An agent-based model of the Foraging Ascomycete Hypothesis.

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Abstract

Most trees host hundreds of species of fungi asymptomatically in their internal tissues, known collectively as fungal endophytes. The Foraging Ascomycete (FA) hypothesis proposes that some fungal endophytes inhabit the internal leaf tissue of forest trees in order to enhance dispersal to substrates on the forest floor, by using leaves as vectors and as refugia during periods of environmental stress. Following the FA hypothesis, many fungi may therefore be in continuous and cyclical flux between life stages as endophytes in the forest canopy and as wood-decomposing fungi on the forest floor. This cycle may represent a very common and previously-ignored process in the ecology of forests, with implications for forest health. The ecological consequences of the FA hypothesis are complex, so we constructed an agent-based model of the FA hypothesis. Our model is intended to serve as both an explicit conceptual explanation of the FA hypothesis, and as an exploration of the conditions in which endophytism and dispersal via leaves may be advantageous for fungi. The model predicts competitive benefits to fungal dispersal via leaves, given sufficient retention of endophyte infections by host trees and with sufficient host trees on the landscape. Loss of these important fungi can result from increased local disturbances of forest canopy, and deforestation.

Keywords: viaphyte, foraging ascomycete hypothesis, fungal foliar endophytes, plant microbiome

Introduction

All large organisms are observed to host microbiomes (Rosenberg et al., 2010). Plants typically host very rich microbiomes, with both epiphytic (external) and endophytic (internal) fungi and bacteria present on and within all tissues (Rodriguez et al., 2009; Rosenblueth and Martínez-Romero, 2006; Vandenkoornhuyse et al., 2015). Additionally, a rich "endobiome" appears to be present at some level in all tissues of all plants. Fungal foliar endophytes (FFE) are an important subset of the plant microbiome, and have a long history of specialized study. We use here a common definition of endophytes: microorganisms that inhabit plant tissues for at least part of their life cycles, but do not cause disease symptoms, at least for an extended part of their existence within the host (Stone et al., 2000; Wilson, 1995). As with the microbiome at large, the FFE community is extremely diverse in most plants (Arnold et al., 2000; Arnold and Lutzoni, 2007), and FFE inhabit virtually all spaces of the leaf, especially in wet tropical ecosystems (Bayman et al., 1998; Gamboa et al., 2003; Gamboa and Bayman, 2001).

Interactions between host and FFE are complex, with relationships ranging from pathogenic to mutualistic (Carroll, 1988). Particular foliar endophytes have been observed to confer pathogen resistance (Arnold et al., 2003; Gazis and Chaverri, 2015; Mejía et al., 2008, 2007), drought resistance (Hamilton and Bauerle, 2012), other environmental stress resistance (Rodriguez and Redman, 2008), and defense against herbivory (Clay, 1988; Estrada et al., 2013; Sumarah et al., 2008). Even in the case of *mostly* commensal, neutral, or weakly antagonistic relationships with their host, the community of FFEs within a plant is hypothesized to act as an important modulator of disease, occupying space within plants that might otherwise be invaded by pathogens (Busby et al., 2016; Mejía et al., 2007). Microbial partners to plants may become more important in the current context of climate-change associated stresses (Busby et al., 2017; Woodward et al., 2012).

Nonetheless, the diversity and ubiquity of fungi living within leaves presents something of an evolutionary riddle. FFE species are often closely related to known plant pathogens, or are pathogens themselves when associated with a different host (Carroll, 1988). Endophytic fungi have been found in the tissues of some of the earliest fossil examples of primitive land plants (Taylor et al., 2005; Taylor and Krings, 2005); for land plants, fungal endophytism may be as old as fungal disease. This makes difficult any clear definition of many fungi found within plant tissues as either pathogen or mutualist, and any general designation of endophytism as an ancestral or derived state is probably therefore a gross simplification.

Further complicating matters, in contrast to the benefits for the host plant, benefits to fungal partners of an endophytic relationship are much less well understood. To be asymptomatic, endophytes must apparently restrict growth and sporulation while within their host (Stone, 1988), and there is evidence that the endophytic phase requires an array of unique metabolites

(Carroll and Petrini, 1983; Kusari et al., 2012; Petrini et al., 1993; Schulz et al., 1999). An endophytic stage must supply some benefit to the fungal partner to outweigh these costs, or endophytism presents an evolutionary dead-end.

The most common answer given to this riddle is the hypothesis that fungal endophytes are latent saprotrophs or pathogens (Carroll, 1988; McMullin et al., 2019; Parfitt et al., 2010; Promputtha et al., 2007). Presumably, fungi living in leaves will have priority access to leaf tissues when host defenses weaken. Many foliar fungi do appear to be latent saprotrophs, meaning that they are very active in at least the early phases of leaf decomposition, consuming some of the more labile components of leaf tissue (Guerreiro et al., 2017; Osono, 2006; Stone, 1987). A portion of resident FFEs then sporulate on the fallen leaves they inhabit. Some of these FFEs are thought to overwinter on their decomposing leaves, sporulate in the spring, and return to the endophytic stage (Unterseher et al., 2013). However, many other fungi observed as FFEs have not been observed to sporulate (i.e., reproduce) on their leaves after senescence (Bayman et al., 1998; Lodge, 1997; Müller et al., 2001). These non-sporulating fungi must escape the leaf to another substrate after “robbing the bank”, or die without reproducing. This is particularly true in the face of intense competition from the diverse and aggressive leaf-decomposing fungi that invade in the later stages of leaf decomposition.

Carroll (1999) proposed that some subset of endophytic fungi may utilize the endophytic phase to increase dispersal and colonization of woody substrates, a concept known as the **Foraging Ascomycete (FA) hypothesis** (Figure 1). He noted that leaves could act as excellent additional vectors for fungi residing within them, given a leaf’s ability to disperse farther from its tree than the majority of fungal spores fall from sporocarps (Ferrari and Sugita, 1996; Galante et al., 2011; Roper et al., 2010). Carroll also proposed that some endophytic fungi utilize the endophytic phase to not only cross spatial gaps to other substrates, but also temporal gaps between available substrate on the forest floor: fungi may take refuge in leaves to endure excessively dry or wet seasons that do not allow extensive decomposition of wood, or persist in leaves when woody substrates are not present. Thomas and Vandegrift et al. (2016) expanded this concept, noting that the humid microclimate provided by the shelter of a fallen leaf could protect endophytic hyphae as they grow out of a leaf, allowing endophytic fungi to escape from its host leaf to woody substrates, thus avoiding the uncertainty inherent in the germination phase of growth from spores. This form of dispersal also may coordinate dispersal times with events in which new substrates become more available, such as with storms that can both bring down new wood and leaves carrying fungi to the forest floor. Here, we use the term ***viaphytic***, recently proposed by Nelson et al. (2019), to describe endophytic fungi that transfer from endophytic infections in leaves to woody substrates, and thus are capable of using leaves as dispersal vectors.

Figure 1. Visualization of the Foraging Ascomycete hypothesis, also known as "viaphytism". Leaves are infected endophytically by spores, then act as dispersal vectors of fungi to wood on the forest floor. Fungi within leaves transfer to wood, decompose the woody substrate, and sporulate. Some of these spores germinate on leaves and colonize leaves again as endophytes.

The Foraging Ascomycete hypothesis centers on the competitive advantage given to fungi that can disperse by "hitchhiking" in leaves. Fungi are increasingly shown to be dispersal limited, and increases in dispersal are therefore increasingly understood as vital for success in competition among fungi (Bruns, 2019). Viaphytism comes with the costs mentioned above that seem to make endophytism a curious bargain for fungi: production of enzymes for penetration of plant tissues and bypassing plant defenses, and subsequent suppressed metabolism and reproduction while occupying plant tissues until leaf senescence. However, for viaphytic fungi, we hypothesize that these costs of the endophytic phase "pay off" energetically and reproductively, because viaphytism externalizes some of the costs of dispersal to host plants, and ultimately results in a very competitive alternative dispersal strategy. Because of this alternative, leaf dispersal strategy, we hypothesize that the selective pressure on spore dispersal of viaphytic fungi is relaxed. Thus in the model presented here viaphytic fungi have a spore dispersal ability (represented in the model by the parameter "*d*", see equation 1) that is generally allowed to be lower than their non-viaphyte competitors. Even if this is not actually the case in natural settings, introducing this handicap of spore dispersal in the model is useful for testing the potential effectiveness of viaphytism.

Conversely, non-viaphytes have evolved other ways to increase dispersal. There are numerous possible adaptations for directly increasing spore dispersal, such as by increasing spore quantities, optimizing spore or spore-bearing structure morphology, synchronizing spore releases, etc. (Fritz Joerg A. et al., 2013; Galante et al., 2011; Pringle et al., 2015; Roper et al., 2010). Most of these rely directly on spores as the main vector for dispersal, and they also come with energetic costs. In the model presented here, all of these strategies increase either the maximum distance or number of spores, or both, meaning greater spore dispersal ability.

The bigger picture

The FA hypothesis is intriguing not only for the clues it may provide to the riddle of endophytes' evolutionary history, but also for the large-scale ecological process it describes, which may be ongoing in forests everywhere around the world. Increasingly, fungi found as foliar endophytes are being located nearby as sexual-state fungi on woody substrates of the forest floor (Bills et al., 2012; Tanney et al., 2016; Thomas et al., 2016), very often *not* on the wood of their previous hosts (Lodge, 1997; Unterseher et al., 2013). The spores from these sexual fungi on the forest floor cause endophyte infections in nearby leaves, but this is not necessarily a one-way exchange. **The FA hypothesis proposes instead that these two great reservoirs of microbial diversity in a forest are in continuous and cyclical flux.** The scale of these processes should not be underestimated: in one Columbian cloud forest system, for example, 4.6 metric tons of leaves fall on a single hectare each year from the canopy, covering the forest floor several times over (Veneklaas, 1991). As all leaves examined so far have been shown to be largely saturated with FFE, this leaf fall represents countless potential transmissions of fungi to substrates on the ground (Nelson et al., 2019).

The process described by the FA hypothesis is not limited to wet tropical forests. The hypothesis was originally formulated to describe dispersal of FFE from conifer needles in the North American Pacific Northwest region (Carroll, 1999), and has been observed as possibly occurring in North American northeastern forests (Tanney et al., 2018). Given the potential common-ness of the viaphytic cycle in forests, the importance of these fungi to the health of their host-trees (and therefore forest systems), and the role of these fungi in decomposing wood and leaf litter in forests, we argue that this ecological cycle has been both under-studied and under-appreciated.

To provide an in-depth theoretical explanation and exploration of the FA hypothesis as currently understood, we employed an Agent-Based Modeling (ABM) approach (Grimm et al., 2005). On a model landscape intended to simulate the site of research of a previous empirical study (Thomas and Vandegrift et al., 2016), we modeled a set of competition "experiments" between viaphytic fungi versus non-viaphytic fungi. We explored the ecological conditions in which viaphytism may endow significant advantage to viaphytic fungi in competition with aggressively dispersed non-viaphytic fungi. Additionally, given the current rapid rates of environmental

change and deforestation throughout the tropics, we examined the resiliency of viaphytes when challenged by deforestation or increased loss of endophyte phase from the canopy.

Methods

Ecological system: fungi in the cloud forest

This model was inspired by an empirical study conducted by the authors in a primary cloud forest site at Reserva Los Cedros (www.reservaloscedros.org), in the northern Andes of Ecuador at 1300 m elevation (Thomas et al., 2016). Rainfall at the site can exceed 3 meters per year, and can occur daily throughout the year, often even during the dry season months of June through November. Forest structure is complex, with downed woody debris of all sizes, with an extremely high woody plant diversity of ~290 tree species per hectare (Peck et al., 2011), and canopy gaps of varying sizes. Fungi, particularly fungi in the family Xylariaceae (Ascomycota, Xylariales), are often observed at this site both (1) as highly visible decomposer fungi, sporulating on woody debris, and (2) as microscopic endophytes within tree leaves overhead (Thomas et al., 2016), making it an obvious location for exploring the FA hypothesis.

Software and computational resources

Model and scripts for simulations were coded in Python3 (www.python.org), using the *Mesa* agent-based model framework (Masad and Kazil, 2015). Additional core packages in the SciPy ecosystem were used to summarize and visualize results: *Matplotlib* (Hunter, 2007), *pandas* (McKinney, 2010), and *NumPy* (van der Walt et al., 2011). Simulations were carried out on the computing cluster in the center for Research Advanced Computing Services at the University of Oregon (https://hpcf.uoregon.edu/).

Documentation:

Much of technical detail of models are available in three online Jupyter notebooks. Online notebooks can be viewed by anyone using the links provided below, and are usually higher in quality than the supplementary pdfs, which are file conversions of the original jupyter notebooks. All code for processes and agents, and original jupyter notebook files used in the viewing links above are also available for download in public GitHub repository for this analysis (https://github.com/danchurch/FA_ABM).

Additional figures, additional results, and code for model runs from **parameter sweeps** of the various scenarios explored below are available as a pdf (S1), or as an online notebook,

viewable at <https://nbviewer.jupyter.org/github/danchurch/FA_ABM/blob/master/parameter_sweeps.ipynb>. Hereafter this is referred to as “notebook 1”.

Additional figures, discussion of calibration, and code for model runs of **dispersal parameters** in the models are available as a pdf (S2), or as an online notebook, viewable at: <https://nbviewer.jupyter.org/github/danchurch/FA_ABM/blob/master/calibratingDispersal.ipynb>. Hereafter this is referred to as “notebook 2”.

Additional figures, and code for calibration of **tree number and placement on the landscape**, including deforestation, are available as a pdf (S3), or as an online notebook, viewable at: <https://nbviewer.jupyter.org/github/danchurch/FA_ABM/blob/master/calibratingForest.ipynb>. Hereafter this is referred to as “notebook 3”.

Here we provide an informal summary description of our model and highlights of results of scenarios explored using the model. A formal Model ODD protocol description with further explanations of model concepts and assumptions is available in supplementary materials (S4).

Model overview

The model landscape is intended to simulate a hectare of Andean cloud forest, after a recent storm or other gap-opening disturbance that has brought down more-than-usual woody debris. A disturbance of this small scale is reflective of actual canopy dynamics in many tropical forests (Espírito-Santo et al., 2014; Hunter et al., 2015; Nicholas V. L. Brokaw, 1982), and also represents the closest-possible “fresh start” scenario as can be imagined in the ancient ecosystem on which the model is based. Such an event may knock down fresh woody debris with lower fungal loads from the canopy to the forest floor, and blow new fungal spores into the site, or agitate the existing spore bank from the soil and debris. Additionally, leaf loss from the storm event and the new exposure due to the new gaps in the canopy at the site may stimulate the production of new, relatively sterile leaves at the site, ready for endophyte colonization.

The model is populated by three types of agents: fungi, trees, and downed wood.

Fungi

Fungal agents are the primary agents of the model. They exist only on substrate (wood agents), and are capable of degrading wood biomass, and sporulating. They can be viaphytic or non-viaphytic (defined above). Some number of fungal agents are present on the landscape at the beginning of the model run, set by user. In all model runs presented here, one fungal agent is present at the beginning of the model run of either viaphyte, non-viaphyte, or one of each, depending on the scenario.

Fungal agents are initiated when a sporulation or leaf fall event successfully inoculates wood on the forest floor. Fungal agents then decompose the wood agent, storing energy with each step as long as the wood agent continues to exist. When they have sufficient energy, fungal agents sporulate. When a wood agent is no longer present, the fungal agent remains, respiring available energy until it dies, or until another wood agent falls onto the site.

Similar to inoculations of wood agents by fungi, tree agents can also be inoculated during a sporulation event. Once a tree agent is successfully inoculated, its infection status changes from negative to positive. Endophytic infections are not directly considered fungal agents, instead these infections are tracked in the positive or negative infection status of a tree agent.

Fungi reproduce and disperse through sporulation events and — if viaphytic — leaf fall events. Neither spores nor leaves are modeled as *agents*; their behavior is modeled instead by the *processes* of sporulation and leaf fall. When a fungal agent reaches sufficient energy to sporulate, all wood agents on the landscape have a chance of being inoculated. If the sporulating fungus is viaphytic, all tree agents on the landscape with a negative infection status are also subject to inoculation. The chance of inoculation is a random variable, defined as:

Eq. 1 $$p(inoculation) = \left(\frac{Ec}{Ei}\right) e^{(-x/d)}$$

Where *x* is distance in meters between sporulating fungal agent and a given wood agent, E_c is currently energy/biomass of the wood agent, E_i is the initial biomass — thus making E_c/E_i a handicap to further inoculation of wood based on the state of decomposition of the wood — and *d* is the coefficient of dispersal that describes how aggressively dispersed a fungus is.

If the sporulating fungal agent is a well-dispersed fungus, it will have a large *d* value, indicating that has a higher maximum radius of dispersal and a higher volume of spores (see Figure 2). The same process occurs for all tree agents on the landscape, if the sporulating fungal agent is viaphytic, without any decomposition handicap. If inoculation of a tree by spores is successful, the tree is infected by the endophyte and will disperse the fungus again to the forest floor via its leaves.

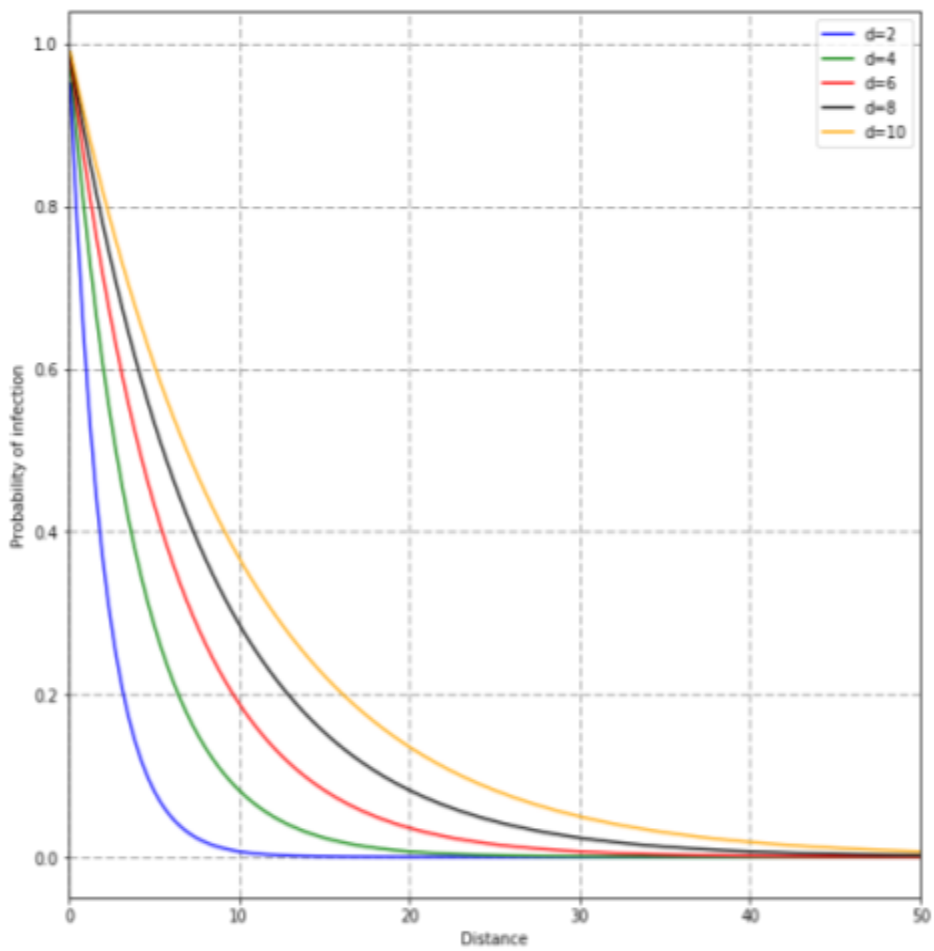


Figure 2. Distribution of probability for several different levels of dispersal ability according to our dispersal equation (Eq1). Distance units are meters. X-axis denotes the distance between a sporulating fungal agent or leaf-releasing tree agent, and a possible substrate. Spores of non-viaphytic fungi were calibrated from available literature and model runs to values from *d*=8 to *d*=10. Falling leaves were calibrated to *d*=4.

Trees

Tree agents are located randomly throughout the landscape, according to a Thomas clustering process (Thomas, 1949), at a density similar to that found in global estimate of wet tropical forests (Crowther et al., 2015). Tree agents persist throughout a model run, unless deforested. Tree agents can be subject to deforestation, in a generally random (thinning) or random clustered (fragmented) model. See S___ or jupyter notebook 3 on tree agent distributions and deforestation for more detail.

If a tree is successfully inoculated by fungal spores, they gain an endophyte infection. Each turn, an infected tree can stochastically lose its endophyte infection, at a probability set by the user. Tree agents shed leaves at regular intervals, capable of causing initiating viaphyte fungal

agents if a tree agent has a positive infection status. Leaves are not agents; instead, leaf fall events are treated similarly to sporulations by fungal agents: they act as probabilistic dispersal events for transfer of endophytes to wood, using the same equation described above (equation 1). However, the dispersal coefficient *d* of leaves is much lower, to reflect the lower rate of leaves dispersed as compared to spores, and the lower maximum distance that leaves reach from the tree as compared to the farthest traveling spores. Additionally, leaf fall occurs every time step, unlike fungal sporulation. For more details about the calibration of leaf-based dispersal of fungi (viaphytism), see the jupyter notebook on dispersal calibration (S___ or jupyter notebook 2).

Wood

New wood agents appear on the landscape at every time step at a user-defined rate, with a random initial biomass. In addition, an initial population of wood agents is deposited at the beginning of every model run, at approximately twice the amount of wood brought in a normal season (three months), to simulate a recent decent disturbance. Wood agents have a single attribute, biomass. Biomass remains stable until wood agents are successfully inoculated with fungal agents either from a sporulation event or leaf fall event. Multiple fungal agents can inhabit a wood agent. Following inoculation, biomass is reduced by decomposition until zero, at a rate of 1 unit of biomass per fungal agent inhabiting the wood agent, until all biomass is respired away, at which point the wood agent is removed.

Scenarios

All scenarios consisted of 100 model runs, where each run consisted of 50 timesteps, except for deforestation scenarios, in which each model run consisted of 100 timesteps. We created scenarios with the model intended to explore the following questions:

1) When is viaphytism a beneficial dispersal strategy for fungi?

We hypothesize that the ability to disperse through leaves alleviates some of the costs associated with sporulation. Thus a fungus that has a viaphytic life stage does not have to “pay” for aggressive dispersal abilities; instead, they can disperse less aggressively through spores because their reproduction and dispersal is augmented by the additional dispersal strategy of using leaves as fungal vectors. To quantify how beneficial viaphytism may be for a fungal species, we compared the minimum threshold of spore dispersal ability necessary to persist on the landscape indefinitely for both non-viaphytic ($\wedge d_{nv}$) and viaphytic ($\wedge d_{v}$) fungal agents. We propose that if d_v is significantly smaller than d_{nv}, viaphytism may well provide dispersal benefits. In this scenario, viaphytic and non-viaphytic fungi were not competed directly against each other, but rather tested in isolation to determine their ability to survive in the default model conditions.

To find the minimal level of dispersal required for a non-viaphytic fungus to survive in the model landscape, we conducted a sensitivity analysis of the effect of spore dispersal abilities ("*d*", equation 1) on the persistence of a non-viaphytic fungi in the default landscape. Resulting values for dispersal ability also were checked to conform to existing empirical data on fungal dispersal (Galante et al., 2011; Norros et al., 2012; Peay et al., 2012; Roper et al., 2010). At this stage we also tested the sensitivity of this "typical" non-viaphytic fungus to variance of initial reserves of woody debris on the landscape.

For a viaphytic fungus, leaf fall was calibrated according to data taken from the site (Thomas et al., 2016) and according to Ferrari et al. (1996). This leaf fall rate was held constant and assumed to be the rate at which viaphytic fungi could augment dispersal via leaves. Spore dispersal for a viaphytic fungus was then simulated in a range of dispersal abilities as with the non-viaphytic fungus.

Refer to notebook 1 (S ___ or jupyter notebook 1) for more details of the simulations to determine minimum threshold of spore dispersal ability necessary to persist on the landscape indefinitely for both non-viaphytic ($\wedge d_{nv}$) and viaphytic ($\wedge d_{v}$) fungal agents. Refer to notebook 2 (S___ or jupyter notebook 2) for comparisons of results to existing literature values.

2) Is viaphytism a competitive dispersal strategy for fungi?

Viaphytic fungi are in competition with other fungal species for woody substrates. In the case of the Xylariaceous fungi that were the inspiration for this model, their competitors are the numerous white-rot basidiomycetous fungi that are rarely recovered as endophytes (Lodge, 1997; Lodge and Cantrell, 1995). We hypothesize that viaphytism may be an important trait for endophytic fungi to disperse to woody substrates, especially in the presence of intense competition from other fungi. In other words, we hypothesize that viaphytism may represent an evolutionary alternative to increasing spore dispersal ability.

A "typical" non-viaphytic fungus that could persist on our model landscape was defined above, in scenario 1. We further defined an "aggressive" non-viaphytic fungus as one that greatly exceeded the level of dispersal ability of this fungus. Thus, an aggressive non-viaphytic fungus was one with a dispersal coefficient *d* set significantly above the threshold needed to persist on the model landscape alone without competition (see results). This "aggressive", non-viaphytic fungus was then the benchmark competition, against which we competed viaphytic fungi with varying levels of dispersal *d* (equation 1). The dispersal ability of viaphytic fungi were incremented in different model runs until both populations consistently coexisted in perpetuity in an equilibrium, neither causing the extinction of the other.

Refer to notebook 1 (S ___ or jupyter notebook 1) for more details of the simulations of competition between viaphytic and non-viaphytic fungal agents.

3) Can viaphytes be lost?

We examined two ways in which viaphytic populations might be lost on a landscape: stochastic loss, and deforestation.

In natural settings, loss of endophytic infections could occur as a result of normal leaf senescence stochastically eliminating a small endophyte infection, or as defoliation events due to herbivory or disease, or in numerous other ways. In the current era of rapid environmental change, disturbances to forests such as disease and herbivory are predicted to increase (Ayres and Lombardero, 2000; Dale et al., 2001; Dukes et al., 2009; Seidl et al., 2017; Weed et al., 2013). Rather than anticipate each of all possible local disturbances which may cause host trees to shed FFE populations, local loss of endophyte infections was modeled as a stochastic process. During every time step, each endophyte-positive tree is at risk of losing its endophyte infection, at a user-set probability of loss. To test sensitivity of a fungal population to stochastic loss, we varied the probability of loss of endophyte infection from zero to extremely-probable (90% chance loss of endophytes per tree per time-step).

Deforestation was modeled in two ways, both intended to represent patterns of deforestation occurring in the region of our empirical study: (1) thinning, where trees are removed singly and throughout the landscape at an even rate, or (2) fragmentation, where contiguous blocks of forest are removed. The first attempts to emulate the results of selective logging, often in the form of "high-grading." This is the most common form of deforestation at the site of research that inspired the model, and occurs continuously at unmeasured rates. The second is intended to model land-use conversions such as homesteading or conversion to pasture (Kettle and Koh, 2014), a generally common type of deforestation throughout the neotropics. Sensitivity of endophyte infections was detected by introducing deforestation into the landscape at the middle time point of 100-timestep model runs, at varying proportions of trees removed, under both styles of deforestation.

Refer to notebook 1 (S ___ or jupyter notebook 1) for more details of the simulations of stochastic loss and deforestation and their effects on viaphytic fungi.

Results

Viaphytism as beneficial dispersal strategy

Viaphytism is a beneficial dispersal strategy as modeled here. A non-viaphyte fungus with a dispersal coefficient of d=8 was found to fit expectations from empirical data and to persist reliably on model landscapes (S ___ or jupyter notebook 1). At this dispersal ability and higher, the fungus usually consumed the default amount of original woody debris on the landscape, then declined in population to match the rate of deposition of new substrates on the landscape.

At lower than *d*=8 dispersal coefficient, populations often went to zero. These *d*<8 populations usually also had not finished decomposing existing wood deposits on the landscape by the end of the model run.

Without competition, fungi with an augmented *d*=10 dispersal ability only very rarely went extinct on the landscape. At this dispersal ability of *d*=10, non-viaphtyic fungus agents were able to fully colonize initial deposits of wood on the landscape, then maintain a steady population where all new woody debris was inoculated as it appeared on the landscape (Figure 3). We therefore considered this an “aggressive” non-viaphyte fungus, to be used in the following competition simulations with viaphytes.

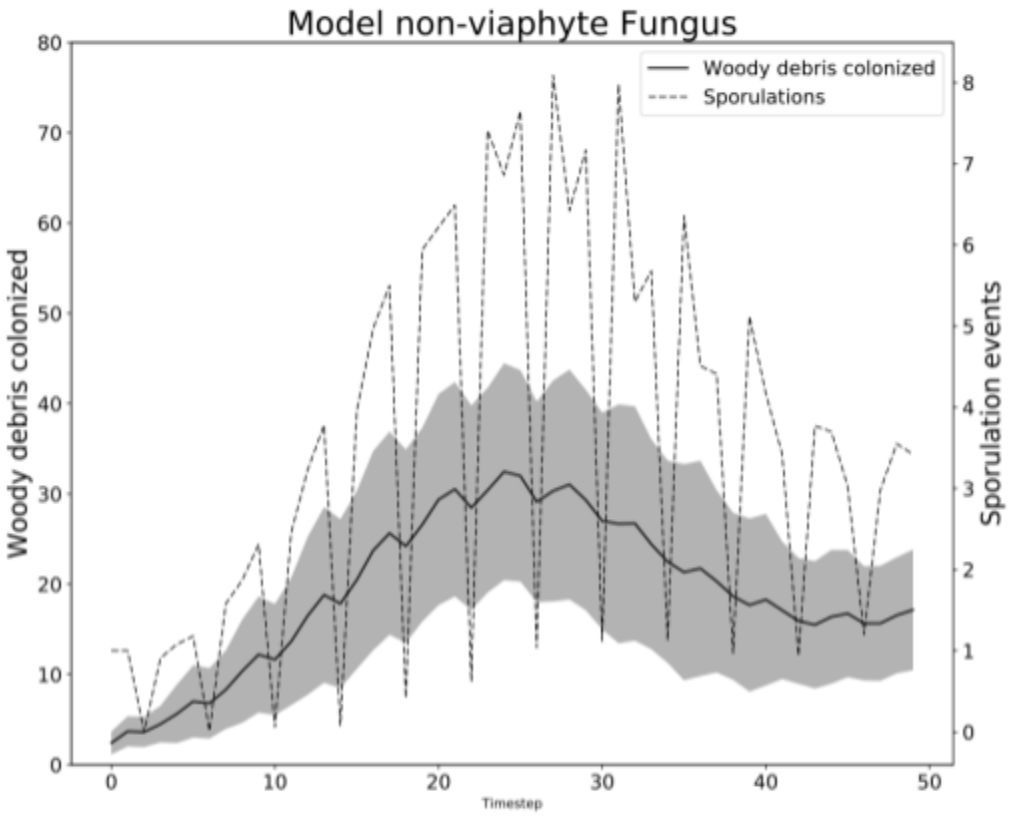


Figure 3. Behavior of an “aggressive” non-viaphytic fungal agents on the default model landscape. Error lines are one standard deviation from the mean. [For a higher resolution image click here](#).

Varying the amount of initial woody debris on the landscape had little effect on long-term behavior of the above “aggressive” non-viaphyte fungus, as fungi typically consumed original

woody debris in approximately the same about of time, though higher peak abundances of fungi were temporarily reached during the decomposition of this wood (Figure 4).

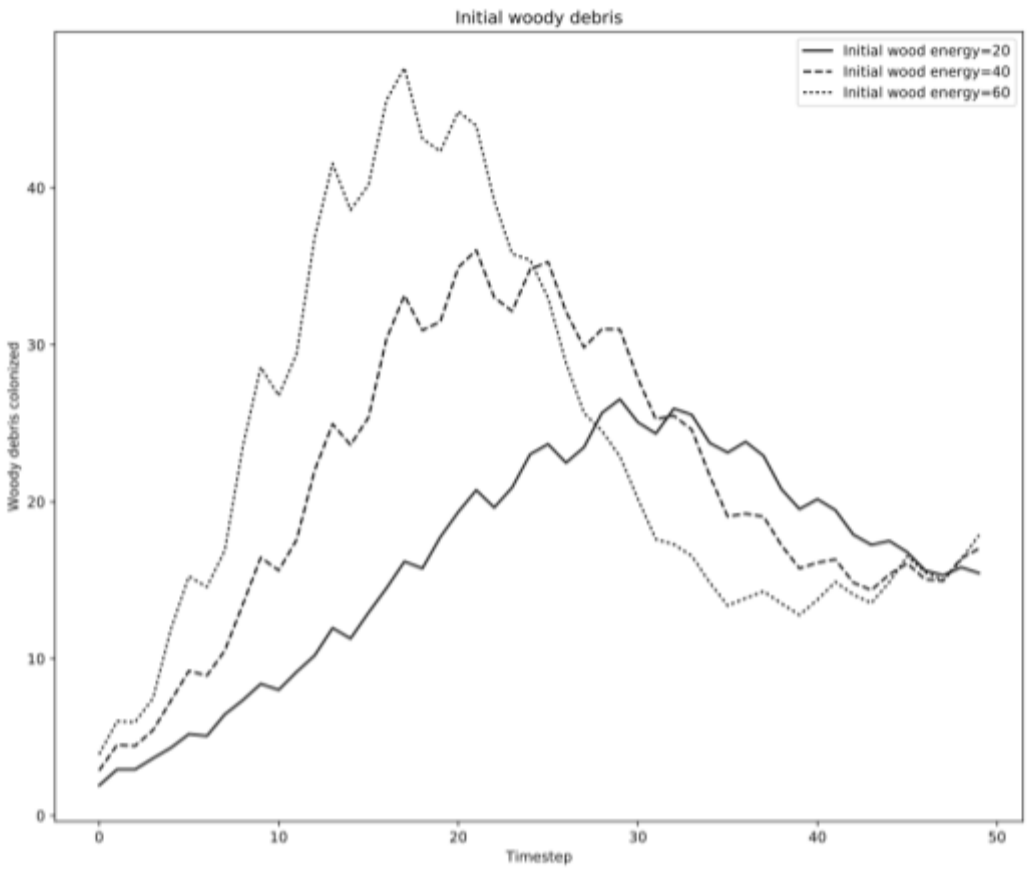


Figure 4. Response by fungi to varying amounts of initial substrate on the landscape. Within the range of values tested, varying the amount of initial amount of woody debris on the landscape changed only the early peak abundance of fungi on the landscape. Following this early peak, fungal populations equilibrate around the same population levels, that is largely governed by the amount of new woody debris deposited on the landscape at each timestep. For a higher resolution image click here.

A viaphytic fungus with a dispersal coefficient of *d*=2 persisted successfully very often on the model landscape, but did not entirely consume the reserves of woody debris on the landscape. (S __, jupyter notebook 1). Viaphytic fungi survived in nearly all model runs and consumed original reserves of woody debris on the landscape before equilibrating to the rate of new wood deposition at *d*=3, just over a third of that necessary for non-viaphytic fungi to achieve the same equilibrium.

Viaphytism as a competitive dispersal strategy

Viaphytic fungi with much lower spore-dispersal abilities compete successfully against aggressive non-viaphytic fungus (Figure 5). At *d*=2, a viaphytic fungus can very often coexist on the landscape with the aggressive non-viaphytic fungus. Below this dispersal level (*d*<2) for viaphytes, non-viaphyte fungus agents clearly outcompete the viaphytes, keeping infected trees and inoculated substrates by viaphytes to near zero levels. A viaphytic fungus with a dispersal coefficient of *d*=3 successfully and consistently outcompetes the non-viaphytic fungus with dispersal coefficient of *d*=10.

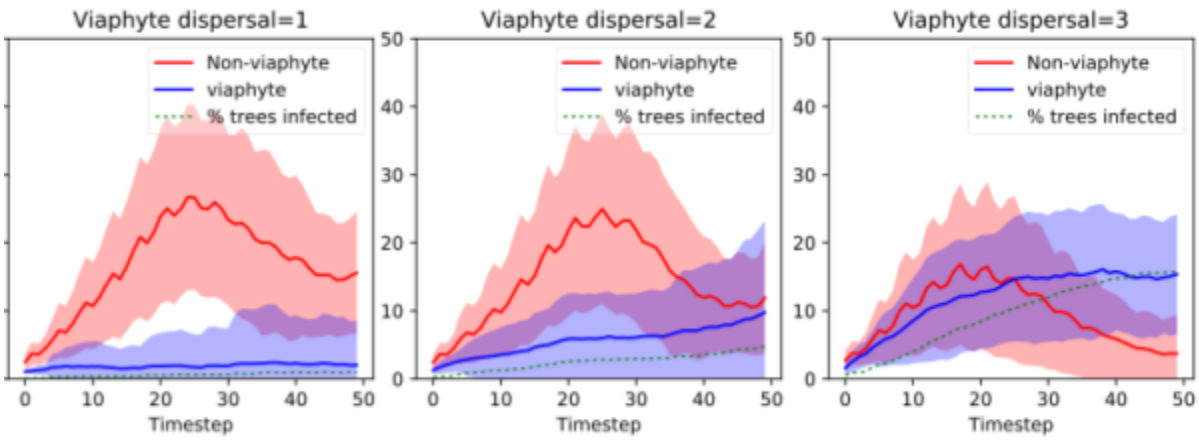


Figure 5. Competition of viaphytic fungi with various dispersal abilities against a model non-viaphytic fungus. For a higher resolution image click here. Error lines are one standard deviation from the mean.

Loss of viaphytes from the landscape

Stochastic loss. All competitive benefits conferred by the endophytic phase to viaphytes as found in scenario 2 are dependent upon persistence of endophytes in the canopy. Under otherwise default settings, a probability of endophyte infection loss greater than 5% by tree agents caused loss of all competitive advantage by viaphytes against non-viaphyte fungal agents (Figure 6).

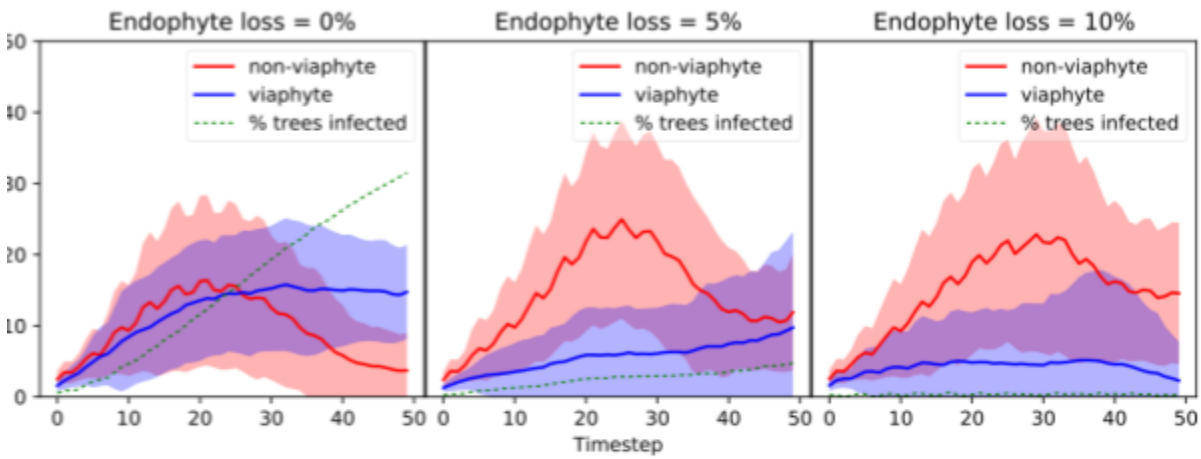
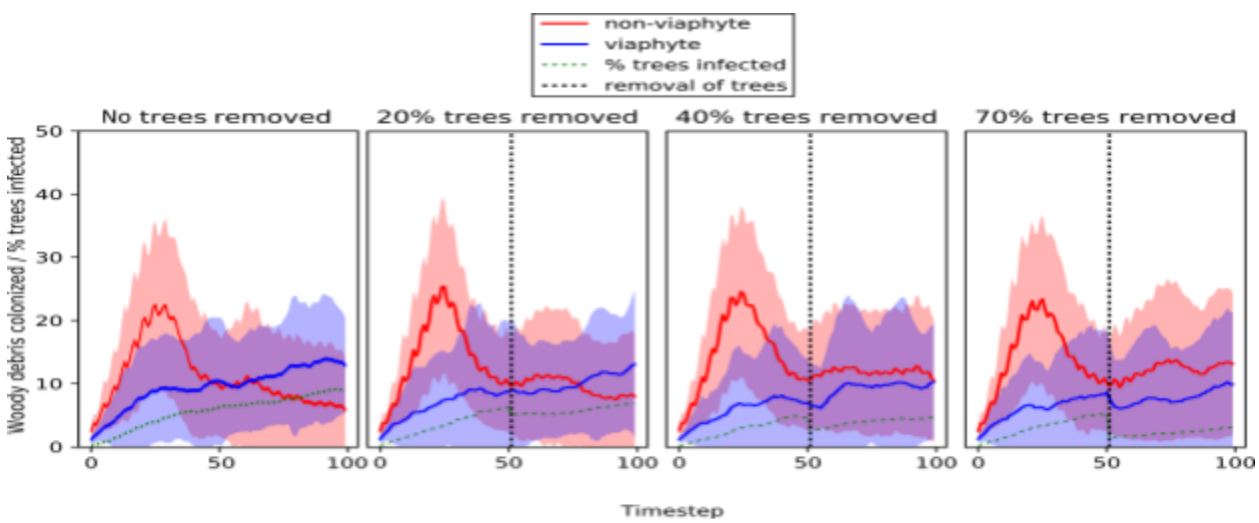


Figure 6. Effect of stochastic endophyte loss on viaphyte success. If trees have a higher than 5% chance of loss For a higher resolution image click here. Error lines are one standard deviation from the mean.

Deforestation. Consequences of removing trees depends on the intensity, timing, and spatial arrangements of the removal of trees. Without any cutting, model viaphytes show an increasingly stable presence on the landscape, as the reservoir of fungus in the canopy incrementally increases (Figure 7). Drastic thins (>70% of trees) reduce this stability, and hobble viaphytic fungi badly in competition with non-viaphytic on the landscape. Lighter thins (10-30%) appear to affect established populations of endophytes minimally. Fragmentation of forest showed similar effect as thinning simulations, on the spatial scale modeled here (S ___, jupyter notebook 3).



Effects of thinning trees from the landscape on viaphytic fungi, as they compete with non-viaphytic fungi. Trees were removed in a single event, at the halfway timestep of the model runs. For a higher resolution image click here. More deforestation scenarios, including continuous thinning and small-scale fragmentation of forest, are detailed in S1 or jupyter notebook 1 . Error lines are one standard deviation from the mean.

Discussion

The model presented here predicts that some fungi may benefit from viaphytism, if endophytic infections can persist in the canopy for sufficient periods of time. As modeled here, the utilization of leaves as dispersal vectors and refugia in times of scarcity can allow a viaphytic fungus to persist and compete on a landscape of other, more aggressive non-viaphytic fungi.

This advantage is due, in large part, to some weaknesses inherent in reproduction by spores as a sole method of dispersal. Fungi without a viaphytic stage must overcome gaps in woody debris over distance and time simply by increasing dispersal distance (or other strategies not examined in this model). This creates a positive feedback in colonization and consumption of substrates that is highly spatially and temporally autocorrelated: since most spores must fall locally in order for some percent to reach farther distances, once established, a fungus typically rapidly colonizes and consumes all local substrate. This “boom and bust” cycle of exponential growth and collapse is risky. If new substrate is not quickly found within dispersal limits, local extinction is very possible. In addition, offspring of a sporulating fungus are modeled as vegetatively incompatible with parents, and are, in one sense, competitors of their own kin.

Viaphytic fungi, alternatively, may take refuge in — and augment dispersal with — an endophyte phase. Neither leaves nor spores of these endophytes are modeled as very widely dispersed: viaphytic fungi rely instead on an incremental but reliable increase over time on the landscape. This effect would surely be increased if wood deposition were spatially linked to the presence of canopy trees; as written the model allows even, random dispersal of wood across the landscape, regardless of the presence of canopy.

Though viaphytism as modeled here is a potentially beneficial strategy, its benefits may only exist under certain conditions. In the model, the potential dispersal benefits of viaphytism require sufficient time for endophytic infections to persist in the canopy. If trees do not maintain stable infections by endophytes in their leaves, viaphytism fails as a competitive strategy of dispersal. This is shown by the high sensitivity of viaphyte populations to greater than a 5% probability of loss from host tree per time step. It might be expected, therefore, that viaphytism is less common in seasonally deciduous forest systems, where yearly leaf fall presumably resets most endophyte populations to zero. In largely deciduous forests, we may instead more commonly see the yearly cycles of reinfection via spores from directly fallen leaves, as predicted by Unterseher et al (Unterseher et al., 2013). This sensitivity also suggests that the increasing disturbance regime predicted in many forests with climate change may impact fungi that rely on a viaphytic strategy for dispersal.

Viaphytism also requires sufficient numbers of trees on the landscape to succeed: if significant numbers of canopy trees are removed from the landscape, a viaphytic life-stage ceases to be useful for overcoming dispersal limitation. Thus the FA hypothesis also points to more complex

implications of deforestation. In such a system as we have modeled here, when a disturbance of the microbial community occurs on the forest floor (such as surface fire) or in the canopy (such as windthrow), recovery of microbial diversity and ecosystem services lost from one habitat may partially depend on the reserves of the other. Disrupting this cycling of microbes by deforestation in a modern, mechanized manner through tree-cutting may have unforeseen consequences to the secondary forest microbiome. Understanding modern deforestation in this way may help explain long-term differences observed in mycobiomes among different types of secondary forests and with nearby primary forests (Chaverri and Vilchez, 2006; Lodge, 1997). Complete removal of both reservoirs of fungal diversity (removal of forest canopies and resulting disturbance/exposure of soil) may mean greater loss of species, and slower regeneration of fungal diversity than smaller scale forms of timber harvesting and habitat conversion like slash-and-burn agriculture.

The work described herein was produced to be a detailed theoretical explanation of the Foraging Ascomycete hypothesis. While this study defends the theoretical potential for this ecological process, further empirical exploration is now needed to gauge the actual importance of this process to forest ecosystem functioning and health. Such work is possible with laborious and invaluable studies such as those by Tanney et al (Tanney et al., 2018, 2016), which involve both classical, culture-based surveys of endophytes and intensive searches for cryptic macrofungi of the forest floor in the vicinity of the endophyte study. Further experimental exploration of the transmission of fungi from an endophytic state to a wood-decomposing state, such as done by Nelson (2019), is also needed.

Author Contributions

D. Thomas, R. Vandegrift and B. A. Roy made wrote the text. D. Thomas wrote python code and ran simulations. B. A. Roy provided institutional support.

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Works cited

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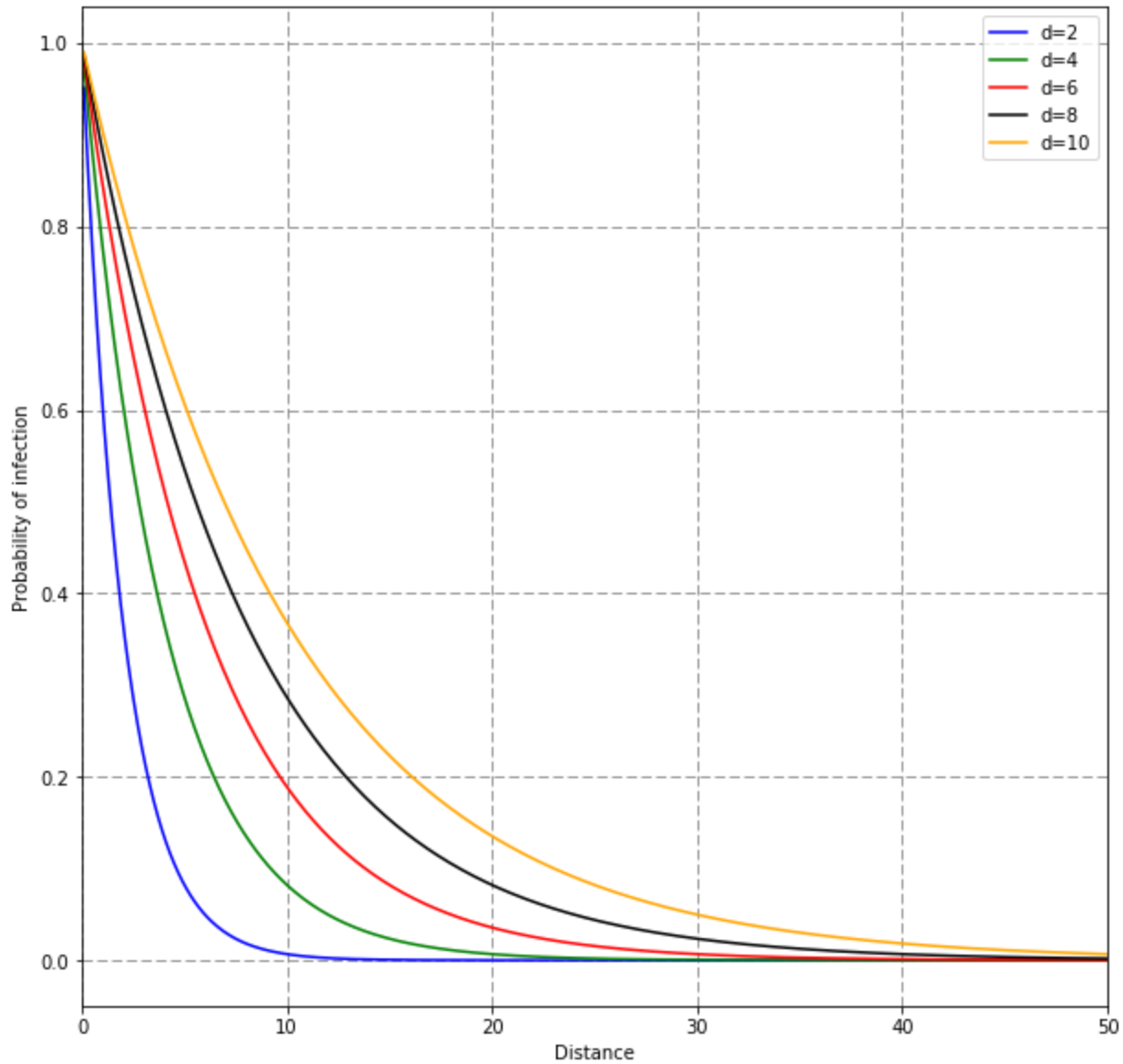
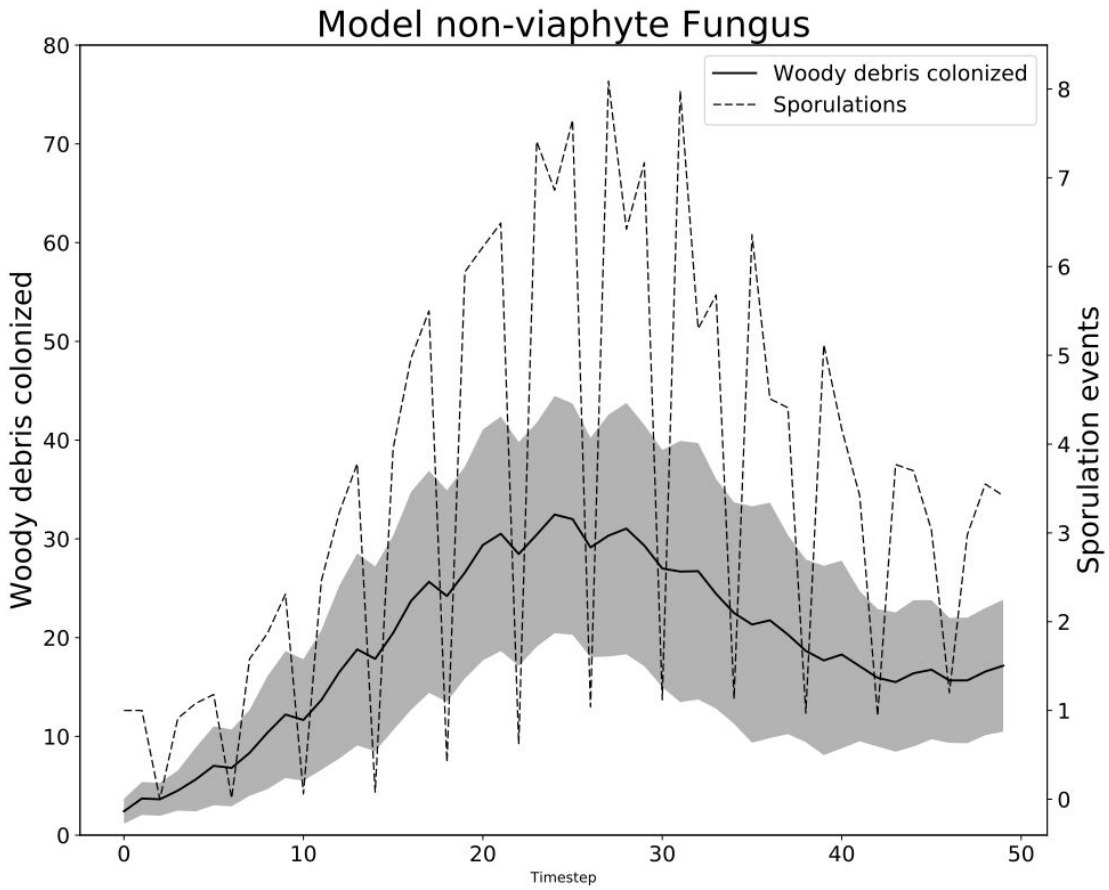
Figures

Figure 2



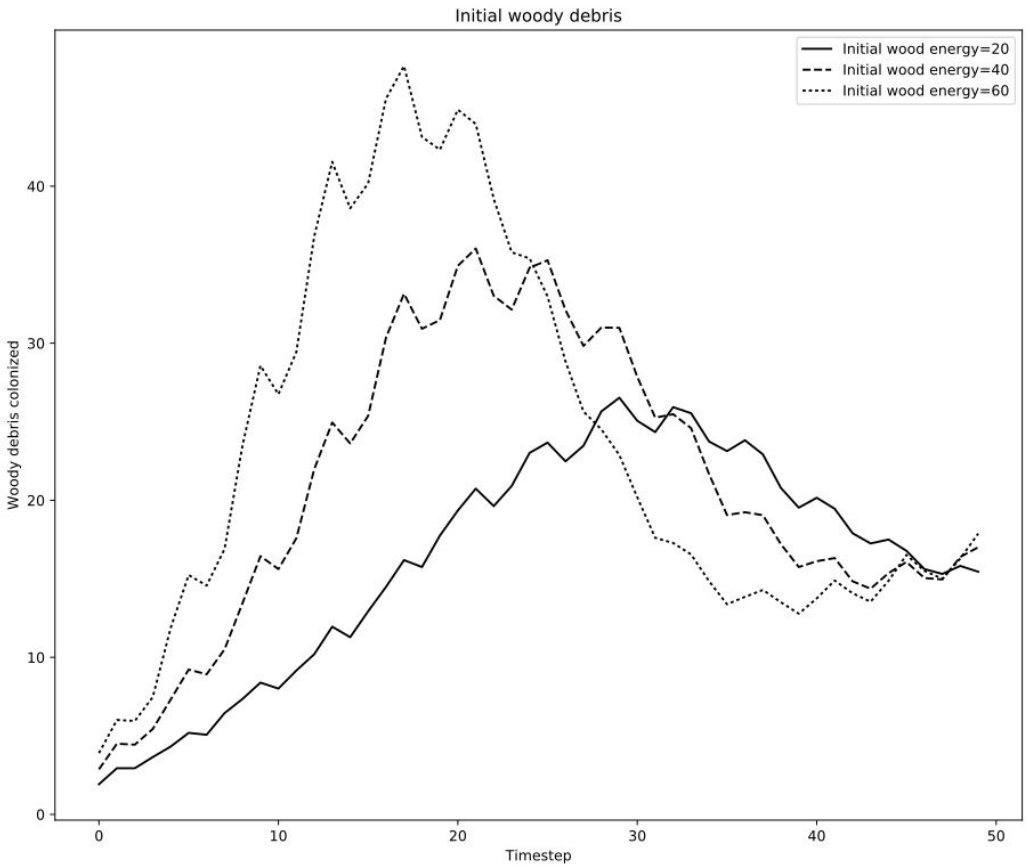
Distribution of probability for several different levels of dispersal ability according to our dispersal equation (Eq1). Distance units are meters. X-axis denotes the distance between a sporulating fungal agent or leaf-releasing tree agent, and a possible substrate. Spores of non-viaphytic fungi were calibrated from available literature and model runs to values from *d*=8 to *d*=10. Falling leaves were calibrated to *d*=4.

Figure 3



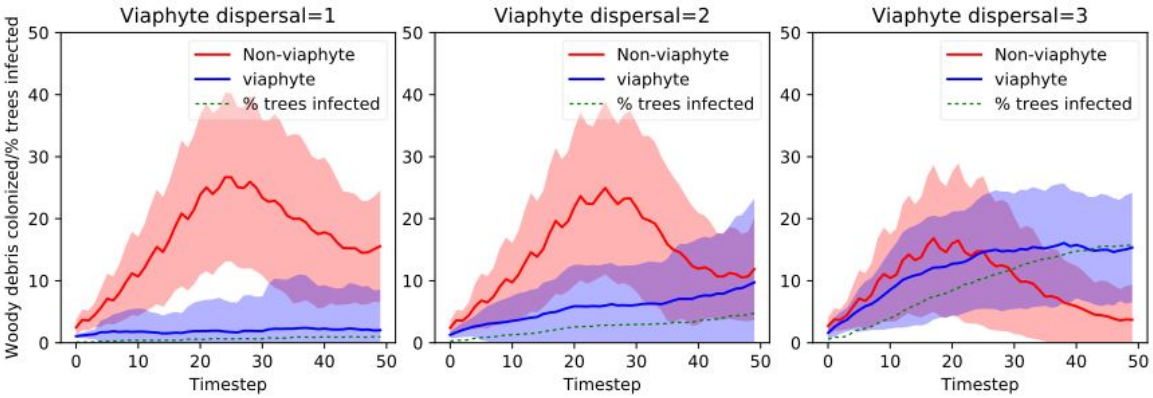
Behavior of an “aggressive” non-viaphytic fungal agents on the default model landscape. Error lines are one standard deviation from the mean. For a higher resolution image click here.

Figure 4



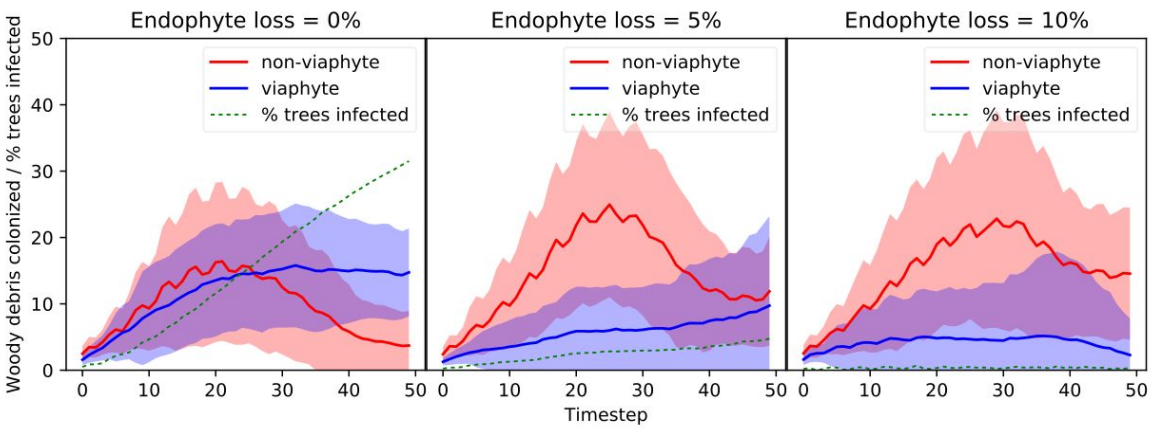
Response by fungi to varying amounts of initial substrate on the landscape. Within the range of values tested, varying the amount of initial amount of woody debris on the landscape changed only the early peak abundance of fungi on the landscape. Following this early peak, fungal populations equilibrate around the same population levels, that is largely governed by the amount of new woody debris deposited on the landscape at each timestep. For a higher resolution image click here.

Figure 5



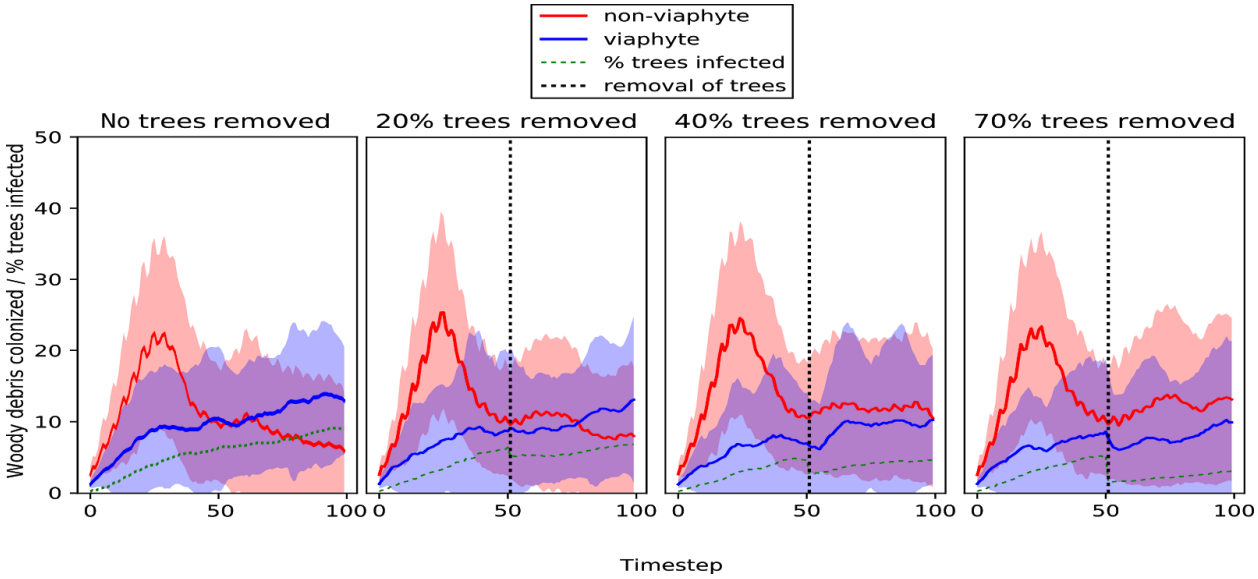
Competition of viaphytic fungi with various dispersal abilities against a model non-viaphytic fungus. [For a higher resolution image click here](). Error lines are one standard deviation from the mean.

Figure 6



Effect of stochastic endophyte loss on viaphyte success. If trees have a higher than 5% chance of loss [For a higher resolution image click here](). Error lines are one standard deviation from the mean.

Figure 7



Effects of thinning trees from the landscape on viaphytic fungi, as they compete with non-viaphytic fungi. Trees were removed in a single event, at the halfway timestep of the model runs. For a higher resolution image click here. More deforestation scenarios, including continuous thinning and small-scale fragmentation of forest, are detailed in S1 or jupyter notebook 1 . Error lines are one standard deviation from the mean.