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Fungal Dispersal Across Spatial Scales

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Abstract

Fungi play key roles in ecosystems and human societies as decomposers, nutrient cyclers, mutualists, and pathogens. Estimates suggest that roughly 3–13 million fungal species exist worldwide, yet considerable knowledge gaps exist regarding the mechanisms and consequences, both ecological and social, of fungal dispersal from local to global scales. In this review, we summarize concepts underlying fungal dispersal, review recent research, and explore how fungi possess unique characteristics that can broaden our understanding of general dispersal ecology. We highlight emerging frontiers in fungal dispersal research that integrate technological advances with trait-based ecology, movement ecology, social–ecological systems, and work in unexplored environments. Outstanding research questions across these themes are presented to stimulate theoretical and empirical research in fungal dispersal ecology. Advances in fungal dispersal will improve our understanding of fungal community assembly and biogeography across a range of spatial scales, with implications for ecosystem functioning, global food security, and human health.

1. INTRODUCTION

Diverse communities of fungi exist in all ecosystems on Earth, aboveground and belowground, and play numerous vital roles in ecosystems from decomposers to mutualists, parasites to predators (Kendrick 1992). Dispersal is a fundamental ecological process driving the abundance and distribution of fungal species at local scales and contributing to biogeographic patterns at global scales (Golan & Pringle 2017, Norros et al. 2012). Dispersal also influences metapopulation dynamics, gene flow, and as a result, micro- and macroevolutionary processes. Knowledge of dispersal mechanisms is also often applied in biodiversity conservation settings (Driscoll et al. 2014). However, dispersal ecology and its theoretical underpinnings are largely based on animal and plant model systems, with extensions and applications in microbial ecology developing only in recent years. With anywhere between 3 and 13 million fungal species existing worldwide (Hawksworth & Lücking 2017) and fungi providing multiple important ecosystem functions, a better understanding of fungal dispersal mechanisms improves our understanding of fungal biodiversity and function through space and time, as well as our ability to conserve the biodiversity of both free-living and symbiotic fungi.

Understanding, observing, and predicting fungal dispersal can be challenging due to the often cryptic and occasionally microscopic life habit of fungi. Unlike animals and plants, for which an individual is discretely defined (but see DeWoody et al. 2008), true fungi (kingdom Eumycota) are defined as absorptive organisms with diffuse filamentous bodies (Kendrick 1992). Separate individuals of fungi are often difficult to define and observe in situ. Fungi, like all modular organisms, defy a unique and unambiguous definition of the individual, since the latter can either be taken as the genet (derived from a single cell or spore) or the ramet (a physiological unit). Furthermore, the spatial scale of discrete fungal bodies, individuals, and genets spans many orders of magnitude. The largest individual of any type of organism on Earth is likely a fungus with a single individual, defined as the genet, documented as covering 600 hectares (Ferguson et al. 2003, Smith et al. 1992). In contrast, a single leaf in certain tropical trees can contain dozens of different asymptomatic fungal endophyte genets, with each individual isolate measuring no larger than 2 mm^2 (Arnold et al. 2000, Rodriguez et al. 2009). The inability to unambiguously define an individual makes understanding and tracking movement and dispersal in a traditionally defined context difficult. The tenuous definition of fungi as microbes (i.e., organisms invisible to the naked eye) further complicates their inclusion in dominant microbial dispersal paradigms such as the "Everything is everywhere" Baas Becking Hypothesis (Peay et al. 2010). Fungal dispersal research often focuses on spores, microscopic reproductive propagules that are able to form new individuals and function as offspring and dispersal agents. Fungi can form spores via specialized macro fruiting bodies (e.g., mushrooms, puffballs), singly from the ends of hyphal branches, or not at all. Spore dispersal represents a mode of fungal movement to consider along with how fungal mycelial networks or individual bodies move. In the early twentieth century, foundational work on fungal dispersal integrated natural history observations of certain Basidiomycota, Ascomycota, and Pilobolus (dung fungi) species with biophysics experiments on spore movement (Buller 1909). Despite an initial lukewarm reception and inability to be published, this early work no doubt paved the way for interdisciplinary research on fungal dispersal and continues to inspire fungal ecological research to this day (Gregory 1961, Lacey 1996, Pringle et al. 2005, Yafetto et al. 2008). Alongside his mycological discoveries, it is also important to note Buller's problematic views as a proponent of eugenics and race purity (Goldsborough 2004). Still, Buller (1909 p. vii) wrote (perhaps foreshadowing), "...showing how closely the various branches of science may be knit together, it is not without interest that the first direct test of Stokes' Law for the fall of microscopic spheres in air has been carried out with the help of a lowly Cryptogam."

Applying traditional dispersal ecology concepts and definitions to fungi can prove challenging due to the unique life forms and life history strategies of fungi. Dispersal is defined as "any movement of individuals or propagules that has potential consequences for gene flow across space" (Saastamoinen et al. 2018, p. 575). In both macro and cryptic fungi, dispersal has been described as having three distinct phases: liberation, transport, and colonization (Buller 1909, Chaudhary et al. 2020, Gregory 1945). The enormous challenges associated with studying dispersal (Nathan 2001) in a manner that incorporates all stages have resulted in mycologists primarily focusing on the transport stage, as well as focusing on fungal spores (Bielčik et al. 2019, Golan & Pringle 2017). But fungal individuals consist of more than spores or sporocarps, and hyphal fragments can also function as propagules (Boddy et al. 2009, Tommerup & Abbott 1981). Movement, on the other hand, is defined as the change in spatial location of an entire individual in time (Nathan et al. 2008). Filamentous fungi are being increasingly incorporated into movement ecology paradigms by acknowledging how they too participate in active movement through integrated growth and foraging in mycelial networks (Bielčik et al. 2019). Movement of spores, sporocarps, and hyphae can be a component of fungal dispersal, but fungal movement can also be independent of dispersal when it functions primarily for the purpose of resource acquisition and does not have consequences for gene flow. Furthermore, some fungi are free living and others are symbiotic, existing in close association of varying dependency with another nonfungal organism; association with a suitable host in the new location is a crucial and little studied step in fungal dispersal research (Koide et al. 2017). Fungal movement can be active, as in the case of fungi that rapidly launch ballistospores (Pringle et al. 2005) or fungi that generate airflow to more efficiently transport spores (Dressaire et al. 2016, Roper et al. 2008), and based in components of behavioral ecology such as communication, cognition, and decision-making (Aleklett & Boddy 2021). Fungal dispersal and fungal movement can also be passive, the result of external abiotic forces (e.g., wind, ocean currents) and biotic vectors (e.g., soil arthropods, birds). In this review, we intentionally refer to both fungal dispersal and movement in an effort to distinguish these fundamentally different but complementary processes. Closer examination of and differentiation between fungal dispersal and fungal movement could aid in illuminating related ecological phenomena (e.g., invasions, migration, range expansion) and reflect a challenging, but exciting, conversation in fungal ecological research.

We have so far addressed only the movement of individual fungi or species; however, given the frequently microscopic habit of fungi, there is also the possibility that fungi move as entire assemblages in what has been termed community coalescence, i.e., the encounter and interaction of entire communities (Rillig et al. 2015). This occurs because portions of the environment colonized by entire fungal communities are routinely moved by a variety of forces (including human-mediated forces but also gravity). While experimental research on this topic has been primarily carried out with bacteria, this is likely due to convenience rather than the presumption that this mode of movement would not also apply to fungi. Falling leaves, for example, full of their fungal endophytes, encounter the soil fungal community upon reaching the soil surface. Animal vectors may also be important for fungal community coalescence dynamics (e.g., topsoil and subsoil mixing by earthworms and fungal assemblage transport across ecosystem boundaries by birds). Perhaps the near-range exchanges of fungal communities in adjacent roots can also be described in this way, rather than by established meta-community paradigms (Rillig et al. 2016). Such dynamics have been investigated for neighboring ectomycorrhizal (EM) communities, in which some EM assemblages exerted strong effects on neighboring communities via taxa transfer (Moeller et al. 2016). A point of distinction between community coalescence and meta-community dynamics is that abiotic changes resulting from environmental mixing are explicitly considered. This is most powerfully exemplified in aquatic ecosystems (Mansour et al. 2018) but may also occur in

soil and other media and influence the fungal taxa that ultimately establish after the coalescence event. Movement and dispersal episodes themselves may constitute important mixing events for community coalescence, the effects of which could have impacts on establishment and community interactions (Castledine et al. 2020). Furthermore, dispersed organisms need not necessarily persist in a new environment to generate long-term community effects; even transient microbial movement in soils leads to feedback loops that result in lasting shifts in community composition and function (Amor et al. 2020). We expect future experimental and conceptual work to embrace community coalescence, adding another layer of complexity to the study of fungal movement.

In this article, instead of exhaustively reviewing 100 years of research on fungal dispersal and movement ecology, we focus on the recent resurgence of research on fungal dispersal (with a focus on cryptic Eumycota), current prevailing conversations in the field, and new frontiers for future research. We cater to a broad ecological audience in an effort to widen the tent of scientific disciplines (e.g., climate change, human health, sustainable agriculture, biodiversity conservation) engaged in addressing fungal dispersal research questions. Outstanding questions are listed in **Table 1** along with selected entrance points into the pertinent literature. We also present the results of quantitative bibliometric analyses of the current state of fungal dispersal research that highlight gaps and trends, as well as cooccurring concepts and citation networks. In addition, hypotheses regarding the relative importance of dispersal vectors at various spatial scales are presented, as well as novel avenues for fungal dispersal research that represent the intersection of methodological and systems advances.

Table 1 Outstanding research questions on fungal dispersal and selected entrance points into the pertinent literature

Question	Reference(s)
How do morphological, physiological, and phenological traits (e.g., spore morphology, mycelial growth strategies, germination seasonality) impact strategies of fungal dispersal at all stages, from liberation to transport to early colonization?	Chaudhary et al. 2020, Deveautour et al. 2020, Juniper & Abbott 2006
How can global science networks be used to monitor and model fungal dispersal? Can these networks predict human disease outbreaks or plant disease pandemics impacting food security?	Abrego et al. 2018, Aguayo et al. 2021, Ristaino et al. 2021
Are specific fungal traits adaptations for movement or dispersal via various vectors?	Bärlocher 2009, Gareth Jones 2006
What are the nature and prevalence of community coalescence, i.e., whole fungal communities moving together? What leads to coalescence events, the moment when the mixing happens?	Castledine et al. 2020, Moeller et al. 2016, Rillig et al. 2015
How does fungal behavior influence dispersal across spatial scales?	Aleklett & Boddy 2021, Bielčik et al. 2019
How is an increasingly globalized world moving and/or homogenizing fungal communities globally?	Santini et al. 2018
How have anthropogenic activities changed the way fungi disperse? How do soil disturbance, fire, or changes in climate impact the way fungi move at various spatial scales?	Bebber et al. 2019, Gorris et al. 2019, Kobziar et al. 2018
How do rivers and major ocean currents contribute to the dispersal of both aquatic and terrestrial fungi?	Allgayer et al. 2021, Chen et al. 2020, LeBrun et al. 2018
Do fungi maintain dispersal mechanisms in novel environments (e.g., cities, agroecosystems) or are new strategies evolving?	McDonald & Stukenbrock 2016
Does temporary or transient movement of fungi have lasting impacts on fungal community dynamics? How do priority effects influence fungal community assembly?	Amor et al. 2020, Debray et al. 2021

2. WHY STUDY FUNGAL DISPERSAL?

Dispersal is fundamental to the spatial arrangement of individuals, populations, and species on Earth. From an ecological perspective, dispersal affects community assembly mechanisms at local and global scales, which has ramifications for ecosystem function. Fungi are essential to terrestrial ecosystems across structural zones: belowground in the maintenance of healthy soil systems, in the litter layer as decomposers, and in aboveground plant and animal host tissues. When these systems become degraded, ecosystem restoration must include the rejuvenation of all ecosystem components, including fungi that are vital to ecosystem functions and services such as nutrient cycling, decomposition, and the maintenance of diversity among primary producers. The year 2021 marked the beginning of the United Nations Environmental Programme's Decade of Restoration, a ten-year call for more action and understanding regarding the process of restoring Earth's ecosystems. Understanding fungal dispersal is key to understanding to what degree human intervention is required for the restoration of healthy and functioning fungal communities. Fungal species with broad dispersal capabilities require less active management during ecosystem restoration, while rare or endemic fungal species with limited dispersal may require more active management for conservation (Hart et al. 2018, May et al. 2018). A better understanding of fungal dispersal improves our understanding of how fungal communities assemble on local to global scales, as well as our ability to manage fungi in natural and managed systems.

Alfred Russel Wallace wrote that biogeographic knowledge, information regarding the geographic distributions of species, was central to conserving biodiversity on Earth; a lack of such knowledge, coined the Wallacean Shortfall, limits our ability to protect species from extinction (Lomolino & Heaney 2004). Because dispersal influences fungal biogeography, an improved understanding of fungal dispersal aids in fungal biodiversity conservation. Efforts to conserve fungi include descriptive estimates of global fungal biodiversity patterns (Tedersoo et al. 2021), work at the global science–policy interface (Mueller & Schmit 2007), and the documentation and management of invasive fungi (Dickie et al. 2016). As symbionts, decomposers, and pathogens, fungi are also critically tied to the conservation of plants and animals. Multiple successive invasions of *Cryphonectria parasitica*, the chestnut blight fungus, led to widespread biodiversity loss in North America and western Europe (Dutech et al. 2012). Certain mycorrhizal or endophytic fungi can also enhance the invasion success of nonnative plant species (Newcombe et al. 2009, Policelli et al. 2019). The rapid spread of *Batrachochytrium dendrobatidis*, a chytrid fungus, has led to population declines in hundreds of amphibian species in Central America, Europe, Australia, and North America (Bower et al. 2017). The introduction from Eurasia of *Pseudogymnoascus destructans*, the fungal pathogen that causes white-nose syndrome, has led to the collapse of bat populations in North America (Hoyt et al. 2021). An improved understanding of fungal dispersal and the ability to predict fungal movement at a variety of spatial scales is of critical concern for not only the conservation of fungal biodiversity but also the conservation of many plant and animal species.

Fungi are of great importance to both agriculture and human health, particularly because many animal- and plant-host species lack natural biodefenses and few antifungal drugs are approved for use in treatments (Almeida et al. 2019). Human trade, human modification of the environment, and an increasingly globalized world are resulting in transmission of both plant and animal pathogenic fungi with significant impacts on human and ecosystem health (Fisher et al. 2012). Fungal pathogens affect crop yield, as well as commodities that influence global trade, with emerging plant diseases (e.g., banana wilt, soybean rust) having profound effects on global food security that disproportionately affect developing nations (Fones et al. 2020). Alternatively, beneficial effects of fungi on crops are also of interest to the growing bioinoculant industry, though knowledge gaps remain regarding ecologically responsible use (Hart et al. 2018). Climate warming and precipitation

regime shifts are expected to expand the incidence of Valley Fever, a fungal disease endemic to the southwestern USA that is caused by inhaling soil-borne spores of the fungus *Coccidioides* (Gorris et al. 2019). Because soil degradation and disturbance release *Coccidioides* spores into the air, Valley Fever disproportionately affects certain communities, such as prison inmates and migrant workers (Cat et al. 2017). Models integrating fungal movement with global change are needed to enhance our ability to predict and prevent potential future pandemics associated with fungal disease in humans.

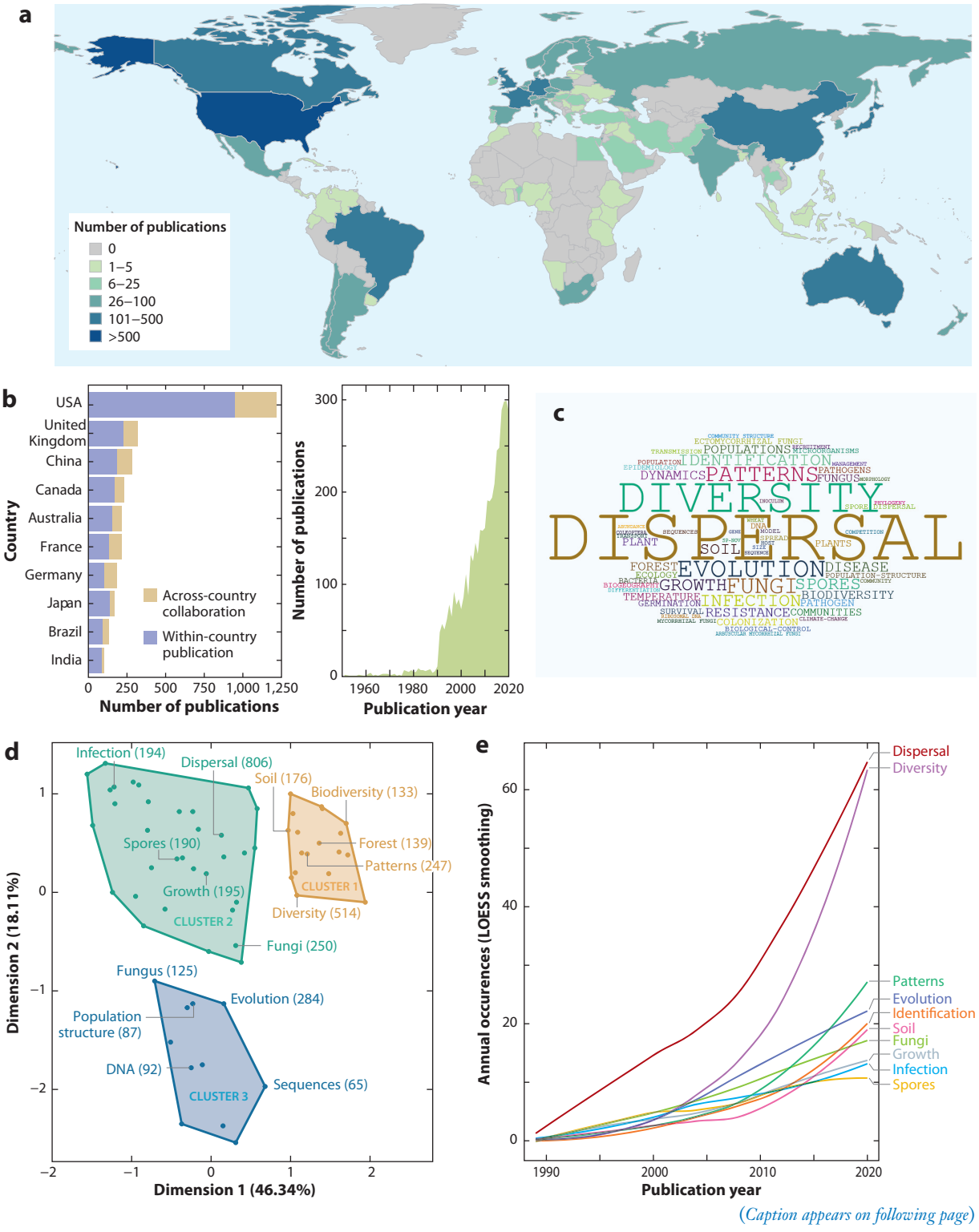
3. TRENDS IN FUNGAL DISPERSAL RESEARCH

Research on the nature and implications of fungal dispersal is on the rise. To quantify and visualize broad trends in this work, we employed a research-weaving approach to combine traditional review methods with bibliometric analyses (Nakagawa et al. 2019). An iterative search approach was applied, with article title screening following each modification to the search string. Search terms were added to the search string to ensure that we captured as many relevant records as possible and excluded nontarget records (e.g., dispersal of plant seeds, insects, moss, or nonfilamentous fungi). Records were accessed and downloaded in BibTeX format from Web of Science on October 5, 2021, using the following search string: "(TS = ((fung* OR conidia OR spore) AND (disperse or dispersal) NOT (yeast OR candida OR biofilm OR fungicide OR moss OR fern OR lichen OR liverwort OR "seed dispersal"))) AND PY = (1900–2020)." Characteristics of the publication collection were analyzed in R using the bibliometrix package (Aria & Cuccurullo 2017).

Our search resulted in a publication collection containing 4,598 records from 1951–2021. Nineteen records were excluded from further analysis: They were listed in our results because they were made available online in 2020 but were actually published in 2021. With the removal of these records, the final number of documents included in the collection was 4,579. The publications derived from 1,194 sources, with an average of 12 years since publication. The majority of publications were classified as articles (88%) and reviews (6%). The number of publications on the topic of fungal dispersal sharply increased in 1990; forty-eight articles were published in that year, whereas from 1951 to 1990, only one to eleven articles were published annually (**Figure 1*b***, inset panel).

The countries that published the most articles on the topic of fungal dispersal were the USA, the United Kingdom, and China (**Figure 1*a*,*b***). The world map shows the global distribution of publications from our collection (defined by the institutional address of the corresponding author, $n = 1$–1,216 articles). The majority of studies come from researchers in the USA, with more than double the amount of publications than the country with the next most publications. Most research was conducted with collaborators from within a single country rather than international research teams; Germany and France have slightly higher proportions of multiple country publications: 44% and 37%, respectively (**Figure 1*b***). These geographic patterns in the publication of fungal dispersal research reflect trends in other scientific disciplines but could contribute to biased knowledge with respect to certain fungal groups or dispersal mechanisms.

We identified the top keywords in our collection, which we defined as those with 50 or more occurrences ($n = 62$) (**Figure 1*c***). A multiple correspondence analysis (MCA) was conducted using these top keywords to investigate patterns in the conceptual structure of our collection of fungal dispersal literature (**Figure 1*d***). MCA is equivalent to principal component analysis but is used for categorical rather than continuous variables. The clusters identified by the analysis are defined by groups of commonly cooccurring keywords, providing insight into the major themes investigated by publications in the collection. The number of clusters ($n = 3$) was selected by examining the topic dendrogram; a cut-off height of 1.5 was applied, leading to three branch divisions (i.e., three



(*Caption appears on following page*)

Figure 1 (*Figure appears on preceding page*)

Bibliometric analyses of metadata from a collection of peer-reviewed publications about fungal dispersal. We queried the Web of Science using the topic search and attempted to capture all relevant research about fungal dispersal; 4,579 articles met our search criteria during the specified publication period of 1951–2020. Analyses include (*a*) the number of publications by country in the fungal dispersal article collection; (*b*, *left*) within- and across-country collaboration for the ten countries with the highest number of publications in the article collection; (*b*, *right*) number of publications per year during the period 1951–2020; (*c*) a word cloud displaying the 62 keywords that appeared in 50 or more publications in our collection; (*d*) a conceptual map, showing clusters of commonly cooccurring keywords, generated by applying a multiple correspondence analysis using keywords that appeared in 50 or more publications. The number of clusters (three) was selected by examining a topic dendrogram of the keywords. The five most frequently occurring keywords in each cluster are labelled, with the number of occurrences as a keyword in the article collection shown in parentheses; (*e*) keyword growth over time for the top ten keywords in the collection.

clusters of keywords). Cluster 1 was defined by 18 terms relating to fungal diversity, communities, and mycorrhizal fungi and included forests and soils. Cluster 2 was the largest cluster, with 33 keywords, many relating to fungal disease (including pathogen, disease, epidemiology, and resistance). The terms "climate change" and "temperature" also grouped with this cluster, though it is unclear whether these studies investigated the effects of climate change on fungal dispersal or on fungal diseases of plants. Cluster 3 included keywords like evolution, phylogeny, and morphology and many terms related to molecular methods (e.g., DNA, ribosomal DNA, sequences). Based on this MCA, it seems that larger bodies of work about fungal dispersal have broadly investigated fungal communities (with many studies of mycorrhizal fungi and/or in terrestrial systems), fungal disease, and the evolution and phylogeny of fungi. We also investigated trends over time for the top 10 keywords, with notable growth in recent years in the use of the keywords "dispersal" ($n = 806$) and "diversity" ($n = 514$) (**Figure 1*e***). While "dispersal" is unsurprising, given that it was one of our search keywords, the frequency of the keyword "diversity" indicates that many studies in our collection investigate fungal communities and not only the dispersal of individual fungal strains or species (as was also indicated by the MCA). Cooccurrence of the terms "dispersal" and "diversity" may also indicate that ecologists are increasingly examining dispersal as an important component of fungal community assembly, the maintenance of diversity in fungal communities, and the role of dispersal in fungal biodiversity conservation.

We also analyzed the local citation network to ascertain which authors within the fungal dispersal literature were most influential. A local citation network provides information about how many times authors and/or publications from within the collection of publications were cited by other publications within the collection. The top cited authors within this collection of fungal dispersal literature are T.D. Bruns, K.G. Peay, M.S. Hovmoller, L. Tedersoo, and L.V. Madden, with between 219 and 345 local citations each. These authors have been influential in the development and application of molecular methodologies for investigating environmental fungal communities or in investigating fungal disease epidemiology in agricultural crops, corresponding to the research themes from clusters 1 and 2 of the MCA.

4. DISPERSAL MECHANISMS FUNCTION AT VARYING SCALES

Ecologists focusing on plant and animal models have long recognized the spatial scale–dependent impacts that different biotic and abiotic dispersal mechanisms have on dispersal (Carlquist 1966). Organisms may have the capacity for determining where, why, when, and how to move, but external biotic and abiotic environmental factors also determine movement and dispersal (Nathan et al. 2008). In fungi, the relative importance of different mechanisms and vectors of dispersal also likely vary depending on spatial scale. We posit theoretical relationships between spatial scale and the relative importance of certain biotic and abiotic vectors and mechanisms of fungal movement and dispersal (**Figure 2**). These relationships are hypotheses intended to be jumping off points for

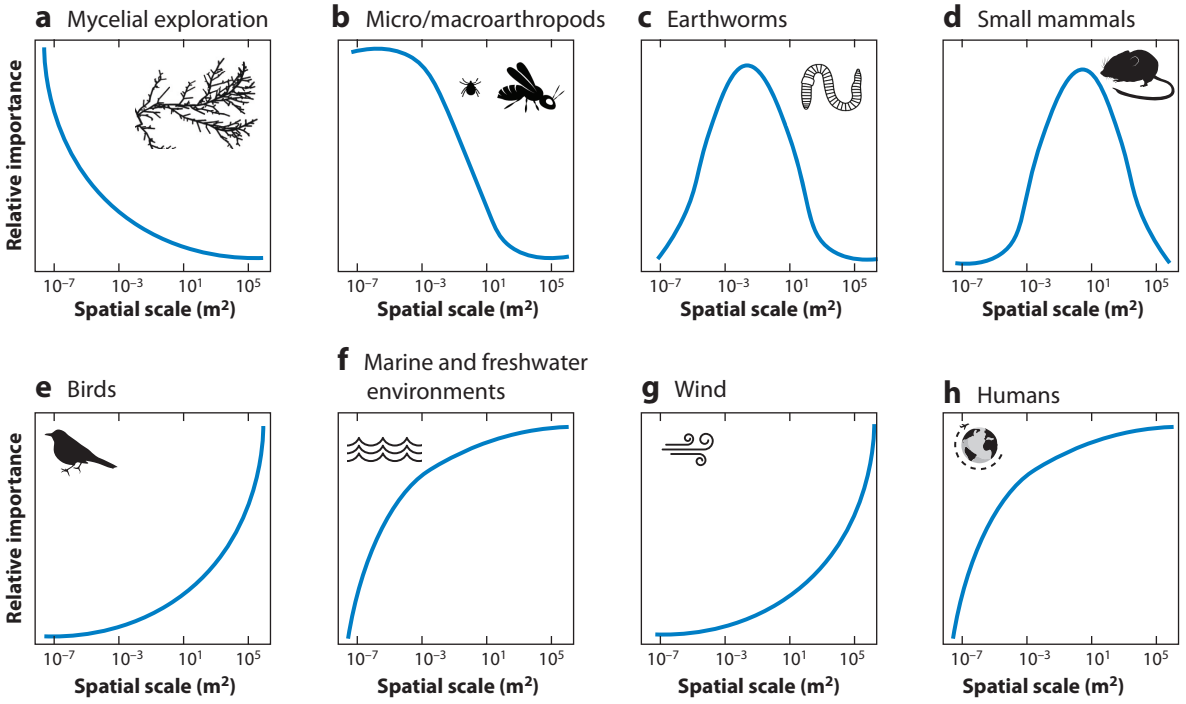


Figure 2

Vectors of fungal movement and dispersal vary with respect to their relative importance across spatial scales. Hypothesized relationships are shown between spatial scale and the relative importance of various mechanisms such as mycelial exploration, arthropods, earthworms, small mammals, birds, marine and freshwater environments, wind, and humans.

future work studying fungal dispersal from microscopic (10^{-7} m^2) to landscape (10^5 m^2) scales. For example, at the smallest, millimeter, spatial scale, hyphal expansion and exploration via the intact mycelium likely play the most important role, relative to other dispersal vectors, in how fungi disperse. Active movement of fungal hyphae in a manner that couples growth with resource foraging (Bielčik et al. 2019) is likely the most important manner of fungal dispersal at these microscopic spatial scales. In soils, strong gradients in pH, moisture, organic and inorganic resource caches, and O_2/CO_2 concentrations can exist at the millimeter scale, influencing how fungal mycelial networks move through the soil matrix. The relative importance of mycelial exploration in fungal movement likely quickly decreases at larger spatial scales of meters and kilometers.

Movement of fungi via invertebrate animal vectors is likely of higher relative importance than mycelial exploration at slightly larger spatial scales. Microarthropods such as collembola (i.e., springtails) transport specific groups of fungi, primarily saprotrophs, via the surface of their bodies and inside their guts (Anslan et al. 2018); macroarthropods like ants and wasps concentrate viable mycorrhizal fungal propagules in their castings and nests (McIlveen & Cole 1976). Microarthropods are likely important for the movement of fungi at meter scales, while macroarthropods, in particular flying species, could contribute to fungal dispersal at kilometer scales. For example, caterpillars feeding on leaves may contribute to the movement of both soil and leaf endophytic fungi (Hannula et al. 2019). Earthworms are ecosystem engineers, producing casts, which are then deposited onto the surface of soil facilitating horizontal dispersal of any fungal propagules contained in the cast material (McIlveen & Cole 1976). Earthworm invasions around the world cause

fundamental changes in ecosystem dynamics at landscape and regional scales (Frelich et al. 2019), with implications for fungal dispersal. Earthworms also demonstrate collective movement, i.e., groups of earthworms traveling in a common direction during migration (Zirbes et al. 2010), a phenomenon that could give rise to fungal community coalescence.

Vertebrates such as small mammals and birds are important vectors for fungal dispersal, with their relative importance likely occurring at larger landscape and even continent scales. Small mammals selectively forage and facilitate fungal dispersal as propagules move through the digestive system (Gehring et al. 2002, Stephens et al. 2021); mammal species can be specialized dispersers for certain fungi or generalists, leading to species-specific dispersal patterns (Stephens et al. 2021). Birds also play important roles in fungal dispersal, particularly at large continental spatial scales, by carrying fungal propagules on their feet and feathers (Nielsen et al. 2016) and even through their digestive tracts after mycophagy (Caiafa et al. 2021). Codispersal of symbiotic mycorrhizal fungi along with seeds of plant hosts has also been documented to occur via birds (Correia et al. 2019).

Movement of fungi at the largest landscape and continent scales is likely primarily facilitated by abiotic vectors, such as wind and water. Wind is capable of moving fungal propagules long distances, even for cryptic fungi and fungi that exist entirely belowground (Allen et al. 1989). Indeed, fungi make up a large proportion of the particulate matter in the air, and fungal aerobiotic communities demonstrate high species turnover and stochastic dispersal patterns over time (Tipton et al. 2019). Global change factors such as climate-intensified wildfires can enhance long-distance aerial movement of fungi through fire-induced convections, as well as triggering fungal germination with heat (Camacho et al. 2018). Water has the potential to act as a fungal dispersal agent in a variety of ways and at multiple spatial scales: Water moves through the soil profile carrying fungal propagules via gravity or capillary forces, rivers transport fungi across continents (LeBrun et al. 2018), ocean currents and tides transport fungi to new locations (Li et al. 2018), and precipitation brings aerial fungi to the surface of the Earth (Bell-Dereske & Evans 2021). Human activity may have the greatest potential to contribute to global-scale dispersal of fungi through the creation of megatrends like globalization (Magyar et al. 2021). Research on the global-scale movement of fungi is growing, but considerable knowledge gaps still remain in our understanding of how wind, water, and even humans influence the movement and dispersal of fungi at global scales.

5. FRONTIERS IN FUNGAL DISPERSAL RESEARCH

Despite the inherent challenges, methodological breakthroughs, systems advances, and areas where these approaches intersect have the potential to further illuminate how fungi disperse on microscopic to global scales (**Figure 3**). Recent advances in trait-based analytics have allowed a better understanding of the mechanisms behind fungal movement and dispersal and the extent of these processes. In particular, analyses of spore traits link form to function, highlighting how different spore morphologies influence dispersal range, survival during dispersal, and the successful establishment in new habitats of several fungal species (Chaudhary et al. 2022). Fungi that form smaller-diameter spores can disperse longer distances by wind than species that form larger diameter spores (Norros et al. 2014), and the presence of spore appendages affects the probability of landing on suitable surfaces (Gareth Jones 2006). Spore surface ornamentation can produce a stationary surface layer of air, increasing effective spore diameter and creating a higher than predicted terminal velocity, while wall thickness, which could alter sphere density, is an important variable in the Stokes's Law equation (Gregory 1945). Spore walls also protect against UV radiation and freezing during dispersal (Norros et al. 2015). Spore physiological traits, such as the quality and quantity of lipid contents (Giovannetti 2000), or spore phenological traits, such as sporulation

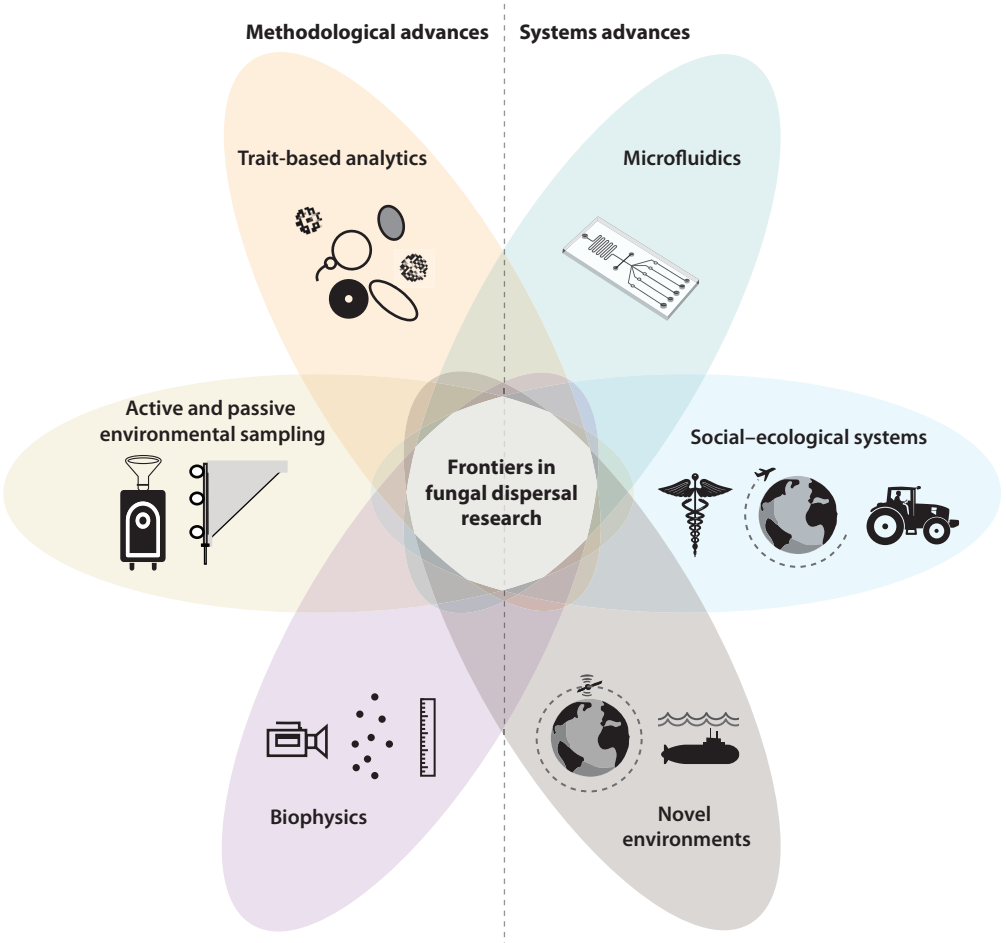


Figure 3

Frontiers in fungal dispersal research employing advances in methodological and systems approaches. Innovative research avenues may arise though the intersection of multiple interdisciplinary approaches, including trait-based analytics, active and passive environmental sampling, biophysics, microfluidics, social–ecological systems, and the exploration of novel environments.

seasonality to avoid higher temperatures and desiccation (Kauserud et al. 2011), ensure survival during dispersal and successful colonization in a new location.

We foresee that advances in trait-based analytics, applied not only to spores but also other structures, will expand the frontier of fungal dispersal research at all spatial scales. At microscopic scales, the use of microstructured environments, a technique mostly used for bacteria, has been recently applied to fungi to determine the search-pattern strategies of individual fungal hyphae in custom-fabricated movement arenas. Rather than observing patterns at the scale of the entire mycelium, this method allows insights into the capabilities of individual hyphae (Aleklett et al. 2018), including dealing with obstacles represented by different angles or structures (Aleklett et al. 2021) or widths of corridors (Fukuda et al. 2021). This approach is uniquely suited for uncovering fundamental constraints to hyphal movement (e.g., hyphae of some species cannot overcome obstacles represented by certain angles and spatial configurations) and for discovering trade-offs between individual hyphal behavior and colony-level growth patterns. Currently, this technique

is focused on physical habitat structure, and a challenging next step is to also include resource heterogeneity or other abiotic gradients in these microstructured movement arenas.

At meso-to-large scales, novel experimental systems allow a detailed understanding of the mechanisms of dispersal. Early mycologists employed elegant contraptions to measure the terminal velocity of spores, such as a small drop tower positioned over a rotating disc with sticky microscope slides (McCubbin 1918). Now, with the increased accessibility of high-speed photography, researchers are again uniting biophysics principles with traits in new experimental settings to study fungal movement (Dressaire et al. 2016, Pringle et al. 2005, Roper et al. 2008). This information can be efficiently processed with the aid of constantly developing computational tools for data extraction (e.g., image-processing algorithms). For example, such tools automate the quantification of spore size, shape, and color, as well as rates of hyphal extension and spore launching speeds, from photographs (Brunk et al. 2018, Deveautour et al. 2020, Vidal-Diez de Ulzurrun et al. 2019) or videos (Stolze-Rybczynski et al. 2009).

Advances in trait-based analytics also help in achieving large-scale data synthesis to characterize dispersal strategies among a wide range of fungal species. Such characterization has been limited to a narrow set of species, as it requires diverse sets of trait data including the physical attributes of dispersal propagules (e.g., spore morphology and structure) and resource and time allocation to reproduction (e.g., number of propagules produced, phenology, and reproductive life span). We believe that recent developments in data extraction and integration are paving the way to achieving large-scale synthesis of dispersal ecology in fungi. For example, image-processing algorithms have the potential to process pictures from large-scale spore-trapping campaigns (De Melo et al. 2019, Korsnes et al. 2016), while text-recognition algorithms and web-scraping tools can be used to extract morphological text data from taxonomic resources (Mora & Araya 2018). Such tools are recognized as being increasingly useful for linking field sampling of fungal spores with in situ measurements of spore traits to make inferences regarding dispersal (Chaudhary et al. 2020) and fungal adaptations to the environment (Deveautour et al. 2020). As these data are integrated, we foresee the expansion, refinement, and further use of large-scale databases. For example, databases such as FunGuild (Nguyen et al. 2016), FUN^{FUN} (Zanne et al. 2019), and FungalTraits (Põlme et al. 2020) are making it increasingly easier to access trait data, including dispersal-relevant information such as spore traits. These trait databases can now be integrated with other databases containing species occurrence data and climate and environmental data to establish relationships between reproductive traits and dispersal extent or preferential occurrence in certain habitats using standard correlative tools (e.g., Peay et al. 2012) or emergent methods (e.g., the joint species distribution models described in Abrego et al. 2017).

Frontiers in fungal dispersal research emerge with the further integration of methodological advances with social–ecological systems approaches and investigations into underexplored environments. Exploration of novel environments for fungi, such as the Earth's upper atmosphere or deep oceans, could also elucidate dispersal mechanisms as we uncover how fungi travel to and persist in extreme environments. Ocean currents disperse marine, freshwater, and terrestrial fungi, with ocean depth and dissolved oxygen identified as factors influencing fungal community structure in oceans (Li et al. 2018). Aircraft, high altitude balloons, and even rockets can be used to assess fungal communities in the upper atmosphere to make inferences regarding long distance fungal dispersal (Smith 2013). In order to develop systems and institutions that result in collective action toward the management of fungal dispersal for sustainable agriculture and human health, a social–ecological systems framework should be employed (Partelow 2018). In this approach, social and ecological variables that influence cooperation for collective action are identified to aid in the development of natural resource governance. Stakeholders should come together to determine how shifting distributions of both mutualistic and pathogenic fungi in the face of interacting

global change factors (e.g., climate change, land use change, globalization) have the potential to influence health and food security.

6. CONCLUSIONS

With applications in health, agriculture, ecosystem restoration, and climate solutions, as well as a burgeoning intersection between methodological and systems advances in fungal ecology, now is an exciting time to study the ecology of the movement and dispersal of fungi. A great deal of unanswered research questions remain regarding the prevalence and mechanisms of fungal dispersal across spatial scales in a changing world (**Table 1**). Approaches addressing these questions span a broad spectrum of empirical and theoretical approaches, from computational analytics to macrosystems biology to controlled ecological or biophysics laboratory experiments to social–ecological system frameworks. Interdisciplinary integration of approaches has the potential to lead to exciting advances that further our knowledge of fungal dispersal mechanisms. It is our hope that students searching for research directions, or even experienced ecologists new to thinking about fungi, will be inspired by these proposed hypotheses and questions on fungal dispersal. We look forward to your future discoveries.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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Errata

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