Long-Distance Dispersal of Fungi

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ABSTRACT Dispersal is a fundamental biological process, operating at multiple temporal and spatial scales. Despite an increasing understanding of fungal biodiversity, most research on fungal dispersal focuses on only a small fraction of species. Thus, any discussion of the dispersal dynamics of fungi as a whole is problematic. While abundant morphological and biogeographic data are available for hundreds of species, researchers have yet to integrate this information into a unifying paradigm of fungal dispersal, especially in the context of long-distance dispersal (LDD). Fungal LDD is mediated by multiple vectors, including meteorological phenomena (e.g., wind and precipitation), plants (e.g., seeds and senesced leaves), animals (e.g., fur, feathers, and gut microbiomes), and in many cases humans. In addition, fungal LDD is shaped by both physical constraints on travel and the ability of spores to survive harsh environments. Finally, fungal LDD is commonly measured in different ways, including by direct capture of spores, genetic comparisons of disconnected populations, and statistical modeling and simulations of dispersal data. To unify perspectives on fungal LDD, we propose a synthetic three-part definition that includes (i) an identification of the source population and a measure of the concentration of source inoculum and (ii) a measured and/or modeled dispersal kernel. With this information, LDD is defined as (iii) the distance found within the dispersal kernel beyond which only 1% of spores travel.

INTRODUCTION
The relative degree to which organisms move is a process operating at multiple temporal and physical scales (1). In recent years dispersal has received a great deal of attention in fields ranging from mathematics and physics to ecology and molecular biology, but only a patchy framework exists to explain dispersal over very large distances. Modeling patterns of long-distance dispersal (LDD) among macroorganisms, ranging from vertebrates and flying insects to seed plants, appears tractable, but documenting the geographic distributions and dispersal dynamics of microscopic propagules and microbes presents multiple theoretical and methodological challenges (2–4). The majority of empirical research directly measuring the dispersal of microbes or microscopic propagules is restricted to relatively short distances, and tracking dispersal at greater spatial scales involves mathematical or genetic models, e.g., in studies of moss (5–9), ferns (10–13), bacteria (14–19), and fungi (19–23). However, fitting dispersal data (e.g., from the tracking of spore movement) to mathematical functions often over- or underestimates LDD and imprecisely describes the trajectory of spore movement across large distances (24–28). Inferences based on population genetics data capture rare instances of successful LDD but incompletely describe underlying demographic processes and typically cannot speak to mechanisms of LDD (1). Besides the limitations of mathematical and genetic methods, important details about the natural history of species are often ignored or remain unknown, leaving many questions unanswered, including, e.g., how ephemeral propagules remain viable while exposed to harsh environments over extended periods of time.

Here we consider LDD as it relates to fungi. Although most research focuses on only a small number of fungi, the kingdom is extremely diverse, housing an estimated 1.5 to 10 million species (29). The ability of fungal dispersal structures (e.g., conidia, basidiospores, ascospores, sclerotia, etc.) to disperse over large distances may be highly context dependent (Fig. 1). Moreover,
FIGURE 1 A framework for understanding fungal LDD.
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while LDD for a rust fungus, e.g., *Puccinia graminis*, may be over several kilometers, LDD for a bird’s nest fungus, e.g., *Crucibulum laeve*, may be only several dozen meters (30, 31). The delimitation of cryptic species by phylogenetic techniques has also in many cases revealed that a fungus once considered widespread in fact consists of several separate species, each with nearly indistinguishable morphological characteristics, and raises questions about the prevalence of LDD (32–34). Further complicating matters, direct evidence for LDD beyond several kilometers is lacking (35). Thus, any discussion of the dispersal dynamics of fungi as a whole is problematic, especially if comparisons are made or inferred between one fungal group and another (e.g., aquatic fungi compared to ectomycorrhizae) (19, 22, 23, 30, 36).

One common feature among sporulating fungi is the tremendous abundance of both sexual and asexual spores (e.g., a single gall of *Ustilago maydis* [corn smut] contains up to 25 billion spores, and a single sporangium of *Rhizopus stolonifer* [common bread mold], up to 50,000) (35). Fungal spores are orders of magnitude smaller than the smallest seeds—smaller than most moss and fern spores and comparable in size to some plant pollen (e.g., *Triticum aestivum*, or wheat, pollen) (37–40) (see Fig. 2 and 5). However, unlike pollen, many fungal spores are short-lived and highly susceptible to desiccation and UV radiation, and it is often unclear whether spores survive, e.g., transcontinental and oceanic transport (41–45).

Given these taxonomic, empirical, and methodological challenges, a sound conceptual framework to guide and synthesize research is urgently needed. Mycologists have yet to integrate the abundant physiological, morphological, and biogeographic data available for hundreds of species into a unifying paradigm of fungal LDD. If comparisons are to be effective or relevant, the highly relative nature of the spatial scales involved must be explicitly acknowledged in any discussion of LDD (46).

**DEFINING Fungal LDD**

In a general framework focused on dispersal, Nathan (28) highlights two general definitions of LDD that are often used in studies of animals and plants: movement exceeding (i) an absolute threshold equivalent to a chosen distance (e.g., 100 km) and (ii) a relative threshold based on a fraction of propagules found at the tail of a dispersal kernel (e.g., 99th percentile and above). However, a translation of these definitions to research on fungi is hindered by the incommensurate priority given to plants and animals in dispersal ecology (cf. 47–49) and by a lack of appropriate empirical data (e.g., spore sources are often inferred through reverse trajectory models that reveal little about source inoculum density, making inferences about fungal dispersal kernels [required by definition ii] difficult) (1, 28, 50). Moreover, definitions involving absolute threshold distances involve discretionary demarcations of LDD, resulting in a lack of consistency among studies. For example, definitions of LDD range from beyond 100 m (*Fusarium graminearum*), to beyond 1,000 m (*Mycosphaerella fijiensis*), to transoceanic transport (*Aspergillus sydowii*) (43, 51, 52). Using definitions based on a relative threshold facilitates comparisons of dispersal kernels of different species, but only if a common percentile is routinely used.

While it may be appropriate to have alternative definitions of fungal LDD for different species, at the moment there is no comprehensive approach to organizing the myriad methods used to think about fungal LDD. An accurate description of successful LDD must include, at a minimum, the magnitude of the source inoculum, the physical and biological probability of LDD (including, e.g., the vector[s] involved and the longevity of spores or tissues), the availability of suitable landing sites, and the probability of establishing a stable population and reproducing (Fig. 1). Any of these variables can prevent successful dispersal, perhaps explaining why fungal LDD appears extremely rare. Additionally, differences between stepwise vs. single-leap LDD must be distinguished. LDD involving sequential, shorter-distance dispersal is likely the more common phenomenon, while LDD involving a single successful spore moving a long distance is a very low-probability event that would coincide with optimal conditions for both fungus and vector.

To unify the disparate approaches used to describe and measure fungal LDD, we propose a synthetic three-part definition built on the framework presented by Nathan (1, 28). Any description of fungal LDD should include (i) identification of the source population and a measure of the concentration of source spores and (ii) a measured and/or modeled dispersal kernel. With this information LDD is defined as (iii) the distance found within the dispersal kernel beyond which only 1% of spores travel (Fig. 3). The 1% threshold provides a useful, common reference point; other choices are possible, but in any discussion the chosen threshold should be clearly identified. Using this standard definition, or discussing how any particular experiment relates to this...
FIGURE 2  Sizes of fungal spores and other airborne particles. Some species are wind dispersed (e.g., P. graminis), while others have other means of dispersal (e.g., Gigaspora rosea). The smallest plant seed, Wolfia angusta, the pollen grains of Hibiscus syriacus and T. aestivum, and a glomerospore of the arbuscular mycorrhizal Gigaspora rosea are provided for comparison. Species labeled with an asterisk are not fungi.
definition, would facilitate an integrated approach to understanding fungal dispersal.

**MEASURING LDD**

Empirical measures of spore dispersal are difficult to make, but direct measures of movement remain critical to understanding the scale of a species’ dispersal as a whole (51-53). It cannot be assumed that spores traveling beyond the limits of an experimental setup are statistically and/or ecologically insignificant. Moreover, while spore viability is often ignored, successful LDD requires that, e.g., a spore that has crossed an ocean is also viable. Novel approaches to measuring both spore trajectories and the probabilities of survival are critically needed, and experiments involving creative thinking, and perhaps taking advantage of new technologies, will likely help to better address the many unanswered questions about fungal LDD.

Once a greater array of empirical dispersal data is available, new dispersal kernels can be developed to better quantify fungal LDD (for a review of kernel functions see reference 54). However, many kernel models are best suited to describe either the source or tail end of dispersal, but not both simultaneously, and when applied to entire trajectories, such models tend to either over- or underestimate LDD (24-27). Describing the mathematics behind these models is outside the scope of this review, but examples of their use can be found in many studies of fungi (31, 45, 55-58).

The majority of studies of fungal LDD employ molecular approaches to compare the genetics of populations across a geographic range. However, genetic inferences reveal little about the underlying biological, physiological, and ecological forces at play and may be less relevant to our proposed definition. Studies often compare allele frequencies among discrete populations to infer dispersal, e.g., among Southern Hemisphere populations of *Ganoderma applanatum-austrole*, globally distributed populations of *Tuber* species, and pan-Arctic populations of many ectomycorrhizal fungi (20, 21, 59, 60). If two populations that are very far away from each other appear closely related in a phylogeny (e.g., Israeli populations appear more closely related to populations from Indiana than they are to Syrian populations), then LDD is inferred (Fig. 4) (61-64). Phylogenetic methods allow inferences of rare LDD to be made with less intensive sampling than the direct capture of spores but cannot provide critical information on spore longevity, nor information about the role of meteorological patterns, spore physiology, putative vectors, and human mediation. Genetic approaches cannot be used to model dispersal kernels and reveal little about dispersal mechanisms, regardless of geographic scale.

However, the best examples of LDD are based on a variety of approaches. Considering the different limitations to direct sampling, statistical modeling, and genetic inference, it is not surprising that the best-known cases of fungal LDD are typically generated using these methods in combination. For example, several reports of fungal trans-Atlantic dispersal in Saharan dust manage to capture viable fungal material, describe a dispersal kernel, and use meteorological backtracking to identify air masses as having originated from Africa (42, 43, 65-67). For other taxa, researchers sample directly from within the planetary boundary layer using towers or aircraft, in addition to tracking the trajectories of air masses (68-71). Genetic methods are also combined with spore capture techniques, usually by first determining the genotype of a specific fungal strain and subsequently allowing it to release spores (58). The relative proportions of that genotype collected by spore traps are then used to construct a dispersal kernel.

**DISPERSAL VECTORS**

**Wind**

Wind is the most commonly considered vector of fungal dispersal. Aerosolized course particles (greater than 2.5 μm in diameter) have been photographed moving hundreds of kilometers from northern Africa across the Atlantic, depositing an estimated 500 million to over 1 billion tons of material per year in the Caribbean and Amazon basin (43, 66). Sand, soil, and, in smaller proportions, biological matter including bacteria and fungal spores have also been found in air samples retrieved from towers or aircraft (36, 68, 71). Further evidence that spores can move in the atmosphere is provided by tracking wind patterns. The biogeography of mosses and ferns, as well as lichens, in the Southern Hemisphere may be better described by wind patterns than by geographic distances between land masses (72), providing indirect evidence for LDD via “wind highways” (45). Wind patterns are also used to infer atmospheric LDD of fungal pathogens, e.g., the introduction of *Hemileia vastatrix* (coffee leaf rust) from Africa to Brazil, and of *Puccinia melanocephala* (sugarcane rust) from West Africa to the Caribbean and the United States (73, 74).

Samples of dust from surfaces are also used to infer fungal LDD. Metabarcoding data taken from North American dust reveal a low percentage of common
Defining and Comparing the Dispersal Kernels of Fungi

Two idealized dispersal kernels

Distance beyond which only 1% of spores travel and beyond which LDD is defined

Spore Source
(e.g. a single mushroom)

Dispersal Distance

A

B

Furthest dispersal distance

Mycosphaerella fijiensis

Fusarium graminearum

Lobaria pulmonaria

Number of Positive Samples

Distance (cm)

Recovery Rate of Retrieved Cone

No. of Resistant Lesions / m² of leaf
species across regions, but some degree of overlap suggests that LDD is a real, albeit rare, phenomenon (19, 23). Alternative hypotheses posit that the ubiquity of some species is caused by short-distance dispersal over long time scales or that species appearing broadly distributed are complexes of cryptic species, each with restricted geographic ranges (75, 76).

Other studies track dispersal in wind by capturing spores. Peay et al. (30, 77) documented the dispersal of ectomycorrhizal assemblages at least 10 kilometers away from their source by placing uninfected “trap” seedlings at different distances from a source population. Data reveal that species richness and trap seeding colonization drop significantly beyond 1 kilometer. Additionally, viable ascospores of the wheat pathogen _F. graminearum_ have been captured 50 meters to 1 kilometer above the Earth’s surface in all seasons in Virginia—even during winter, when its plant host is absent. The capture of spores during winter suggests that the source of spores is kilometers away, because there was no wheat in the vicinity of the experimental setup when the _F. graminearum_ spores were collected (68, 70, 71).

The most complete picture of wind LDD emerges from research on _A. sydowii_, the causal agent of aspergillosis of the Caribbean sea fan, _Gorgonia ventalina_. An outbreak of the disease occurred during the 1980s and coincided with the highest recorded deposition of African dust in the Caribbean Sea (42). Air samples taken from African dust plumes revealed the presence of _A. sydowii_ conidia, and by inoculating _G. ventalina_ in laboratory assays, these same dust-borne conidia were shown to cause the same symptoms of aspergillosis as occurring in the Caribbean (42, 67). Furthermore, only samples derived from African air masses moving over the Caribbean contained viable _A. sydowii_ material, while samples from air masses of different origins did not (78).

Atmospheric LDD may involve more than wind and may be facilitated by a combination of meteorological phenomena, including cloud, storms, and precipitation. In fact, spores may serve as rain- and cloud-forming nuclei, although the limited evidence for this phenomenon is debated, and it is still unclear how water can condense on the potentially hydrophobic

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**FIGURE 3** To integrate the disparate approaches used to describe and measure fungal LDD, we propose a synthetic three-part definition building on the general framework presented by Nathan (1, 26). A description of fungal LDD should include (i) identification of a source population and measure of source inoculum concentration (e.g., the number of spores in a single rust pustule), (ii) a measured and/or modeled dispersal kernel, and (iii) a measure of the distance, based on the dispersal kernel, past which only 1% of spores travel. Adopting a standard approach would mitigate the confusion caused by differing definitions and measurements of LDD and facilitate comparisons among the dispersal kernels of different species. In the illustration, the blue and red dispersal kernels demonstrate idealized kernels for two hypothetical species. LDD is defined per species at distances A and B, respectively—the distance beyond which only 1% of spores travel. We next used our approach with real dispersal data of _M. fijiensis_ (measured as the number of resistant lesions per square meter of banana leaf measured from a source to 1,000 m) (52), _Fusarium graminearum_ (measured as the recovery rate of ascospores of a unique clone released from a source to 1,000 m) (58), and _Lobaria pulmonaria_ (measured as the proportion of DNA from snow samples identical to an isolated source of soredia up to a distance of 40 m [193]) to estimate dispersal kernels and identify LDD for each species. We smoothed the published data to estimate an approximate dispersal kernel, and the distance beyond which 1% of spores traveled was found by integrating the area under each kernel from 0 m to the distance at which 99% of spores had been captured. Although both _M. fijiensis_ and _F. graminearum_ are capable of dispersing to approximately 1,000 m, the proportion of spores that fit our definition of LDD varies considerably, because LDD is defined past 714 m for _F. graminearum_ and past 250 m for _M. fijiensis_. A holistic comparison of the two dispersal kernels suggests that different dynamics will shape the effective reach of each species. The dispersal kernel of _L. pulmonaria_ illustrates how truncated experimental setups can impact measures of LDD. At the furthest collection point (40 m), a large proportion of samples tested positive, and the best dispersal kernel that can be modeled from the data (193) provides what is likely an underestimate of LDD, at approximately 39 m (15% of the positive samples collected at 0 m were detected). Ideally, the tail end of a modeled dispersal kernel should very closely approach a horizontal line at y = 0.
outer surface of spores (see section below on morpho-
logical, biophysical, and physiological properties influ-
encing LDD).

Fire may also play a role in initiating LDD because it can rapidly heat air and cause high-velocity up-
drafts (79). For example, back trajectory modeling of air masses suggests that viable spores captured from smoke over the Gulf Coast of Texas originated 1,500 km away in forest fires in the Yucatán Peninsula, Mexico (80). Sugarcane agriculture provides an excellent model for exploring how fire promotes LDD, because fields are frequently burned prior to harvest and are often plagued by one of the most widely referenced putative long-distance dispersers, P. melanocephala—among the first fungal species described as having undergone trans-Atlantic dispersal (79, 81). Fire-borne updrafts, perhaps often caused by humans, may facilitate the spread of P. melanocephala, challenging hypotheses of the unassisted dispersal of spores across oceans (cf. 73, 74).

Plants
Plants are another agent of fungal dispersal, and their ability to vector fungi is unsurprising given the close

![Figure 4](image-url)
ecological association between the two kingdoms. Fungi inhabit both living and dead plant tissues, and there are many opportunities for fungi to codisperse, e.g., with seeds, senesced leaves, or branches.

Driftwood is an often overlooked substrate in which fungi disperse. Saprotrophic fungi are often found in decaying logs floating in bodies of water, and if hyphae or spores are able to withstand saline conditions, driftwood may be able to transport species across oceans. For example, Rämä et al. (82) sampled logs from across the North Sea and successfully cultured 147 fungal operational taxonomic units of Ascomycota, Basidiomycota, Mucormycotina, and Chytridiomycota, 50% of which were identified as terrestrial (nonmarine). Driftwood kept afloat by ice flows during the late Weichselian or early Holocene is suggested as a mediator of LDD for several trans-Arctic plant species and likely also their fungal symbionts (83). Data already support the long-distance movement of driftwood; e.g., Hellman et al. (84) show that logs collected in Greenland and Svalbard originated from western and central Siberia and North America. However, the majority of wood was logged, again suggesting that humans play a key role in many different kinds of LDD. The problem of driftwood-associated fungi remains a promising area for future research, and open questions concern patterns of driftwood movement and their possible relationship to fungal introductions and whether some logging practices increase the likelihood of LDD.

Living plant material transported by ocean currents is another putative mediator of fungal LDD. Symbiotic fungi are associated with plant roots as mycorrhizae and with leaves, stems, and seeds as endophytes. Thus, ocean-dispersed plant material, including floating seeds, asexual propagules, or entire root balls, may explain the geographic range of some fungi that are found on two sides of, e.g., an ocean. Little to no direct evidence for this phenomenon has been collected to date, and phylogenetic analyses testing whether plants and fungi disperse together are, surprisingly, lacking (85). Anecdotal evidence of arbuscular mycorrhizae occurring most frequently and with greater biomass on Hawaiian endemic beach grass species has been used to suggest fungus-plant long distance codispersal (86, 87). However, Koske and Gemma (87) provide alternative hypotheses such as concurrent, independent dispersal and sea bird-mediated dispersal of arbuscular mycorrhizae. A codispersal hypothesis is also suggested as an explanation for evidence of recent gene flow between island and mainland ectomycorrhizae, though vectors such as wind cannot be ruled out (85, 88).

Oceans, Rivers, and Lakes

Large bodies of water can act as vectors of fungal dispersal. Oceans and lakes provide large areas across which some fungi can freely travel by, e.g., moving with microcurrents and upwelling, while rivers and streams provide continuous movement in the direction of their flow. The number of fungi specifically adapted to an aquatic or amphibious lifestyle is estimated at more than 10,000 species, although only approximately 500 have been formally described (89). Aquatic species are informally divided into two major groups: Ingoldian fungi, found on decaying leaves in streams and lakes, and aquatic ascomycetes (traditionally referred to as hyphomycetes), found on submerged wood (90). The uncommon shapes of many aquatic fungal spores may facilitate dispersal, as well as adherence to various substrates, in aquatic environments. Conidia are typically sigmoid or tetraradial, while ascospores are generally fusiform with bipolar mucilaginous pads (see Fig. 5N) (91).

Whether spores are passively or actively released remains unclear. Most marine ascomycetes appear to release their spores passively, while many tropical freshwater ascomycetes actively eject their spores away from the fungal thallus (92). A possible explanation for this pattern may involve wind dispersal of spores during seasonal drying of streams and rivers. Alternatively, storms can cause flooding and the accumulation of substrate on, e.g., riverbanks and subsequently expose ascocarps to airflows once waters subside (92). In both cases spores are hypothesized to be sometimes dispersed by air, although the interplay between aquatic and terrestrial habits of these kinds of fungi requires further study.

At least a few Ingoldian fungi appear to have cosmopolitan ranges, suggesting they may be capable of LDD (90). For example, recent phylogenetic methods have elucidated that there is no geographic structure to populations of the widely distributed marine fungus Lignicola laevis, hinting that the species may be a long-distance disperser. However, only two loci were used in the study, and including several more genetic regions may reveal more restricted population assemblages (75, 76, 89). Pang et al. (89) list several other species which seem to have similar cosmopolitan distributions—Aniptodera cheasapeakensis, Ceriosporopsis halima, Corollospora maritima, Savoryella lignicola, Torpedospora radiata, and Zalerion maritima—suggesting that aquatic fungal LDD may be an as yet undescribed phenomenon.

Aquatic environments may be an ideal place for LDD to occur considering that fungal dispersal is often
limited by spore desiccation, UV damage, and harsh temperatures. Water temperature fluctuates more slowly than that of air, and water attenuates light penetration at relatively shallow depths (especially in highly trophic waters). Moreover, water provides a greater degree of buoyancy than air, increasing the time before spore sedimentation. Aquatic dispersal is perhaps the least commonly considered mechanism of LDD, and future studies might address the coupling of, e.g., spore hydrodynamics with river flow velocity, as well as the population structure of putatively cosmopolitan aquatic fungi.

Animals
Animals are also vectors of fungal dispersal. Many animals migrate across continents on an annual basis and may transport fungi either internally or externally as spores, hyphae, sclerotia, or symbionts (93–98). Fungal propagules sheltered deep within fur or feathers are potentially protected from some harsh environments as they move over large distances.

Flying animals clearly serve as fungal vectors, and there is a great deal of evidence for birds and insects as mediators of fungal dispersal, especially of pathogens. Examples in arthropods include the spread of Entomophaga maimaiga, an introduced pathogen of gypsy moths used for biocontrol in North America (99); Aspergillus flavus, which infects desert locusts in India (100); Sphaeropsis sapinea, a pathogen of conifers worldwide that is spread by the pine engraver beetle (101); Ophiostoma spp. and Knoxaviesia proteae, commensal species of mites secondarily vectored by beetles in South Africa (102, 103); and many others. However, dispersal by insect vectors tends to be restricted within a localized range, e.g., a few hundred kilometers, while dispersal across, e.g., continents or oceans, is more commonly caused by the human-mediated movement of insects and fungi together (103, 104).

Migrating birds are another common agent of animal-mediated dispersal. Examples include Gibberella fujikuroi (Fusarium moniliforme), a pathogen of rice vectored by hummingbirds (105); Encephalitozoon and Enterocytozoon spp., microsporidian human pathogens collected from several bird species (106, 107); and 2,337 filamentous fungi isolated from 216 migrating Mediterranean birds, of which Cladosporium cladosporioides, Alternaria alternata, and Aspergillus niger were the most abundant (108).

The recent spread of white-nose syndrome in North America, caused by Pseudogymnoascus destructans (Geomyces destructans), is another example of flying animal-mediated fungal dispersal. The mycosis appears to be spread among congregating bats and by their subsequent movement to other caves (109). The recent emergence of the disease in North America has resulted in the death of millions of bats, but it is unclear if the epidemic has resulted from the introduction of a European species or from the recent emergence of a newly virulent North American strain (110). In either case, the disease is spreading on a continental scale, and in addition to bats, humans may play a role in its spread (109).

Finally, the spread of chytridiomycosis of amphibians, caused by Batrachochytrium dendrobatidis, is perhaps the most commonly cited example of putative animal-mediated LDD. In recent years chytridiomycosis has spread rapidly, perhaps facilitated by a changing climate, as shown in Central America (111). The disease is heterogeneously distributed across all continents except Antarctica, but the reasons for its disjointed distribution are unknown (112, 113). It is not entirely clear how the fungus moves over large spatial scales, but its spread may be caused by a combination of localized amphibian movement coupled with, again, human mediation via the international trade of Xenopus laevis (the African clawed frog) and other amphibians (114–116).

FIGURE 5 Images of various fungal spores. (A) Basidiospores of Agaricus bisporus (brown powder) next to seeds of Wolfia borealis (seicsmolecules) and sugar crystals (white cubes). (B) Urediniospores of Puccinia menthae (Fig. 1 of reference 194). Conidia of (C) Alternaria solani and (D) A. alternata. A. alternata is a putative long-distance disperser, while A. solani (10X in size) is not (courtesy of Steve Jordan). (E) Glomerospore of Glomus irregulare (Fig. 5i of reference 195). (F) Conidium of C. herbarum (Fig. 5c of reference 196). (G) Teliospore of Tilletia controversa (Fig. 9 of reference 197). (H) Urediniospore of H. vastatrix (Fig. 1e of reference 198). (I) Urediniospore size, shape, and ornamentation of P. melanocephala (Fig. 1d of reference 199). (J) Zoospores of chytrid Rhizophyllum elyensis (200). (K) Ascospores of Ascosbolus denuudatus (200). (L) Sporangiospores of Rhizophus microsporus var. chinesis (200). (M) Basidiospores of Boletellus taiwanensis still on soredia (200). (N) Conidia of the aquatic ascomycete Nawawi dendroides (Fig. 66 of reference 92).
Humans

Ancient fungal dispersal mediated by human migrations is suggested by data on population structures ([117–119]). The range expansion of the fungal pathogen *Coccioides immitis* into South America parallels human migration routes during the Pleistocene ([120–122]). Similarly, the diversification of *Saccharomyces cerevisiae* strains mirrors their use and movement with human populations ([123]).

Contemporary dispersal mediated by human vectors merits special consideration as the inadvertent transport of biological materials continues at unprecedented spatial and temporal scales. Plant disease epidemics caused by introduced fungal pathogens are among the clearest examples of the impact of human-mediated LDD, e.g., *Cryphonectria parasitica* (chestnut blight), *Ophiostoma ulmi* and *Ophiostoma novo-ulmi* (Dutch elm disease), and *Cronartium ribicola* (white pine blister rust) ([124–127]). But human-mediated LDD is not restricted to pathogens. For example, Vellinga et al. ([128]) show that many genera of ectomycorrhizae have also been introduced to novel ranges and spread globally by the human movement of plants and soil.

The global transport of agricultural products, as well as exotic plants, animals, and soil, all serve either indirectly or directly as platforms by which fungi can disperse over large distances at an accelerating rate. Modern transportation enables fungi—including fungal tissue that cannot independently disperse—to traverse continents in less than 24 hours. For instance, fruits and vegetables grown in North America typically spend a maximum of 5 days in intracontinental transit following harvest, and the transport time of produce grown in the Southern Hemisphere for U.S. consumption can take as little as a few days, depending on the mode of transportation ([46]).

Although many examples of human-mediated fungal dispersal are well documented, circumstantial evidence points to an even greater array of human-mediated dispersal events that are less well understood. Examples include *M. fijensis* (black sigatoka) and *Mycosphaerella graminicola* (septoria leaf blotch), *Puccinia striiformis* f. sp. *tritici* (wheat yellow rust), *P. melanocephala* (sugarcane rust), *H. vastatrix* (coffee rust), and *Rhynchosporium secalis* (barley scald) ([59, 63, 64, 73, 74, 129–131]). Many of these species are intimately associated with agriculture, are planted over vast areas, and are regularly moved (either superficially on or within plant tissue) on a global scale. These same species are also frequently cited as prime examples of fungi capable of LDD ([25]). However, few to no data on fungal characteristics enabling or inhibiting LDD are available; to travel, e.g., across oceans, spores must presumably surmount considerable biophysical constraints. Many of these pathogens are also globally distributed—as are their crop hosts—and an alternative hypothesis explaining what appears as LDD would involve a global network of commerce that provides multiple opportunities for infectious material to be transported between locations.

Consider the global populations of *M. graminicola* studied by Zhan et al. ([64]), of which, e.g., populations in Syria and Uruguay are genetically less distant from each other than geographically close populations sampled from both eastern and western Australia ([Fig. 4]). The fact that geographically distant populations of *M. graminicola* are grouped together, e.g., Uruguayan populations are grouped with Algerian and Syrian populations, suggests movement by humans. *M. graminicola* infects a highly traded agricultural product, wheat, and its ascospores cannot survive prolonged exposure to, e.g., dry air ([132]). However, with enough time, if gene flow were to completely halt, geographic populations could diverge and no longer appear as nested populations, although relationships between genetic and geographic distances would remain difficult to interpret. Highlighting the connection between human-mediated LDD and its effects on population structure may prove itself as a key variable to consider when trying to determine vectors and mechanisms of fungal LDD.

MORPHOLOGICAL, BIOPHYSICAL, AND PHYSIOLOGICAL PROPERTIES INFLUENCING LDD

Spore Size and Shape

The most obvious and perhaps most important agent of dispersal is the spore, whose size and shape may critically affect movement over large distances ([Fig. 5]) ([133]). A spore’s ability to reach airflows, remain aloft, and then land in a suitable location is influenced by aerodynamic forces operating at a microscopic scale, and such forces may be harnessed by manipulating spore morphology ([133, 134]). Although Jenkins et al. ([135]) report no correlation between propagule size and dispersal distance in general cases, aspects of spore morphology are clearly optimized for movement. For example, Fritz et al. ([136]) have shown that among some Ascomycetes, spore dimensions precisely fit apical ring size to maximize launch distance with minimal energy. Others show that spore size can also be correlated to environmental parameters in ways that might maximize the probability...
of LDD. For example, Kauerud et al. (137, 138) show a relationship between spore size and the calendar date of sporulation and reason that spore morphology enables some fungi to take full advantage of seasonal wind velocities. However, when we compiled data on spore sizes and dispersal distances claimed as fungal LDD (Table 1) we found no relationship between spore morphology and dispersal distance (Fig. 6), but we hypothesize that the lack of any apparent correlation reflects the different measures and definitions of LDD used in the literature and not necessarily the lack of a biological relationship.

There is likely a compromise between small spore size, which can enable dispersal over longer distances, and large spore size, which can facilitate settling onto a favorable substrate (Fig. 5C, D). In principle, smaller spores should remain aloft for greater time intervals, but their reduced mass makes landing more difficult and increases their susceptibility to adverse environmental pressures, including UV exposure and desiccation (139). Greater and improved data on a range of spore parameters—emphasizing spore size, shape, longevity, and density—are required to further explore the tradeoffs involved in successful LDD. Often, the aerodynamic diameter (defined as the diameter of a spherical particle with equal density and terminal velocity to the particle of interest) of a spore is the sole parameter considered in estimates of spore dispersal (140). The focus on aerodynamic diameter may be problematic because many spores are not spheres, and also because density measurements specific to species of interest are not available but are necessary for accurate extrapolations of dispersal in heterogeneous airflows (140–142).

Successful fungal dispersal appears also to rely on a critical interplay between drag reduction (to maximize launch height) and drag maintenance (to maximize flight time). Roper et al. (143) have shown that explosively launched spores of many Ascomycetes have drag-minimizing shapes. Drag minimization enables spores to breach the boundary layer of still air surrounding sporocarps to reach more turbulent air layers. However, once aerosolized, successful LDD may require spores to remain aloft for extended periods (133). Wong et al. (144) have shown that remaining aloft is more a function of spore volume than of shape and have observed that the drag constants of spores are surprisingly proportional to their surface area (discounting shape and type of particle). Therefore, spore size appears to have, overall, a greater effect on settling velocity than do shape and density, suggesting that the latter characteristics may be less important in determining sedimentation rates (140, 142). An exciting direction for future research involves more thorough testing of whether or how fungi have adapted to take advantage of aerodynamic principles, especially among putative long-distance dispersers.

A Spore’s External Surface

Additional aspects of morphology that may influence spore dispersal include ornamentation and hydrophobicity, although these features appear to be more rarely studied than shape and size, despite limited data suggesting their key role in dispersal. For example, Hallwachs et al. (145) report that asymbiotic agaric species tend to be more ornamented than ectomycorrhizal agars, while the latter tend to have smoother, more pigmented spore walls; differences may reflect distinct dispersal dynamics; e.g., ectomycorrhizae may require more pigmentation for UV protection while dispersing greater distances to find a plant host (but see reference 146 for criticisms related to methodology). The many unanswered questions surrounding ornamentation and its potential impact on dispersal include, How does a spore’s outer morphology affect spore-to-spore aggregation, surface impaction, and dry or wet deposition (147) (Fig. 2)?

Slightly more is known about spore surface hydrophobicity. Aimanianda et al. (148) have shown that hydrophobic surface proteins on fungal spore walls allow many species to remain dormant inside animal lungs without causing an immune response. While spores rarely escape from lungs, spore hydrophobicity may protect spores in other animal cavities, e.g., the gut, and hydrophobins may enable survival over the relatively large distances covered by many animals. If spores remain undetected and viable in animal digestion tracts until excretion, spore hydrophobicity may well play a role in long-range movement of fungi within animals (149, 150).

Spore surface hydrophobicity also raises questions about whether spores can play a role in meteorological phenomena, either as cloud-condensing nuclei or ice nuclei (143, 151, 152). Spores can theoretically disperse within cloud formations, e.g., at the core of an ice particle, but how water would condense on hydrophobic spore walls remains an open question (153–155). Some kinds of plant pollen do act as cloud-condensing nuclei in high-humidity environments, despite a waxy outer layer. Pope (156) hypothesizes that the small pores found on pollen surfaces (approximately 1 µm in diameter) cause a localized reduction in vapor pressure and, as a result, capillary condensation. Similar morphologies are seen on ornamented fungal spores and,
### TABLE 1 Spore parameters for putative long-distance dispersers

<table>
<thead>
<tr>
<th>Putative LDD fungal species</th>
<th>Spore type</th>
<th>Spore dimensions&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Shape</th>
<th>Habit</th>
<th>Pigment</th>
<th>Clump</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>B. graminis f. sp. tritici</td>
<td>Ascospore</td>
<td>20–30 μm (l) × 10–13 μm (w)</td>
<td>Ellipsoid</td>
<td>Plant pathogen</td>
<td>Hyaline</td>
<td>Yes</td>
<td>201</td>
</tr>
<tr>
<td>Gibberella zeae/Fusarium gramineum</td>
<td>Ascospore</td>
<td>13–28 μm (l) × ~4 μm (w)</td>
<td>Long ellipsoid</td>
<td>Plant pathogen</td>
<td>Light brown to hyaline</td>
<td></td>
<td>202</td>
</tr>
<tr>
<td>M. fijiensis</td>
<td>Ascospore</td>
<td>11.5–16.5 μm (l) × 2.5–5 μm (w)</td>
<td>Fusiform</td>
<td>Plant pathogen</td>
<td>Hyaline</td>
<td></td>
<td>41</td>
</tr>
<tr>
<td>M. graminicola/Septoria tritici</td>
<td>Ascospore</td>
<td>8–10 μm (l) × 2–2.5 μm (w)</td>
<td>Fusiform</td>
<td>Plant pathogen</td>
<td>Hyaline to light brown</td>
<td></td>
<td>65</td>
</tr>
<tr>
<td>Mycosphaerella musicola</td>
<td>Ascospore</td>
<td>14.9 μm (l) × 4.6 μm (w)</td>
<td>Fusiform</td>
<td>Plant pathogen</td>
<td>Dark brown</td>
<td></td>
<td>203</td>
</tr>
<tr>
<td>Phaeosphaeria nodorum</td>
<td>Ascospore</td>
<td>20–31 μm (l) × 4–5 μm (w)</td>
<td>Fusiform</td>
<td>Plant pathogen</td>
<td>Yellow-brown</td>
<td></td>
<td>129</td>
</tr>
<tr>
<td>Sclerotinia sclerotiorum</td>
<td>Ascospore</td>
<td>12 μm (l) × 6 μm (w)</td>
<td>Ellipsoid</td>
<td>Plant pathogen</td>
<td>Hyaline</td>
<td>Yes</td>
<td>204</td>
</tr>
<tr>
<td>Venturia inaequalis</td>
<td>Ascospore</td>
<td>11–15 μm (l) × 5–7 μm (w)</td>
<td>Ellipsoid</td>
<td>Plant pathogen</td>
<td>Brown</td>
<td></td>
<td>205</td>
</tr>
<tr>
<td>G. applanatum-austre</td>
<td>Basidiospore</td>
<td>Applanatum: 6.5–8.5 μm (l) × 4.5–6 μm (w); austreale: 8–13 μm (l) × 5.5–9 μm (w)</td>
<td>Ellipsoid</td>
<td>Saprotroph</td>
<td>Brown</td>
<td></td>
<td>88</td>
</tr>
<tr>
<td>Laccaria amethystina</td>
<td>Basidiospore</td>
<td>6.16–8.47 μm (diam)</td>
<td>Globose, ornamented</td>
<td>Mycorrhiza</td>
<td>White</td>
<td></td>
<td>206</td>
</tr>
<tr>
<td>A. alternata</td>
<td>Conidia</td>
<td>20–63 μm (l) × 9–8 μm (w); often produced in chain of more than 5 conidia</td>
<td>Obclavate to obpyriform</td>
<td>Plant pathogen</td>
<td>Beige to brown</td>
<td>Yes</td>
<td>19</td>
</tr>
<tr>
<td>A. sydowii</td>
<td>Conidia</td>
<td>2.5–4.0 μm (diam)</td>
<td>Globose</td>
<td>Animal biotroph</td>
<td>Hyaline</td>
<td></td>
<td>68</td>
</tr>
<tr>
<td>C. herbarum</td>
<td>Conidia</td>
<td>1–12 μm (l) × 1–10 μm (w) with 50–100 nm × 50–400 nm bundle-like structures</td>
<td>Ellipsoid</td>
<td>Plant pathogen</td>
<td>Melanized</td>
<td>Yes</td>
<td>19</td>
</tr>
<tr>
<td>R. secalis</td>
<td>Conidia</td>
<td>12–20 μm (l) × 2–4 μm (w)</td>
<td>Fusiform</td>
<td>Plant pathogen</td>
<td>Hyaline</td>
<td></td>
<td>131</td>
</tr>
<tr>
<td>Peronospora hyoscyami f.sp. tabacinat</td>
<td>Oosporre</td>
<td>17–28 μm (l) × 13–17 μm (w)</td>
<td>Globose</td>
<td>Plant pathogen</td>
<td>Hyaline</td>
<td></td>
<td>207</td>
</tr>
<tr>
<td>Sporisorium scitamineum</td>
<td>Teliospore</td>
<td>5 μm (diam)</td>
<td>Ovoid</td>
<td>Plant pathogen</td>
<td>Brown</td>
<td>Yes</td>
<td>208</td>
</tr>
<tr>
<td>Ustilago nuda</td>
<td>Teliospore</td>
<td>6.5 μm (l) × 5.8 μm (w)</td>
<td>Subglobose</td>
<td>Plant pathogen</td>
<td>Golden brown</td>
<td></td>
<td>197</td>
</tr>
<tr>
<td>H. vastatrix</td>
<td>Urediospore</td>
<td>29.7–34.5 μm (l) × 18.9–37.3 μm (w)</td>
<td>Ellipsoid</td>
<td>Plant pathogen</td>
<td>Yellow</td>
<td>Yes</td>
<td>198</td>
</tr>
<tr>
<td>Phakospora pachyrhizi</td>
<td>Urediospore</td>
<td>18–34 μm (l) × 15–24 μm (w)</td>
<td>Globose</td>
<td>Plant pathogen</td>
<td>Pale yellow to hyaline</td>
<td>Yes</td>
<td>209</td>
</tr>
<tr>
<td>P. graminis f.sp. tritici</td>
<td>Urediospore</td>
<td>28.3 μm (l) × 17.5 μm (w)</td>
<td>Globose</td>
<td>Plant pathogen</td>
<td>Brown</td>
<td>Yes</td>
<td>210</td>
</tr>
<tr>
<td>P. melanocephala</td>
<td>Urediospore</td>
<td>28–33 μm (l) × 18–23 μm (w)</td>
<td>Globose</td>
<td>Plant pathogen</td>
<td>Cinnamon brown</td>
<td></td>
<td>162</td>
</tr>
<tr>
<td>P. striiformis f.sp. tritici</td>
<td>Urediospore</td>
<td>14–36 μm (l) × 13–23 μm (w)</td>
<td>Ellipsoid</td>
<td>Plant pathogen</td>
<td>Yellow to brown</td>
<td>Yes</td>
<td>211</td>
</tr>
<tr>
<td>B. dendrobatidis</td>
<td>Zoospore</td>
<td>3–5 μm (diam); posterior flagellum (19–20 μm long)</td>
<td>Ovoid</td>
<td>Animal pathogen</td>
<td>Hyaline</td>
<td></td>
<td>212</td>
</tr>
</tbody>
</table>

<sup>a</sup>Dimensions are given for major (l) and minor (w) axes or, when spherical, for diameter (diam). †, oomycete.
famously, on the adaxial surface of many basidiospores (143, 157–159). These structures may affect nucleation, although to date no study has tested whether spore wall ornamentation drives water condensation.

**Do Spores “Clump?”**

Dispersal may also be influenced by the ability of spores to aggregate, or form clumps. Clumping is reported for a variety of species, including *P. graminis*, *P. striiformis*, *A. alternata* (Fig. 5D), *Cladosporium herbarum* (Fig. 5F), *Blumeria graminis*, *Phakopsora pachyrhizi* (Fig. 5I), and *H. vastatrix* (Fig. 5H) (160–163). Clumping may improve individual fitness by stimulating germination (164) and may facilitate impaction on substrates by providing greater inertial mass (150, 165). Moreover, the outermost spores in airborne clumps may shield the innermost spores from harmful environmental conditions, e.g., solar radiation (163). However, whether clumping provides a net benefit to spores remains unknown. While the lower mass of a single spore may facilitate launch into turbulent air layers, the greater mass of clumped spores may shape horizontal displacement and deposition. Moreover, data on clumping are limited to a handful of fungal species (164, 165), and more research is needed to understand when, how, and how commonly spore clumps form.

**FIGURE 6** Comparing spore sizes to reported maximum dispersal distances. Spore volume in square micrometers is measured on the left-hand vertical axis, and spore Q-ratio (the ratio of spore length to width) is measured on the right. Data points were calculated from the parameters listed in Table 1. There is a poor correlation between approximate maximum dispersal distance and both average spore volumes ($R^2 = 0.0167, P = 0.5568$) and Q-ratios ($R^2 = 0.1113, P = 0.1198$). The lack of any correlation likely reflects inconsistent definitions and measurements of LDD, rather than any biological reality.
The Physiological Hardiness of Spores
Fungal LDD may be constrained by the physiological tolerances of spores to solar radiation (especially UV), air moisture (relative humidity), and temperature. The resilience of a spore to any of these variables will vary according to species or taxonomic group. For example, urediniospores of *P. striiformis* var. *tritici* die quickly when exposed to high solar radiation, while ascospores of *Gibberrella zeae* are more susceptible to low relative humidities, and urediniospores of *P. pachyrhizi* cannot tolerate cold temperatures (166–168).

Because of the diversity of physiologies involved, the ability of species to withstand stresses must be tested individually. For example, if a species is hypothesized to have traveled from West Africa to Brazil by wind (cf. 73), verifying whether the spores of that particular species can withstand the UV, relative humidities, and temperatures likely encountered over the predicted path of flight is a critical and simple check on the plausibility of LDD. These kinds of data would complement evidence of inferred LDD, e.g., population genetics data, and enable a more comprehensive understanding of the likelihood of dispersal.

Sporocarp Properties Influencing LDD
Whether sporocarps influence LDD depends on the context in which dispersal occurs. Fungal species whose dispersal is animal-mediated, whether externally or internally, have evolved sporocarps with specific mechanisms to attract vectors. For example, *Tuber* spp. synthesize volatiles to encourage fungivory by mammals, while *Phallus* spp. produce foul aromas to attract insects (169–173).

Intriguingly, recent evidence suggests that sporocarps also play an active role in mediating wind dispersal. Within Ascomycetes, despite the diversity of spore and ascus apical ring shapes involved, the launch velocity of 90% of ascospores is within 2% of optimal energy conservation, so the morphology of the ascus facilitates ascospore penetration beyond the boundary layer of still air surrounding an ascocarp (Fig. 7F) (133, 136). Apothecia can also synchronize the release of spores, enabling groups of spores to move through still air to heights that could not be reached by the forcible discharge of a single spore (134). Basidiomycete mushrooms also appear to manipulate dispersal by using water evaporation from the pileus to generate convective airflows and move spores by at least several centimeters vertically (Fig. 7A) (174).

Less clear is whether sporocarps can control the timing of spore release to take advantage of local weather that might enhance the probability of LDD. Using a Lagrangian stochastic model, Savage et al. (175) show that fungal spores released during the hottest times of day are most likely to undergo LDD, presumably because updrafts formed by heated low-altitude air masses can lift spores into turbulent flows at higher altitudes. Extreme weather events, including thunderstorms and tornados, can also generate intense vertical updrafts and lift air into the upper troposphere. Anecdotal evidence suggests that fungi may release a greater concentration of spores just before thunderstorms (when updrafts are prevalent), and there are records of asthma outbreaks caused by fungal spores specifically prior to thunderstorms (40, 176–179). Efforts to track the timing and number of spores released during atmospheric updrafts, and in relation to other meteorological phenomena, remain an interesting direction for future research and may offer additional perspectives on the ability of fungi to manipulate LDD.

### UNKNOWN AND CONFOUNDING VARIABLES: FREQUENCY OF LDD, VICARIANCE, AND CHANGING PATTERNS OF HUMAN-MEDIATED DISPERSAL

The frequency of LDD for any particular species often remains unknown. Frequent LDD requires movement to be unhindered by (i) physical barriers, (ii) lack of vectors, or (iii) unsuitable habitat. If LDD is frequent enough and occurs on a global scale, it results in what appears as a global population structure (32). Rare LDD might involve a single stochastic founding event and would be
reflected in population structures where shared alleles become rare over time. Different rates of LDD are important because they result in very different dynamics when, e.g., a novel adaptive mutant (e.g., a genotype able to take advantage of a novel host) arises in one population.

When population structure is determined by geological events, rather than the movement of organisms themselves, the concept of vicariance is often invoked. Vicariance is typically defined as the fragmentation of a single population by changes in a landscape, causing limited to no gene flow between the resulting disjunct populations (180–183). Vicariance is relevant to a discussion of LDD because when data do not suggest vicariance, LDD often emerges as the default explanation for population structures. If populations appear related, despite a clear physical barrier (e.g., an ocean separating populations of the same species on two continents), LDD is often hypothesized to be the process causing the observed population structures (60, 184–187) (Fig. 4).

As discussed previously, when LDD is inferred from genetic data, the mechanism of LDD remains unknown. Natural vectors, especially wind, are typically invoked as an explanation, but the literature on vicariance and LDD may provide strong indirect evidence for the role humans play in mediating dispersal across extreme physical barriers, e.g., oceans and mountain ranges. This hypothesis is seldom discussed, but the inability of physical and/or genetic data to explain contemporary population structures for many species is highly suggestive of humans playing an expanding role in fungal LDD (20, 129, 131). As the entire field of invasion biology attests, there are different dynamics at play when humans become involved in mediating dispersal (188). Technology (e.g., commercial aircraft, ocean vessels, etc.) facilitates the movement of goods, and in recent times the spatial and temporal scales of potential fungal dispersal have clearly amplified. Understanding whether apparent gene flow is a function of changing human behaviors, and not part of an autonomous pattern more typical of the past thousands or millions of years, would usefully inform our understanding of, e.g., disease and changing patterns of biodiversity.

CONCLUSIONS: UNANSWERED QUESTIONS AND FUTURE DIRECTIONS

Many unanswered questions remain, including, What shapes the end stages of successful LDD (defined as the growth and reproduction of an individual following its dispersal) (Fig. 1)? Dispersal can mitigate intraspecific competition and parent-offspring conflict, but dispersal to new habitats also involves demographic risks, e.g., the lack of mates, inbreeding depression, and other problems of small populations. Difficulties may be especially acute for individuals establishing at the tail end of a dispersal kernel. Other unanswered questions include, Which characteristics have evolved in some fungi to optimize the likelihood of LDD, and do some fungi take advantage of stochastic meteorological events, e.g., storms, or other local environments, to facilitate LDD?

Our definition of fungal LDD simplifies comparisons among species because it provides a relative measure of LDD for any species under consideration. LDD may involve tens of meters (e.g., a soil yeast) to kilometers (e.g., a smut fungus), and exact scales depend on the measured dispersal kernel for any given fungus. While our definition does not explicitly account for differences in the number of propagules found in, e.g., a mushroom, an infected plant, a field, etc., theoretically, a well-defined dispersal kernel will scale proportionately with the number of spores released. But whether the concentration of spores at a source affects the shape of a fungal dispersal kernel remains an open question. Greater numbers of spores may change the shape of a kernel if more spores increase the likelihood of, e.g., clumping, spore-to-spore wind entrainment, and wet deposition.

As global change affects the current ecological ranges of species, and biological materials continue to be moved on a global scale, defining LDD and understanding the mechanisms by which it occurs emerge as key research priorities. Fungal LDD has the potential to impact international food security and public health, as witnessed by emerging threats to soybeans in the United States and increasing cases of mucormycosis across the globe (132, 189–192). Human-mediated dispersal may drive current fungal LDD (cf. 28), though mycologists seem reluctant to mention the likely role of humans as dispersal agents. A mushrooming realization of the breadth of fungal biodiversity suggests that much is still to be learned about fungal dispersal.

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