

Exploring fungal invasions: observational and theoretical insights and unanswered questions

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Abstract

Despite invasive fungi’s dramatic effects on native biodiversity and ecosystem processes, the extent of fungal invasions and the mechanisms behind them are unclear. We address this gap by synthesizing documented global macrofungal invasions to assess which fungal traits and lifestyles contribute to invasions across fungal guilds. Specifically, we analyze global observations of non-native fungi to show the extent of introduced fungal range areas for the first time, finding that EM fungi’s introduced ranges concentrate in Australia and South America, while fungal introduced ranges of saprotrophs and pathogens cluster more heavily in North America. We then consider the unified framework of biological invasions proposed by Blackburn et al. (2011), which describes the stages and barriers non-native organisms must pass through to become invasive, from an explicitly fungal point of view. Finally, we evaluate the extent to which seven established hypotheses explain the mechanisms by which non-native fungi overcome invasional barriers. In doing so, we highlight emerging research priorities, provide insight into common pathways through which fungi become invasive, and spotlight how major fungal guilds may proceed through stages of invasion differently. This work is an important step toward integrating fungi into invasion biology research, and, more broadly, assessing microbial fit into invasion theory that has historically focused on macroorganisms.

Section 1: Introduction

As we populate maps of fungal distributions across the globe, the spread and impacts of invasive fungi can be investigated more clearly (Steidinger et al., 2020; Van Nuland et al., 2025). For centuries, humans have intentionally (Sitta & Floriani, 2008; Trutmann, 2012) and unintentionally moved fungi around the Earth. Outside of their native range, invasive fungi can dramatically alter their new environments ecologically and economically. Human-mediated dispersal of mycorrhizal fungi, for instance, allowed the establishment of ectomycorrhizal (EM) tree plantations in many parts of the southern hemisphere, which, in turn, have drastically reshaped biogeochemical cycles and lead to the spread of EM fungi to nearby native forests (Dickie et al., 2014). Other unintentional fungal invasions have led to stand-replacing pathogen outbreaks (e.g., Chestnut blight caused by *Cryphonectria parasitica*; Anagnostakis, 1987). These examples are just a few among many lines of evidence that invasive fungi can have dramatic effects on biodiversity and ecosystem carbon and nutrient cycling. However, the extent and frequency of fungal invasions is still under-described across fungal functional groups, limiting our ability to understand, predict, and manage fungal invasions beyond specific ecosystems or case studies. Here, we document the magnitude and extent of macrofungal invasions globally and synthesize knowledge on which traits, lifestyles, and growth forms influence the extent of invasion across the fungal kingdom.

Observational Evidence of Macrofungal Invasions

Occurrence data on macrofungi (e.g., fungi with visible fruiting bodies) has been documented on iNaturalist for at least a decade. Using these data, we characterized the introduced ranges of 178 fungal taxa, each with at least 30 observations, across the globe (Supplemental Materials 1). These fungal taxa ranged across three functional guilds: EM fungi (**Figure 1a**, $n = 57$ taxa, and 29,767 unique observations), pathogens (**Figure 1b**, $n = 55$ taxa and 19,207 unique observations), and saprotrophs (**Figure 1c**, $n = 66$ taxa and 61,173 unique observations) and 98 genera. Altogether, there were over 110,000 records of introduced fungi globally on every continent except Antarctica, demonstrating the ubiquity and large magnitude of fungal introductions around the world. Fungal guilds contrasted in their introduced distributions. EM fungi were more likely to be introduced in Australia and South America, whereas introduced pathogens and saprotrophs were more prevalent in North America.

Data on introduced fungi are inherently biased by many factors. Investigators can only determine which fungi are invasive in places where native communities are well described. This bias could explain why more introduced fungi are reported from Australia and North America relative to other countries. These data also rely on iNaturalist observations, which require cell phone service and a smartphone, potentially excluding observations from developing regions of the world. Fungi themselves vary in coloration, size, phenology, and nutritional mode, which can all influence observations. For example, brightly colored, larger fruiting bodies that grow on substrates near human heights and for longer in the growing season may be detected more often than cryptic fruiting bodies. Furthermore, while data on introduced mushrooms are currently the only reliable data on non-native fungal distributions, these data likely represent just a fraction of introduced fungi in the world, which are often found as microscopic hyphae for part or the whole portion of their life cycles (Veerabahu et al. 2025). Finally, introduced fungi with larger impacts on plants and ecosystems (e.g., destructive pathogens, or beneficial EM fungi) might attract more attention and thus documentation worldwide. Altogether, the large spatial extent exhibited by introduced macrofungi in iNaturalist records here is most likely a substantially conservative estimate of the spatial extent and prevalence of introduced fungi worldwide.

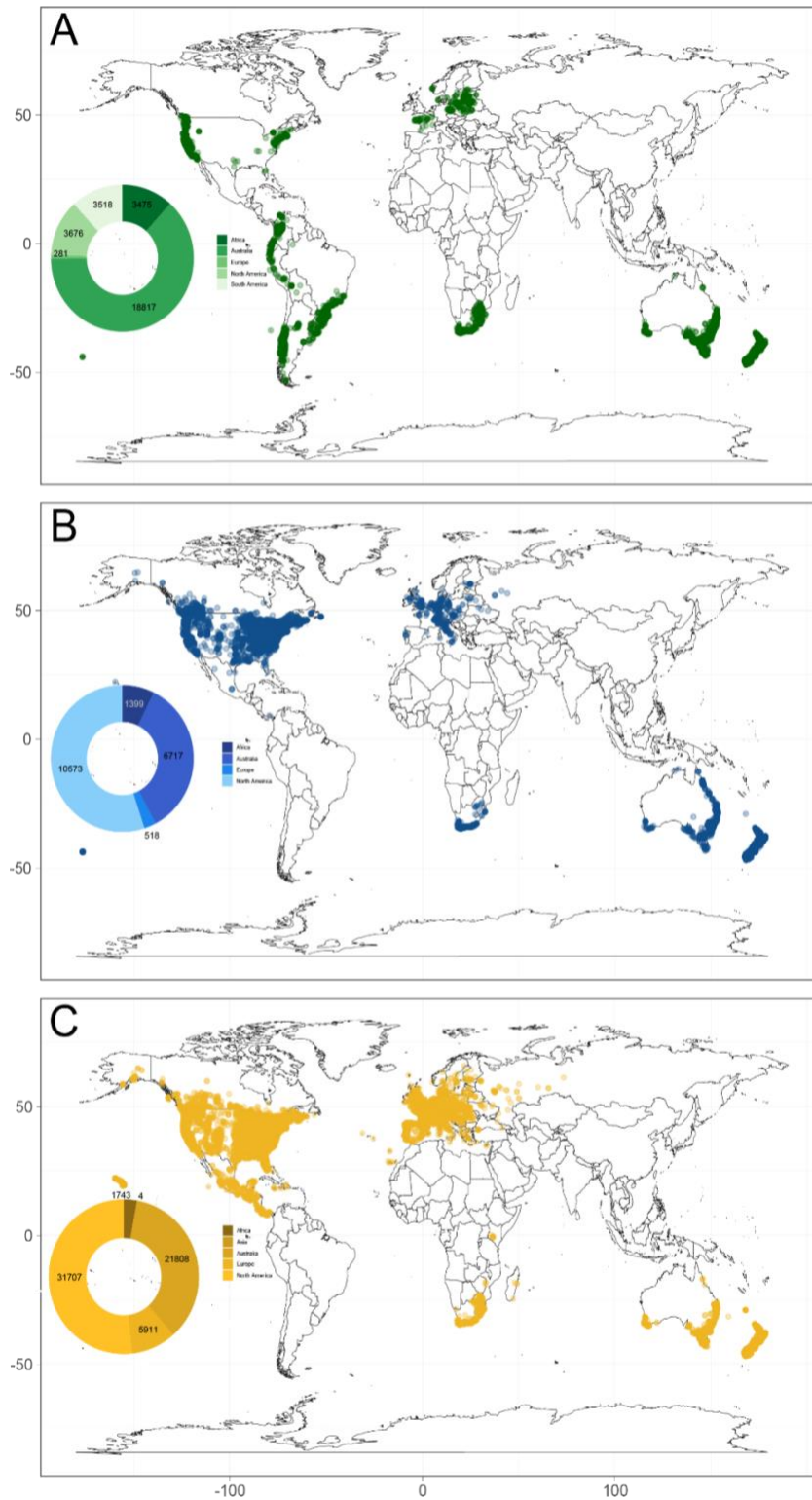


Figure 1 Observations of non-native fungi gathered from iNaturalist. Introduced ranges of a) EM fungi, b) fungal pathogens, and c) fungal saprotrophs cluster heavily in North America, Europe, South Africa, and Australia

Integrating fungi into existing invasion biology theory to predict new fungal invasions

Global change increases uncertainty associated with emergence of new fungal invasions. Rising temperatures, in combination with a continually high rate of global trade and land use change, may trigger new fungal invasions and modify effects of existing ones. Because climate heavily influences fungal ranges, reproduction, growth, and phenology, many more fungi may become invasive in the future (Damialis et al., 2015; Feng et al., 2022; Kauserud et al., 2012). Climate and land use changes may also alter recipient communities to make the spread of invasive fungi more likely. Elevated CO₂, for example, enhances fungal pathogens' negative effects on plant hosts (Raza & Bebber, 2022). Disturbances can also increase non-native plant coverage in mountainous regions worldwide by increasing the prevalence of arbuscular mycorrhizal (AM) relationships (Clavel et al., 2021, 2024). As transport of fungi to novel environments continues at high rates globally, predicting which fungi will become invasive is both important for proactive management and difficult due to underdeveloped theory on fungal invasions.

The field of invasion biology provides well-tested hypotheses describing mechanisms of plant and animal invasions, but leveraging this body of work to predict fungal invasions requires evaluating the extent to which fungal invasions unfold similarly to those of macroorganisms. Desprez-Loustau et al. (2007) were among the first to consider the fungal dimensions of invasion biology by reviewing examples of mostly pathogenic invasive fungi to posit that fungi could follow established frameworks and hypotheses as other invasive species do. Since then, advancements in sequencing and growing interest among biologists have greatly increased knowledge on general fungal ecology, distributions, and non-pathogenic fungal invasions. Meanwhile, other reviews have added to understanding of fungal invasions by examining population genetics underlying fungal invasions (Gladieux et al., 2016), ecological impacts of fungal invasions (Loo, 2009; van der Putten et al., 2007), traits that make pathogenic fungi more likely to become invasive (Philibert et al., 2011), patterns and consequences of global fungal transport (Ladau et al., 2025; Pringle et al., 2009; Schwartz et al., 2006; Vellinga et al., 2009), biology of linked plant-fungal invasions (Dickie et al., 2017; Policelli et al., 2019), and potential strategies for management of invasive fungi (Dickie et al., 2016). Recent work has revived calls for the integration of microbes into greater invasion biology theory (Ladau et al., 2025), but we still lack a comprehensive synthesis of evidence evaluating whether fungi follow invasion biology theory similarly to other organisms and a discussion of how fungal traits may cause them to diverge from theoretical expectations.

Here, we consider the unified framework of biological invasions proposed by Blackburn et al. (2011), which describes the stages and barriers non-native organisms must pass through to become invasive, from an explicitly fungal point of view. We also evaluate the extent to which seven established hypotheses explain the mechanisms by which non-native fungi overcome invasional barriers. In doing so, we provide insight into common pathways through which fungi become invasive, how mechanisms of invasion differ among fungal guilds, and research priorities in the field of fungal invasions. Because fungi share many traits with other microbial taxa such as bacteria and algae, considering how fungi fit into Blackburn's unified framework and its corresponding hypotheses will also likely improve understanding of how other microbial taxa may invade new environments.

Section 2: How do fungi proceed through invasional stages and barriers?

Historically, separate theoretical frameworks described how introduced species of different kingdoms invade. Plant invasion theory often follows the framework from Richardson et al. (2000), which defines different stages of invasion based upon the geographic, abiotic, and biotic barriers a plant

must overcome to become naturalized or invasive. Discussions of how animals invade, however, tend to follow Williamson's (1996) description of the stages of biological invasions (arrival, establishment, spread). To better address the taxonomic divide within the field, Blackburn et al. (2011) proposed a unifying framework that merged conceptual approaches from plant and animal invasion literature into a single theoretical approach. The unified framework begins with transport of the invasive organism, where the organism must overcome geographic barriers to reach new habitats. Then, after introduction to a new habitat, the organism must escape captivity and cultivation to establish beyond the introduction site. Establishment depends on successful survival and reproduction, while the final stage, spread, requires invasive organisms to disperse and colonize new environments in their invasive ranges.

Although this unified framework technically includes all human-mediated invasions, it disproportionately emphasizes plants and animals in its discussion and application, limiting its use for predicting invasions of microbial taxa. Broadly, we expect fungal invasions to follow the same stages and barriers outlined in Blackburn's unified invasion framework, but we also expect fungal-specific traits to cause their invasions to proceed through stages and barriers of invasions differently than plants and animals (Table 1).

Table 1. Stages and barriers of biological invasions with special considerations for fungi

Stage	Barrier	Common characteristics across taxa	Special considerations for fungi
Transport	Geography	-Human trade and travel are common vectors that lead to transport of non-native species to new ranges. -Quarantine and visual inspection programs aim to limit spread of non-native species across international borders.	-Because fungi are often microscopic, and fungal saprotrophs, endophytes, and mutualists will not cause visible symptoms in hosts, border control programs are not designed to limit spread of non-native fungi. -Fungal spores and mycelia can remain viable through a broad range of environmental conditions, allowing fungal spread to occur independently from their hosts'. -Fungi's long distance dispersal capabilities may also facilitate their transport to new ranges to a much greater extent than plant and animal long distance dispersal.
Introduction	Captivity or cultivation	-Escape from captivity and cultivation should increase with the frequency and size of introductions (<i>i.e.</i> , propagule pressure).	-Outside of edible mushroom-forming fungi and bioinoculants, most fungi are not intentionally cultivated so should skip directly from the transport to establishment stage.
Establishment	Survival and reproduction	-Survival depends on the presence of mutualists, the presence of enemies, and	-Fungi reproduce in extremely large numbers and can transfer genetic material horizontally, which likely

		abiotic conditions, while reproduction depends on mating system, mate availability, and abiotic conditions. -Abiotic and biotic specialists require a narrower range of conditions for establishment than generalists.	allows them to adapt to novel environments much more rapidly than macroorganisms. -Different fungal guilds have extremely diverse mechanisms of resource acquisition, levels of host and abiotic specificity, and systems of reproduction, which requires guilds to be considered separately when evaluating likelihood of establishment.
Spread	Dispersal and environment	-Organisms capable of long-distance dispersal should more readily reach new habitat, while others must rely more heavily on interactions with other organisms.	-EM fungi, pathogens, and saprotrophs have small spores that can travel long distances through the wind. -Mushroom-forming EM fungi and saprotrophs are likely dispersed by larger fungivores. -AM fungi, which do not form mushrooms and whose spores are too large to travel through the atmosphere, should rely most heavily on consumption by soil fauna and ectozoochory on larger fauna for dispersal.

Stage: Transport

Barrier: Geography

The first stage of Blackburn's unified invasion framework is transport, in which organisms must overcome geographic barriers between home and new ranges. Human vectors of fungal transport are likely similar to those that transport invasive plant and animal species over continental scales: trade and travel (Bradshaw et al., 2021). Compared to plants and animals, however, fungi are extraordinarily difficult to detect and may be more resilient during the transport process. Outside of edible and mutualistic fungi transported for agricultural purposes, fungi are rarely intentionally moved over large geographic scales (Desprez-Loustau et al., 2007). Instead, they may hitchhike as pathogens of other organisms, as saprotrophs in decaying material, or as endophytic or mycorrhizal fungal symbionts of plants (Dickie et al., 2017). While organizations like the U.S. National Invasive Species Council recommend protocols that ostensibly screen for all potentially invasive taxa during trade, including "spores, or other biological material capable of propagating species", the vast majority of screening practices in place worldwide are not designed to detect microbes. Nations with the most comprehensive screening programs in place recognize a large number of potential invasive species and visually inspect or quarantine imports to identify those species (Early et al., 2016). Fungal spores are much smaller than plant seeds, usually by an order of magnitude, rendering visual inspections largely ineffective for their detection (J. J. Golan & Pringle, 2017). Pathogenic fungi frequently appear on regulated species lists, and

quarantine protocols may limit the spread of these fungi if their hosts are symptomatic during quarantine (Cline & Farr, 2006). Non-pathogenic fungi, on the other hand, are largely unregulated, do not cause visible symptoms in hosts, and consequently, face minimal border controls (Blanchette et al., 2025). Fungi can also adhere to non-living objects: sequencing of decorative wood products imported into the United States for use in aquariums revealed 123 fungal taxa, including 21 potential plant pathogens, 37 saprotrophs, 34 unknown taxa, and 31 species never previously reported in the U.S., indicating that in some cases, fungal transport occurs independently from that of living hosts (Blanchette et al., 2025). Because both mycelia and spores can propagate new populations, and both are generally robust to environmental conditions (*e.g.*, dormancy), fungi likely have high survival rates during trade and travel-mediated transport over large scales (J. J. Golan & Pringle, 2017; Nara, 2009).

To a much greater extent than plants and animals, fungi's own long-distance dispersal also facilitates their transport to new ranges. Fungal spores reach new continents through wind, freshwater currents, and marine currents (Chaudhary et al., 2022). The degree to which different fungal species rely on any particular mode of dispersal is still poorly understood, but theory and some evidence suggest that spore traits and reproductive strategy influence dispersal type (Paz et al., 2021). AM fungal spores are large and lack structures that allow them to stay airborne, so AM fungi rely most on vectors of dispersal other than wind (Paz et al., 2021). EM, saprotrophic, and pathogenic fungal spores are smaller and can travel through the wind over scales that range from meters to continents (J. K. M. Brown & Hovmøller, 2002; Kivlin et al., 2014; Nordén & Larsson, 2000; Horton, 2017). Spore traits that increase resilience to wind and water dispersal (*e.g.*, melanin and large spores may protect against UV radiation and salinity, respectively) should also predict fungi's abilities to successfully establish in new ranges following long-distance dispersal (Davison et al., 2018; Onoda et al., 2024). Overall, through human movements and fungi's own dispersal capabilities, transport of alien and potentially invasive fungi to new habitats likely occurs extremely frequently around the globe.

Stage: Introduction

Barrier: Captivity or cultivation

In the introduction stage, organisms must escape captivity or cultivation to encounter wild ecosystems. This stage does not apply to organisms that are not intentionally held in captivity or cultivated; therefore, because the vast majority of fungi transported over large geographic scales are not moved for any agricultural purpose, most invasive fungi will not pass through this stage and will instead skip from transport to establishment (Blackburn et al., 2011). Notable exceptions include mycorrhizal fungi used to inoculate crops, EM fungal *Tuber* spp. grown as edible truffles, and saprotrophic edible fungi, such as lion's mane (*Hericium erinaceus*), shiitake (*Lentinula edodes*), golden oyster (*Pleurotus citrinopileatus*) and king oyster (*Pleurotus eryngii*) mushrooms, grown from kits and in large-scale agriculture in Europe and North America (Reyna & Garcia-Barreda, 2014; Schwartz et al., 2006; Veerabahu et al., 2025). Chances of these fungi spreading beyond their sites of cultivation increase with the number and size of imports, as discussed in the Propagule Pressure hypothesis section below.

Stage: Establishment

Barriers: Survival and reproduction

For populations to establish in new habitats, organisms must survive and reproduce in their introduced conditions. Plant and animal survival typically depends on the presence of both mutualists and enemies and the degree to which their abiotic niches overlap with that of the new environment (Hutchinson, 1957). Species with higher abiotic or biotic specificity require a narrower range of environmental conditions or community compositions, respectively, to establish in new habitat.

Biotic interactions and abiotic niche size similarly affect fungal survival, but fungi's diverse methods of reproduction and nutrient acquisition, rapid life cycles, and abilities to transfer genetic material horizontally likely provide alternate mechanisms and considerations for fungal establishment. While plants primarily obtain carbon through photosynthesis, and animals primarily obtain carbon through heterotrophy, fungi are divided into guilds with extremely diverse methods of resource acquisition. Fungal pathogens parasitize plant or animal hosts, saprotrophs decompose organic material, arbuscular mycorrhizal (AM) fungi transfer water and inorganic forms of nutrients to AM host plants in exchange for photosynthetically-derived carbon, and ectomycorrhizal (EM) fungi exchange water and both organic and inorganic nutrients to EM host plants for carbon (Boddy & Hiscox, 2016; Smith & Read, 2010). Outside of mechanisms of resource acquisition, these guilds vary widely in other traits that affect their abilities to successfully establish in new habitats. Generally, fungal pathogens and EM fungi display high host and abiotic specificity, AM fungi tend toward generalism, and saprotrophs range from generalists to specialists, with some saprotrophs colonizing only one specific structure of a limited number of plant species (*i.e.*, *Magnolia* spp. cones; Boddy & Hiscox, 2016; Ju et al., 2018; Laine, 2007; Segal & Kivlin, 2025). Therefore, EM and pathogenic fungi may be most likely to establish in habitats with abiotic conditions and hosts that are similar to those in their native ranges, AM fungi may be able to colonize a more diverse range of habitats, and saprotroph establishment will likely depend on their enzymatic abilities and available substrates. Because of vast differences among fungal guilds, predicting fungal invasions will likely require considering fungal guilds separately when evaluating non-native fungi's likelihood of surviving in new habitat.

Compared to plants and animals, fungi also have enhanced ability to adapt to new environments rapidly, which may increase their ability to persist in novel habitats. Fungi reproduce in extremely large numbers, with some wood-decay fungi producing 100,000 spores per cm² of mushroom per hour at peak production and some plant pathogens producing 100,000-1,000,000 spores per mL of broth media (Norros et al., 2023; Pistininzi et al., 2014). Large population sizes augment fungi's evolutionary potential by heightening genetic diversity, increasing the likelihood of beneficial mutations, and quickening the rate at which adaptive traits can spread through populations (Kusch et al., 2024; McDonald & Linde, 2002). Different fungi can also reproduce asexually (*i.e.*, AM fungi), sexually, or through mixed mating systems, and each form of reproduction carries different benefits for fungal establishment. Sexual reproduction maximizes genetic diversity through recombination of alleles, while asexual reproduction allows fungi to reproduce quickly without the constraint of finding a compatible partner. Mixed mating systems, in which fungi sexually reproduce and then asexually divide, likely increase fungal potential for invasiveness most, as sexual recombination produces a large number of genotypes and asexual division allows the most beneficial genotypes to quickly become prevalent (McDonald & Linde, 2002).

Hyphal anastomosis, or fusion of interacting hyphae, provides another mechanism for recombination for fungi of all mating types (Chagnon, 2014). Generally, hyphal anastomosis occurs when interacting hyphae are genetically similar: whether interacting alleles at heterokaryon incompatibility, or *het*, genes are compatible determines whether hyphae fuse to form stable heterokaryons or whether their fusion degrades via cell death (Aanen et al., 2010). Successful fusions result in genetic transfer between

hyphae, which can confer increased tolerance of abiotic conditions, expanded ability to interact with new hosts and substrates, and, in the case of pathogenic fungi, traits that allow evasion of hosts' defenses (Anagnostakis, 2001; Chagnon, 2014; Mehrabi et al., 2011; Wang & McCallum, 2009). Because somatic incompatibility increases with genetic distance between interacting fungi, fungi with low phylogenetic similarity or that originate from locations far from fungi in a given community may have reduced ability to anastomose, which could limit the frequency of hyphal anastomosis as a mechanism for rapid evolution in invasive fungi (Chagnon, 2014; Roper et al., 2011). That said, anastomosis has been documented between native and non-native fungi and may generate heterokaryons with novel genetic combinations that have large impacts on local communities (Anagnostakis, 1987). Overall, frequent, diverse, and large reproduction events likely allow non-native fungi to evolve adaptations to new conditions much more rapidly than plant or animal populations, which can broaden the range of mechanisms that allow them to establish in new locations.

Spread

Barriers: Dispersal and environment

After non-native populations establish, their ability to spread to and persist in new locations determines whether they become invasive. In addition to human-mediated dispersal and fungi's own long-distance dispersal through wind and water, fungi can disperse through mycelial exploration and movements of earthworms, arthropods, mammals, and birds (Chaudhary et al., 2022; Vašutová et al., 2019). Non-native fungi capable of long-distance wind dispersal may readily reach new habitats following reproduction, while those not suited to airborne dispersal may rely more on interactions with organisms in their invaded range. Various animals disperse both AM and EM fungi after intentionally consuming them and by chance, after consuming other organisms or otherwise coming into contact with them unintentionally (e.g., ectozoochory; Vašutová et al., 2019). Because AM fungi do not produce mushrooms, and EM fungi do, AM fungal consumers are more likely to be soil fauna, whereas larger vertebrates may prefer EM fungi (Vašutová et al., 2019). Larger vertebrate consumers likely disperse EM fungi, and possibly mushroom-forming saprotrophs, over larger distances (e.g., S. Ashkannejhad & Horton, 2006; Nuñez et al., 2013), while AM fungal dispersal may depend more on ectozoochory for longer animal-mediated dispersal. If fungivores in invaded ranges preferentially consume native fungi, then animal dispersal of invasive fungi from all fungal guilds may decrease relative to their native ranges. Until mechanisms of fungal dispersal are better characterized, however, the extent to which dispersal will facilitate or limit fungal invasions is unclear.

Once invasive fungi disperse to new locations in the invaded range, they again must establish. Blackburn et al. (2011) note that greater dispersal distance correlates with greater change in environmental conditions. As in the establishment stage, fungi with larger abiotic niches and greater ability to rapidly adapt to new conditions will likely have increased ability to establish in novel environments. This stage may separate non-native fungi well-suited to their initial establishment site from those capable of persisting across diverse landscapes.

Monitoring fungal invasions

While monitoring is not a stage of invasion and is therefore not mentioned in the unified framework, some fungal traits will prevent traditional survey methods from characterizing fungal invasions; consequently, monitoring fungal invasions represents one of the largest hurdles to integrating

fungi into traditional invasion frameworks. Due to fungi's cryptic nature, fungal ranges are difficult to describe. Because definitions of invasive species stipulate that species in question must be non-native, confusion over fungi's native distributions can prevent a species from being labeled invasive in the first place (Vellinga et al., 2009). Most fungal ranges are still unmapped, and humans have moved soil and microorganisms for centuries, which limits our ability to infer native ranges from current distributions. However, recent advancements in DNA sequencing have led to breakthroughs in mapping current fungal distributions (*i.e.*, Kivlin et al., 2011; van Galen et al., 2025), and phylogeographic analyses of fungal population genetics are becoming a key tool in identifying the native range of fungi (Nickles et al., 2026). For instance, phylogenetic analyses were used to determine that widespread populations of *Amanita phalloides* on the North American west coast are likely native to Europe (Pringle et al., 2009).

Difficulties in detecting fungi also complicate efforts to monitor ongoing fungal invasions. State of the art techniques to detect outbreaks of other invasive species include chemical cues, remote sensing, coordinated monitoring by government agencies, eDNA, and citizen science observations (Larson et al., 2020). For mushroom-forming invasive fungi, such as *A. phalloides*, combinations of historical records and modern observations can enable inference of spread rates, while observation of hyphal length can be indicative of whether fungal spread occurs sexually or asexually (J. J. Golan & Pringle, 2017; Pringle et al., 2009). Most invasive fungi, however, are not visible to the human eye, which precludes use of remote sensing, surveys, and citizen science observations. Currently, chemical cues are mostly only capable of detecting insect species, while eDNA has successfully identified invasive fungi, but its high cost limits widespread use (NISC 2016, (Larson et al., 2020; Shestibratov et al., 2018). As sequencing costs fall, eDNA may become a valuable tool for monitoring changes in fungal distributions.

Even when invasive fungi are detected, delineations between fungal individuals and species are nebulous, which complicates efforts to describe population sizes and growth rates. While plant and animal individuals can be thought of as physically distinct units, fungal anastomosis blurs boundaries between previously physiologically distinct fungal individuals (Todd & Rayner, 1980). Boundaries between fungal species are also unclear, as horizontal gene transfer allows neighbors to influence each other's genetics (Fitzpatrick, 2012). Additionally, some fungi, like the *Glomeromycotina*, reproduce entirely asexually, which renders species concepts that rely on reproduction between individuals or diversity between genomes non-applicable (Corradi et al., 2025; Rosendahl, 2008). Overall, murky boundaries between fungal individuals and species may force invasion frameworks to consider fungal invasive status using an integrative approach beyond simple marker gene sequence identity or observable morphology, such as whole genome sequencing (Drees et al., 2017).

Section 3: Evaluating existing invasion hypotheses from a fungal perspective

Hypotheses exist within invasion biology to examine how introduction effort, traits of the recipient community and environment, and species traits aid in the successful establishment and spread of non-native plants and animals. These hypotheses offer alternative explanations for how invasive species overcome the barriers associated with each of the invasion stages outlined in Blackburn's unified framework. Below, we synthesize seven hypotheses that are widely tested for invasive plants and animals, identify the evidence that exists for fungi, and evaluate alternative considerations, when relevant, that may influence each hypothesis' ability to predict fungal invasions.

Propagule Pressure

What is the hypothesis?

The propagule pressure hypothesis predicts that increased propagule number (the number of individuals in a release event) and propagule frequency (the number of release events per unit of time) increases non-native species' likelihood of successful invasion (Simberloff, 2009; Williamson, 1996). Propagule pressure offers an explanation for why certain populations of introduced species establish while others do not; with repeated introductions the probability of introducing a new genotype that can withstand novel environmental conditions increases (Lockwood et al., 2005).

What evidence exists for fungi following this hypothesis?

Several case studies demonstrate links between fungal invasions and high introduction intensity. Analysis of numerous studies of population genetics of fungal invasions revealed that the majority of fungal invasions stem from introductions of multiple populations, with enhanced genetic diversity linked to greater virulence in pathogens and greater tolerance of diverse environmental conditions across fungal groups (Gladieux et al., 2016). However, more recently, whole-genome sequencing used to characterize population genetics of *Pleurotus citrinopileatus* (golden oyster mushroom) throughout its invasive range demonstrated that populations hundreds of kilometers apart had extremely similar genotypes, indicating that multiple introductions of the same commercial strain likely launched many small invasions at once (Bruce, 2018). These examples suggest that propagule size and number play an important role in facilitating fungal invasions of natural systems, whether or not genetic diversity increases with introduction intensity. Laboratory experiments have also demonstrated that high propagule pressure is often necessary for invading microbes to overcome priority effects to establish in existing microbial communities (Acosta et al., 2015).

Alternative considerations for fungi

Fungi's ability to rapidly and asexually reproduce in large numbers may lower the propagule pressure necessary for non-native fungi to invade. In instances where genetic diversity in the founding population of non-native fungi is low, their reliance on asexual reproduction may allow non-native individuals to persist in the environment until new individuals - and genes - are introduced (Gladieux et al., 2016). Although clonal populations may be more susceptible to local extinction in the face of stochasticity or unsuitable climatic and environmental niches, hyphal anastomosis or other means of hybridization may allow clonal individuals to incorporate genetic materials from native species (Chagnon, 2014). These mechanisms may lower the propagule load required to launch invasions of fungi relative to those of macroorganisms. Spore size may also be important to consider when applying concepts of propagule pressure to invasive fungi, as spores of varying sizes have different advantages that can alter population dynamics. AM fungi, for instance, tend to have large spores, which provide them with greater nutrients and increased resistance to desiccation (Davison et al., 2018; Pehim Limbu et al., 2025), while smaller EM fungal spores can disperse farther, potentially increasing interconnectedness between populations.

Untested research frontiers

- *Can we use horticultural records (import records, shipping intensity, etc.) to estimate the propagule pressure of fungi intentionally transported to non-native ranges?*
- *How can we better quantify the propagule size and number for fungi unintentionally introduced through global trade?*
- *How does fungi's rapid evolution and anastomosis influence the introduction intensity necessary to launch fungal invasions?*

Invasional Meltdown

What is the hypothesis?

Invasional meltdown asserts that introduced species can facilitate the spread of other non-native species through synergistic interactions with one another (Simberloff & Von Holle, 1999). Therefore, the hypothesis predicts that the number of invasive species positively accumulates with introduction of new species. In the context of the unifying framework, invasional meltdown plays an important role in not only helping non-native species spread, but in cases of close association (e.g., *Pinus* and their associated EM fungi), can also determine whether two species can establish in a new environment (Vellinga et al., 2009).

What evidence exists for fungi following this hypothesis?

Possibly the most famous example of invasional meltdown in fungal ecology is that of the facilitative co-invasions of *Pinus* and EM fungi in the southern hemisphere, where EM trees are not historically found. In Isla Victoria, Argentina, dense plantations of non-native *Pinus* species were established in 1925, but, despite *Pinus* species' well-known invasive potential and high fecundity (Richardson et al., 1994), no pines had established outside of the plantations almost 100 years later. The spread of the pines was limited by a lack of compatible EM fungi outside of the plantation (Nuñez et al., 2009, Nuñez et al., 2013). When pine invasion occurs, a small group of co-invasive fungal taxa, most commonly the Suilloid fungi (*i.e.*, *Suillus* and *Rhizopogon*; Policelli et al., 2019), facilitate the proliferation of pines outside of their native range and drive cascading impacts on native fungal communities (Mujic et al., 2023). Therefore, the success of pine invasions is heavily contingent upon the establishment and spread of invasive EM fungal symbionts (Dickie et al., 2010; Hayward et al., 2015; Nuñez et al., 2009; Nuñez & Dickie, 2014; Policelli et al., 2023; Policelli et al. 2026; Sapsford et al., 2022). While other plant-fungal co-invasions have not received as much attention, non-native mycorrhizal fungi have also been found in higher abundances near multiple (non-*Pinus*) invasive tree species in New Zealand and the Iberian Peninsula, illustrating that invasional meltdown may be a common vector for mycorrhizal fungal invasions around the world (Bogar et al., 2015; Díez, 2005). Host invasions may similarly allow pathogenic and saprotrophic fungi to invade new ranges.

Invasive fungi also participate in invasional meltdowns through interactions with invasive taxa other than their host species, which result in beneficial niche modification and dispersal. Non-native mammals, including wild boar, deer, possums, and hares ingest and transport non-native EM fungal spores, expanding their invaded ranges (Aguirre et al., 2021; Livne-Luzon et al., 2017; Nuñez et al., 2013; Soteras et al., 2017; Wood et al., 2015). Invasive species also facilitate invasive fungi's establishment indirectly by altering abiotic conditions. For instance, the invasive black locust (*Robinia pseudoacacia*) enriched soil nitrogen content via associations with nitrogen-fixing bacteria in the introduced range,

creating an island effect which facilitated proliferation of other non-native plant species and suppressed native fungal communities, possibly creating openings for non-native fungal invasions (Grove et al., 2017; Guisande-Collazo et al., 2016; Von Holle et al., 2006; Wolfe et al., 2008).

Alternative considerations for fungi

Fungi have been featured in examples of invasional meltdowns with plants and animals, but research rarely considers that fungi are capable of engineering conditions that favor their own success. For instance, fire-adapted fungi slow decomposition relative to non-fire-adapted fungal communities, which allows fuel build-up and increases the likelihood of recurrent fire (Hopkins et al., 2025). While it is untested, it is possible that invasive fungi can promote their own growth, colonization, and spread by altering abiotic conditions (i.e., faster decomposition) and native community structure (Mujic et al., 2023; Veerabahu et al., 2025; Vietorisz et al., 2025), paving the way for invasions of other fungi.

Untested research frontiers

- *To what extent can invasive fungi engineer abiotic conditions to promote their own invasions?*
- *Is it common for invasive fungi to benefit from invasion-induced disturbance?*
- *What is the potential for invasive fungi to facilitate the spread of other invasive fungi?*

Enemy of my enemy

What is the hypothesis?

A closely related concept to invasional meltdown is the enemy of my enemy hypothesis (EEH). EEH draws upon the proverb “the enemy of my enemy is a friend” to capture how the presence of an invasive species’ natural enemy in their introduced range can promote invasion success for both species (Colautti et al., 2004). EEH differs from invasional meltdown in that co-invading species are not mutualists but natural enemies. However, due to their past co-evolution, the invasive species has resistance to its natural enemy, whereas native species in their invaded range lack defenses. Thus, the natural enemy decimates native populations, decreasing the invasive host’s competition and facilitating its spread.

What evidence exists for fungi following this hypothesis?

One example of EEH is the interaction between *Lithobates catesbeianus* (the North American bullfrog) and the pathogenic fungus *Batrachochytrium dendrobatidis* (Bd) (Miaud et al., 2016). In Europe, non-native North American bullfrogs act as a reservoir for Bd. While severe Bd infections can be lethal to North American bullfrogs, the mortality rate for infected European amphibians is much higher than in the invasive bullfrogs. Because Bd disproportionately impacts native European amphibians, both the non-native North American bullfrogs and, consequently, the pathogenic fungi they carry, can more easily invade new European environments.

Untested research frontiers

- *Are there instances in which the fungal species acts not as the enemy, but as the reservoir?*

- How can researchers link population growth of the invasive fungi to the presence of its native enemy or reservoir?

Enemy Release

What is the hypothesis?

The enemy release hypothesis (ERH) asserts that introduced species may be able to grow and spread more widely outside of their native range because their natural enemies are absent, releasing them from herbivory, predation, or pathogenic pressures (Keane & Crawley, 2002).

What evidence exists for fungi following this hypothesis?

When fungi are included in research on ERH, they are typically featured as the enemies from which invasive plants and animals are escaping. Yet, fungal populations are also controlled by natural enemies, including other fungi, bacteria, viruses, and soil macrofauna like mollusks, nematodes, and arthropods (Nakamori & Suzuki, 2005; Vašutová et al., 2019). Such enemies can out-compete fungi, induce infections, produce harmful chemicals, act as parasites, or consume fruiting bodies or fungal hyphae, damaging the individual and interrupting spore dispersal (Vašutová et al., 2019; Thambugala et al., 2020).

Consistently, fungal species can more easily invade new environments in the absence of their natural enemies, as demonstrated by the disproportionate severity of the Dutch Elm epidemic in North America compared to Europe. While the pathogenic fungus responsible for Dutch Elm disease, *Ophiostoma ulmi*, was initially widespread across both continents, North American Dutch Elm infections continued to rise while European elm populations experienced a sharp decline in mortality. Evidence now suggests that the differential outcomes were due to deleterious mitoviruses that attacked the European, but not North American, populations of *O. ulmi* (Brasier & Buck, 2001).

The success of biological control efforts, in which researchers deliberately introduce enemies of invasive fungi to prevent their spread, further illustrates the role of enemy release in fungal invasions. For instance, chestnut blight, caused by the fungal pathogen *Cryphonectria parasitica*, was more severe in North America than Europe, which is partially due to European biocontrol efforts. Because a co-evolved hypovirus constrains *C. parasitica* in its native range, European researchers attempted to use an RNA virus of the fungus, *Cryphonectria hypovirus 1* (CHV1) as a biocontrol agent. Sampling efforts across Croatia revealed that when *C. parasitica* is infected with CHV1, the pathogenic fungus induces a weakened version of chestnut blight that produces smaller lesions in trees (Ježić et al., 2024). CHV1 was not introduced early enough in North America to effectively control *C. parasitica* (Ježić et al., 2024). In addition to introducing viruses, researchers have also introduced other antagonistic fungi, including over 100 species of *Trichoderma*, *Ampelomyces quisqualis*, and *Phlebiopsis gigantea*, to control fungal plant pathogens like *Rhizoctonia solani*, *Sclerotinia americana*, powdery mildew, and root rot (Elad et al., 2025; Thambugala et al., 2020; Carbó et al., 2020; Thambugala et al., 2020; Kälviä et al., 2018; Thambugala et al., 2020). These efforts to control invasive fungi which were otherwise free from enemy pressures has led to increased commercialization of biocontrol agents in the form of globally available powders, dusts, and liquid-based biopesticides (Ardakani et al., 2009; Thambugala et al., 2020).

Research frontiers

- How relevant is enemy release for nonpathogenic fungi?
- How can we improve selection of host-specific biocontrol agents for invasive fungi?
- How does the phylogenetic relatedness between biocontrol agents and native communities predict its ability to control invasive fungi?

EICA

What is the hypothesis?

The evolution of increased competitive ability (EICA) hypothesis expands upon ERH, predicting that in the absence of native enemies, introduced species do not need to invest in defense and instead allocate more resources into growth and reproduction, increasing their competitive ability (Blossey & Notzold, 1995). Consequently, if individuals of a species taken from their introduced range are grown under identical growing conditions to individuals from their native range, the introduced individuals will produce greater biomass. Experimental tests of EICA commonly show plants increasing growth and/or reproduction in their introduced ranges (Callaway et al., 2022), but demonstrating reduced defense is also critical.

What evidence exists for fungi following this hypothesis?

Very few studies of invasive fungi have investigated whether patterns of growth or reproduction differ in fungi's invasive and native ranges, and consequently, little evidence exists to evaluate EICA from a fungal perspective. Pathogenic fungi may differ in reproductive mode in native and invasive ranges, switching from frequent sexual reproduction in native ranges to often almost entirely clonal reproduction in invasive ranges (Ali et al., 2010; Fisher et al., 2009; Singh et al., 2021). Ali et al. (2010) demonstrated a genetic basis to this reproductive switch by inoculating the same cultivar of wheat (*Triticum aestivum*) with *Puccinia graminis* f.sp. *tritici* (PST) pathogens sourced from throughout Europe and Asia and finding that PST pathogens from the native range had much higher production of sexual structures than those from the invaded range (Ali et al., 2010). Invasive pathogens' switch to asexual reproduction could be a result of enemy release, as fungi do not need sexual reproduction to evade specialized enemies (Gladieux et al., 2014), which would be consistent with EICA; alternatively, evolution of clonality could be due to lack of compatible sexual partners in the new range, preservation of heterozygosity in small founder populations, or decreased need for the production of sexual spores for dispersal (Gladieux et al., 2016). Asexual reproduction may also grant invasive pathogens a competitive advantage in their new range by allowing them to reproduce more rapidly than they would through sexual reproduction. Conversion to asexual reproduction is only sometimes seen in invasive populations of other fungal guilds, however. EM fungal *A. phalloides* heavily relies on sexual reproduction in its invasive range but has also been shown to reproduce asexually, while saprotrophic *P. citrinopileatus* mainly relies on sexual reproduction in both its native and invasive range (Bruce, 2018; J. Golan et al., 2024). AM fungi always reproduce asexually (Chagnon, 2014). Whether or not reproductive output increases in fungi's invasive ranges regardless of reproductive method has not been evaluated.

Alternative considerations

EICA also states that organisms evolve increased allocation of resources to growth when released from enemies in invasive ranges, but for fungi thus far, any differences in growth traits between native and invasive ranges are unmeasured. However, grazing, or lack thereof, can alter fungal growth phenotypes. For example, when four species of wood-decomposing fungi were exposed to four different grazers and a non-grazing control, fungal species' mycelial network architecture varied between 1% and 30% across treatments (Aguilar-Trigueros et al., 2025). If fungi experience decreased grazing pressure in their new ranges, it follows that their growth patterns could shift, perhaps allowing fungal individuals to produce larger mycelia or even invest in alternative hyphal exploration strategies.

To support an increase in allocation of resources to growth, EICA predicts a tradeoff in which a population evolves to invest less into defense. Since biosynthesis of chemical effectors is energetically expensive, production of chemical defenses often only begins after an attack; therefore, in the absence of enemies, non-native fungi's defense capabilities may weaken over generations (Kempken & Rohlf, 2010; Künzler, 2018). Testing differential resource allocation to defense compounds between the native and invasive ranges of fungi (Kaya et al., 2015), could potentially elucidate whether energetic tradeoffs between growth and defense serve as a primary mechanism underlying fungal invasion.

Research frontiers

- Do fungi that change their reproductive modes in invasive ranges increase their reproductive output, or do reproductive switches result from a lack of compatible partners in invasive ranges?
- How does release from enemy pressures in the invasive range alter fungal growth morphology?
- Do invasive fungi decrease their production of defensive compounds in invasive ranges?

Novel Weapons

What is the hypothesis?

The novel weapons hypothesis is an alternative to enemy release and EICA that suggests that instead of allocating extra resources into growth and reproduction, invasive species may intensify their production of chemical defenses in their introduced ranges (Callaway & Ridenour, 2004). Increased allelopathy can suppress surrounding community members, reducing the intensity of interspecific competition that the invader faces. This release from competition is further perpetuated by species in the introduced range lacking resistance to chemical weapons since native communities did not co-evolve with the invader (He et al., 2009).

What evidence exists for the hypothesis?

Not only can fungi facilitate plant invasions through the transport of allelochemicals (Aschehoug et al., 2014; Cipollini et al., 2012), but they can also promote their own invasions through the production of defense compounds. Fungi employ numerous chemical weapons to suppress competitors (i.e., diffusible organic compounds), and these weapons can slow competitors' growth and degrade their cell walls, sometimes leading to their death (Boddy & Hiscox, 2016; Sharma et al., 2011). Whether production of these compounds varies in invasive and native ranges has only rarely been considered, but existing evidence supports the application of the novel weapons hypothesis to fungi. For example, comparison of native European populations and invasive Californian populations of *A. phalloides* revealed that the invasive fungi had significantly different toxin allele frequencies than European

populations, indicating genetic divergence from native populations, potentially as an artifact of founder effects (Drott et al., 2023). Similarly, while the MSDIN genes responsible for producing toxins such as α -amanitin, β -amanitin, phalloidin, and phallacidin were highly conserved across all individuals, the presence of accessory genes varied across populations, suggesting diversifying selection played a role in developing unique chemical signatures for fungal individuals living in invasive versus native ranges (Drott et al., 2023). Although additional work is needed to clarify whether the evolution of such accessory chemical defenses in Californian populations is helping to drive the invasion of *A. phalloides* and whether altered defense profiles in invasive populations require greater energetic investment, these findings are foundational for future tests of novel weapons.

Research frontiers

- Is the evolution of novel weapons in the introduced range predictive of increased invasion success?
- Do populations of fungi in their invasive range allocate more energy to the production of chemical weapons than native populations?
- Does the naivety of recipient communities correlate with invasive fungi's energetic investment in weapons?

Biotic resistance

What is the hypothesis?

The biotic resistance hypothesis predicts that communities with high biodiversity can better resist biological invasions because an increase in species interactions such as competition, herbivory, and parasitism prevents or slows new species' establishment in the community (Levine et al., 2004).

What evidence exists for fungi following this hypothesis?

Because engineering desirable microbiomes is a high research priority in microbiology, many laboratory experiments have demonstrated that altering existing microbial communities is more difficult when communities are diverse (Albright et al., 2020; Henry & Bergelson, 2025; Ye et al., 2025). Diverse communities inhibit colonization of invading microbes through competition and priority effects that allow microbes to create environments that are less suitable for invaders (Ye et al., 2025). Fungi are significantly worse at overcoming biotic resistance in laboratory environments than bacteria, suggesting that biotic resistance from native microbial communities may pose a significant barrier to fungal invasions (Albright et al., 2020).

High diversity of microbes and other taxa also weaken fungal invasions in natural ecosystems. Priority effects, for instance, strongly govern AM and EM fungal colonization of tree roots to the exclusion of late-arriving mycorrhizal fungi (Kennedy et al., 2010; Werner & Kiers, 2015). Similarly, root and leaf microbial communities deter colonization of pathogenic fungi by out-competing enemies for carbon, nutrients, and space, triggering production of defense compounds, and quickening plants' recovery from herbivory and disease (Delavaux et al., 2017; Dowarah et al., 2022; Zabalgoeazcoa, 2008). Given that certain microbes specialize in just one or some of these defense mechanisms (Zabalgoeazcoa, 2008), overall defenses against pathogenic fungi should increase with microbial community species richness. Finally, pathogenic fungal invasions are more frequent and severe in

agricultural communities, where host plants are often conspecific and have low genetic diversity, than forests, where lower density of hosts decreases pathogens' colonization and spread (Desprez-Loustau et al., 2007).

Research frontiers

- Which groups of microbes provide the most biotic resistance against fungal invaders in natural ecosystems?
- Alternatively, do we see patterns of biotic acceptance, in which higher native fungal diversity correlates with higher invasive fungal diversity?
- How does the phylogenetic diversity of the recipient community impact the success of fungal invasions?
- Do different guilds of fungi vary in their ability to overcome biotic resistance in invasive ranges?

Section 4: Open questions in fungal invasions:

In addition to unresolved questions surrounding the extent to which theoretical invasion frameworks and hypotheses predict fungal invasions, numerous aspects of spatial and temporal patterns of fungal invasions are unclear. We also consider whether other microbial invasions unfold similarly to fungal invasions and whether intentional transport of fungi contributes to fungal invasions differently than natural dispersal.

Biogeography of fungal invasions

Which areas are most susceptible to fungal invasions?

As classically demonstrated with plants (Lonsdale, 1999), certain environments are more susceptible to invasions than others. For instance, when adjusted for area, islands tend to have more non-native species than their mainland counterparts (Denslow, 2003; Lonsdale, 1999). The vulnerability of islands to invasions is partially explained by the ecological naivety of their native species, who evolved in the absence of herbivores or predators found in the mainland, and consequently lack the necessary defenses to withstand pressures from introduced enemies (Bowen & Vuren, 1997; Freedman et al., 2024; Moser et al., 2018; Simberloff, 1995; Walsh et al., 2012). Disturbed environments also tend to be more invadable, as the removal of individuals from the community often leads to higher resource availability, including increased space and light (Davis et al., 2000). Theory suggests that competition intensity is inversely related to resource availability, meaning that invasive species experience less competition in disturbed environments (Davis et al., 2000). Our current understanding of whether non-native fungal species are more likely to invade the same areas as non-native plants and animals (islands, disturbed environments, etc.) is limited. Previous research has suggested that response to disturbance is guild-specific; fungal pathogens, for instance, have been positively correlated with increased disturbance (Shi et al., 2019), whereas ectomycorrhizal fungi diversity decreases (Rodriguez-Ramos et al., 2021). Trends also vary across systems; saprotrophic diversity decreased along a disturbance gradient in a tropical rainforest in China (Shi et al., 2019), but increased in a temperate forest invaded with garlic mustard (Anthony et al., 2020). Future work is critical for clarifying which areas are most susceptible to invasions by non-native fungi, as well as the mechanisms underpinning such patterns.

Where do fungal centers of diversity exist globally?

Though great progress has been made in mapping fungal distributions (Edwards et al. 2026; Ordiozola et al., 2026; Van Nuland et al., 2025), centers of global fungal diversity remain unclear. Diversity of other taxa, including terrestrial plants, mangrove trees, marine protists, reptiles, coral, arthropods, fish, birds, and mammals, famously peak in the tropics and decrease with latitude (Willig et al., 2003). However, notable exceptions to this rule exist (*i.e.*, conifers, crayfish, ichneumonid wasps, etc.; J. H. Brown, 2014). EM fungi, which are not commonly found in tropical regions, are another clear exception, but where diversity of other fungal guilds concentrates is unknown. Uncovering centers of fungal diversities is important for predicting fungal invasions, as regions with the highest fungal diversity may both have increased resistance to invasion (*i.e.*, biotic resistance) and species with increased likelihood of becoming invaders themselves due to greater probability of one of a larger number of species being a successful invader and because species in more diverse environments may evolve increased competitive ability (Huston, 1994).

Temporal aspects of fungal invasions

Do fungal invasions unfold more quickly than those of other taxa?

Lag times, or the amount of time in between a non-native organism's arrival in a new habitat and its spread as an invasive species, exist in all invasions. Because detecting and responding to invasions early is essential for controlling the spread of invasive species (Crooks, 2005), the length of lag times informs how frequently monitoring must occur to eradicate non-native species before invasions begin. Lag times stem from non-native species' inherent population growth rates and rates of adaptation, as well as the occurrence of chance environmental release events (Crooks & Soulé, 1999). While chance environmental release events likely impact fungi at similar frequencies as other organisms, fungi's rapid rates of population growth and adaptation may greatly shorten their lag times. That said, fungal lag times are currently unknown.

Other microbial invasions

Do other microbial invasions operate similarly to fungal invasions?

Other microbial taxa, including bacteria, protists, and algae, can also be invasive (Acosta et al., 2015; Law et al., 2000; Rodríguez-Echeverría, 2010). While limited case studies provide evidence that invasions of non-fungal microbial groups can follow trajectories predicted by hypotheses (*i.e.*, invasional meltdown of co-invading legumes and N-fixing bacteria), invasion dynamics of these taxa have not been examined in natural systems as often as fungi (Rodríguez-Echeverría, 2010; Thakur et al., 2019). As a result, comparing invasion trajectories of different microbial groups is difficult. While microbial groups are united by common traits, like large population sizes and rapid reproductive rates, microbial groups also differ in traits that may impact their procession through invasional stages. For example, bacteria have smaller body sizes than protists and fungi; because reduced body size is associated with greater passive dispersal rates, larger population sizes, and increased rates of evolution, bacteria may have increased ability to rapidly colonize non-native environments (Luan et al., 2020). Evaluating how other traits of

other microbial groups impact their invasion trajectories is necessary to fully integrate microbes into existing invasion biology theory.

Conclusion

Given that existing fungal invasions have severe ecological and economic consequences, transport of fungi to new ranges occurs at high rates around the world, and global change will alter future fungal invasions, understanding how fungal invasions unfold is of high concern. Decades of research outline the mechanisms that underpin plant and animal invasions, but the extent to which this body of work describes fungal invasions is unclear. In this paper, we synthesize research on general fungal ecology and invasions of multiple fungal guilds to review Blackburn's unified invasion framework and seven well-established hypotheses in invasion biology from a fungal perspective. We find that invasion biology theory generally applies to fungi, but that fungi have traits that merit special attention when considering fungi's place in invasion frameworks and hypotheses. In particular, fungi are difficult to detect, have extremely diverse modes of reproduction and resource acquisition, and are capable of rapid evolution, and these characteristics modify their passage through every invasional stage. Other microbial groups, such as bacteria, algae, and protists, share similar qualities, suggesting that some features of invasions may be microbe specific. While advancements in sequencing and increased interest among biologists have enabled great strides in characterizing fungal invasions in recent years, many aspects of invasion hypotheses and greater invasion theory remain unexplored for fungi. We therefore present some of the highest priority research questions in the field of fungal invasions, including whether the same areas most susceptible to invasions by plants and animals are also at higher risk for fungal invasions, and whether fungi invade more rapidly compared to other taxa.

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Statements and Declarations

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Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Author contributions

All authors conceived of the idea for the manuscript. ECS and LMP drafted the manuscript. SNK and SDO curated and analyzed the data on invasive fungal range sizes. All authors edited the manuscript.

Supplemental Materials

Supplemental Materials 1

Records of introduced fungi were downloaded from iNaturalist from January 1st, 2026 through September 30th, 2026. Occurrence records were obtained individually for each fungal species with the condition “Introduced = yes”. We only retained data for fungal species with at least 30 total observations in iNaturalist. Records were then curated by first ensuring they matched the fungal species of interest (species name identity confirmed in the “scientific_name” column). We then determined the continent(s) on which each fungal species occurred. We only retained records of fungi’s presence on a continent when there were at least 10 observations of the fungus on that continent, unless the distribution was contiguous in space (e.g., Europe to Asia). This threshold confirmed that species identities were supported by at least 10 user observations and therefore was more rigorous than iNaturalist’s Research Grade observations, which only require 3 unique observations. We further corroborated fungi’s continent-level introduced distributions by searching the primary literature to verify the introduced status of that species on that continent (reported in Supplemental Table 1). This resulted in 110,147 verified records of fungal introductions across 178 species.

Fungal distribution maps were created with ggplot2 in R for each fungal guild using the WGS 84 projection. Donut plots report the number of occurrences on each continent.