</i> sp. 1	SFC20220920-B257	Muan	ITS	OP598053

Fungal phyla are in bold font

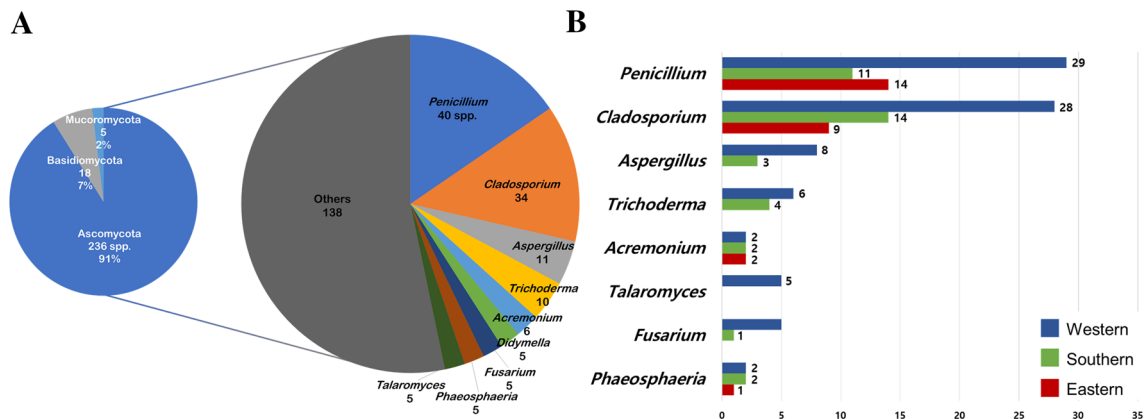


Fig. 2 **A** The proportion of isolated fungal species by phylum and genus. **B** Predominant fungal species diversity from three seashores of the Korean Peninsula

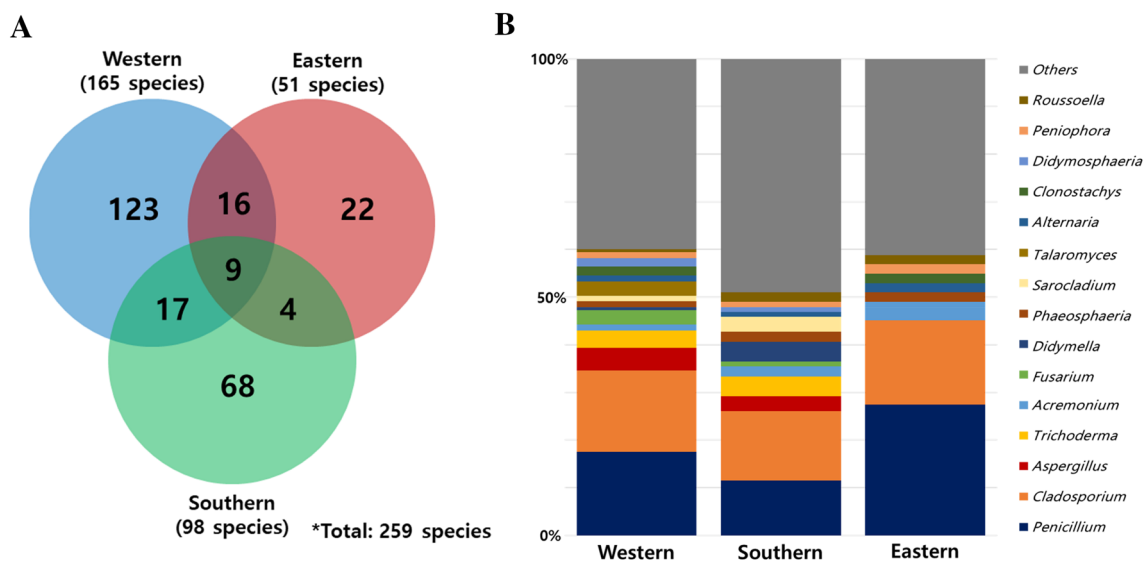


Fig. 3 **A** Venn diagram of the total, unique, and shared fungal species obtained from each seashore. **B** Proportions of fungi by seashores (western, southern, eastern)

Further, 123 species were isolated only from the western seashore, and 68 and 22 species were isolated only from the southern and eastern seashores, respectively. *Cladosporium*

and *Penicillium* were found abundantly in all areas (Fig. 3B). Among the 34 species of *Cladosporium*, 23 were uniquely detected from only one of the seashores: 18 from the western

seaside and four from the southern seaside; *C. macadamiae* was only detected from the eastern seaside. For *Penicillium*, 18, five, and four unique species were detected in the western, southern, and eastern seashores, respectively. Additionally, 11 species of *Aspergillus* were found, of which 8 and 3 were respectively found only on the western and the southern seaside. Other species also showed apparent distributional differences depending on the seaside.

The alpha diversity indices, species abundance, Chao1 richness, and Shannon's diversity were all highest in the western seaside and lowest in the eastern seaside (Fig. 4A). However, statistically significant differences were not found in the ANOVA and post-hoc tests between seashores. A clear separation between seashores was found in the CAP ordination plot, but significant differences were not found between seashores for the different ocean currents in the PERMANOVA test ($p=0.075$, $R^2=0.095$; Fig. 4B).

Discussion

Beach sands are exposed to a highly dynamic environment that changes daily or even with the tidal cycle. Quantitative research showed that beach sands of the Korean Peninsula possess a high diversity of arenicolous fungi despite the nutrient-poor sand dune with high salinity, fluctuating temperature, and tidal currents. Notably, the fungal diversity on the coasts of the Korean Peninsula was higher than on other beach sands (Ghinsberg et al., 1994; Vogel et al., 2007; Walker & Robicheau, 2021; Yee et al., 2016). Most species isolated in this study were classified into the Ascomycota phylum. Ascomycota species are major marine fungi, commonly found in the marine environment, such as sediment, seawater, and salt marsh (Calabon et al., 2021; Tisthammer et al., 2016; Velez et al., 2021), and many are facultative

marine fungi. These marine fungi are responsible for decomposing woody substrates and other marine organisms (Hyde et al., 1998; Patyshakuliyeva et al., 2019).

Penicillium and *Cladosporium* were the most abundant genera in the beach sand. *Penicillium* species have been repeatedly reported in various marine environments, such as sand, seawater, and macroalgae (Park et al., 2014, 2019). *Penicillium* strains isolated from the intertidal zone have cellulase and protease activity, indicating that they act as decomposers in marine environments (Park et al., 2019). *Cladosporium* species inhabit marine environments, such as sediments, seawater, seaweed, and mangrove forests for their halotolerant and osmotolerant activities (Araújo et al., 2020; Cunliffe et al., 2017; Marchese et al., 2021; Thirumalanadhuni & Palempalli, 2018; Zalar et al., 2007).

Following the classification of marine fungi (obligate and facultative), Velez et al. (2022) also categorized MAFs into obligate and facultative MAFs: obligate MAFs complete their life cycles in the intertidal and subtidal region of marine sandy beaches, whereas facultative MAFs are terrestrial- and freshwater-borne fungi with active growth in sandy beaches. Only one obligate MAF, *Corollospora gracilis*, was identified in this study. *Corollospora* species are mostly found in marine habitats, especially sand grains and shell fragments (Kohlmeyer & Kohlmeyer, 1979; Velez et al., 2022). *Corollospora gracilis* also form ascoma and attach to thick and hard materials such as sand grains (Hsieh et al., 2007). *Paradendryphiella arenariae* is the only facultative MAF species reported in Korea (Lee et al., 2019b), but it was not detected in this study. The MAF types of the remaining isolated species are unknown, i.e., whether they are obligate or facultative. Nonetheless, many fungal species, including *Penicillium* and *Cladosporium*, are frequently found in marine environments such as beach sand. Thus, as suggested by Jones et al. (2015) and Velez et al. (2022),

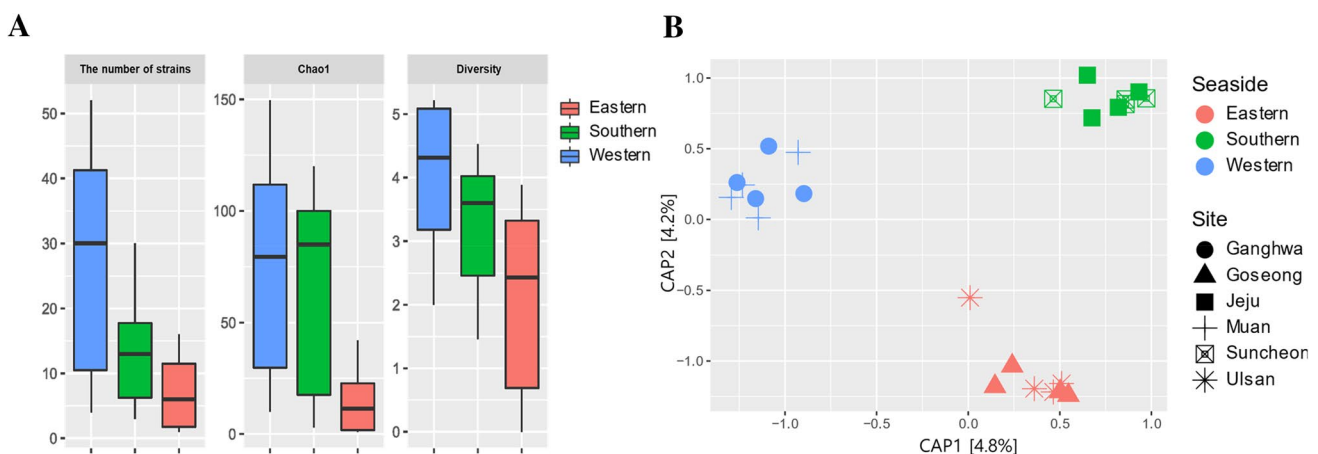


Fig. 4 **A** Alpha diversity indices of fungi from the three seashores. **B** Constrained analysis of principal coordinates (CAP) plots for fungal communities based on Jaccard distance

fungi repeatedly isolated from beach sand environments may be reevaluated as facultative MAFs.

Some species are predicted to have come from the terrestrial inland. *Alternaria angustiovoidea* species were known to have pathogenicity on coastal sand inhibiting plants, leafy spurge, which are distributed along the coast of the Korean Peninsula (Yang et al., 1993). Other common species, such as *Cladosporium anthropophilum* and *Penicillium fructuariae-cellae* inhabit terrestrial niches (Lee et al., 2019a; Lorenzini et al., 2019). Isolates belonging to Basidiomycota and Mucoromycota were mostly saprotrophic fungi, which are commonly found in decayed woods, leaf litter, or soil in surrounding forests. These fungi may be introduced to beach sand by other organisms or wind and survive the harsh conditions in beach sands in dormant states or as spores (Mysyakina et al., 2016; Nguyen, 2018).

The different composition and number of fungi by seashores may be explained by the differential characteristics of each seashore. GH and MA in the West Sea and SC in the South Sea, with high biodiversity, have wide tidal flats beside the beach sand. Meanwhile, the species diversity is low in GS and US in the East Sea and JJ in the South Sea, where all three sites only consist of beach sand. The tidal flats are biodiversity hotspots and have high microbial diversity (Li et al., 2019; Lv et al., 2016; Ryu et al., 2011). Therefore, the presence of a tidal flat may have influenced the MAF abundance and diversity of the nearby beach sands.

In addition to the coastal characteristics, the dynamic ecosystems of the intertidal zone are usually influenced by natural forces, such as ocean currents, wind (Brand et al., 2020), or input of adjacent environments (Colombini & Chelazzi, 2003). Similarly, natural forces seem to affect marine fungi inhabiting beach sands. As mentioned above, some species appear to be of terrestrial origin. However, most terrestrial Ascomycota species are frequently reported in marine environments. They are likely to have settled on beach sands by ocean currents. Therefore, we isolated fungi from three seashores, considering the ocean currents. Only 9 of 259 species were found in all three seashores, and many species were found unique to each seashore.

In *Penicillium*, 27 out of 40 species were distributed differently depending on the coast. For example, *Penicillium jejuense*, first reported from Jeju Island located in the southern Korean Peninsula (Park et al., 2015b), was detected only from the southern seashore in this study. *Penicillium menonorum* strains were found exclusively in the western seashore in this study; the species were also found in a tidal flat adjacent to the sampling site (Park et al., 2020). A similar result was found in our previous study: the *Penicillium* community displayed a significant variation relative to the seashore (western and southern coast; Park et al., 2019). The obligate MAF, *Corollospora gracilis*, was found only in the East Sea in this study and a

previous study (Lee et al., 2019b). Given that distribution of many marine-inhabiting species is affected by ocean currents (Li et al., 2018; Nakagiri et al., 1999; Park et al., 2019), our results show that the composition of MAFs varied by the different ocean currents flowing along each coast. However, the sampling site exerted no statistically significant effect on the fungal community. This might be because fungi of terrestrial origin were included in the statistical analysis. A more precise conclusion may be drawn when the MAFs of marine origin are clearly defined.

In conclusion, our study provides information on MAFs associated with three different seashores on the Korean Peninsula. Using a culture-based approach, we isolated 603 fungal strains and identified them as 259 fungal species based on phylogenetic analysis. These results indicate that many MAFs inhabit the beach sand, and each seashore has a distinct fungal composition. The abundance and diversity of MAFs were influenced by the presence of the tidal flat, and the compositions of MAFs were shaped by the ocean currents. By extending the list of the Korean arenicolous fungal species, this study provides a basis for further research on arenicolous fungal communities and distributions on seashores.

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Data availability The authors confirm that the data supporting the findings of this study are available within this article.

Declarations

Conflict of interest The authors have no conflict of interest to report.

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