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Title: Decadal survival of tropical pioneer seeds in the soil seedbank is accompanied by fungal infection and dormancy release.

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Abstract

1. Neotropical pioneer trees require high-light environments for successful seedling establishment. Their seeds often persist in the soil seed bank (SSB) for periods ranging from several weeks to decades. How they survive despite extensive pressure from seed predators and soilborne pathogens remains an intriguing question.

2. The aim of this study was to test the hypotheses that decades-old seeds collected from the SSB in a lowland tropical forest remain viable by i) escaping infection by fungi, which are major drivers of seed mortality in tropical soils, and/or ii) maintaining high levels of seed dormancy and seed coat integrity when compared to inviable seeds.

3. We collected seeds of *Trema micrantha* and *Zanthoxylum ekmanii* at Barro Colorado Island, Panama, from sites where reproductive trees previously occurred in the past 30 years. We used carbon dating to measure seed age and characterized seed coat integrity, seed dormancy, and fungal communities.

4. Viable seeds from the SSB ranged in age from 9 to 30 years for *T. micrantha*, and 5 to 33 years for *Z. ekmanii*. We found no evidence that decades-old seeds maintain high levels of seed dormancy or seed coat integrity. Fungi were rarely detected in fresh seeds (no soil contact), but phylogenetically diverse fungi were detected often in seeds from the SSB. Although fungal infections were more commonly detected in inviable seeds than in viable seeds, a lack of differences in fungal diversity and community composition between viable and inviable seeds suggested that viable seeds are not simply excluding fungal species to survive long periods in the SSB.

5. *Synthesis.* Our findings reveal the importance of a previously understudied aspect of seed survival, where the impact of seed-microbial interactions may be critical to understand long-term persistence in the SSB.

KEYWORDS: Ascomycota, lowland tropical forest; pioneer trees; seed coat integrity; seed dormancy; seed-fungal interactions; seed long-term persistence; soil seed bank.

1 | INTRODUCTION

Tropical pioneer trees colonize and establish in treefall gaps and other forest disturbances. In old-growth forests, treefall gaps typically result from seasonal blow-downs and lightning strikes (Gora et al., 2021) and are rare at the landscape level (Lobo and Dalling, 2013). Their rarity limits recruitment opportunities for seeds of pioneer trees in space and time. Therefore, some species of pioneer trees compensate for infrequent recruitment opportunities by prolonging seed persistence in the soil.

In the seed ecology literature, it is often stated that seed dormancy improves the chances of survival by delaying germination until conditions are favorable for seedling establishment and growth, thus reducing the risk of reproductive failure (e.g., Long et al., 2015). Mechanisms of dormancy differ among species: for example, physically dormant seeds are enclosed inside a water-impermeable layer that prevents germination, whereas physiologically dormant seeds are permeable but can only germinate in response to specific chemical or environmental cues (Thompson, 2000). Seed persistence, defined as the time between soil arrival and germination, ranges from a few weeks to a few decades for tropical pioneer trees (Dalling and Brown, 2009; Long et al., 2015). Burial experiments and carbon-dating of seed coats of pioneer species from

69 the lowland tropical forests in Panama suggest that decadal seed persistence may be common
70 among larger seeded pioneers that have either physical or physiological seed dormancy (Dalling
71 and Brown, 2009; Zalamea et al., 2018).

72 After reaching the soil, seeds can be attacked by granivores or infected by microbes,
73 including soilborne fungi that are significant causes of seed mortality in tropical forest soils
74 (Dalling et al., 1998, 1997). Thus, seeds have a range of defensive strategies, with the production
75 of hard and fibrous external layers or investment in chemical defenses fine-tuned to limit
76 predation and pathogen infection (Dalling et al., 2020). Our recent work on tropical seeds has
77 revealed how investments in physical and chemical seed defenses vary with seed dormancy type,
78 reflecting the importance of seed permeability as a key trait (Zalamea et al., 2018). Seed
79 mortality due to fungi is widespread across pioneer species (Dalling et al., 1998; Gallery et al.,
80 2010). However, recent evidence also suggests that non-dormant (i.e., quiescent) seeds of
81 *Cecropia* species may be particularly dependent on protection from certain soil-borne, seed-
82 infecting fungi (Dalling et al., 2020; Gallery et al. 2007; Zalamea et al., 2021). Thus, fungal
83 infections may have positive or negative effects, with the outcome of interactions between seeds
84 and fungi (i.e., functional specificity, Sarmiento et al., 2017) highly dependent on host species
85 identity.

86 Seed burial experiments often are used to study seed fate in the SSB (Long et al., 2015).
87 However, they are usually short in time and therefore do not address mechanisms of long-term
88 seed persistence. Census data collected from long-term forest dynamics plots contain fine-scale
89 data on the past locations of trees, which allows sampling of potentially decades old SSBs. Using
90 this approach in the 50-ha forest dynamics plot on Barro Colorado Island (BCI), Panama, Dalling
91 and Brown (2009) found that physiologically dormant seeds of *Croton billbergianus, Trema*

92 *micrantha,* and *Zanthoxylum ekmanii* collected at or near the soil surface (< 3 cm soil depth) can
93 survive for at least 38, 31, and 18 years, respectively. Seed burial experiments at BCI that
94 excluded seed predators but allowed microbial colonization also showed that seeds of *T.*
95 *micrantha* and *Z. ekmanii* did not lose viability after 30 months of burial (Zalamea et al., 2018).
96 However, little is known about the effect of dormancy status and microbial colonization on the
97 fate of decades-old seeds with seed dormancy from the natural SSB.
98 The aim of this study was to test the hypotheses that decades-old seeds collected from the
99 SSB in a lowland tropical forest remain viable by i) escaping infection by fungi and/or ii)
100 maintaining high levels of seed dormancy and seed coat integrity when compared to inviable
101 seeds. We focused on *Trema micrantha* and *Zanthoxylum ekmanii*, which are pioneer species
102 that have seeds that can persist in the soil seed bank for decades, produce physiologically
103 dormant seeds, and differ in their investment in chemical defenses (Dalling and Brown, 2009;
104 Zalamea et al., 2018). We collected seeds of each species from sites at BCI where conspecific
105 reproductive trees had occurred over the previous 30 years, and used carbon dating to measure
106 seed age and characterized seed coat integrity, seed dormancy, and fungal communities to test
107 three predictions. First, if dead seeds accumulate saprobic infections, we predicted that seed
108 infection rates of old seeds would be higher for dead seeds than live seeds. Second, if dead seeds
109 can be colonized by opportunistic fungi, but viable seeds are mainly colonized by a narrower
110 pool of endophytes or pathogens that can impact seed survival, inviable seeds should have higher
111 fungal diversity when compared to viable seeds. Third, as long-term seed persistence can be
112 achieved by having permeable seeds that are well-defended chemically or by having
113 impermeable seeds that are well-defended physically (Zalamea et al., 2018), we predicted that
114 viable old seeds of *T. micrantha* and *Z. ekmanii* should maintain high levels of seed dormancy

and seed coat integrity. Finally, we explored if the focal plant species harbor distinct seed-associated fungal communities as our previous work suggested for other pioneer seed species (Sarmiento et al., 2017; Zalamea et al., 2021).

2 | METHODS

2.1 | Study site and species selection

This study was conducted in a seasonally moist lowland tropical forest on Barro Colorado Island (BCI), Panama (9°10'N, 79°51'W). Rainfall on BCI averages 2600 mm/year, with a pronounced dry season from January to April (Windsor, 1990). The BCI 50-ha forest dynamics plot on the central plateau of the island was established in 1980 with all trees >1 cm diameter at breast height (DBH) identified, mapped, and censused every five years.

Trema micrantha (Cannabaceae) and *Zanthoxylum ekmanii* (Rutaceae) are medium- to large-seeded pioneer species that retain high seed viability in burial experiments (Dalling et al., 1997; Zalamea et al., 2018). *Trema micrantha* is a rare canopy tree in old-growth forest at BCI. Its fruits are produced year-round and seeds, with an average seed mass of 3.2 mg, are dispersed by birds. *Zanthoxylum ekmanii* is a relatively common dioecious canopy tree in old-growth forest at BCI. Its fruits are produced annually and seeds, with an average mass of 16.2 mg, are dispersed primarily by primates and secondarily by ants (Dalling and Brown, 2009; Ruzi et al., 2021, 2017; Zalamea et al., 2018).

2. 2 | Seed sampling

We used the BCI 50-ha plot census data to locate sites occupied in the past by reproductive-sized individuals of *T. micrantha* and *Z. ekmanii*. Sites were selected to ensure that at least one

reproductive-sized individual of each tree species died at least 5 years before the seed sampling, with no subsequent recruitment, mature conspecifics in the immediate area.

We collected soil cores between July and December 2014 from five individual localities where *T. micrantha* occurred previously, and six localities where *Z. ekmanii* occurred. We collected 0.5 L cores consisting only of surface soil layers (0–3 cm depth) to ensure that seeds were collected at depths from which emergence can successfully occur (Pearson et al., 2002; Ruzi and Suarez, 2022). For each sampled site, soil cores were collected from at least three haphazardly chosen areas in a 5 m by 5 m quadrat.

2.3 | Seed germination, seed viability, isolation of seed-associated fungi, and seed fracture resistance

Seeds were extracted from soil cores by rinsing the soil with tap water under a series of sieves, with a minimum pore diameter of 2 mm for *Z. ekmanii* and 1 mm for *T. micrantha*. Seeds were identified to species and then partitioned for tests of i) seed viability and identification of seed-associated fungi (692 and 593 seeds of *T. micrantha* and *Z. ekmanii*, respectively), ii) germination and carbon dating (a total of 239 and 196 seeds of *T. micrantha* and *Z. ekmanii*, respectively), and iii) seed fracture resistance as a measure of seed coat integrity (224 and 142 seeds of *T. micrantha* and *Z. ekmanii*, respectively).

Fungal isolation and seed viability assessment followed Sarmiento et al. (2017). About 60% of seeds recovered from each soil core were haphazardly selected, surface-sterilized (95% ethanol, 10 sec; 0.7% $NaClO^-$, 2 min; 70% ethanol, 2 min), and allowed to surface-dry under sterile conditions. Surface-sterilizing the seeds allowed us to isolate fungi that had colonized the interior of the seed while eliminating fungi that were restricted to the seed surface. Surface-

sterilized seeds were cut in half under sterile conditions. Half of each seed was used to score seed viability via staining with tetrazolium (TZ; 2, 3, 5-triphenyl tetrazolium chloride), such that both infection status and viability were scored for each seed. For viability testing, seed halves were placed in Petri dishes lined with filter paper, saturated with 0.5% TZ immediately after cutting, and kept in the dark at ca. 22°C for 24 h prior to scoring as viable or inviable. Dishes were sealed with Parafilm® throughout incubation to avoid seed desiccation. The other half of each seed was placed on 2% malt extract agar (MEA) in an individual 1.5 mL microcentrifuge tube for fungal isolation. Tubes were incubated at room temperature (ca. 22°C) with natural light-dark cycles for at least 12 months. If growth was observed, we excised a small piece of fresh mycelium from each emergent culture under sterile conditions. Fungi were isolated into pure culture, vouchered as living mycelium in sterile water, and processed for DNA extraction and Sanger sequencing (see below). All vouchers have been archived at the Robert L. Gilbertson Mycological Herbarium, University of Arizona (MYCO-ARIZ).

To score seed germination we placed seeds in groups of ~10 into a Petri dish lined with paper towel and moistened with sterile distilled water. Each Petri dish was sealed with two layers of Parafilm® (Zalamea et al., 2015). Dishes were incubated in a shade house on BCI under ca. 30% sunlight, high red:far-red irradiance ca. 1.4, and ambient temperature (23–30°C). Germination (i.e., radicle protrusion) was scored weekly for six weeks. The maximum temperature recorded on the germination bench was ca. 38°C, similar to the temperature near the soil surface in large treefall gaps on BCI (Marthews et al., 2008).

We measured seed fracture resistance (defined as the minimum force required to initiate seed rupture) as a quantitative measure of physical protection. Seed fracture resistance was measured by an Instron Single Column Testing System Model 3342 (Instron Company, USA).

Each seed was loaded between the anvil and the compression probe and then compressed until the seed coat ruptured. The seed coat rupture creates a sudden drop in force, such that the instrument can precisely record the force causing the fracture. After measuring seed fracture resistance, we scored seed viability via TZ staining in old seeds, so that seed viability and seed fracture resistance could be examined in tandem.

To determine baseline values of initial fungal infection rates, fungal diversity, dormancy levels, and seed fracture resistance we also collected fresh seeds (i.e., seeds that did not have soil contact) of *T. micrantha* and *Z. ekmannii* from at least five different maternal sources per species. For each species we evaluated 200 seeds for fungal infection rates and fungal diversity, 200 seeds for germination, and 35 seeds for seed fracture resistance.

2.4 | Age determination of seeds

To determine seed ages we followed Dalling and Brown (2009). Seed coat samples from germinated seeds or seed halves from viable seeds used for fungal isolation were cleaned and dated by accelerator mass spectrometry (AMS) at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory. By directly counting ^{14}C ions AMS yields high-precision $^{14}C/^{13}C$ measurements from very small amounts of sample carbon. The measured $^{14}C/^{13}C$ ratios were converted to $F^{14}C$ values following standard conventions (Stuiver and Polach, 1977; Reimer et al, 2004). The calendar year dates of carbon fixation for the samples were determined through comparison of the sample $F^{14}C$ values to a long-term Northern Hemisphere atmospheric ^{14}C record. Seed ages obtained with this technique are conservative because we assume that carbon fixation occurred during the period of declining $^{14}C/^{13}C$ (post-1963) rather than ascending $^{14}C/^{13}C$ (1953–1963). Because of the cost of AMS, we evaluated 18

individual seeds: we selected three sites per species representing the highest number of seeds recovered from soil cores and dated three individual seeds per site (Table 1). We averaged dates for sites that included three seeds if the ages differed. For the other two sites for *T. micrantha* and three for *Z. ekmannii,* we selected the census year when the tree under which we collected the soil was first reported dead. Carbon-dated seeds were consistently older than expected from the date of tree death recorded in the 50-ha census data, suggesting that this is a conservative age for the seeds that were not carbon-dated.

2.5 | Seed-associated fungal communities

Total genomic DNA was extracted from ground mycelium of each culture with the REDExtract-N-Amp Plant PCR kit (Sigma-Aldrich, Saint Louis, MO, USA). We used the polymerase chain reaction (PCR) with primers ITS1F and LR3 to amplify the nuclear ribosomal internal transcribed spacers and 5.8S gene (ITS rDNA) and an adjacent portion (ca. 600 bp) of the large subunit (LSU rDNA). If amplification failed with these primers, PCR was repeated with primers ITS5 and LR3. PCR reaction mixture and cycling reactions followed Sarmiento et al. (2017). PCR products were verified by staining with SYBR Green I (Molecular Probes, Invitrogen, Carlsbad, CA, USA) followed by electrophoresis on a 1% agarose gel. All products that yielded single bands were cleaned using 1 μL of ExoSAP-IT reagent (Affymetrix, Inc., Cleveland, OH, USA), quantified, normalized, and sequenced bidirectionally at the University of Arizona Genetics Core with the original sequencing primers. We assembled contigs and verified base calls from chromatograms following Sarmiento et al. (2017).

Isolation frequency was calculated as the number of isolates divided by the number of examined seeds. Operational taxonomic units (OTUs) were defined by 97% similarity in the

Sanger clustering workflow of the Mobyle SNAP Workbench (Monacell & Carbone, 2014) following Zalamea et al. (2021). Diversity was measured as Fisher's alpha, which is robust to variation in sample size and is appropriate given the relative abundance of OTUs (Sarmiento et al., 2017).

In total, 692 and 593 seeds of *T. micrantha* and *Z. ekmanii* were screened for fungal growth. Overall, 174 and 220 fungal strains were isolated from each species, and high-quality sequence data were obtained from 100% of all strains (Table 1, Table S1). A total of 129 OTUs were defined at 97% sequence similarity. All OTUs were included in measures of diversity.

Seed-associated fungal communities were defined as fungal isolates from seeds of a given plant species, tree site, and seed viability status. By definition, rare OTUs could not be present in all plant species or all communities; thus, we excluded singletons and fungal communities with fewer than three isolates from analyses of community structure, with a resulting pool of 55 OTUs and 13 communities.

2.6 | Data analysis: linking isolation frequency, fungal diversity, seed germination, physical protection, seed age, and seed-associated fungal communities

We used linear mixed effect models to test whether isolation frequency, fungal diversity, proportion of dormant/germinating seeds, and seed fracture resistance varied by plant species, seed viability status, and their interaction. For each response variable, we coded each tree site as a random effect and plant species, seed viability status, and their interaction as fixed effects. We also used linear regression analysis to determine if fungal isolation frequency and fungal diversity were associated with seed age. Analyses were implemented in R version 4.0.4 (R Development Core Team, 2021) using the package *nlme* (Pinheiro et al., 2023).

We used a multivariate generalized linear model (GLM) to test the extent to which each factor (i.e., plant species, tree site, or seed viability) was relevant to fungal community structure. We used a negative-binomial GLM based on sequence count data and a binomial GLM based on presence–absence data, performed with the R package *mvabund* (Wang et al., 2012). We complemented the results from the multivariate GLM with non-metric multidimensional scaling (NMDS) and variation-partitioning analyses performed with the R package *vegan* (Oksanen et al., 2019). The NMDS was performed using the function metaMDS with the dissimilarity matrix calculated using the Morisita–Horn index and the parameter *k* set to three dimensions (for graphical representations, we only included the first two dimensions). Variance-partitioning analyses were performed using the function *varpart*, with plant species, tree site, and seed viability coded as explanatory factors. Finally, taxonomic annotation of the sequences was based on T-BAS v. 2.1 (Carbone et al., 2019).

3 | RESULTS

Viable seeds from the SSB ranged in age from 9 to 30 years for *T. micrantha*, and 5 to 33 years for *Z. ekmanii* (Table 1). Fresh unburied seeds had low levels of fungal infection and fungal diversity, suggesting that most of the fungi colonized the seeds in the soil (Figs 1a, b).

We predicted that fungal isolation frequency in decades-old seeds would be higher on dead (inviable) seeds than on live (viable) seeds. In agreement with this prediction, we found that the frequency of fungal infections was higher in inviable seeds than in viable seeds collected from the SSB ($F_{1,11} = 5.21$, $p = 0.043$), a trend that is consistent for both species (species, $F_{1,11} = 0.39$, $p = 0.542$; species x seed viability, $F_{1,11} = 0.26$, $p = 0.622$; Fig 1a). When fungal isolation frequency was regressed against seed age there was a significant negative association for both

276 viable and inviable seeds (inviable, $r^2 = 0.51$, n = 11, p = 0.008; viable, $r^2 = 0.43$, n = 11, p =
277 0.017; Figs 2a and b).
278 We also predicted that among old seeds, inviable seeds would have higher fungal
279 diversity when compared to viable seeds. Contrary to this prediction, we did not find differences
280 in fungal diversity between viable versus inviable seeds collected from the SSB ($F_{1,3} = 0.67$, p =
281 0.471). Diversity of seed-associated fungi also did not differ between plant species ($F_{1,3} = 2.68$,
282 p = 0.200), and there was no evidence for a meaningful interaction between seed viability and
283 seed species ($F_{1,3} = 0.27$, p = 0.640; Fig 1b). Fungal diversity and seed age were not associated
284 for inviable or viable seeds (inviable, $r^2 = 0.02$, n = 7, p = 0.79; viable, $r^2 = 0$, n = 5, p = 0.92;
285 Figs 2c and d).
286 Seed viability differed between *T. micrantha* and *Z. ekmanii* ($F_{1,7} = 6.95$, p = 0.033; Fig
287 1c). Overall, 62% of *T. micrantha* and 28% of *Z. ekmanii* seeds recovered from soil cores were
288 viable. We found no evidence that decades-old seeds maintain high levels of seed dormancy and
289 seed coat integrity. Instead, we found that dormancy levels were less than 2% for *T. micrantha*
290 and 1% for *Z. ekmanii* old seeds, while they were over 75% and 30% in fresh unburied seeds
291 respectively (Fig 1c).
292 Our expectation of high seed coat integrity received only partial support: viable seeds
293 were harder than inviable seeds ($F_{1,4} = 8.02$, p = 0.047; Fig 1d), but this pattern was not
294 observed in both species (species x seed viability; $F_{1,4} = 15.52$, p = 0.017; Fig 1d). When seed
295 coat integrity values for old seeds were compared to fresh unburied seeds we found mixed
296 results: old seeds were harder than fresh seeds in *T. micrantha,* but softer in *Z. ekmanii* (Fig 1d).
297 We found that seed-associated fungal communities differed between the focal plant
298 species (negative binomial GLM; $df_{1,11}$, Dev = 161.1, p < 0.01; Fig 3a). However, seed-

associated fungal communities did not differ among localities ($df_{1,10}$, Dev = 70.3, p = 0.23) or as a function of seed viability ($df_{1,9}$, Dev = 87.3, p = 0.16). Plant species alone explained 25% of the total variance in OTU abundance while tree locality only explained 5% and seed viability 3% of the total variance (Fig 3b).

Fungi isolated from old seeds represented a broad range of phylogenetic lineages (Fig 4, Table S1). The three most abundant classes of Ascomycota isolated from *T. micrantha* and *Z. ekmanii* seeds were the same, but the ranking and abundances were different between species (Fig 4a). Sordariomycetes was the most abundant class isolated from both species, followed by Dothideomycetes in *T. micrantha*, and Eurotiomycetes in *Z. ekmanii* (Fig 4a). Hypocreales and Xylariales were the most abundant orders isolated from both species (Fig 4b).

4 | DISCUSSION

Soil borne fungal pathogens (including the fungus-like Oomycota) are a major source of seed and seedling mortality in tropical forests (Augspurger, 1984; Dalling et al., 1998; Bagchi et al., 2014). This study explored how seeds of pioneer trees can survive in the soil seed bank for decades in a lowland tropical forest. Working with decades-old seeds collected from the SSB in a lowland forest in Panama, we tested the hypotheses that viable seeds escape infection by fungi and/or maintain high levels of seed dormancy and seed coat integrity. We found support for neither hypothesis. Instead, seeds of *Trema micrantha* and *Zanthoxylum ekmanii*, associate with different fungi, including in seeds that are viable after many years of soil contact. Thus, our results highlight the importance of a previously understudied aspect of seed survival, where the impact of seed-microbial interactions that may not necessarily be negative, may be critical to understanding long-term persistence in the SSB.

We used AMS to carbon-date seeds of *T. micrantha* and *Z. ekmanii* that were extracted from undisturbed soil seed banks in the 50-ha forest dynamics plot on BCI. Seed ages reported here were consistent with seed ages reported by Dalling and Brown (2009) for *T. micrantha*, but extended the measured duration of seed persistence from 18 to 33 years for *Z. ekmanii*. Decades-long persistence has been hypothesized as a common trait among large-seeded tropical pioneers that produce physiologically or physically dormant seeds (Zalamea et al., 2018). Our results are consistent with this hypothesis and suggest that at least some large-seeded tropical pioneer species overcome enemy-mediated and environmental pressures by selecting trait combinations that permit long-term persistence (Zalamea et al., 2018; Dalling et al., 2020).

Treefall gaps in tropical lowland forests are rare, resulting in limited recruitment opportunities for pioneer species. In the seed ecology literature, dormancy has often been proposed as an essential mechanism for long-term persistence by which plants can decouple the timing of seed dispersal from the availability of conditions conducive to successful germination and recruitment (Baskin and Baskin, 1998). Over 80% of viable fresh seeds of *T. micrantha* and *Z. ekmanii* were dormant at the time of dispersal, but contrary to our prediction, we found that decades-old viable seeds of both species do not maintain high levels of seed dormancy. These results suggest that in addition to seed dormancy, long-term persistence is achieved through other mechanisms.

The maintenance of seed dormancy plays an important role in seed persistence in weed species in agricultural fields, desert and grassland ecosystems, where opportunities for successful seed germination are frequent, but where post-germination conditions are unpredictable (Long et al., 2015). For pioneer trees in lowland tropical rain forest, the long lifespan of canopy trees (and therefore time interval between treefall gaps), means that seeds likely only experience suitable

345 germination conditions a single time during their lifetime. The avoidance of germination through
346 seed dormancy is therefore unlikely to increase fitness.

347 We used seed fracture resistance as a proxy for seed coat integrity and found opposing
348 results for seeds of *T. micrantha* and *Z. ekmanii*. Fracture resistance was similar between viable
349 and inviable old seeds of *T. micrantha*, but higher in viable seeds of *Z. ekmanii*. Compared to
350 freshly collected seeds, seed fracture resistance was higher in old seeds of *T. micrantha*, but
351 lower in old seeds of *Z. ekmanii*. The seed coat is the primary barrier isolating the seed interior
352 from the physical environment. It has often been stated that hard seed coats protect the seed from
353 mechanical stresses and pathogen infections (e.g., Mohamed-Yasseen et al., 1994). Our previous
354 research found that freshly collected seeds of *T. micrantha* and *Z. ekmanii* are permeable
355 (Zalamea et al., 2018). Collectively, results from this contribution and our previous findings
356 suggest that maintaining hard and impermeable seeds is not necessarily critical to long-term
357 persistence.

358 Based on previous studies, we hypothesized that microbially-induced defenses and the
359 degree to which microbial defenses are carried over time could be a fruitful inquiry in future seed
360 ecological research (Dalling et al., 2020; Zalamea, in press). Germination data acquired in a 30-
361 month burial experiment on BCI, including the focal species *T. micrantha* and *Z. ekmanii,*
362 showed that the proportion of dormant seeds decreased through time, while seed viability
363 remained unchanged (Zalamea et al., 2018). The observation that decades-old viable seeds in this
364 study harbor fungal infections and have low levels of seed dormancy highlights the need for
365 further exploration of seed-fungal interactions in achieving long-term persistence in seeds of *T.*
366 *micrantha* and *Z. ekmanii*, and possibly other species too.

Seeds from tropical pioneers often associate with a wide variety of soil-borne fungi (Gallery et al., 2010; Sarmiento et al., 2017). Sarmiento et al. (2017) found that the composition of fungal communities that infect seeds of nine species of trees is strongly determined by plant species rather than by soil type, forest characteristics, or time spent in the soil. Zalamea et al. (2021) found that seed-associated fungal communities were also strongly structured by plant species, even among three congeneric species of *Cecropia*. Here, we found that decades-old seeds of *T. micrantha* and *Z. ekmanii* harbor distinctive fungal communities adding empirical support to previous research findings.

Seed endophytes are primarily filamentous Ascomycota (mainly Pezizomycotina), including many species of Sordariomycetes (Nelson, 2018; Simonin et al., 2022; Zalamea et al., 2021). Although the relative abundance of fungal classes varied considerably among plant species, seed microbiome studies consistently find that seed-infecting fungi of crop and tropical tree species are often represented by many species within a few fungal classes (Simonin et al., 2022; Zalamea et al., 2021). We found that major fungal groups at the class and order levels isolated from decades-old seeds of *T. micrantha* and *Z. ekmanii* are similar between these species and previous seed microbiome studies (Sarmiento et al., 2017; Nelson, 2018; Simonin et al., 2022; Zalamea et al., 2021). Thus, our results suggest that future studies might focus on understanding the functional impact of a few fungal classes on seed survival and persistence.

4.1 | Conclusions

Seeds are often colonized by soil-borne fungi in both wild and agricultural systems (e.g., Sarmiento et al., 2017; Nelson, 2018; Simonin et al., 2022). Seed microbial community assembly is the result of complex interactions (Bergmann & Leveau, 2022). Previous studies suggest that

the diversity of seed-infecting fungi is comparatively low to other plant tissues such as leaves (Arnold et al., 2003; Newcombe et al., 2018). The low microbial richness of seeds compared to other plant tissues makes individual seed-microbial interactions potentially more meaningful to study the impact of these interactions on survival and persistence. Contrary to our expectations, long-term persistent seeds of two tropical pioneer trees did not maintain high levels of seed dormancy, high levels of seed coat integrity, or avoid fungal colonization. Instead, we documented that a broad range of fungal species colonizes old, viable seeds. This finding supports previous studies that showed that seed infections by non-lethal fungi are common in tropical ecosystems (Sarmiento et al., 2017; Zalamea et al., 2021). Microbially-induced defenses in seeds remain a topic of great potential in the ecological literature. Still, we consider that with the improvement in methodological approaches to studying plant-microbial interactions, future research inquiries can benefit from a closer look at the impact of these interactions on seed survival and persistence.

AUTHOR CONTRIBUTIONS

JWD and PCZ conceived and designed the study; VK, CD, CS, TB, and PCZ collected the data; CS and PCZ analysed the data; PCZ wrote the manuscript with contributions from JWD, AEA, ASD and CS. All authors contributed substantially to revisions and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

Sequences used in this study will be deposited in NCBI GenBank.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

436 **Table and figure legends**

437

438 Table 1. Seed ages, number of viable and inviable seeds processed, number of cultivable fungi,
439 number of sequences, number of operational taxonomic units (OTUs) isolated, and fungal
440 diversity obtained from old seeds of *Trema micrantha* and *Zanthoxylum ekmanii* collected from
441 the soil seed bank in lowland tropical forest on Barro Colorado Island.

442

443 Figure 1. (a) Isolation frequency of fungi recovered from fresh unburied and decades-old seeds
444 of *Trema micrantha* and *Zanthoxylum ekmanii.* Old seeds were collected from the soil seed bank
445 in lowland tropical forest on Barro Colorado Island. Isolation frequency was calculated as the
446 number of fungal isolates divided by the number of seeds processed in each collection point and
447 seed viability class. (b) Diversity of fungi isolated from fresh unburied and old seeds. Fisher's
448 alpha was calculated with all sequenced isolates from each plant species and seed viability. (c)
449 Percentage of seeds that were dormant and germinable from fresh and old seeds. (d) Seed
450 fracture resistance (SFR; Newtons (N)) of fresh and old seeds. SFR was calculated by viability
451 class in old seeds. Error bars represent the standard error.

452

453 Figure 2. Relationship between isolation frequency of fungi recovered from seeds and seed age
454 for (a) inviable and (b) viable seeds. Relationship between the diversity of fungi isolated from
455 seeds and seed age for (c) inviable and (d) viable seeds. The lines represent significant
456 relationships and shaded areas represent the 95% confidence interval around the lines.

457

Figure 3. Structure of seed-associated fungal communities isolated from old seeds. (a) Non-metric multidimensional scaling (NMDS) analysis representing Morisita-Horn dissimilarity among fungal communities (points) isolated from old seeds of *Trema micrantha* and *Zanthoxylum ekmanii*. Fungal communities are color-coded to represent plant species; stress = 0.084. Ellipses represent a standard deviation of point scores relative to their centroid. (b) Venn diagram represents the percent of variation in fungal community composition explained by plant species, tree locality (collection site), and seed viability. If the percent of variation is zero, values are not represented in the figure.

Figure 4. Stacked bars represent the relative frequency and taxonomic composition of seed-associated fungi isolated from old viable and inviable seeds at the (a) class and (b) order levels. Numbers on top of each bar represent the number of isolates for which we obtained sequences.

Table S1. Sequence accession numbers (GenBank) and taxonomy of fungi isolated from decades-old seeds. Fungal isolates were obtained from seeds of *Trema micrantha* and *Zanthoxylum ekmanii* extracted from soil cores collected from five and six independent localities on Barro Colorado Island, respectively. Operational taxonomic units (OTU) were defined at 97% sequence similarity. For each sequence we provide the GenBank accession number.

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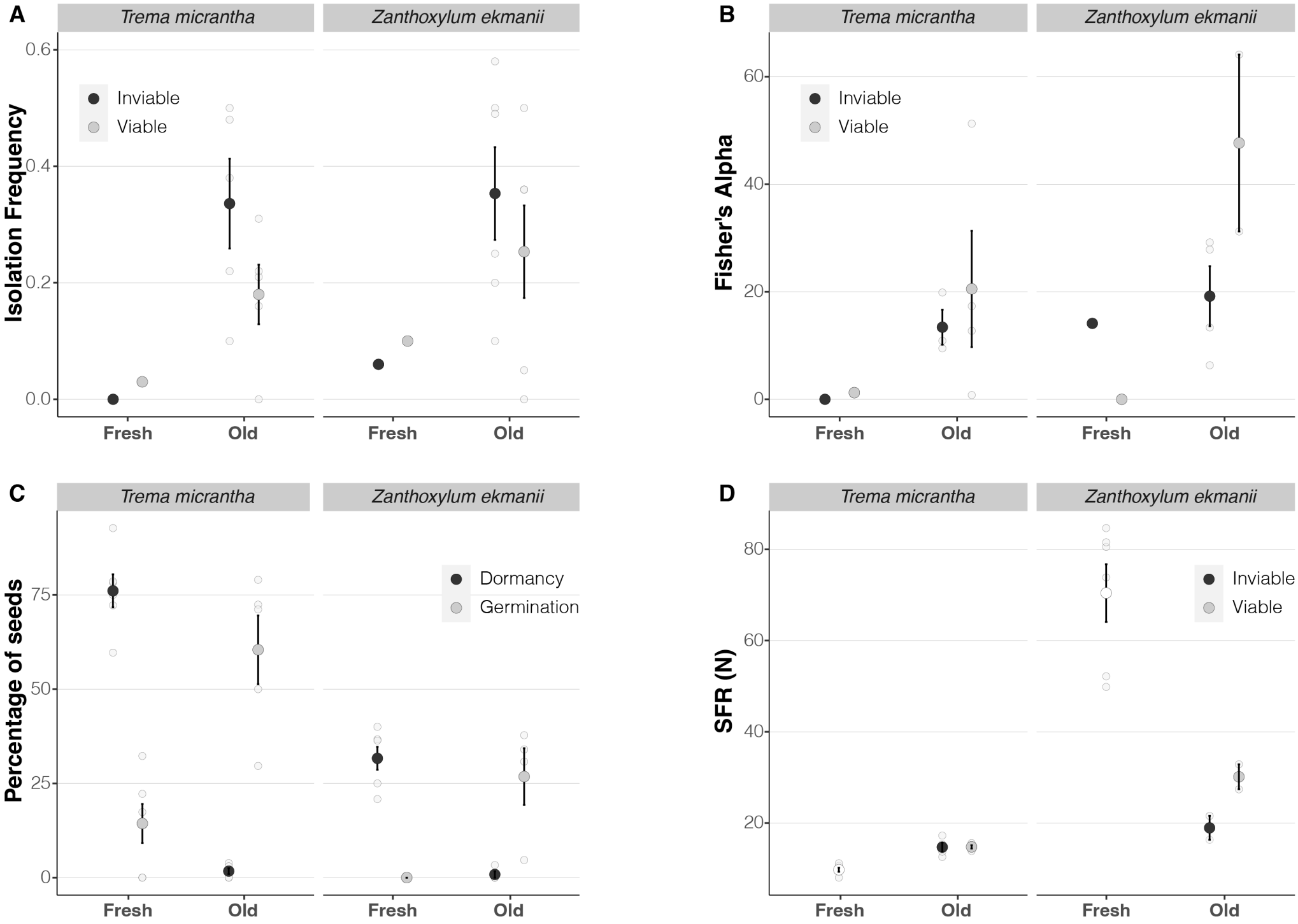
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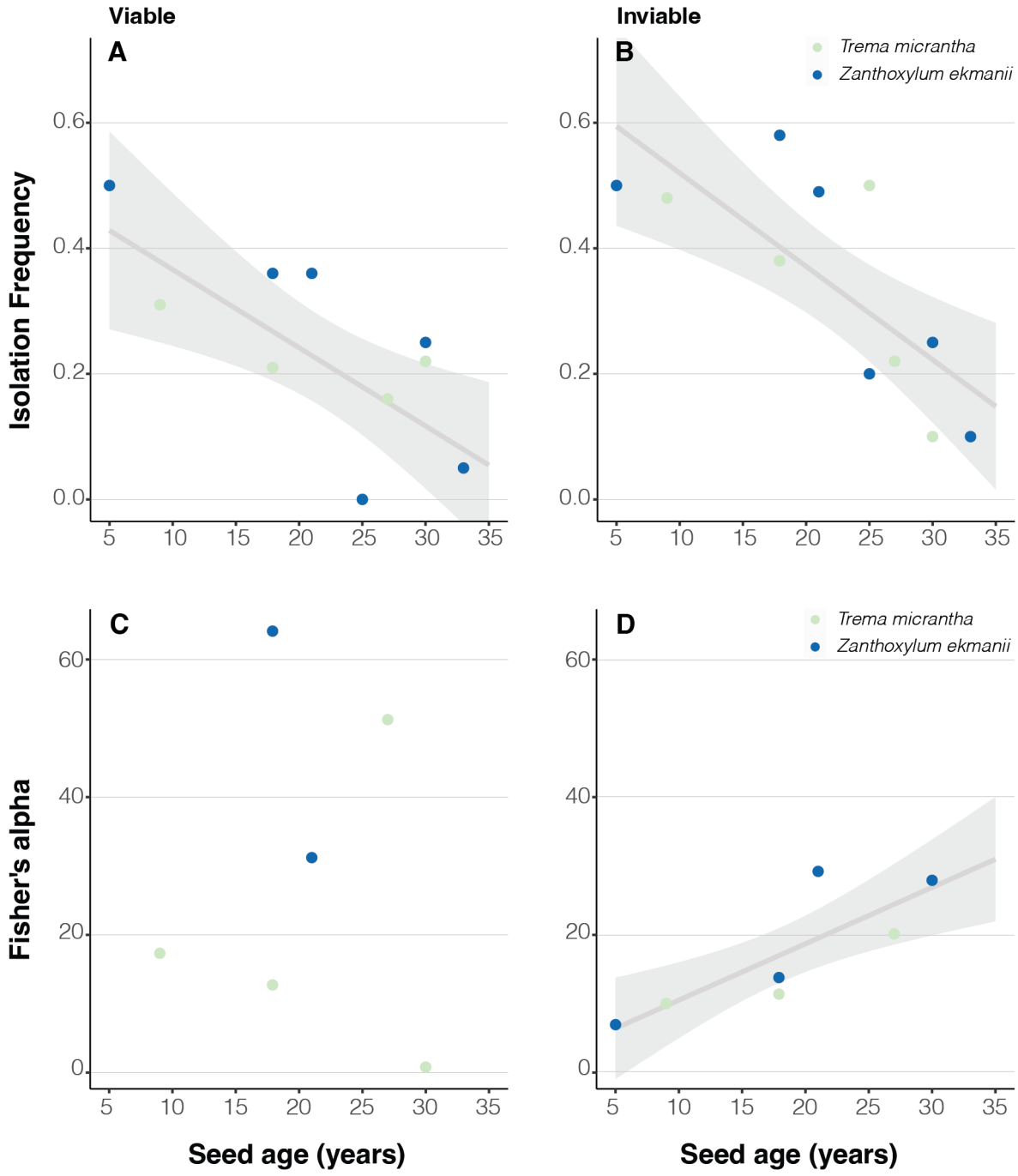
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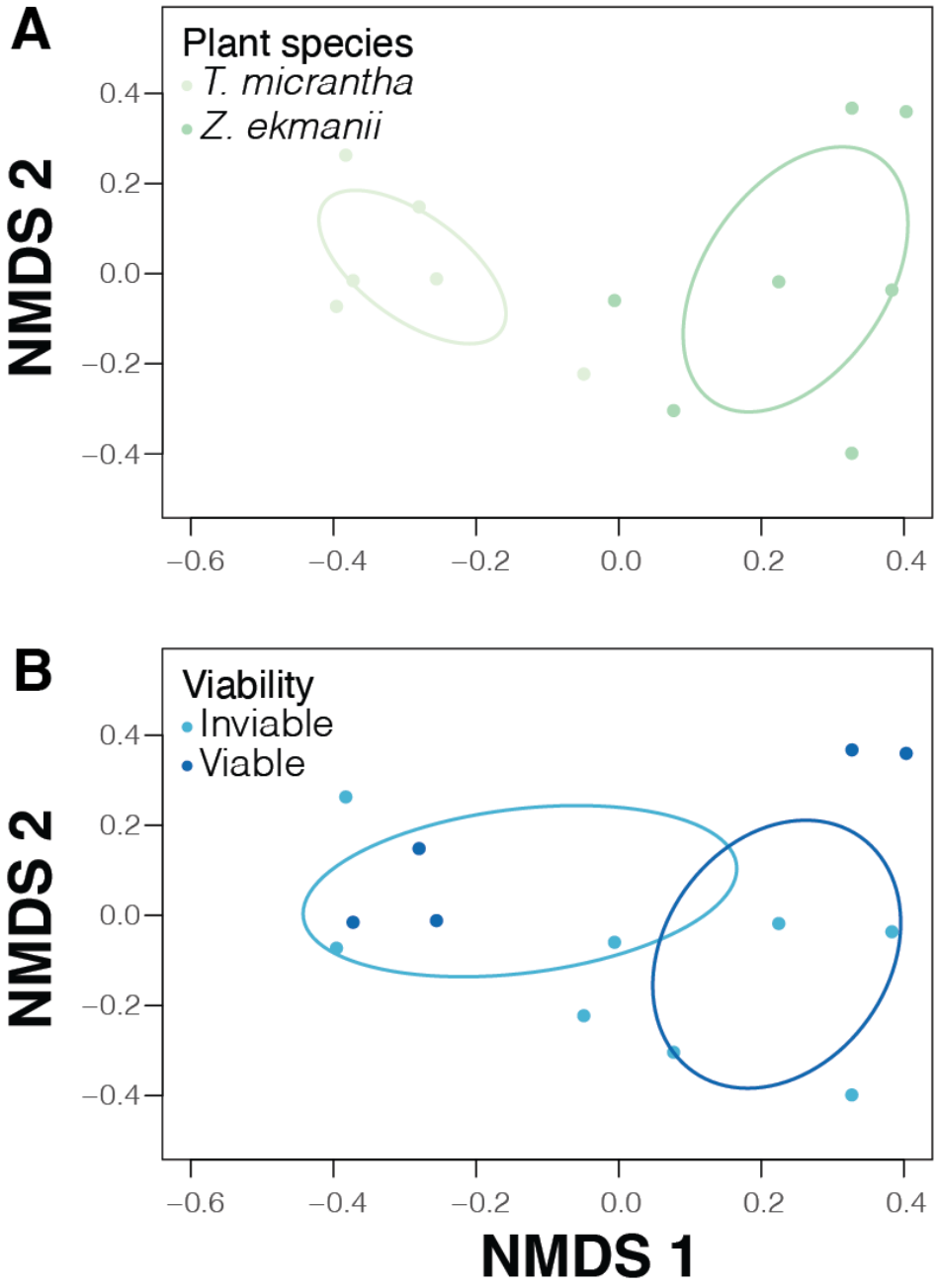
Table 1.

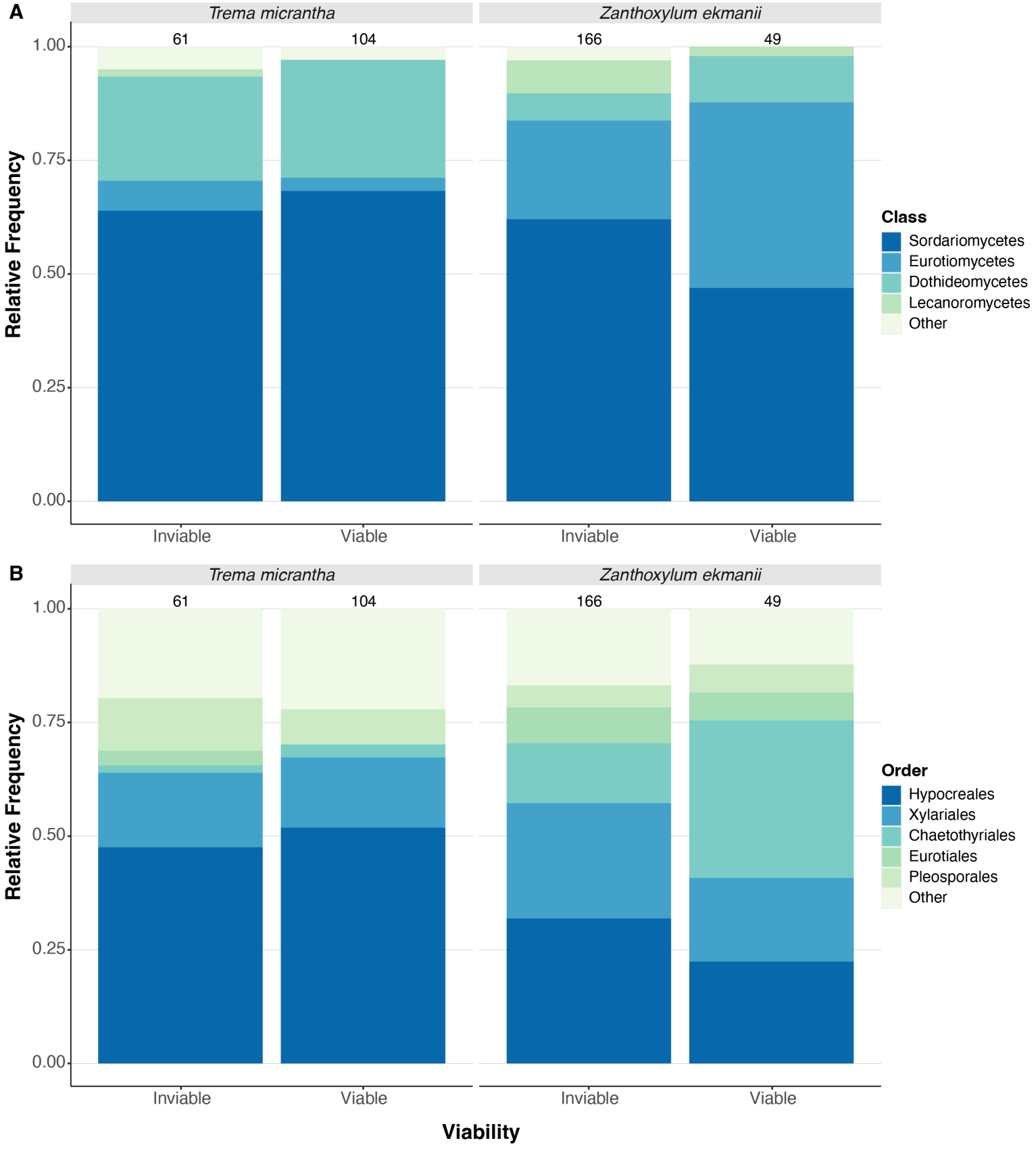
Species	C-dated Seed age (y)	95% CI	Viability	Number of seeds	Number of cultivable fungi	% of seeds with cultivable fungi	Number of sequences	Total number of OTU	Fisher's alpha
Trema micrantha	9	+/- 2	Inviable	66	32	48	32	14	9.5
			Viable	154	47	31	47	23	17.3
	18	+/- 2	Inviable	37	14	38	14	9	10.9
			Viable	156	33	21	32	16	12.7
	25	*	Inviable	2	1	50	1	1	NA
			Viable	2	0	0	NA	NA	NA
	27	+/- 2	Inviable	79	17	22	13	10	19.9
			Viable	167	26	16	23	19	51.3
	30	*	Inviable	20	2	10	2	2	NA
			Viable	9	2	22	2	1	0.8
Zanthoxylum ekmannii	5	*	Inviable	20	10	50	10	6	6.3
			Viable	2	1	50	1	1	NA
	18	+/- 2	Inviable	38	22	58	22	13	13.3
			Viable	33	12	36	12	11	64.1
	21	+/- 1.5	Inviable	233	115	49	112	46	29.2
			Viable	94	34	36	34	23	31.2
	25	*	Inviable	5	1	20	1	1	NA
			Viable	1	0	0	NA	NA	NA
	30	*	Inviable	60	15	25	15	12	27.9
			Viable	4	1	25	1	1	NA
	33	+/- 1.5	Inviable	81	8	10	8	8	NA
			Viable	22	1	5	1	1	NA

* These seeds were not C-dated. We selected the census year when the tree under which we collected the soil was first reported to be dead.


A
Trema micrantha
Zanthoxylum ekmanii
Isolation Frequency
0.6
0.4
0.2
0.0
Inviable
Viable
Fresh
Old
B
Fisher's Alpha
60
40
20
0
C
Percentage of seeds
75
50
25
Dormancy
Germination
D
SFR (N)
80
60
40
20


Viable
Inviable
A
B
C
D
Trema micrantha
Zanthoxylum ekmanii
Isolation Frequency
Fisher's alpha
Seed age (years)
Seed age (years)
0.0
0.2
0.4
0.6
0
20
40
60
5
10
15
20
25
30
35


A
Plant species
T. micrantha
Z. ekmanii
NMDS 2
0.4
0.2
0.0
−0.2
−0.4
−0.6
−0.4
−0.2
0.0
0.2
0.4
B
Viability
Inviable
Viable
NMDS 2
NMDS 1
C
Plant species
Tree locality
39%
1%
8%
Viability
Residuals = 60%


A
Trema micrantha
Zanthoxylum ekmanii
61
104
166
49
1.00
0.75
0.50
0.25
0.00
Relative Frequency
Inviable
Viable
Class
Sordariomycetes
Eurotiomycetes
Dothideomycetes
Lecanoromycetes
Other
B
Order
Hypocreales
Xylariales
Chaetothyriales
Eurotiales
Pleosporales
Other
Viability

Sequence ID	Accession number	OTU 97%	Plant species	Seed age (years)	Seed viability
VPS001		0	*Trema micrantha*	9	1
VPS002		1	*Trema micrantha*	9	1
VPS004		2	*Trema micrantha*	9	0
VPS005		3	*Trema micrantha*	9	0
VPS007		4	*Trema micrantha*	9	1
VPS013		0	*Trema micrantha*	9	0
VPS014		3	*Trema micrantha*	9	0
VPS016		0	*Trema micrantha*	9	0
VPS017		0	*Trema micrantha*	9	1
VPS018		5	*Trema micrantha*	9	0
VPS019		6	*Trema micrantha*	9	1
VPS020		7	*Trema micrantha*	9	0
VPS021		5	*Trema micrantha*	9	0
VPS022		0	*Trema micrantha*	9	1
VPS024		8	*Trema micrantha*	9	1
VPS025		9	*Trema micrantha*	9	1
VPS026		10	*Trema micrantha*	9	1
VPS027		11	*Trema micrantha*	9	1
VPS028		12	*Trema micrantha*	9	0
VPS029		13	*Trema micrantha*	9	1
VPS032		14	*Trema micrantha*	9	0
VPS033		15	*Trema micrantha*	9	1
VPS034		12	*Trema micrantha*	9	1
VPS035		16	*Trema micrantha*	9	1
VPS038		17	*Trema micrantha*	9	0
VPS041		18	*Trema micrantha*	9	1
VPS042		19	*Trema micrantha*	9	1
VPS043		5	*Trema micrantha*	9	1
VPS044		12	*Trema micrantha*	9	1
VPS046		20	*Trema micrantha*	9	1
VPS047		10	*Trema micrantha*	9	1
VPS048		21	*Trema micrantha*	9	1
VPS049		0	*Trema micrantha*	9	1
VPS050		12	*Trema micrantha*	9	0
VPS054		0	*Trema micrantha*	9	0
VPS054		0	*Trema micrantha*	9	0
VPS055		22	*Trema micrantha*	9	1
VPS056		9	*Trema micrantha*	9	0
VPS057		20	*Trema micrantha*	9	1

VPS058	23	*Trema micrantha*	9	0
VPS059	9	*Trema micrantha*	9	1
VPS062	9	*Trema micrantha*	9	1
VPS063	24	*Trema micrantha*	9	1
VPS065	12	*Trema micrantha*	9	0
VPS066	9	*Trema micrantha*	9	1
VPS067	12	*Trema micrantha*	9	1
VPS068	8	*Trema micrantha*	9	1
VPS069	24	*Trema micrantha*	9	1
VPS070	9	*Trema micrantha*	9	0
VPS071	9	*Trema micrantha*	9	1
VPS072	25	*Trema micrantha*	9	0
VPS074	9	*Trema micrantha*	9	1
VPS075	9	*Trema micrantha*	9	0
VPS076	26	*Trema micrantha*	9	0
VPS077	0	*Trema micrantha*	9	1
VPS078	27	*Trema micrantha*	9	0
VPS079	15	*Trema micrantha*	9	0
VPS080	28	*Trema micrantha*	9	1
VPS081	9	*Trema micrantha*	9	1
VPS083	9	*Trema micrantha*	9	1
VPS084	23	*Trema micrantha*	9	1
VPS085	29	*Trema micrantha*	9	1
VPS086	5	*Trema micrantha*	9	0
VPS087	5	*Trema micrantha*	9	0
VPS089	15	*Trema micrantha*	9	0
VPS090	0	*Trema micrantha*	9	1
VPS091	9	*Trema micrantha*	9	1
VPS092	5	*Trema micrantha*	9	1
VPS093	5	*Trema micrantha*	9	0
VPS095	5	*Trema micrantha*	9	1
VPS096	5	*Trema micrantha*	9	0
VPS097	30	*Trema micrantha*	9	1
VPS099	9	*Trema micrantha*	9	1
VPS100	5	*Trema micrantha*	9	1
VPS101	5	*Trema micrantha*	9	0
VPS102	12	*Trema micrantha*	9	0
VPS103	5	*Trema micrantha*	9	0
VPS104	5	*Trema micrantha*	9	0
VPS105	0	*Trema micrantha*	9	1
VPS105	0	*Trema micrantha*	9	1
VPS183	9	*Trema micrantha*	27	1
VPS188	9	*Trema micrantha*	27	1

VPS189	40	*Trema micrantha*	27	1
VPS191	5	*Trema micrantha*	27	1
VPS192	15	*Trema micrantha*	27	0
VPS197	0	*Trema micrantha*	27	1
VPS202	41	*Trema micrantha*	27	1
VPS203	15	*Trema micrantha*	27	1
VPS204	20	*Trema micrantha*	27	1
VPS206	42	*Trema micrantha*	27	1
VPS209	43	*Trema micrantha*	27	1
VPS214	20	*Trema micrantha*	27	1
VPS215	34	*Trema micrantha*	27	0
VPS217	9	*Trema micrantha*	27	0
VPS219	34	*Trema micrantha*	27	0
VPS220	15	*Trema micrantha*	27	0
VPS221	41	*Trema micrantha*	27	0
VPS225	19	*Trema micrantha*	27	1
VPS226	0	*Trema micrantha*	27	0
VPS227	13	*Trema micrantha*	27	1
VPS229	1	*Trema micrantha*	27	1
VPS232	9	*Trema micrantha*	27	0
VPS233	44	*Trema micrantha*	27	0
VPS235	44	*Trema micrantha*	27	1
VPS236	45	*Trema micrantha*	27	1
VPS237	46	*Trema micrantha*	27	1
VPS239	47	*Trema micrantha*	27	0
VPS240	9	*Trema micrantha*	27	1
VPS242	37	*Trema micrantha*	27	0
VPS243	48	*Trema micrantha*	27	0
VPS245	34	*Trema micrantha*	27	1
VPS246	49	*Trema micrantha*	27	0
VPS247	9	*Trema micrantha*	27	1
VPS249	50	*Trema micrantha*	27	1
VPS250	51	*Trema micrantha*	27	1
VPS252	52	*Trema micrantha*	27	1
VPS108	5	*Trema micrantha*	30	1
VPS111	3	*Trema micrantha*	30	0
VPS112	5	*Trema micrantha*	30	1
VPS113	9	*Trema micrantha*	30	0
VPS116	8	*Trema micrantha*	18	1
VPS120	0	*Trema micrantha*	18	0
VPS121	15	*Trema micrantha*	18	1
VPS123	13	*Trema micrantha*	18	0
VPS124	0	*Trema micrantha*	18	1

VPS125	0	*Trema micrantha*	18	1
VPS127	31	*Trema micrantha*	18	0
VPS128	0	*Trema micrantha*	18	0
VPS130	32	*Trema micrantha*	18	1
VPS132	12	*Trema micrantha*	18	1
VPS133	33	*Trema micrantha*	18	1
VPS134	34	*Trema micrantha*	18	1
VPS137	9	*Trema micrantha*	18	1
VPS138	8	*Trema micrantha*	18	1
VPS139	10	*Trema micrantha*	18	0
VPS143	35	*Trema micrantha*	18	0
VPS144	36	*Trema micrantha*	18	0
VPS145	37	*Trema micrantha*	18	0
VPS146	10	*Trema micrantha*	18	0
VPS147	5	*Trema micrantha*	18	1
VPS148	38	*Trema micrantha*	18	1
VPS149	10	*Trema micrantha*	18	1
VPS150	8	*Trema micrantha*	18	0
VPS151	0	*Trema micrantha*	18	1
VPS152	11	*Trema micrantha*	18	1
VPS153	0	*Trema micrantha*	18	0
VPS154	9	*Trema micrantha*	18	1
VPS158	9	*Trema micrantha*	18	0
VPS159	9	*Trema micrantha*	18	0
VPS160	0	*Trema micrantha*	18	1
VPS161	10	*Trema micrantha*	18	1
VPS163	0	*Trema micrantha*	18	1
VPS164	19	*Trema micrantha*	18	1
VPS165	0	*Trema micrantha*	18	1
VPS166	0	*Trema micrantha*	18	0
VPS167	13	*Trema micrantha*	18	1
VPS168	20	*Trema micrantha*	18	1
VPS169	10	*Trema micrantha*	18	1
VPS170	20	*Trema micrantha*	18	1
VPS171	34	*Trema micrantha*	18	1
VPS174	10	*Trema micrantha*	18	1
VPS175	12	*Trema micrantha*	18	1
VPS176	15	*Trema micrantha*	18	1
VPS178	39	*Trema micrantha*	18	1
VPS180	0	*Trema micrantha*	18	1
VPS181	34	*Trema micrantha*	18	1
VPS115	9	*Trema micrantha*	25	0
VPS332	53	*Zanthoxylum ekmanii*	33	0

VPS340	54	*Zanthoxylum ekmanii*	33	0
VPS344	72	*Zanthoxylum ekmanii*	33	0
VPS346	65	*Zanthoxylum ekmanii*	33	0
VPS350	73	*Zanthoxylum ekmanii*	33	0
VPS351	74	*Zanthoxylum ekmanii*	33	0
VPS353	5	*Zanthoxylum ekmanii*	33	0
VPS354	15	*Zanthoxylum ekmanii*	33	1
VPS356	75	*Zanthoxylum ekmanii*	33	0
VPS254	53	*Zanthoxylum ekmanii*	25	0
VPS299	13	*Zanthoxylum ekmanii*	5	0
VPS300	15	*Zanthoxylum ekmanii*	5	0
VPS301	54	*Zanthoxylum ekmanii*	5	0
VPS302	12	*Zanthoxylum ekmanii*	5	0
VPS303	5	*Zanthoxylum ekmanii*	5	0
VPS304	10	*Zanthoxylum ekmanii*	5	0
VPS305	13	*Zanthoxylum ekmanii*	5	1
VPS306	54	*Zanthoxylum ekmanii*	5	0
VPS307	15	*Zanthoxylum ekmanii*	5	0
VPS308	12	*Zanthoxylum ekmanii*	5	0
VPS309	12	*Zanthoxylum ekmanii*	5	0
VPS362	67	*Zanthoxylum ekmanii*	21	0
VPS363	76	*Zanthoxylum ekmanii*	21	0
VPS364	77	*Zanthoxylum ekmanii*	21	0
VPS366	78	*Zanthoxylum ekmanii*	21	1
VPS368	79	*Zanthoxylum ekmanii*	21	1
VPS369	80	*Zanthoxylum ekmanii*	21	0
VPS370	81	*Zanthoxylum ekmanii*	21	0
VPS371	81	*Zanthoxylum ekmanii*	21	1
VPS372	82	*Zanthoxylum ekmanii*	21	1
VPS374	29	*Zanthoxylum ekmanii*	21	1
VPS376	83	*Zanthoxylum ekmanii*	21	0
VPS377	12	*Zanthoxylum ekmanii*	21	1
VPS378	56	*Zanthoxylum ekmanii*	21	1
VPS379	12	*Zanthoxylum ekmanii*	21	0
VPS380	77	*Zanthoxylum ekmanii*	21	0
VPS381	84	*Zanthoxylum ekmanii*	21	0
VPS382	85	*Zanthoxylum ekmanii*	21	1
VPS383	86	*Zanthoxylum ekmanii*	21	1
VPS384	87	*Zanthoxylum ekmanii*	21	0
VPS387	88	*Zanthoxylum ekmanii*	21	0
VPS388	12	*Zanthoxylum ekmanii*	21	0
VPS389	56	*Zanthoxylum ekmanii*	21	1
VPS390	89	*Zanthoxylum ekmanii*	21	0

VPS391	37	*Zanthoxylum ekmanii*	21	0
VPS392	29	*Zanthoxylum ekmanii*	21	1
VPS393	77	*Zanthoxylum ekmanii*	21	0
VPS395	77	*Zanthoxylum ekmanii*	21	0
VPS396	29	*Zanthoxylum ekmanii*	21	1
VPS401	67	*Zanthoxylum ekmanii*	21	0
VPS402	29	*Zanthoxylum ekmanii*	21	0
VPS403	90	*Zanthoxylum ekmanii*	21	0
VPS404	91	*Zanthoxylum ekmanii*	21	0
VPS406	92	*Zanthoxylum ekmanii*	21	1
VPS409	91	*Zanthoxylum ekmanii*	21	0
VPS410	60	*Zanthoxylum ekmanii*	21	0
VPS412	85	*Zanthoxylum ekmanii*	21	0
VPS413	93	*Zanthoxylum ekmanii*	21	1
VPS414	94	*Zanthoxylum ekmanii*	21	0
VPS415	64	*Zanthoxylum ekmanii*	21	0
VPS416	85	*Zanthoxylum ekmanii*	21	1
VPS417	61	*Zanthoxylum ekmanii*	21	0
VPS418	15	*Zanthoxylum ekmanii*	21	0
VPS419	15	*Zanthoxylum ekmanii*	21	0
VPS422	5	*Zanthoxylum ekmanii*	21	0
VPS424	83	*Zanthoxylum ekmanii*	21	0
VPS425	95	*Zanthoxylum ekmanii*	21	0
VPS426	87	*Zanthoxylum ekmanii*	21	0
VPS427	92	*Zanthoxylum ekmanii*	21	1
VPS428	85	*Zanthoxylum ekmanii*	21	0
VPS429	12	*Zanthoxylum ekmanii*	21	0
VPS430	12	*Zanthoxylum ekmanii*	21	0
VPS431	81	*Zanthoxylum ekmanii*	21	0
VPS433	85	*Zanthoxylum ekmanii*	21	0
VPS434	94	*Zanthoxylum ekmanii*	21	0
VPS435	83	*Zanthoxylum ekmanii*	21	1
VPS436	56	*Zanthoxylum ekmanii*	21	0
VPS437	5	*Zanthoxylum ekmanii*	21	0
VPS438	67	*Zanthoxylum ekmanii*	21	0
VPS440	53	*Zanthoxylum ekmanii*	21	0
VPS441	67	*Zanthoxylum ekmanii*	21	0
VPS441	67	*Zanthoxylum ekmanii*	21	0
VPS442	96	*Zanthoxylum ekmanii*	21	0
VPS443	82	*Zanthoxylum ekmanii*	21	0
VPS445	97	*Zanthoxylum ekmanii*	21	0
VPS446	98	*Zanthoxylum ekmanii*	21	0
VPS447	62	*Zanthoxylum ekmanii*	21	0

VPS448	99	*Zanthoxylum ekmanii*	21	0
VPS451	77	*Zanthoxylum ekmanii*	21	0
VPS452	49	*Zanthoxylum ekmanii*	21	0
VPS453	37	*Zanthoxylum ekmanii*	21	0
VPS454	70	*Zanthoxylum ekmanii*	21	0
VPS456	56	*Zanthoxylum ekmanii*	21	0
VPS457	100	*Zanthoxylum ekmanii*	21	0
VPS458	77	*Zanthoxylum ekmanii*	21	0
VPS459	56	*Zanthoxylum ekmanii*	21	0
VPS460	5	*Zanthoxylum ekmanii*	21	0
VPS461	29	*Zanthoxylum ekmanii*	21	0
VPS462	101	*Zanthoxylum ekmanii*	21	0
VPS463	85	*Zanthoxylum ekmanii*	21	0
VPS464	37	*Zanthoxylum ekmanii*	21	0
VPS465	64	*Zanthoxylum ekmanii*	21	1
VPS467	37	*Zanthoxylum ekmanii*	21	0
VPS469	56	*Zanthoxylum ekmanii*	21	0
VPS470	62	*Zanthoxylum ekmanii*	21	0
VPS471	57	*Zanthoxylum ekmanii*	21	0
VPS472	85	*Zanthoxylum ekmanii*	21	0
VPS473	61	*Zanthoxylum ekmanii*	21	0
VPS476	83	*Zanthoxylum ekmanii*	21	0
VPS477	102	*Zanthoxylum ekmanii*	21	0
VPS478	53	*Zanthoxylum ekmanii*	21	0
VPS480	70	*Zanthoxylum ekmanii*	21	0
VPS481	56	*Zanthoxylum ekmanii*	21	1
VPS483	67	*Zanthoxylum ekmanii*	21	0
VPS484	56	*Zanthoxylum ekmanii*	21	0
VPS486	57	*Zanthoxylum ekmanii*	21	0
VPS487	103	*Zanthoxylum ekmanii*	21	0
VPS488	91	*Zanthoxylum ekmanii*	21	0
VPS489	10	*Zanthoxylum ekmanii*	21	1
VPS490	54	*Zanthoxylum ekmanii*	21	0
VPS491	77	*Zanthoxylum ekmanii*	21	0
VPS492	56	*Zanthoxylum ekmanii*	21	0
VPS493	104	*Zanthoxylum ekmanii*	21	0
VPS494	66	*Zanthoxylum ekmanii*	21	0
VPS495	29	*Zanthoxylum ekmanii*	21	0
VPS496	37	*Zanthoxylum ekmanii*	21	0
VPS497	93	*Zanthoxylum ekmanii*	21	0
VPS498	85	*Zanthoxylum ekmanii*	21	0
VPS499	105	*Zanthoxylum ekmanii*	21	0
VPS501	12	*Zanthoxylum ekmanii*	21	0

VPS502	85	*Zanthoxylum ekmanii*	21	0
VPS503	56	*Zanthoxylum ekmanii*	21	0
VPS504	56	*Zanthoxylum ekmanii*	21	1
VPS505	106	*Zanthoxylum ekmanii*	21	1
VPS506	77	*Zanthoxylum ekmanii*	21	0
VPS507	56	*Zanthoxylum ekmanii*	21	0
VPS509	15	*Zanthoxylum ekmanii*	21	1
VPS510	107	*Zanthoxylum ekmanii*	21	1
VPS511	62	*Zanthoxylum ekmanii*	21	0
VPS512	5	*Zanthoxylum ekmanii*	21	0
VPS513	5	*Zanthoxylum ekmanii*	21	0
VPS514	108	*Zanthoxylum ekmanii*	21	0
VPS515	79	*Zanthoxylum ekmanii*	21	1
VPS516	109	*Zanthoxylum ekmanii*	21	1
VPS518	92	*Zanthoxylum ekmanii*	21	1
VPS519	94	*Zanthoxylum ekmanii*	21	1
VPS521	53	*Zanthoxylum ekmanii*	21	1
VPS522	85	*Zanthoxylum ekmanii*	21	0
VPS523	110	*Zanthoxylum ekmanii*	21	1
VPS524	29	*Zanthoxylum ekmanii*	21	0
VPS525	29	*Zanthoxylum ekmanii*	21	1
VPS526	111	*Zanthoxylum ekmanii*	21	1
VPS527	15	*Zanthoxylum ekmanii*	21	0
VPS528	5	*Zanthoxylum ekmanii*	21	0
VPS529	5	*Zanthoxylum ekmanii*	21	0
VPS530	2	*Zanthoxylum ekmanii*	21	0
VPS531	5	*Zanthoxylum ekmanii*	21	0
VPS532	5	*Zanthoxylum ekmanii*	21	0
VPS533	83	*Zanthoxylum ekmanii*	21	0
VPS534	5	*Zanthoxylum ekmanii*	21	0
VPS535	5	*Zanthoxylum ekmanii*	21	0
VPS536	0	*Zanthoxylum ekmanii*	21	1
VPS537	5	*Zanthoxylum ekmanii*	21	0
VPS538	29	*Zanthoxylum ekmanii*	21	1
VPS539	112	*Zanthoxylum ekmanii*	21	0
VPS256	54	*Zanthoxylum ekmanii*	18	1
VPS257	1	*Zanthoxylum ekmanii*	18	1
VPS258	55	*Zanthoxylum ekmanii*	18	0
VPS259	56	*Zanthoxylum ekmanii*	18	0
VPS261	15	*Zanthoxylum ekmanii*	18	0
VPS262	57	*Zanthoxylum ekmanii*	18	1
VPS263	29	*Zanthoxylum ekmanii*	18	0
VPS264	37	*Zanthoxylum ekmanii*	18	0

VPS265	6	*Zanthoxylum ekmanii*	18	1
VPS267	12	*Zanthoxylum ekmanii*	18	0
VPS268	58	*Zanthoxylum ekmanii*	18	0
VPS269	5	*Zanthoxylum ekmanii*	18	0
VPS271	37	*Zanthoxylum ekmanii*	18	0
VPS272	12	*Zanthoxylum ekmanii*	18	0
VPS273	59	*Zanthoxylum ekmanii*	18	0
VPS275	60	*Zanthoxylum ekmanii*	18	1
VPS276	61	*Zanthoxylum ekmanii*	18	1
VPS277	29	*Zanthoxylum ekmanii*	18	0
VPS278	62	*Zanthoxylum ekmanii*	18	1
VPS279	29	*Zanthoxylum ekmanii*	18	1
VPS280	56	*Zanthoxylum ekmanii*	18	1
VPS282	63	*Zanthoxylum ekmanii*	18	0
VPS283	56	*Zanthoxylum ekmanii*	18	0
VPS285	5	*Zanthoxylum ekmanii*	18	0
VPS286	12	*Zanthoxylum ekmanii*	18	0
VPS287	64	*Zanthoxylum ekmanii*	18	0
VPS288	15	*Zanthoxylum ekmanii*	18	0
VPS291	10	*Zanthoxylum ekmanii*	18	1
VPS292	65	*Zanthoxylum ekmanii*	18	0
VPS293	53	*Zanthoxylum ekmanii*	18	0
VPS294	15	*Zanthoxylum ekmanii*	18	0
VPS295	29	*Zanthoxylum ekmanii*	18	1
VPS296	66	*Zanthoxylum ekmanii*	18	1
VPS297	29	*Zanthoxylum ekmanii*	18	0
VPS310	67	*Zanthoxylum ekmanii*	30	0
VPS311	5	*Zanthoxylum ekmanii*	30	0
VPS312	68	*Zanthoxylum ekmanii*	30	0
VPS313	15	*Zanthoxylum ekmanii*	30	0
VPS314	69	*Zanthoxylum ekmanii*	30	0
VPS315	10	*Zanthoxylum ekmanii*	30	0
VPS318	15	*Zanthoxylum ekmanii*	30	0
VPS319	56	*Zanthoxylum ekmanii*	30	1
VPS321	70	*Zanthoxylum ekmanii*	30	0
VPS322	58	*Zanthoxylum ekmanii*	30	0
VPS323	71	*Zanthoxylum ekmanii*	30	0
VPS325	70	*Zanthoxylum ekmanii*	30	0
VPS326	35	*Zanthoxylum ekmanii*	30	0
VPS327	35	*Zanthoxylum ekmanii*	30	0
VPS328	37	*Zanthoxylum ekmanii*	30	0
VPS330	12	*Zanthoxylum ekmanii*	30	0

Class	Order	Genus
Sordariomycetes	Hypocreales	*Neocosmospora*
Dothideomycetes	Botryosphaeriales	*Lasiodiplodia*
Sordariomycetes	Xylariales	*Kretzschmaria*
Dothideomycetes	Pleosporales	*Medicopsis*
Sordariomycetes	Hypocreales	*Ilyonectria*
Sordariomycetes	Hypocreales	*Fusarium*
Dothideomycetes	Pleosporales	*Medicopsis*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Diaporthales	*Gnomonia*
Dothideomycetes	Pleosporales	*Septoriella*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Moelleriella*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Xylariales	*Microdochium*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Sordariomycetes	Hypocreales	*Fusarium*
Leotiomycetes	Rhytismatales	*Cudonia*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Dothideomycetes	Pleosporales	*Wettsteinina*
Dothideomycetes	Venturiales	*Verruconis*
Sordariomycetes	Hypocreales	*Metarhizium*
Sordariomycetes	Xylariales	*Arthrinium*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Dothideomycetes	Capnodiales	*Pseudocercospora*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Mariannaea*
Sordariomycetes	Hypocreales	*Neocosmospora*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Pochonia*
Dothideomycetes	Abrothallales	*Abrothallus*
Dothideomycetes	Capnodiales	*Pseudocercospora*

Dothideomycetes	Pleosporales	*Pyrenochaetopsis*
Dothideomycetes	Abrothallales	*Abrothallus*
Dothideomycetes	Abrothallales	*Abrothallus*
Sordariomycetes	Hypocreales	*Pochonia*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Dothideomycetes	Abrothallales	*Abrothallus*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Pochonia*
Dothideomycetes	Abrothallales	*Abrothallus*
Dothideomycetes	Abrothallales	*Abrothallus*
Eurotiomycetes	Eurotiales	*Penicillium*
Dothideomycetes	Abrothallales	*Abrothallus*
Dothideomycetes	Abrothallales	*Abrothallus*
Sordariomycetes	Hypocreales	*Neocosmospora*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Eurotiomycetes	Chaetothyriales	*Cyphellophora*
Sordariomycetes	Hypocreales	*Moelleriella*
Sordariomycetes	Hypocreales	*Moelleriella*
Dothideomycetes	Pleosporales	*Pyrenochaetopsis*
Eurotiomycetes	Chaetothyriales	*Minimelanolocus*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Dothideomycetes	Abrothallales	*Abrothallus*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Dothideomycetes	Pleosporales	*Murilentithecium*
Dothideomycetes	Abrothallales	*Abrothallus*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Moelleriella*
Sordariomycetes	Hypocreales	*Moelleriella*

Sordariomycetes	Hypocreales	*Aquanectria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Eurotiomycetes	Chaetothyriales	*Capronia*
Sordariomycetes	Hypocreales	*Fusarium*
Dothideomycetes	Capnodiales	*Pseudocercospora*
Dothideomycetes	Pleosporales	*Medicopsis*
Dothideomycetes	Pleosporales	*Pseudodidymocyrtis*
Dothideomycetes	Capnodiales	*Pseudocercospora*
Sordariomycetes	Hypocreales	*Clonostachys*
Dothideomycetes	Abrothallales	*Abrothallus*
Sordariomycetes	Hypocreales	*Clonostachys*
Sordariomycetes	Hypocreales	*Fusarium*
Eurotiomycetes	Chaetothyriales	*Capronia*
Sordariomycetes	Xylariales	*Arthrinium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Dothideomycetes	Botryosphaeriales	*Lasiodiplodia*
Dothideomycetes	Abrothallales	*Abrothallus*
Dothideomycetes	Trypetheliales	*Trypethelium*
Dothideomycetes	Trypetheliales	*Trypethelium*
Sordariomycetes	Xylariales	*Pestalotiopsis*
Dothideomycetes	Pleosporales	*Massariosphaeria*
Eurotiomycetes	Eurotiales	*Penicillium*
Dothideomycetes	Abrothallales	*Abrothallus*
Lecanoromycetes	Lecanorales	*Metus*
Dothideomycetes	Pleosporales	*Arthopyrenia*
Sordariomycetes	Hypocreales	*Clonostachys*
Sordariomycetes	Hypocreales	*Penicillifer*
Pezizomycetes	Pezizales	*Genea*
Dothideomycetes	Venturiales	*Ochroconis*
Dothideomycetes	Capnodiales	*Neodevriesia*
Dothideomycetes	Pleosporales	*Curvularia*
Sordariomycetes	Xylariales	*Kretzschmaria*
Dothideomycetes	Pleosporales	*Medicopsis*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Hypocreales	*Moelleriella*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*

Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Purpureocillium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Xylariales	*Annulohypoxylon*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Dothideomycetes	Pleosporales	*Pseudodidymocyrtis*
Sordariomycetes	Hypocreales	*Clonostachys*
Sordariomycetes	Hypocreales	*Moelleriella*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Dothideomycetes	Pleosporales	*Biatriospora*
Eurotiomycetes	Sclerococcales	*Fusichalara*
Leotiomycetes	Rhytismatales	*Cudonia*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Xylariales	*Kretzschmaria*
Leotiomycetes	Rhytismatales	*Cudonia*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Xylariales	*Microdochium*
Sordariomycetes	Hypocreales	*Fusarium*
Pezizomycetes	Pezizales	*Peziza*
Pezizomycetes	Pezizales	*Peziza*
Sordariomycetes	Hypocreales	*Moelleriella*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Xylariales	*Arthrinium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Dothideomycetes	Capnodiales	*Pseudocercospora*
Sordariomycetes	Hypocreales	*Fusarium*
Dothideomycetes	Capnodiales	*Pseudocercospora*
Sordariomycetes	Hypocreales	*Clonostachys*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Xylariales	*Microdochium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Clonostachys*
Sordariomycetes	Hypocreales	*Moelleriella*
Sordariomycetes	Xylariales	*Hypoxylon*

Sordariomycetes	Hypocreales	*Clonostachys*
Sordariomycetes	Xylariales	*Annulohypoxylon*
Eurotiomycetes	Chaetothyriales	*unclassified*
Eurotiomycetes	Chaetothyriales	*Cyphellophora*
Sordariomycetes	Boliniales	*Camarops*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Trichoderma*
Sordariomycetes	Xylariales	*Hypoxylon*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Clonostachys*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Clonostachys*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Sordariomycetes	Hypocreales	*Mariannaea*
Eurotiomycetes	Chaetothyriales	*Phialophora*
Sordariomycetes	Hypocreales	*Purpureocillium*
Dothideomycetes	Pleosporales	*Hobus*
Eurotiomycetes	Chaetothyriales	*Capronia*
Lecanoromycetes	Rhizocarpales	*Rhizocarpon*
Sordariomycetes	Togniniales	*Phaeoacremonium*
Sordariomycetes	Togniniales	*Phaeoacremonium*
Lecanoromycetes	Rhizocarpales	*Rhizocarpon*
Eurotiomycetes	Chaetothyriales	*Minimelanolocus*
Sordariomycetes	Hypocreales	*Cosmospora*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Sordariomycetes	Xylariales	*Xylaria*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Sordariomycetes	Hypocreales	*Purpureocillium*
Eurotiomycetes	Chaetothyriales	*Exophiala*
Eurotiomycetes	Eurotiales	*Talaromyces*
Eurotiomycetes	Chaetothyriales	*Exophiala*
Eurotiomycetes	Eurotiales	*Talaromyces*
Schizosaccharomycetes	Schizosaccharomycetales	*Schizosaccharomyces*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Sordariomycetes	Xylariales	*Xylaria*
Sordariomycetes	Microascales	*Petriella*

Lecanoromycetes	Lecanorales	*Metus*
Eurotiomycetes	Chaetothyriales	*Minimelanolocus*
Sordariomycetes	Hypocreales	*Purpureocillium*
Sordariomycetes	Hypocreales	*Purpureocillium*
Eurotiomycetes	Chaetothyriales	*Minimelanolocus*
Sordariomycetes	Hypocreales	*Mariannaea*
Eurotiomycetes	Chaetothyriales	*Minimelanolocus*
Sordariomycetes	Unclassified	*Barbatosphaeria*
Sordariomycetes	Xylariales	*Hypoxylon*
Eurotiomycetes	Chaetothyriales	*unclassified*
Sordariomycetes	Xylariales	*Hypoxylon*
Eurotiomycetes	Chaetothyriales	*Cladophialophora*
Eurotiomycetes	Eurotiales	*Talaromyces*
Eurotiomycetes	Eurotiales	*Talaromyces*
Eurotiomycetes	Chaetothyriales	*Capronia*
Eurotiomycetes	Chaetothyriales	*Capronia*
Eurotiomycetes	Eurotiales	*Talaromyces*
Eurotiomycetes	Chaetothyriales	*Cyphellophora*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Hypocreales	*Cosmospora*
Sordariomycetes	Chaetosphaeriales	*Menispora*
Eurotiomycetes	Eurotiales	*Talaromyces*
Eurotiomycetes	Chaetothyriales	*unclassified*
Eurotiomycetes	Eurotiales	*Talaromyces*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Sordariomycetes	Togniniales	*Phaeoacremonium*
Eurotiomycetes	Eurotiales	*Talaromyces*
Eurotiomycetes	Chaetothyriales	*Capronia*
Sordariomycetes	Hypocreales	*Cosmospora*
Sordariomycetes	Xylariales	*Xylaria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Hypocreales	*Mariannaea*
Sordariomycetes	Xylariales	*Hypoxylon*
Sordariomycetes	Hypocreales	*Mariannaea*
Sordariomycetes	Hypocreales	*Mariannaea*
Sordariomycetes	Togniniales	*Phaeoacremonium*
Dothideomycetes	Jahnulales	*Jahnula*
Eurotiomycetes	Eurotiales	*Aspergillus*
Dothideomycetes	Venturiales	*Ochroconis*
Sordariomycetes	Xylariales	*Xylaria*

Eurotiomycetes	Sclerococcales	*Fusichalara*
Sordariomycetes	Hypocreales	*Purpureocillium*
Sordariomycetes	Hypocreales	*Penicillifer*
Lecanoromycetes	Lecanorales	*Metus*
Leotiomycetes	Rhytismatales	*Cudonia*
Sordariomycetes	Xylariales	*Xylaria*
Eurotiomycetes	Chaetothyriales	*unclassified*
Sordariomycetes	Hypocreales	*Purpureocillium*
Sordariomycetes	Xylariales	*Xylaria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Eurotiomycetes	Chaetothyriales	*Minimelanolocus*
Eurotiomycetes	Eurotiales	*Talaromyces*
Eurotiomycetes	Eurotiales	*Talaromyces*
Lecanoromycetes	Lecanorales	*Metus*
Eurotiomycetes	Chaetothyriales	*Capronia*
Lecanoromycetes	Lecanorales	*Metus*
Sordariomycetes	Xylariales	*Xylaria*
Sordariomycetes	Xylariales	*Xylaria*
Dothideomycetes	Pleosporales	*Pseudochaetosphaeronema*
Eurotiomycetes	Eurotiales	*Talaromyces*
Eurotiomycetes	Chaetothyriales	*Cyphellophora*
Sordariomycetes	Hypocreales	*Cosmospora*
Sordariomycetes	Xylariales	*Hypoxylon*
Sordariomycetes	Xylariales	*Hypoxylon*
Leotiomycetes	Rhytismatales	*Cudonia*
Sordariomycetes	Xylariales	*Xylaria*
Sordariomycetes	Hypocreales	*Mariannaea*
Sordariomycetes	Xylariales	*Xylaria*
Dothideomycetes	Pleosporales	*Pseudochaetosphaeronema*
Eurotiomycetes	Chaetothyriales	*Exophiala*
Sordariomycetes	Xylariales	*Hypoxylon*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Clonostachys*
Sordariomycetes	Hypocreales	*Purpureocillium*
Sordariomycetes	Xylariales	*Xylaria*
Eurotiomycetes	Chaetothyriales	*Cladophialophora*
Dothideomycetes	Pleosporales	*Medicopsis*
Eurotiomycetes	Chaetothyriales	*Minimelanolocus*
Lecanoromycetes	Lecanorales	*Metus*
Eurotiomycetes	Eurotiales	*Talaromyces*
Eurotiomycetes	Eurotiales	*Talaromyces*
Sordariomycetes	Xylariales	*Nemania*
Sordariomycetes	Hypocreales	*Gliocladiopsis*

Eurotiomycetes	Eurotiales	*Talaromyces*
Sordariomycetes	Xylariales	*Xylaria*
Sordariomycetes	Xylariales	*Xylaria*
Sordariomycetes	Hypocreales	*Gliomastix*
Sordariomycetes	Hypocreales	*Purpureocillium*
Sordariomycetes	Xylariales	*Xylaria*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Xylariales	*Annulohypoxylon*
Sordariomycetes	Xylariales	*Xylaria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Diaporthales	*Diaporthe*
Eurotiomycetes	Chaetothyriales	*Capronia*
Sordariomycetes	Boliniales	*Camarops*
Eurotiomycetes	Chaetothyriales	*unclassified*
Eurotiomycetes	Chaetothyriales	*Capronia*
Sordariomycetes	Xylariales	*Hypoxylon*
Eurotiomycetes	Eurotiales	*Talaromyces*
Sordariomycetes	Hypocreales	*Moelleriella*
Eurotiomycetes	Chaetothyriales	*Minimelanolocus*
Eurotiomycetes	Chaetothyriales	*Minimelanolocus*
Dothideomycetes	Abrothallales	*Abrothallus*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Hypocreales	*Cosmospora*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Xylariales	*Kretzschmaria*
Eurotiomycetes	Chaetothyriales	*Minimelanolocus*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Clonostachys*
Dothideomycetes	Botryosphaeriales	*Lasiodiplodia*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Xylariales	*Xylaria*
Sordariomycetes	Hypocreales	*Fusarium*
Dothideomycetes	Pleosporales	*Pseudochaetosphaeronema*
Eurotiomycetes	Chaetothyriales	*Minimelanolocus*
Leotiomycetes	Rhytismatales	*Cudonia*

Sordariomycetes	Diaporthales	*Diaporthe*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Lecanoromycetes	Lecanorales	*Metus*
Sordariomycetes	Xylariales	*Kretzschmaria*
Lecanoromycetes	Lecanorales	*Metus*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Leotiomycetes	Helotiales	*Ascocoryne*
Eurotiomycetes	Chaetothyriales	*Cladophialophora*
Eurotiomycetes	Chaetothyriales	*Cyphellophora*
Eurotiomycetes	Chaetothyriales	*Minimelanolocus*
Sordariomycetes	Xylariales	*Xylaria*
Eurotiomycetes	Chaetothyriales	*Minimelanolocus*
Sordariomycetes	Xylariales	*Xylaria*
Dothideomycetes	Pleosporales	*Arthopyrenia*
Sordariomycetes	Xylariales	*Xylaria*
Sordariomycetes	Xylariales	*Kretzschmaria*
Sordariomycetes	Hypocreales	*Gliocladiopsis*
Eurotiomycetes	Chaetothyriales	*Capronia*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Eurotiomycetes	Chaetothyriales	*unclassified*
Sordariomycetes	Xylariales	*Hypoxylon*
Sordariomycetes	Hypocreales	*Fusarium*
Eurotiomycetes	Chaetothyriales	*Minimelanolocus*
Dothideomycetes	Pleosporales	*Medicopsis*
Eurotiomycetes	Chaetothyriales	*Minimelanolocus*
Sordariomycetes	Hypocreales	*Mariannaea*
Sordariomycetes	Xylariales	*Kretzschmaria*
Dothideomycetes	Pleosporales	*Pseudochaetosphaeronema*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Ophionectria*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Hypocreales	*Fusarium*
Sordariomycetes	Xylariales	*Xylaria*
Lecanoromycetes	Lecanorales	*Metus*
Lecanoromycetes	Lecanorales	*Metus*
Dothideomycetes	Pleosporales	*Hobus*
Lecanoromycetes	Lecanorales	*Metus*
Dothideomycetes	Pleosporales	*Biatriospora*
Dothideomycetes	Pleosporales	*Biatriospora*
Lecanoromycetes	Lecanorales	*Metus*
Sordariomycetes	Hypocreales	*Gliocladiopsis*