The high diversity of *Scedosporium* and *Lomentospora* species and their prevalence in human-disturbed areas in Taiwan

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Abstract

Scedosporium and *Lomentospora* are important opportunistic pathogens causing localized or disseminated infection in humans. Understanding their environmental distribution is critical for public hygiene and clinical management. We carried out the first environmental survey in urbanized and natural regions in Taiwan. Overall, *Scedosporium* and *Lomentospora* species were recovered in 132 out of 267 soil samples (48.5%) across Taiwan. We morphologically and molecularly identified four *Scedosporium* species and one *Lomentospora* species. All four major clinical relevant species were isolated with high frequency, i.e. *S. apiospermum* (41.7%), *S. boydii* (28.8%), *L. prolificans* (12.3%), and *S. aurantiacum* (4.9%); a clinically minor species, *S. dehoogii*, had moderate incidence (12.3%). These fungal species have high incidence in urban (48%) and hospital (68%) soil samples, and have limited distribution in samples from natural regions (5%). Multivariate analysis of the fungal composition revealed strong evidence of the preferential distribution of these fungi in urban and hospital regions compared to natural sites. In addition, strong evidence suggested that the distribution and abundance of these fungal species are highly heterogeneous in the environment; samples in vicinity often yield varied fungal communities. Our results indicated that these fungal species are prevalent in Taiwan and their occurrences are associated with human activities. Hygiene sensitive places such as hospitals should be particularly aware of the high frequency of the clinical relevant species.

1. Introduction

Scedosporium and *Lomentospora* are two fungal genera that accommodate pathogenic species to immunocompromised and occasionally immunocompetent hosts. These fungal pathogens cause a broad range of clinical manifestation including colonization of respiratory tract, cutaneous infections, allergic reactions, and severe localized or disseminated mycoses. Mortality rates of infected hosts are generally high. In a meta-analysis of 264 infection causes, mortality rate was reported at an average of 22.2% in immunocompromised and of 14% in immunocompetent patients (1). In disseminated infections, mortality rate can be extreme as high as up to 80% (2). Treatments of *Scedosporium* and *Lomentospora* are challenging due to their low susceptibility to many current antifungal drugs such as 5-flucytosine, amphotericin B, and triazole drugs (2). In conjunction with their prevalence in the environment, *Scedosporium* and *Lomentospora* are imperative, emerging pathogens that call for research input in improving the diagnostic methods, developing effective therapies, and systematically surveying their distribution in the environment.

Scedosporium and *Lomentospora* are ubiquitous soil dwellers in temperate regions and are less frequently encountered in tropics (3, 4). Their distribution in the environment is often associated with nutrient-rich substrates such as agricultural and garden soils (3, 5), crude oil-contaminated soil (6), and manure of livestock, poultry or cattle (7–9). In addition, they can be isolated from low aerated and high osmotic substrates such as sewage sludge (10, 11), polluted pond bottoms (12), brackish water (13), coastal tidelands (14), and wastewater treatments (15, 16). Their prevalence in soil environments manifests in the cases of their occurrence in tissues of small wildlifes such as lizards (17), gerbils (18), donkey (19), and pigeons (20). In contrast, surveys of their occurrence in indoor water and air samples indicated that they are limited distributed in these samples (10, 12, 21, 22), while again, are

63 abundant in the soil of potted plants (21). Due to their prevalence in human active regions,
64 *Scedosporium* was proposed as an indicator species for anthropogenic impacts (23). Given
65 the pathogenic nature of these fungi, their occurrence in the environment are of concern,
66 especially in hospital and indoor settings, where they are posing potential hazard to people
67 with chronic respiratory disease and/or immunocompromised (24, 25).

68 Different *Scedosporium* and *Lomentospora* species pose different clinical relevances. Four
69 species, *S. boydii*, *S. apiospermum*, *S. aurantiacum* and *L. prolificans* are the most clinically
70 relevant species that account for most infections in reported cases (26, 27). With a few case
71 reports, *S. dehoogii* can cause subcutaneous and osteoarticular infections (28, 29). To
72 effectively distinguish clinical species from other clinically minor species, recent efforts have
73 made substantial taxonomic revisions and species delimitation of *Scedosporium* and
74 *Lomentospora* based on their morphological and molecular distinction (3, 30, 31). To date,
75 there are 13 distinct *Scedosporium* species: *S. americanum*, *S. apiospermum*, *S. aurantiacum*,
76 *S. boydii*, *S. cereisporum*, *S. dehoogii*, *S. desertorum*, *S. haikouense*, *S. hainanense*, *S.*
77 *minutisporum*, *S. multisporum*, *S. rarisporum*, *S. sanyaense*. Three species, *S. ellipsoideum*,
78 and *S. fusoideum*, *S. angustum*, are hypothesized cryptic species in the *S. boydii* species
79 complex but without provision of proper nomenclature requirements, and therefore invalid
80 (32). *Lomentospora* accommodates two species including *L. prolificans* and a recently
81 reported *L. valparaisensis* (33).

82 Research on their environmental distributions, compared to the clinical studies (e.g.
83 pathology, diagnosis, antifungal resistance), have been less emphasized. To date, there were a
84 few systematic surveys conducted in Australia (34), Europe (35, 36), South America (37, 38),
85 Africa (39), and Southeast Asia (40, 41). These studies have revealed a high variation of
86 species assemblies among samples, locations, and countries [see reviews such as Luplertlop

87 (2018) (42) and Rougeron et al (2018)]. This, coupled with a few non-targeted environmental
88 disclosures of these species in close proximity to human living habitats (5, 22, 43, 44), has
89 emphasized the importance of recognizing these potential infection sources in the
90 environment.

91 Studies of *Scedosporium* and *Lomentospora* species in Taiwan are limited. There were only a
92 few clinical case reports (45–52) and an environmental survey (25). This study, therefore,
93 aimed to survey the occurrence of these species in the soil environment across Taiwan. To
94 assess the risk factor of these species in varied facilities, we compared the species distribution
95 between natural and urbanized areas. We explicitly tested: (1) Do human-disturbed regions
96 accommodate more fungal species than in natural areas? (2) Do hygiene-sensitive areas (e.g.
97 hospital) harbor more fungal species compared to other urbanized regions?

98 2. Materials and Methods

99 2.1 Sampling sites

100 During 2014 to 2016, we collected soil samples from 79 locations across Taiwan (Table 1).
101 Sampling sites were selected to represent different levels of human activities (urban and
102 natural); in particular, we stressed the hospital samples as another sub-category in urban
103 samples as we wanted to highlight the distribution of these potential opportunistic fungi in the
104 hygiene sensitive places. In each site,1 – 14 sampling units were randomly chosen. For each
105 sampling unit, five points with 10 – 20 cm intervals from the center were randomly selected
106 to represent the fungal community of each unit. Soil was sampled with a metal spatula,
107 sterilized with 70% ethanol between samples to avoid cross contamination. Soil was sampled
108 at a depth of 7 – 10 cm beneath the soil surface, put in a sterile plastic bag and gently

109 squeezed to mix; the pooled soil sample was then filled in a 50 ml sterile Falcon tube. Soil
110 samples were stored at 4 °C until the fungal isolation.

111 2.2 Fungal isolation and fungal burden determination

112 For each soil sampling unit, ten grams of soil was air dried at room temperature for 1 – 2
113 days, placed in a 100 ml flask and homogenized with 90 ml sterilized water with 1 – 2 drops
114 of Tween 20. The mixture was thoroughly vortexed and left to stand for 15 minutes. 250 µl of
115 suspension of mixture were inoculated onto five plates of modified *Scedosporium* selective
116 medium (SceSel+) (53), comprised of malt extract, 6.25 g; maltose, 6.25 g; mono-potassium-
117 phosphate, 1.25 g; yeast extract, 1.0 g; magnesium sulfate heptahydrate, 0.625 g; soy
118 peptone, 0.625 g; chloramphenicol, 0.1 g; streptomycin sulfate, 0.1 g; dichloran, 2 mg;
119 benomyl, 6 mg; agar, 20.0 g; and reverse osmosis water, 990 ml. Plates were incubated at
120 37°C for 5 – 7 days and inspected at intervals for the emergence of characteristic colonies of
121 *Scedosporium*. All *Scedosporium* colonies on five plates of each sampling unit were counted,
122 from which the fungal burdens were determined based on the mean value of CFU per gram of
123 soil dry weight.

124 2.3 DNA extraction, PCR, sequencing, and phylogeny reconstruction

125 Fungal tissues (5 – 20 mg) were lysed using mechanical beads (mix of 1 mm and 0.5 mm
126 beads at 1:1 ratio) beating at 1800 rpm for 4 min using a Retsch mixer mill MM400. DNA
127 extraction of the lysed cells were carried out using ZymoBIOMICS™ (CAT#D4306) with a
128 ZiXpress 32 automated nucleic acid purification instrument following the manufacturer's
129 instructions. Quantity and quality of eluted DNA were measured using Qubit dsDNA BR
130 Assay kit and Qubit Flex Fluorometer 4.0 (Thermo Fisher Scientific) following the
131 manufacturer's instructions.

132 For molecular identification, we employed the Multi-Locus Sequence Typing (MLST)
133 approach (54) and amplified four housekeeping gene loci including internal transcribed
134 spacer (ITS), β-tubulin (TUB), RNA polymerase II second largest subunit (RPB2), and
135 calmodulin (CAL). Primer pairs and their references used for PCR amplification are shown in
136 Table S1 (54–61). Amplification was performed with a two-step barcoding approach
137 according to Herbold et al. (62). The first-step PCR reaction mixture volume was 25 µl,
138 consisted of 1 µl of DNA template, 1 µl of each primer, 12.5 µl of 2X Tools Supergreen PCR
139 master mix (CAT#TTC-PA31-10), and 9.5 µl of ddH_2O. Amplification were carried out as
140 following steps: initial denaturation at 95 °C for 2 min, 25 cycles with denaturation at 95 °C
141 for 30 s, annealing at 64 – 66 °C for 30 s, primer extension at 72 °C for 1 min, and final
142 extension step was 7 min at 72 °C. The second-step PCR reaction mixture was 25 µl,
143 consisted of 1 µl of the first-step DNA product as template, 2.5 µL pre-mixed barcoded
144 primers, 10.75 µL of 2X Tools Supergreen PCR master mix, and 10.75 µl of ddH_2O. The
145 barcoded amplification products were purified using Ampure Xp Beads with 0.4X product to
146 bead volume ratio, both procedures followed the manufacturer's protocol. Sequencing was
147 carried out on a Oxford Nanopore Technologies GridION sequencer using the manufacturer's
148 library preparation kit.

149 We reconstructed the phylogeny of the isolated species using their concatenated ITS and β-
150 tubulin genes. We retried sequences of type specimens of *Scedosporium* and *Lomentospora*
151 species from NCBI. Sequences of *Petriellopsis africana* (CBS311.72), *Petriella setifera*
152 (CBS 385.87), *Petriella sordida* (CBS 144612) were selected as the outgroup. We carried out
153 the phylogenetic analysis using an online phylogenetic service platform NGPhylogeny.fr
154 (63). Concatenated sequences were aligned using MAFFT with automatic flavor (64).
155 Phylogenetic informative regions were selected using Block Mapping and Gathering with
156 Entropy, a sliding window size of 3, and maximum entropy of 0.5 (65). Phylogenetic trees

157 were reconstructed using MrBayes (66) with recommended partition parameters. Two
158 MCMC runs of four chains were executed simultaneously from a random starting tree for
159 1000000 generations, every 500 generations were sampled resulting in 2000 trees, and 500
160 trees were discarded during burn-in. Posterior probabilities were estimated from the retained
161 1501 trees. Trees were visualized using Interactive Tree of Live version 4 (67).

162 2.4 Community analysis

163 We hypothesized that *Scedosporium* and *Lemontospora* species are more abundant in human-
164 ditrubed regions than in natural regions. To test this hypothesis, we conducted a distance-
165 based permutational multivariate analysis of variance (PERMANOVA) between the species
166 distance matrix of urban and natural samples. This test measures if groups of observations
167 differ in their composition. From our hypothesis, we expected to see a significant difference
168 of species composition between urban and natural samples. The test was implemented on a
169 Euclidean distance matrix using adonis() function of the vegan package for R (68). We then
170 carried out a PERMANOVA pairwise post hoc test using pairwise.perm.manova() on the
171 species distance matrix to test the differences of groups pairwisely (69). We further
172 conducted a homogeneity test on the species community matrix using betadisper() function.
173 Because the betadisper method is less sensitive to the variances among groups, it can help
174 justify the significant result from PERMANOVA that is a result of compositional difference
175 between samples, rather than within group variations. We presented Rsq and P-values and
176 discussed their inferences using the language of "evidence" following the recommendation in
177 Muff et al. (70)

178 To test for the effects of detecting *Scedosporium* and *Lomentospora* species in each location,
179 location types (i.e. urban, hospital, and natural), and each sampling unit, we conducted a
180 linear model-based analysis of the recovered species assemblage. We used the manyglm()

181 function of the mvabund package of R (71) to fit individual negative binomial linear models
182 for the species abundance of each detected fungal species. This approach provides an overall
183 multivariate test of the effect of location and location type on the composition of the
184 recovered fungal assemblage, as well as individual tests of the location, location types, and
185 sampling units on the abundance of each fungal species with adjusted P-value to account for
186 multiple comparisons. Three models were tested: (1) the effect of location type, (2) the
187 effects of location type, location, and their interaction, and (3) the effects of location,
188 sampling unit, and their interaction.

189 3. Results

190 3.1 Fungal isolation and fungal burden determination

191 164 *Scedosporium* and *Lomentospora* isolates were recovered from 267 sampling units in 79
192 locations, including 67 urban sites, six hospitals, and six natural sites across Taiwan (Table
193 1). The presence and abundance of these fungal species seems to be highly associated with
194 human activities. They were detected in 48% of urban samples, 68% of hospital samples, and
195 5% of natural samples (Fig. 1A). Likewise, the highest fungal burden was revealed in
196 hospital samples with average 20.8 CFU/g, followed by urban samples with 10.29 CFU/g; in
197 contrast, natural samples had only 0.11 CFU/g.

198 We identified five *Scedosporium* and *Lomentospora* species based on their morphological
199 and molecular characteristics, they were *S. apiospermum*, *S. boydii*, *S. aurantiacum*, *S.*
200 *dehoogii*, and *L. prolificans*. Of all 164 isolates, the *S. apiospermum* was the most frequently
201 recovered species (n = 68, 41.7%), followed by *S. boydii* (n = 47, 28.8%), *L. prolificans* (n =
202 21, 12.3%), *S. dehoogii* (n = 20, 12.3%), and *S. aurantiacum* (n = 8, 4.9%) (Fig. 1B). The

203 occurrence of these fungal species among locations were highly varied (Fig. 2 & 3). All five
204 species were detected in urban samples, ranging from one species in 14 locations, two species
205 in 11 locations, three species in 10 locations, four species in three locations, and all five
206 species in Tunghai University. All hospital samples revealed the occurrence of these fungal
207 species, ranging from one species in Linkou Chang Gung Memorial Hospital, two species in
208 Taichung Tri-service Hospital, three species in four hospitals (Taichung Veterans Hospital,
209 Taichung Hospital, Taichung Chung Shan Hospital, and China Medical University). In
210 contrast, *S. apiospermum* was the only species recovered from the natural samples from
211 Lotus Pond in Nantou.

212 Notably, the detected five fungal species exhibited some exceptionally high fungal burdens in
213 varied locations. For example, high fungal burden of *S. apiospermum* were detected in five
214 sampling locations including the British Consulate at Takow (365 CFU/g), Chishang Hakka
215 Cultural Park (250 CFU/g), Rushan Visitor Center (186 CFU/g), Meilun (112 CFU/g), and
216 Taichung Park (106 CFU/g). *Lomentospora prolificans* was high in three locations, they were
217 Taichung Veterans Hospital (325 CFU/g), Taichung Park (313 CFU/g), and Taichung
218 Hospital (149 CFU/g). *Scedosporium boydii* was high in Chishang Hakka Cultural Park (250
219 CFU/g). *Scedosporium aurantiacum* was abundant in Rushan Visitor Center (183 CFU/g),
220 and *Scedosporium dehoogii* showed it abundance in the British Consulate at Takow (460
221 CFU/g) (Figure 3).

222 3.2 Fungal community distribution analysis

223 Our analysis indicated there was an evident variation in the species composition of
224 *Scedosporium* and *Lomentospora* within and between locations. Overall, there was strong
225 evidence for the species composition in different location types (i.e. urban, hospital, and
226 natural samples), while it accounted for a limited portion of the explained variation (adonis:

227 df=2, F=5.3980, R^2=0.0375, P=0.001). While explaining much of the compositional
228 difference, there was no evidence showing the species composition varied among locations
229 (adonis: df=75, F=1.0991, R^2=0.2870, P=0.245)(Table 2). In a pairwise PERMANOVA
230 analysis, species composition in natural samples was distinct from that in urban and hospital
231 samples, while no difference was detected between the urban and hospital samples (Table 3).
232 The homogeneity test further indicated that species assemblage between natural-urban and
233 natural-hospital samples were significantly different in their homogeneity; instead, no
234 dispersion effect was found between urban and hospital samples (Figure 4) (betadisper: df=2,
235 F=9.8585, P=7.3809e-05). The dissimilarity of species composition was also indicated by the
236 clustering of natural samples, which were separated from the urban and hospital samples, on
237 the NMDS plot (Figure 5). Altogether, these results suggested that *Scedosporium* and
238 *Lomentospora* had different composition profiles in natural regions compared to human-
239 dominated regions, i.e. urban and hospital samples.

240 General linear model-based analysis indicated a evident effect of location types (i.e. urban,
241 hospital, and natural samples) on the multivariate composition of the recovered *Scedosporium*
242 and *Lomentospora* assemblages (P = 0.001) (Table 4, model 1). In addition, the univariate
243 test indicated that *S. apiospermum* (P = 0.006), *S. boydii* (P = 0.007), *L. prolificans* (P =
244 0.007), and *S. dehoogii* (P = 0.006) showed moderate-strong evidence of its preferred
245 distribution in urban regions (including urban and hospital site) (Table 5, model 1). Similar to
246 the result of PERMANOVA analysis, we found no evidence that the recovered fungal
247 composition was explained by location (P = 0.582) and its interaction term with location type
248 (P = 0.798) (Table 4, model 2). In the further test using location and sampling unit as factors
249 (model 3), we found moderate-strong evidence of the location effect (P = 0.022) and strong
250 evidence of the sampling unit effect (P = 0.001) on the recovered fungal composition.
251 Furthermore, there was strong evidence indicating that *S. apiospermum* is preferentially

252 recovered from certain sampling units ($P = 0.001$), and moderate-strong evidence for *S.*
253 *boydii* (P = 0.032)(Table 5, model 3).

254 4. Discussion

255 *Scedosporium* and *Lomentospora* species were prevalent in soil samples in Taiwan. Their
256 occurrence in the environment were mostly in human disturbed areas, i.e. in urban and
257 hospital samples in the present study. In contrast, natural regions had limited distribution of
258 these fungal species. While detecting *Scedosporium* and *Lomentospora* species in hospital
259 regions in the present study, our results indicated that these hygiene-sensitive areas, in
260 general, possessed no more fungal burden than nearby urban regions; lessening the need of
261 taking precautionary approach at this point.

262 *Scedosporium* and *Lomentospora* are prevalent and are heterogeneous 263 distributed in the environment

264 Overall, half of soil samples in the present study yield *Scedosporium* and *Lomentospora*
265 species. Their distribution was not only on the main island, but also on the outlying islands
266 such as Penghu and Kinmen. Although with less density of human population on these
267 islands, we recovered a comparable amount of *Scedosporium* and *Lomentospora* species as
268 that on the main island. Whether the fungal community of these species on the outlying island
269 is endemic or is brought via human activities, and if so the disseminating route, await further
270 investigations.

271 Distribution of *Scedosporium* and *Lomentospora* species in the environment appear to be
272 highly heterogeneous, even sampling sites in vicinity often yielded varied compositions of
273 these fungal species, as suggested in the homogeneity test (Fig. 4). Notably, we did not

274 observe apparent patterns explaining the high fungal burden of these species in certain
275 sampling sites. We found, for example, *S. apiospermum* and *L. prolificans* are abundant in
276 sampling sites in parks where birds are fed and are routinely roosting in; these are places
277 where they may accumulate high nitrogen contents that can encourage the population of
278 *Scedosporium* and *Lomentospora* species (36, 39). Other than this putative factor, we found
279 in some tourist visiting sites (e.g. British Consulate at Takow, Chishang Hakka Cultural Park,
280 and Rushan Visitor Center) and hospitals (e.g. Taichung Veterans Hospital and Taichung
281 Hospital) where they accommodate exceptionally high fungal burden of these species (Fig.
282 3). While again, the distribution of *Scedosporium* and *Lomentospora* species are highly
283 variable in sites of these high fungal burden places. The heterogeneous distribution of these
284 fungal species in the environment invites analysis of the physical and chemical properties of
285 soil samples in the future studies.

286 As in many previous studies, *S. apiospermum* is the most common species in the environment
287 (34, 36, 38–41). The prevalence of this species in the environment has been repeatedly
288 revealed in varied countries across continents and climatic zones, and by using varied
289 selective culturing methods, i.e. dichloran rose bengal chloramphenicol (DRBC) media,
290 *Scedosporium*-selective media (SceSel), and Scedo-Select III culture medium (36, 39, 72).
291 All together, it suggests that *S. apiospermum* appears to be the dominant species in the soil
292 environment globally regardless of geographical and climatic regions. This, in conjunction
293 with their prevalence in human disturbed regions (e.g. sewage, wastewater treatment plants,
294 and landfills), suggests their potential as the indicator species for anthropogenic disturbance
295 or pollution in areas worldwide (23).

Scedosporium and *Lomentospora* have limited distribution in natural regions

In the present study, we isolated *S. apiospermum* from a natural region. As opposed to previous studies, in which no *Scedosporium* and *Lomentospora* species were isolated from the natural/pristine areas (35, 36). The only three cases of recovering *Scedosporium* from natural regions were samples from Argane forests in Souss-Massa, forests in Maamoura, and beaches in Casablanca, all in Morocco (39, 73, 74). These places, however, appeared to exhibit anthropogenic activities, especially in the highly visited Casablanca beach; it may explain the presence of *Scedosporium* species in these regions. Similar to the case in Morocco, the detected sample in the natural region in Taiwan was from Lotus Pond, where is a recreation place with moderate tourist vistings, the low recovery rate and abundance (16 CFU/g) of *Scedosporium* species was therefore plausible. The other five natural places, Cui-Feng, Daxueshan, Baimaoshan, Kuantaoshan, and Liu-Long-Tou, are relatively high-elevated and with lesser tourist visitings; we therefore did not find the fungi in the present study. Intriguingly, few samples from a recreation area (Moon World) with the Badlands landscape exhibit the distribution of *S. apiospermum* (16 CFU/g) and *L. prolificans* (8 CFU/g). Though with low fungal burden for both species, their presence in such an arid region suggest the tolerance of *Scedosporium* and *Lomemtospora* species to many adverse environments.

Surveys in different countries revealed varied community profiles of *Scedosporium* and *Lomentospora*

The four clinical relevant species, i.e. *S. apiospermum* (41.7%), *S. boydii* (28.8%), *L. prolificans* (12.3%), and *S. aurantiacum* (4.9%), accounted for 87.7% of the recovered fungal species in the present study; the clinically minor species, *S. dehogii*, accounted for the rest

319 12.3%. This recovered fungal community profile in Taiwan is different from that in different
320 countries. For example, an environmental survey in Morocco revealed a similar fungal profile
321 of *S. apiospermum* (56%), *S. aurantiacum* (17%), *S. boydii* (18%), and *S. dehogii* (9%) (39);
322 in Thailand revealed a profile of *S. apiospermum* (87%), *S. aurantiacum* (7%), *S. dehogii*
323 (6%) (40); in France revealed a profile of *S. dehogii* (39.4%), *S. aurantiacum* (21.6%), *S.*
324 *boydii* (19.7%), and *S. apiospermum* (18.9%) (35); in Australia revealed a profile of *S.*
325 *aurantiacum* (54.6%), *L. prolificans* (43%), *S. boydii* (2.1%), *S. dehogii* (0.3%), and *S.*
326 *minutispora* (0.004%) (34); and in Austria, a profile of *S. apiospermum* (69.8%), *S. dehoogii*
327 (19.8%), *S. aurantiacum* (6.3%), *S. boydii* (2.2%), and *S. minutispora* (1.9%) was revealed
328 (36).

329 Intriguingly, the disclosed fungal profile of *Scedosporium* and *Lomentospora* in countries
330 appear to echo the clinical cases attributed to certain species. For example, patients with
331 chronic lung disease in Australia were mostly colonized by *S. aurantiacum (34)*. Clinical
332 cases in Austria were mostly attributed to *S. apiospermum* (36). Infections in Taiwan were
333 diagnosed with *S. apiospermum* and *S. boydii* as the culprits (Sun et al. unpublished). While
334 discrepancy happens such as the case in France where *S. boydii* is the major cause of
335 infections but the dominant species was *S. dehoogii* in the environmental study. The exact
336 link between environmental and clinical strains warrants future studies using a more rigorous
337 experimental design coupled with approaches such as molecular population genetics.

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587 # Legends

588 **Figure 1**. Culture-dependent isolation from soil samples in the present study. (A) Percentage
589 of culture-positive samples of *Scedosporium* and *Lomemtospora* species in different types of
590 sampling sources (urban, hospital, and natural) across Taiwan. (B) Proportion of each
591 isolated *Scedosporium*/*Lomemtospora* species in the 164 isolates.

592 **Figure 2**. Mean CFU of *Scedosporium*/*Lomemtospora* species from samples in each location
593 across Taiwan. Names of locations with mean CFU more than 40 are labeled. Circle sizes
594 represent the sampling size in each location. * measured values of CFU/g.

595 **Figure 3**. Heatmap showing the mean CFU of each *Scedosporium*/*Lomemtospora* species in
596 each location sampled in the present study; types of sampling sources (urban, hospital, and
597 natural) were labeled next the location name on x-axis.

598 **Figure 4**. Homogeneity test on the species assemblage in different types of sampling sources
599 (urban, hospital, and natural); the p-value generated via pairwise comparisons using post hoc
600 t-test were shown above the bars.

601 **Figure 5**. NMDS ordination showing the dissimilarities of species assemblage in soil samples
602 from each location.

603 **Table 1**. Sampling locations, assigned categories (urban, hospital, and hospital) of each
604 sampling location, geographic coordinate, and sample sizes of each location.

605 **Table 2**. Degree of freedom, F-values, determination coefficients, and P-values of tested
606 factors (location type and location) that influence the species assemblage observed in each
607 location.

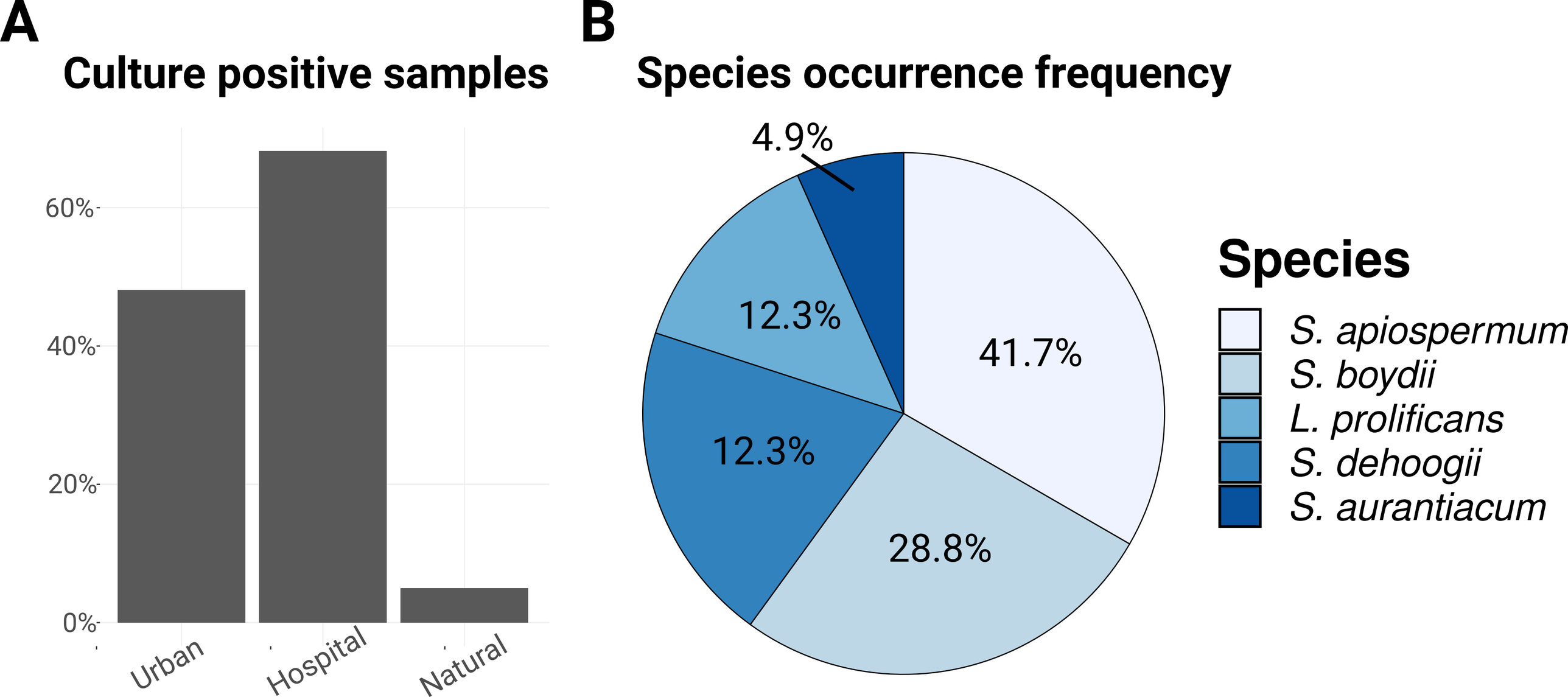
608 **Table 3**. F-values, determination coefficients, and P-values of pairwise test of species
609 assemblage observed in urban, hospital, and natural regions.

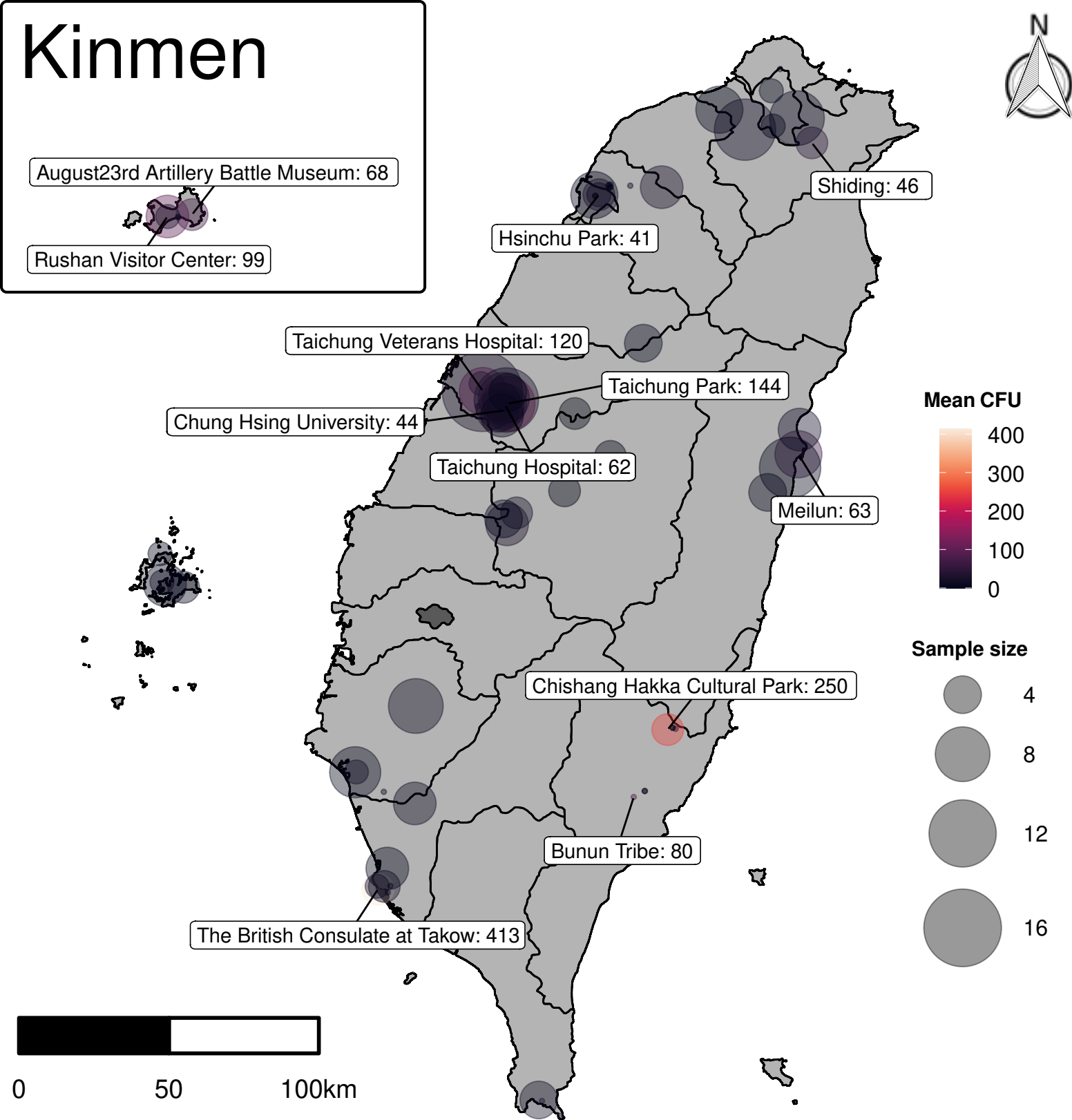
610 **Table 4**. Three models using the general linear-model-based analysis tested the occurrence
611 differences of *Scedosporium* and *Lomentospora* species explained by the effect of location
612 type (model 1); location type, location and the interaction term (model 2); location, sampling
613 unit, and the interaction term (model 3). Degree of freedom, deviance, and alpha- corrected
614 P-values of multivariate tests were shown.

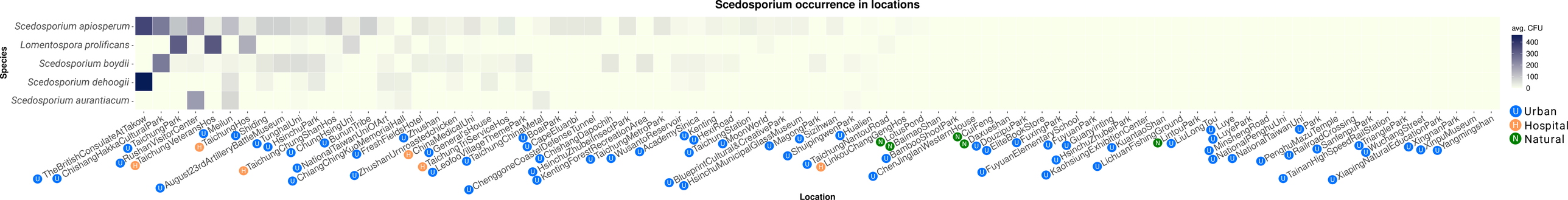
615 **Table 5**. Three models using the general linear-model-based analysis tested the occurrence
616 differences of *Scedosporium* and *Lomentospora* species explained by the effect of location
617 type (model 1); location type, location and the interaction term (model 2); location, sampling
618 unit, and the interaction term (model 3). The alpha- corrected P-values of univariate tests
619 were shown.

620

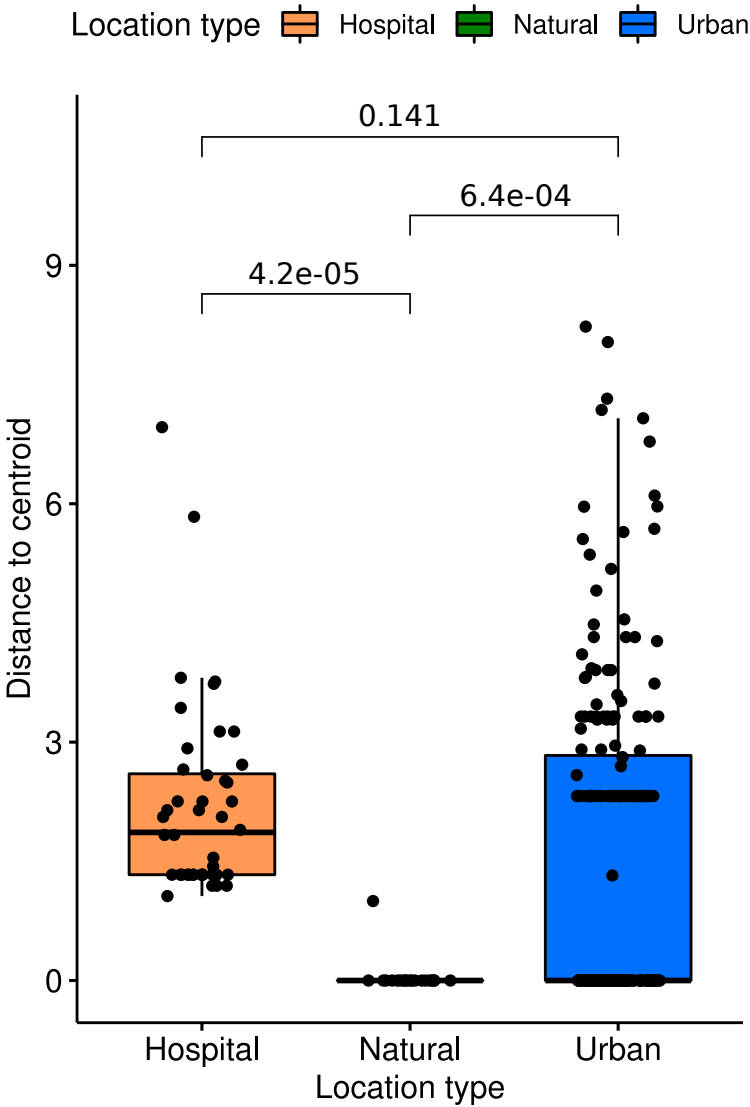
621 **Table S1**. Primer names and their sequences used in the present study.

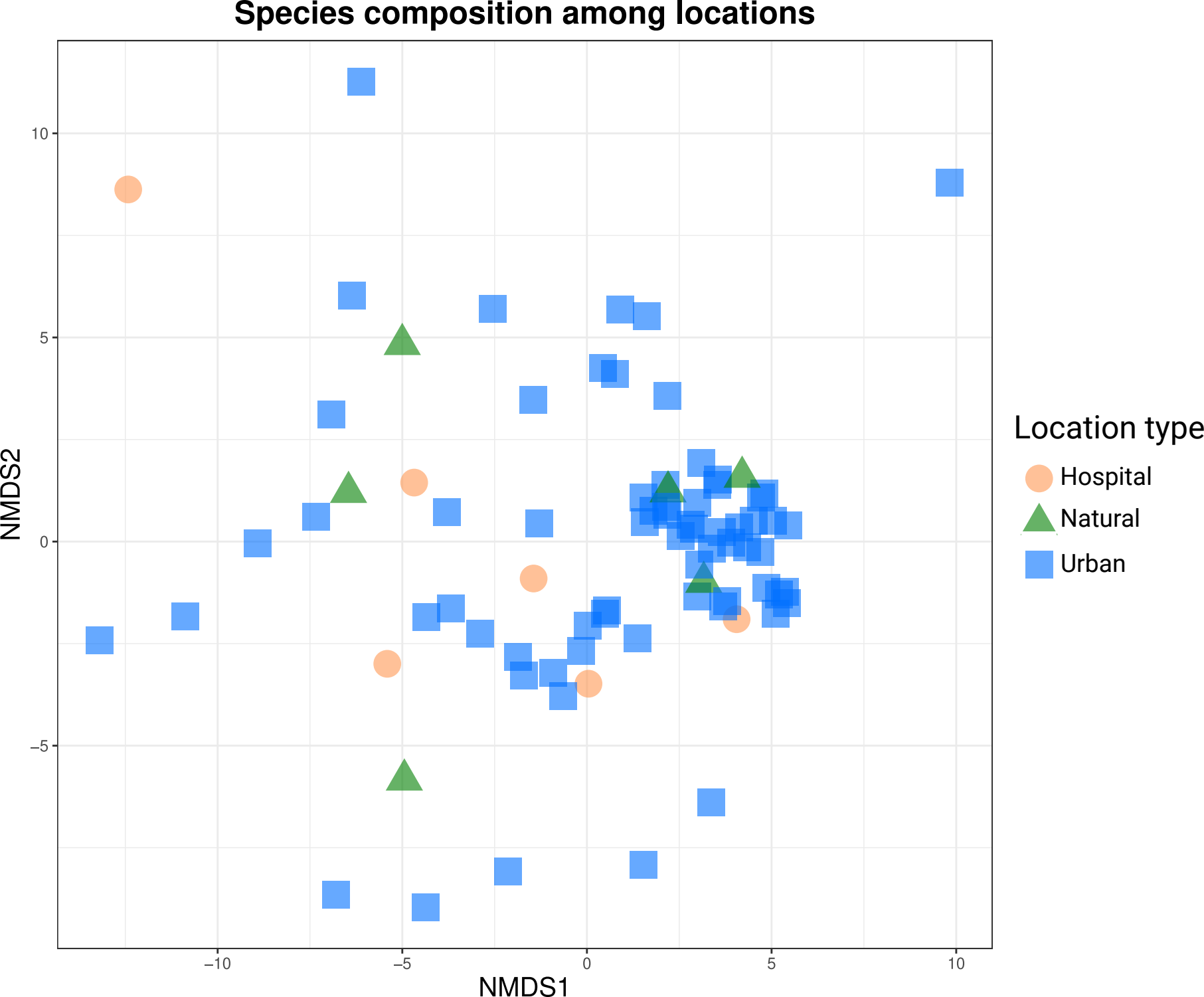

A
Culture positive samples
60%
40%
20%
0%
Urban
Hospital
Natural
B
Species occurrence frequency
4.9%
12.3%
41.7%
12.3%
28.8%
Species
S. apiospermum
S. boydii
L. prolificans
S. dehoogii
S. aurantiacum


Kinmen
August23rd Artillery Battle Museum: 68
Rushan Visitor Center: 99
N
Shiding: 46
Hsinchu Park: 41
Taichung Veterans Hospital: 120
Taichung Park: 144
Chung Hsing University: 44
Taichung Hospital: 62
Meilun: 63
Mean CFU
400
300
200
100
0
Sample size
4
8
12
16
Chishang Hakka Cultural Park: 250
Bunun Tribe: 80
The British Consulate at Takow: 413
0
50
100km



Scedosporium occurrence in locations
Species
Scedosporium apiosperum
Lomentospora prolificans
Scedosporium boydii
Scedosporium dehoogii
Scedosporium aurantiacum
Location
avg. CFU
400
300
200
100
0
Urban
Hospital
Natural
TheBritishConsulateAtTakow
ChishangHakkaCulturalPark
TaichungPark
RushanVisitorCenter
TaichungVeteransHos
Meilun
TaichungHos
Shiding
August23rdArtilleryBattleMuseum
TunghaiUni
HsinchuPark
TaichungChungShanHos
ChungHsingUni
BununTribe
NationalTaiwanUniOfArt
ChiangChingKuoMemorialHall
FreshFieldsHotel
Zhushan
ZhushanUnroastedchicken
ChinaMedicalUni
GeneralsHouse
TaichungTriServiceHos
LeofooVillageThemePark
TaichungChinaMetal
BoaiPark
CapeEluanbi
ChengggoneCoastelDefenseTunnel
ChishangDapochih
HsinchuZhubeiInsectPark
KentingForestRecreationArea
TaichungMetroPark
WusantoReservoir
AcademySinica
Kenting
HexiRoad
TaichungStation
MoonWorld
BlueprintCultural&CreativePark
HsinchuMunicipalGlassMuseum
MagongPark
Sizihwan
ShuipingwenPark
Hualien
TaichungNantouRoad
LinkouChangGengHos
LotusPond
BaimaoShan
BambooShootPark
ChenJinglanWesternHouse
CuiFeng
Daxueshan
DouzipuPark
EliteBookStore
FuxingPark
FuyuanElementarySchool
FuyuanPark
Guanyinting
HsinchuZhubeiPark
KaohsiungExhibitionCenter
KuantaoShan
LichuanFishingGround
LintouPark
LiuLongTou
Luye
LuyePark
MinshengRoad
NationalPenghuUni
NationalTaiwanUni
Park
PenghuMazuTemple
RailroadCrossing
SanfenpuPark
TainanHighSpeedRailStation
TrianglePark
WuchangStreet
XiapingNaturalEducationPark
XingnanPark
XinpuMuseum
Yangmingshan


Location type
Hospital
Natural
Urban
0.141
6.4e-04
4.2e-05
9
6
3
0
Distance to centroid
Hospital
Natural
Urban
Location type


Species composition among locations
NMDS2
NMDS1
10
5
0
−5
−10
−5
0
5
10
Location type
Hospital
Natural
Urban