


Factors in the Distribution of Mycorrhizal and Soil Fungi

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Abstract: Soil fungi are crucial microorganisms in the functioning of ecosystems. They shape the soil properties, facilitate nutrient circulation, and assist with plant growth. However, their biogeography and distribution studies are limited compared to other groups of organisms. This review aims to provide an overview of the main factors shaping the spatial distribution of soil fungi (with a special focus on mycorrhizal fungi). The review also tries to identify the field frontier where further studies are needed. The main drivers of soil fungal distribution were classified and reviewed into three groups: soil properties, plant interactions, and dispersal vectors. It was apparent that ectomycorrhizal and arbuscular fungi are relatively overrepresented in the body of research, while the other mycorrhiza types and endophytes were grossly omitted. Notwithstanding, soil pH and the share of ectomycorrhizal plants in the plant coverage were repeatedly reported as strong predictors of mycorrhizal fungal distribution. Dispersal potential and vector preferences show more variation among fungi, especially when considering long-distance dispersal. Additionally, special attention was given to the applications of the island biogeography theory to soil fungal assemblages. This theory proves to be a very efficient framework for analyzing and understanding not only the soil fungal communities of real islands but even more effective islands, i.e., isolated habitats, such as patches of trees discontinuous from more enormous forests.

Keywords: soil fungi; microbial ecology; mycorrhiza; island biogeography



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1. Introduction

Soil fungi are crucial actors in the functioning of terrestrial ecosystems. Studies have indicated that fungi can constitute up to 30% of the soil microorganism biomass [1]. This includes various functionally diverse groups, ranging from saprotrophic to pathogenic, parasitic, and symbiotic [2]. In addition to the most recognizable role soil fungi play, i.e., decomposing organic matter and facilitating carbon and nitrogen circulation, they are crucial to supporting plant life; about 80% of plant species depend on soil fungal associates in their development [3]. All these functions are addressed by a great diversity of fungal species, estimated to be over six million [4]. This exceeds the diversity of a much better understood group such as plants (ca. 450,000 species) more than tenfold [5].

The distribution patterns of all organisms are tied to their ecology. The spatial and temporal availability of resources, e.g., water or nutrients, limits the distribution of individual species differently, depending on their demand for these resources. Similar in their effect on organism distribution are some edaphic factors, such as the soil's chemical properties or aeration [6]. Likewise, climate factors, such as temperature and its amplitude or precipitation, can affect species distribution respective to their tolerance [7]. The presence of other interacting organisms may affect species distribution negatively (e.g., competition and predation) or positively (e.g., mutualism and commensalism) [8]. Dispersal abilities of individual species are crucial to their distribution; effectively, they determine whether geographical obstacles, e.g., mountains, bodies of water, or open spaces, become barriers these species cannot cross [6]. Of course, all this is also true for fungi. Thus, understanding the fungal ecology (their lifestyle, interactions with the environment and other organisms,

and propagation mechanisms) is intrinsically tied to understanding their biogeography and distribution patterns.

Fungal biology, ecology, and distribution are not sufficiently studied (Appendix A, Table A1). To date, about 150,000 species of fungi have been described, i.e., less than 3% of the estimated 6 million; this is even more striking compared to plants, where more than 50% of the species are known and described [9]. Fungi are underrepresented in academic research. Not even 10% of the published studies of eukaryotes relate to fungi [10]. However, the reasons for fungi being seemingly neglected by researchers are not hard to see. Many fungal species are inconspicuous, sometimes forming only microscopic-scale structures [11]. Their morphological characteristics may be highly misleading, as one species can develop vastly different forms across its life cycle, yet numerous species can be virtually indistinguishable [12], barring molecular identification. Some fungi form obligate relations with other organisms, making them onerous to grow and study in laboratory conditions [13]. These challenges, alongside fungi's limited exposure in biology education, make it so few people decide to study this group [10].

All the difficulties above also apply to studying soil fungi. While some species of soil fungi form eye-catching sporocarps, many (including entire functional groups such as arbuscular mycorrhizal fungi or endophytic fungi) can only be observed under a microscope. Moreover, the sporocarp taxonomic diversity tends to significantly diverge from the belowground community structure [14]. Because of soil fungi's obscure morphology, molecular identification methods are long adopted [15,16]. In contemporary studies, environmental meta-sequencing is a routine practice (e.g., [17]). In addition to allowing easy identification of a wide range of fungal species, meta-sequencing also helps record the species of low prevalence, which could otherwise be missed due to their patchy distribution in soil. However, this approach also comes with its disadvantages; provided identification is of a low taxonomic resolution (usually up to the genus level), taxa present only in the form of inviable propagules can be detected by providing false identifications. Additionally, information about the spatial distribution of the fungi within soil layers and distribution in relation to interacting plants is often lost [18].

This review presents the available information on soil fungi distribution patterns. Various known biotic and abiotic factors directly influencing the distribution of soil fungi were gathered and summarized. The observations made in the relevant body of research were analyzed considering the most prominent paradigm in biogeography, the island biogeography theory [19]. While initially formulated for oceanic and sea islands, the mechanisms described in the island biogeography theory were found to also apply to ecological islands—habitats effectively separated from one another not by a body of water but by a space lacking suitable niches for an organism in question to inhabit [20–24]. The main objective of the present review is to make the link between soil fungi's distribution patterns and ecology more explicit, thus aiding and inspiring future research in the field.

2. Soil Properties

2.1. Soil Chemistry and Nutrient Gradients

Variables most often reported to correlate with soil fungal distribution are pH, soil organic matter, organic and inorganic carbon, nitrogen, and phosphorus (e.g., [25–28]). These are the most often measured variables in studies of soil fungal communities. Additionally, the concentration of exchangeable cations is sometimes reported to affect the fungal distribution in soil. Studies measuring cation concentrations most often report the levels of Ca, K, and Mg (e.g., [27,28]). It is important to note that general fungal diversity, diversity of individual functional groups, and abundance of individual fungal taxa can—and often do—differ in their relation to soil chemistry and nutrient gradients [27]. This can be easily understood in light of the competitive exclusion principle [29]. The response of broader groups reflects the average habitat preference of the taxa they include. In contrast, the individual taxa often diverge from this average as an adaptation to avoid intraclass competition. This mechanism also explains why, compared to the diversity of

fungal functional groups, the abundance of numerous individual fungal taxa correlates significantly with a higher number of soil variables.

Soil fungi tolerate large ranges of soil pH values compared to other microorganisms such as bacteria. This is attributable to both individual fungal taxa drastically differing in their optimal pH range and many fungal species capable of withstanding more than a 5 unit pH difference [30]. Soil fungi generally display higher diversity in lower-pH environments [30,31]. This could be attributed to increased competition with soil bacteria in higher-pH soils rather than a direct effect of pH itself [30,32]. However, recent large-scale studies indicate soil pH, next to local plant diversity, as one of the key factors explaining soil fungal community structure [27]. Most notably, different ranges of soil pH seem to promote discrete trophic guilds of soil fungi. Soil saprotrophs show higher diversity in lower pH, litter saprotrophs and ectomycorrhizal fungi close to neutral pH, and arbuscular mycorrhizal and plant pathogenic fungi in higher pH [27]. It is essential to consider that plant community composition can significantly shape local pH values. Thus, to a degree, the impact of pH on soil fungal assemblages may be regarded as an indirect effect of plant community composition [33].

Soil organic matter is particularly important to saprotrophic fungi, independent from other organisms in nutrient acquisition. As a result, saprotrophic fungi often prefer high concentrations of soil organic matter or proximity to recalcitrant detritus deposits [34,35]. Many mycorrhizal fungi show no correlation or are negatively correlated with soil organic matter content. This might be related to competition with saprotrophic fungi [36] as, unlike them, mycorrhizal fungi are provided with carbohydrates by their plant partners. Certain mycorrhizal fungi retain limited saprobic potential, e.g., ectomycorrhizal *Piloderma* spp. and *Tylospora* spp. [37] or most orchid mycorrhiza [38]. Some mycorrhizal fungal taxa may also decompose organic matter for non-C nutrients, mostly N [36].

Soil mineral nutrient gradients are oft highly related to mycorrhizal fungi distribution patterns. While all fungi require numerous mineral macro- and micronutrients, this is especially true for mycorrhizal fungi, which dispatch mineral nutrients to their host plants [39]. Compared to other mycorrhizal fungal guilds, ectomycorrhizal fungi abundance seems to be more strongly correlated to soil exchangeable ions levels (most significantly Ca) [27]. Increased Ca ion concentration is known to stimulate the growth of some ectomycorrhizal fungal taxa, such as *Hebeloma* [40]. Additionally, the soil Ca ion concentration plays a role in the sporocarp formation of some fungi, as in *Tuber* [41]. The concentration of Ca in soil may further affect these taxa's distribution and dispersal potential through this mechanism.

Some fungi show little correlation with soil nutrient concentration. Most notably, this includes generalist saprotrophic fungi. Moll et al. [42] identified some opportunistic taxa living on simple carbohydrates from plant root exudates, e.g., some *Candida* or *Mortierella* spp., relatively equally distributed among all soil compartments analyzed in the study. Depending on the environmental conditions, arbuscular mycorrhizal fungi may also fall into this category. In harsh, limiting conditions, rather than the soil properties, only the distance from arbuscular mycorrhizal plants was found to relate significantly to the arbuscular fungal distribution [43].

2.2. Soil Moisture

As all organisms require water to live, the moisture level is a critical aspect regulating the structure of soil biota communities. The soil water conditions can also greatly vary on a local scale. However, it is long established that fungi tend to be prevalent regardless of soil water content [44]. This is due to various discrete water conditions to which particular fungi are adapted. Studies in the desert and other arid ecosystems report all trophic guilds of fungi present, with a notable share of mycorrhizal (arbuscular and ectomycorrhizal) fungi in the local communities [45]. Most desert fungi are found in local plants' rhizospheres, and a mutualistic lifestyle is a great adaptation advantage in these adverse conditions. Fungi may also play an active role in transforming the water conditions of the inhabited dry soils. Both arbuscular [46] and ectomycorrhizal [47] fungi actively transport and distribute water

in dry soils. Even saprotrophic fungi (*Agaricus bisporus*) were found to redistribute water in the soil, allowing fewer drought-resistant microorganisms to inhabit otherwise unavailable soil niches [48]. After arid ecosystems, wetlands are the other extreme in terms of soil water level. In wetlands, mycorrhizal fungi are still common [49], but saprotrophic fungi also play a more significant role [50]. Although, across the entire gradient of soil humidity, some well-adjusted fungi can be found thriving, studies of soil microbial communities in Central Europe indicate a soil moisture content of 60% (soil maximum water capacity) to be the optimal value for the general growth of soil fungal communities [51].

However, despite specific fungal groups being adjusted to most ranges of soil humidity, fungal communities seem susceptible to sudden drought stress. Temporary drying of the soil was reported to negatively affect soil fungal communities much more than bacterial communities in terms of their richness and composition. The impact of a drought period on a fungal community seems to persist even after soil hydration is restored; this effect is called drought legacy [52]. Several factors might contribute to this. Generally, fungal communities tend to be more persistent than ephemeral bacterial communities [53,54]. Some fungi could require more time to re-establish themselves after a drought event. Additionally, a study of drought stress priming in saprotrophic fungal species revealed that some fungal species, e.g., *Penicillium chrysogenum*, drastically limit their metabolism and growth in prolonged periods following drought events [55]. The nutrients saved in the process may be used to prepare the fungus to withstand follow-up drought waves.

Soil fungi differ in their hyphal surface properties and hydrophilicity [56]. This may lead to changes in community composition in response to the local water conditions. It is known that ectomycorrhizal fungi distribution responds to soil moisture level, with ectomycorrhizal taxa with hydrophobic properties becoming more prevalent as there is more water in the environment [49,57]. The hydrophobic/hydrophilic properties of ectomycorrhizal fungi are primarily associated with their exploration types; moving from contact type to short, medium, and long type, the fungal structures tend to become more hydrophobic [56]. Soil fungi are also known to synthesize different quantities of hydrophobins, highly hydrophobic proteins. These proteins can be presented on the surface of various fungal structures, increasing their hydrophobicity, or be released into the soil, changing its properties [58].

In addition to being related to water access, soil moisture also regulates soil aeration. Due to slow gas diffusion in liquids, high soil moisture levels may lead to low oxygen concentration regions forming anaerobic conditions [59]. Most soil fungi are highly restricted by reduced oxygen availability [60]. However, studies in flooded soils revealed several facultatively anaerobic microfungi predominant in similar conditions. Most of these microfungi are saprotrophic or pathogenic (e.g., genera *Mucor*, *Rhizopus*, and *Fusarium*), but some are plant-associated mutualists (e.g., *Trichoderma*) [61].

2.3. Soil Structure

Propagating hyphae through the soil and upkeeping robust hyphal networks require metabolic energy. As a result, the soil structure (density, porosity) is also essential for fungal distribution. A study of *Rhizoctonia solani* showed that, while its hyphae can extend across open spaces without support, it tends to grow alongside the soil pore walls [62]. Some explanations suggest that extending while supported by an outer structure presents a lower metabolic cost for the hyphae, or that adhering to the soil pore walls is preferred as it increases the hyphal surface capable of absorbing nutrients from the soil [59]. Regardless of the mechanism, this preference leads to *R. solani* growing more extensively and extending further in soils with higher bulk density; more soil particles and smaller diameter of soil pores provide more support to the extending hyphae.

Moreover, soil structure may affect fungal distribution indirectly; small invertebrates (e.g., mites and nematodes) grazing on fungal hyphae may be able to access them if the pores are large enough for them to fit [59]. The effect of invertebrates grazing on the biomass and growth of soil fungi seems to be very inconsistent among fungal taxa, even

for taxa in the same trophic guild. However, in cases of some mycorrhizal fungi, grazing can impair the efficiency of the mutualistic relation with plants; arbuscular mycorrhizal fungi seem most susceptible to its effects [63]. Nevertheless, soil invertebrates accessing fungal hyphae may contribute positively to soil fungal distribution. As a result of coming into contact with or consuming hyphae or spores, they may serve as important vectors for the dispersal of soil fungal propagules [64].

In addition, soils tend to feature distinctly stratified structures. Fungi are known to vary greatly in their abundance among soil layers, yet few studies addressed this [35,42,65,66]. This is mainly because soil layers differ in terms of the previously described variables, i.e., chemical properties, nutrient gradients, moisture level, density, and aeration. Studies in grasslands indicate that, while general soil fungal communities are significantly stratified among soil horizons, this is not true for Basidiomycota communities, which are little affected by the sampling depth [65,66]. Moll et al. [42] reported arbuscular mycorrhizal fungi as the trophic guild with the most stratified communities on arable soils. Notably, arbuscular mycorrhizal taxa, particularly susceptible to soil disturbance, e.g., *Glomus*, show a preference for deeper soil horizons. Some fungi are reported to occur exclusively in direct proximity to plant roots, regardless of soil depth. In addition to mycorrhizal fungi, these might include other plant-interacting specialized fungal taxa, e.g., pathogenic genera *Microdochium*, *Mycochaetophora*, or *Periconia* or endophytes such as some Helotiales [42]. In North American temperate forests, a significant shift from saprotroph dominance to mycorrhizal fungal dominance alongside soil depth was reported. A similar trend was observed in both arbuscular mycorrhizal and ectomycorrhizal-dominated forests. This pattern seems to result from the soil organic matter distribution, decreasing in the deeper horizons [35].

3. Plant Relations

Local flora composition is well established as one of the main determiners of the diversity and structure of the soil fungal communities [25,27,67]. In addition to interacting with some fungal trophic guilds directly (e.g., mycorrhizal and pathogenic), plants affect local soil environments by exuding carbohydrates through roots [42], shedding foliage that affects soil acidity and nutrient content [33], or forming deposits of dead wood and organic matter [37]. As soil fungal trophic guilds vary in the degree to which they interact with plants, plant diversity affects their distribution differently [27].

Most studies analyzing the relationship between local plant and soil fungal communities focused on mycorrhizal fungi. Arbuscular (e.g., [42,43]) and ectomycorrhizal fungi (e.g., [28,68,69]) tend to be most often studied in this regard, followed by orchid mycorrhiza (e.g., [38]). Others, such as ericoid mycorrhizal fungi, have rarely been studied independently and are often grouped with ectomycorrhizal fungi [70]. Arbuscular and ectomycorrhizal fungi show a similar strong relation to the distribution of compatible plant hosts. This seems less of a factor for orchid mycorrhizal fungi, probably due to their strong affinity to a saprotrophic lifestyle.

The relationship between the ectomycorrhizal fungal community and trees is usually analyzed from the perspective of the trees' taxonomic identity. This is commonly referred to as the host effect [28,68]. While some ectomycorrhizal fungal taxa are generalists equally associating with all ectomycorrhizal trees (e.g., *Cenococcum geophilum*), other taxa show a strong preference toward specific hosts (e.g., *Tuber* spp.) or are host-specific, only interacting with a single tree genus or species (e.g., *Suillus* spp.) [71]. As a result, each ectomycorrhizal host tree species provides niches of a distinct character. However, host identity is not the only plant-related factor influencing ectomycorrhizal fungi. While not studied to the same extent, the age of interacting trees was reported to significantly matter for the makeup of associated ectomycorrhizal fungal communities [17,18]. Rudawska et al.'s [18] study of ectomycorrhizal communities in monoculture *Pinus sylvestris* stands of different ages indicates that, as the host tree ages, young-stage fungal taxa (e.g., *Suillus* spp.) get replaced by old-stage ones (e.g., *Russulaceae* spp.). While the fungal community

diversity is not affected by the individual host tree age, it can be affected by the forest age. As forests get older, more trees of different ages are present, opening distinct niches to ectomycorrhizal fungi.

Arbuscular fungi tend to be more generalist than ectomycorrhizal fungi. As such, soil conditions tend to be the primary determiner of arbuscular fungal distribution in standard environments where arbuscular/mycorrhizal plants are relatively densely distributed. However, more extreme conditions and sparse vegetation result in distance from arbuscular plants being the dominant factor behind arbuscular fungal distribution [43]. Somewhat similarly, studies on arable soils indicate that arbuscular fungi abundance drastically drops in the seasonal absence of compatible plants [42]. These observations can be explained by the fact that, while other mycorrhizal fungi may retain the potential to decompose organic matter, arbuscular fungi receive all their carbon from plant partners [72]. This extreme dependency on their plant hosts can also explain why the abundance of arbuscular fungi in any given site is correlated to the local proportion of arbuscular and ectomycorrhizal plants more strongly than the abundance of ectomycorrhizal fungi [27].

Orchid mycorrhizal fungi are the least dependent on their plant partners among the mycorrhizal types. Most orchid mycorrhizal fungi have other primary ways of acquiring carbon, either by also forming ectomycorrhizal symbiosis (e.g., *Tomentella* spp.) or leading a saprotrophic lifestyle (e.g., *Auricularia* spp.), and they often end up providing carbon to mycoheterotrophic orchid species [73]. Accordingly, the orchid mycorrhizal fungal distribution shows no correlation to compatible orchid distribution [38].

Fungal endophytes are a relatively understudied group of soil fungi. They are essential mutualistic partners of plants. However, as they only recently started receiving wide scientific attention, few studies of factors informing their distribution were performed. Most fungal endophytes are generalists, seemingly colonizing all plant taxa [74]. Nevertheless, U'Ren et al. [75] indicated the importance of clade-level plant host identity to fungal endophytes' global distribution, particularly in the boreal regions.

While saprotrophic fungi are less directly involved with plants than mycorrhizal fungi or endophytes, their distribution is still highly related to the local plant communities. Plants are a significant source of organic matter, becoming the carbon source for saprobes. The two primary plant-based substrates for saprotrophic fungi are dead wood and litter. Many wood-decomposing fungal taxa tend to prefer some tree species [34]. Interestingly, a strong negative relation between ectomycorrhizal plants and saprotrophic soil fungi was repeatedly reported [27,36,76]. This was attributed to competition between saprotrophic and ectomycorrhizal fungi [36]. While saprotrophs are more efficient in organic matter decomposition, both trophic guilds are capable. At the same time, ectomycorrhizal fungi have the advantage of not being dependent on organic matter decomposition for acquiring carbon. Additionally, leaf litter of many ectomycorrhizal tree species, particularly conifers, reduces the local soil pH, inhibiting many saprotrophic fungal taxa [27].

4. Dispersal Vectors and Limitations

Dispersal capabilities seem to be one of the most crucial factors behind fungal distribution patterns, in many studies outweighing all other distribution pattern drivers. Soil fungi utilize several dispersal vectors. These may include wind [22,77–80], water, with waves carrying the propagules [81], animals transporting propagules after consuming a part of the fungus [22,64,79,82] or attached to their surface [64,83], or soil hyphal outgrowth [77]. Each of the dispersal methods is limited in different ways, leading to the emergence of different obstacles and restricting the distribution by a specific vector.

4.1. Wind Dispersal

Airborne dispersal is the most apparent soil fungal propagule dispersal type. The majority of conspicuous epigeous sporocarps produce spores that, to a certain extent, can be transported by air currents; this includes ectomycorrhizal fungi [22,77,84], saprotrophic fungi [79,80], and pathogenic/parasitic fungi [78,80]. Wind dispersal may require low

energy investments or interaction with other organisms. Additionally, fungi have special adaptations to increase the efficiency of their spores' wind dispersal. In some cases, spores can be actively ejected (most notably puffballs like *Lycoperdon* spp.); often, they are sent upward by air currents caused by the water transpiration from sporocarps [85].

Soil fungal trophic guilds seem to differ in their affinity toward specific dispersal vectors. Comparative studies of ectomycorrhizal and saprotrophic fungi's spore structure indicate that saprobes depend on wind dispersal to a higher degree and have their spores adapted fittingly [79,83]. Compared to the spores of ectomycorrhizal fungi, saprotrophic fungal spores tend to be smaller, be elongated in shape, and feature darker pigmentation, protecting the spores from losing viability [79,86]. In turn, even the ectomycorrhizal fungi capable of wind spore dispersal tend to feature adaptations helping with animal vector dispersal, e.g., hydrophobic ornamentation. This differentiation persists even after correcting for phylogenetic distance [79,83].

While some fungal taxa were reported to potentially have their spores transported over thousands of kilometers [78,87], most soil fungal species have their range of effective airborne dispersal limited to a much smaller scale. In addition to the physical limit on how far the wind can carry a spore, this effect can be attributed to the gradual loss of spore viability over the traveled distance [84,88]. In the case of ectomycorrhizal fungi, Peay et al. [88] indicated a 50% decrease in fungal diversity for sites 1 km from the source of propagules. Effective spore dispersal distance seems to depend on the fungal species identity. Even discrete species from the same genera seem to differ significantly in their dispersal potential. For example, *Suillus pungens* was effective at long-distance colonizing, while *S. tomentosus* or *S. pseudobrevipes* were found to have limited dispersal capabilities [84]. As some crucial factors negatively influencing fungal spores over time are sunlight and air turbulences, many fungal taxa can time their spore release to increase their viability. In fact, many fungal taxa are known to release spores late in the evening or at night [80].

The wind mainly transports spores distributed seasonally. This puts it at a disadvantage compared to the mycelium spread distribution, which can occur almost constantly. Studies of *Suillus bovinus* communities in forest stands of different history suggest that spore propagation is most prominent in young stands. However, as the fungi are already present in local soil, mycelium spread becomes more significant. This was indicated by the number and size of individual *S. bovinus* genetets, which were less numerous and covered more extensive areas in older forest stands [77].

4.2. Animal Dispersal

Animal vectors in soil fungal dispersal are probably equally important to wind. Especially in the case of ectomycorrhizal fungi, the most significant way of spore dispersal seems to depend on animal agents [79,83]. As ectomycorrhizal fungal spores need to germinate in the vicinity of compatible host trees, they tend to feature surface ornamentation allowing them to stick to soil invertebrates [83]. Soil invertebrates have long been recognized as a crucial vector in ectomycorrhizal fungal dispersal after forest disturbance, either carrying the spores on their surface or in their digestive systems [64].

Many ectomycorrhizal fungi depend on their sporocarps being consumed and spores being dispersed with animal droppings. The most striking example of this adaptation is hypogeous fungi, such as *Tuber* spp. or *Rhizopogon* spp. [89]. Growing underground, these are not exposed to airflow, and their spores tend to be produced inside the sporocarps. As such, the sporocarps need to be consumed for spore dispersal to be possible. However, even epigeous ectomycorrhizal fungi capable of wind dispersal of spores tend to prefer animal dispersal following sporocarp consumption. This is suggested by the fact that the sporocarps of ectomycorrhizal fungal species tend to be larger than those of saprotrophic fungi, even when correcting for phylogenetic distance, making them more attractive to consumers [90]. Such importance of cervine consumption in spore dispersal was confirmed for *Suillus* spp., otherwise wind-dispersed taxa [82].

Birds may be essential vectors in long-distance soil fungal dispersal. In a study of arbuscular fungal communities on an artificial Baltic Island, Peberholm, it was found that the fungal propagules—spores and inoculated plant fragments—were brought there by migratory geese resting on the island [91]. The taxonomic structure of the local arbuscular fungal community bore a high resemblance to the fungal taxa diversity detected from goose droppings. An essential feature of birds as symbiotic fungi dispersal vectors is that they may be co-dispersing compatible plant host propagules, facilitating the formation of suitable niches for the fungi in the colonized sites [92]. Birds also play a role in the dispersal of ectomycorrhizal [93] and saprotrophic [94] fungi.

4.3. Water Dispersal

Fungal propagules can be dispersed across bodies of water by waves and currents. However, few studies investigated this dispersal vector in soil fungi. A necessary adaptation to such dispersal, particularly over long distances, seems to be a large spore size. Studying arbuscular fungal communities on remote oceanic islands revealed taxa producing relatively large spores to be overrepresented compared to mainland communities [81]. This has been attributed to large spores having increased resilience to adverse environmental conditions and retaining viability for many years [95].

Water might also have a potential role in fungal propagule dispersal within soils. Soil fungal spores differ in their wettability depending on the species; this has been suggested to be an adaptation to their precipitation-facilitated dispersal in soil [96]. Later studies suggest that this way of dispersal might be negligible in natural conditions [64]. However, cases of water-facilitated lateral transport of soil fungal spores have been reported. A plant fungal pathogen, *Phytophthora cinnamomi*, was found to have its propagules transported over a significant distance by the subsurface water flow following heavy rainfall in Australia [97].

5. Ecological Islands

The implications of the island biogeography theory broadly apply to soil fungal communities, although the body of research is skewed toward mycorrhizal guilds. In addition to studies analyzing the fungal distribution across real-life islands, both oceanic [81,91,98] and inland [54,99], the island biogeography paradigm is often applied in studying fungi in effective islands, i.e., isolated habitats such as discontinuous patches of trees [20–24,84,88]. While many similarities can be found between fungal communities in real-life and effective islands, some diversity-shaping effects, most notably the species–area relation, manifest themselves differently. An evident difference between the two systems is their scale, ranging from square kilometers for ocean islands to single trees; in fact, some of the studies themselves suggest that specific island biogeography effects in soil fungal communities may only manifest themselves on particular scales [54,81].

5.1. Real-Life Islands

A Japanese study indicated that the communities of saprotrophic and ectomycorrhizal Basidiomycota in sea islands differ in response to island area [98]. While the community richness of both saprotrophic and ectomycorrhizal fungi showed a strong positive correlation with island area size, ectomycorrhizal fungi were found only on larger islands; 630 m² was indicated as the minimal island size for ectomycorrhizal fungi. Additionally, while saprobes' species–area slope was shallower (0.316), closer to values usually observed for mobile organisms such as birds, the slope for ectomycorrhizal fungi was steeper (0.469) and more typical of sedimentary organisms such as plants [100]. This could be attributed to the mycorrhizal fungal communities being strongly influenced and dependent on the local flora. The island area was found to significantly affect the taxonomic structure of saprotrophic but not ectomycorrhizal fungal communities. Ectomycorrhizal fungal communities' taxonomic makeup depends on the local plant diversity. Communities of neither trophic guild seemed to be affected by the island isolation.

The diversity of arbuscular fungal communities in oceanic islands seems to be little affected by the isolation and island area. Island communities of this trophic guild tend to be subsets of mainland communities, with very few island-endemic taxa and an overrepresentation of large-spored taxa. As such, it has been suggested that effective long-distance dispersal and colonization events for arbuscular fungi on the oceanic scale outweigh the importance of extinction and speciation events [81]. However, it is crucial to note that all the islands analyzed in the Davison et al. [81] study were relatively large. The authors suggest that area effects could play a more significant role in islands smaller than 1 km². While arbuscular fungal communities on the artificial island Peberholm (1.3 km²) were reported to be less diverse [91], it must be noted that the island was constructed at the end of the 20th century, and both its plant and fungal communities are still in relatively early successional stages.

Li et al. [54] compared the inland island communities of soil bacteria and fungi on the Thousand Island Lake in China. For bacteria and fungi, island size but not distance from the mainland was correlated to the community richness. However, the two groups of organisms displayed different patterns of decreasing diversity in smaller islands. Bacterial richness tended to be lower in each individual sample as the island size was smaller, translating to a decrease in α diversity. Conversely, individual samples tended to contain a similar number of fungal taxa regardless of the island size, but the smaller the island was, the fewer differences among the samples were observed, i.e., a decrease in β diversity. Li et al. [54] linked the difference to a different temporal characteristic of the two organism groups, with fungi being more persistent than bacteria. The authors indicate factors contributing to the species–area relation on inland islands. Smaller islands involve more environmental stress as edge habitats are more prevalent. On the other hand, large islands benefit from the sampling effect and habitat heterogeneity effect.

A study of arbuscular fungal communities on Panama's Gatun Lake islands indicated that all island fungal communities were similar regardless of island size or distance from the mainland [99]. However, the island fungal communities significantly differed from the mainland communities. No environmental variables significant in shaping the differences were identified.

5.2. Effective Islands

While the idea of applying island biogeography theory to effective islands in studies of fungal communities already appeared in older work [101], a long-going series of studies in Point Reyes National Seashore in California [20,23,84,88] seems to be the most influential in bringing this approach forward. As ectomycorrhizal fungi need to associate with compatible host trees, Peay et al. [20] suggested that patches of ectomycorrhizal trees discontinuous from a larger forest function as islands, in the sense that, to colonize them, fungal propagules need to traverse an inhabitable space. The number of niches available is limited due to the tree patch's small size. In that case, immigration and extinction events would play a key role in shaping the ectomycorrhizal fungal communities' diversity in tree islands. This first study in the series confirmed this hypothesis, indicating island area as the main predictor of local fungal taxonomic richness. The distance from the forest edge was only significant in multiple regression, including the island size. The subsequent study focused more on the distance from the forest edge [88]. To control for the island size, isolated single trees were studied. The study reported a drastic decrease in fungal taxonomic richness alongside increasing island isolation, indicating a 50% decrease in the number of species for islands only 1 km from the forest edge, a value confirmed by subsequent studies [84]. The isolated island communities shared their low richness, but no similarities could be found in their composition. The authors attributed this to the random nature of colonization events. Further analysis suggested that while most ectomycorrhizal fungi rarely successfully colonize remote islands, few species, e.g., *Suillus pungens*, do it consistently [84]. This aspect of the competition–colonization tradeoff was vital in maintaining ectomycorrhizal fungal diversity [23].

A study in subalpine forests in Yosemite National Park, California, indicated that, even in the case of single isolated trees, the tree size affects the ectomycorrhizal fungal communities analogous to the island size [22]. Interestingly, even older trees analyzed in the study were primarily associated with pioneer-stage ectomycorrhizal fungal species. This was attributed to environmental stress and adverse conditions; as the local extinction events were prominent, the communities were dominated by fungal taxa consistent with dispersal and colonizing. Most ectomycorrhizal fungi found with high frequency were predominately animal-dispersed taxa, e.g., *Rhizopogon* spp. This is a critical observation for understanding ectomycorrhizal fungal communities on effective islands, as other similar studies tend to be biased toward wind dispersal in their experimental design [23,84].

Effective island systems are almost exclusively studied for ectomycorrhizal fungi due to the unique biology of this trophic guild. Other studies of fungal communities on effective islands have been published, but the fungi involved were not inhabiting soil. Most often, these look at fungal communities specific to certain plant organs, such as leaves [101] or flowers [21].

6. Other Factors

While this review explored and summarized some of the most fundamental factors shaping mycorrhizal fungal distribution, many others remain. These factors range from apparent ones such as climate effects [102] or elevation [24] to less evident ones such as slope aspect [103]. Taking all the environmental variables into consideration, particularly the distinguishing features of any given study site, is essential in the studies of soil fungi. Additionally, the temporal characteristics and seasonal changes of soil microbial communities mentioned in this review but not explored in detail (e.g., [17,42,54,77]) are important aspects explaining the soil fungal distribution patterns.

One prominent element missing from the review is human activity. Anthropogenic factors are potent agents shaping the diversity and distribution of all organisms, including soil microorganisms [104]. Human activity impacts fungi by manipulating and affecting the previously described factors, e.g., soil properties or plant coverage. Most apparent are the effects of agricultural [42,105] and forestry [106,107] practices, as well as the effects of pollution [108]. Additionally, people can serve as vectors transporting fungal propagules over large distances [78]. An interesting case of human-facilitated soil fungi propagation can be seen in plant–fungal co-introduction [109]. This includes the purposeful introduction of plants to new habitats (e.g., establishing tree plantations in regions outside of the distribution range of these trees), resulting in the unintentional introduction of fungi associated with these trees. Fully exploring the extent of human impact on soil fungal assemblages deserves a separate review.

The mechanisms shaping the soil fungal distribution are still poorly understood in many ways. While mycorrhizal fungi receive more scientific attention than other soil fungi, even in their case, many aspects of their ecology remain unclear. Hopefully, this review could help and inspire researchers interested in furthering our understanding of this critical topic.

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Appendix A

Table A1. The number of results following keyword combination searches on Scopus and Google Scholar (GS). The results are based on searches conducted on 5 December 2022. In columns, the main keywords representing groups of soil fungi are represented. The verses include secondary keywords that were used in combination with primary keywords. The '[BLANK]' rows represent searches without the inclusion of secondary keywords. The '%' columns indicate the number of search results featuring secondary keywords as a proportion of the number of search results where only the respective primary keyword was used. All searches were completed with the default settings.

Scopus	Soil Fungi		Mycorrhiza		Arbuscular Mycorrhiza		Ectomycorrhiza		Root Endophyte Fungi		Saprotrophic Fungi		Orchid Mycorrhiza		Ericoid Mycorrhiza	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
[BLANK]	55,587		26,428		19,178		7272		2797		1737		774		562	
Distribution	21,765	39%	11,648	44%	8285	43%	4026	55%	1263	45%	943	54%	455	59%	290	52%
Biogeography	4421	8%	2135	8%	1287	7%	1307	18%	247	9%	328	19%	114	15%	94	17%
Propagation	940	2%	1029	4%	614	3%	171	2%	125	4%	17	1%	198	26%	10	2%
GS	Soil Fungi		Mycorrhiza		Arbuscular Mycorrhiza		Ectomycorrhiza		Root Endophyte Fungi		Saprotrophic Fungi		Orchid Mycorrhiza		Ericoid Mycorrhiza	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
[BLANK]	3960,000		203,000		126,000		78,300		74,200		30,100		19,400		9060	
Distribution	3,250,000	82%	143,000	70%	73,600	58%	52,600	67%	43,800	59%	23,700	79%	18,900	97%	6170	68%
Biogeography	70,700	2%	22,300	11%	11,000	9%	12,700	16%	11,600	16%	19,400	64%	4030	21%	1240	14%
Propagation	1,200,000	30%	36,000	18%	21,700	17%	10,900	14%	19,100	26%	3680	12%	10,400	54%	1550	17%

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