An agent-based model of the Foraging Ascomycete Hypothesis.

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Abstract

Plant-fungal interactions are of paramount importance. Building useful ecological models of plant-fungal interactions is challenging, due to the complexity of habitat, varying definitions of biological basic units of interest, various spatial scales of dispersal, and non-linear, emergent properties of plant-fungal systems. Here we show that the bottom-up approach of agent-based models is useful for exploring the ecology of fungi. We constructed an agent-based model of the Foraging Ascomycete hypothesis, which proposes that some fungi maintain an endophytic life stage to enhance dispersal and bridge gaps in substrate in space and time. We characterized the general conditions in which dispersal through leaves may be worth the metabolic and fitness costs of endophytism. We also modeled possible effects of deforestation on leaf endophytes, highlighting how agent-based models can be useful for asking questions about changing ecosystems.

Introduction

Plant-fungal symbioses are ancient (Stukenbrock 2008, Redecker 2000), ubiquitous, and important (Vandenkoornhuyse 2015). All large organisms are observed to host complex microbiomes (Rosenburg 2010), and plants are no exception, with both epiphytic and endophytic fungi and bacteria present on and within all tissues (Rodriguez 2009, Rosenbleuth 2006). These symbionts are known to be extremely diverse (Arnold 2000, Arnold 2007) and some are important to plant health (Mejia 2008, Arnold 2003a, Porras-Alfaro 2011, Rodriguez 2009).

Extensive literature has explored benefits conferred to plant hosts by endophytic fungi and bacteria. However, benefits conferred to the endophytic microbes themselves are not as well explored. In particular, the reduced reproductive activity, and costly array of unique metabolites produced by fungal endophytes to maintain the endophytic phase (Carroll 1983, Kusari 2012) make the endophytic lifestyle seem like an uncertain investment, from the fungal perspective.

Nevertheless, diverse fungi are observed that can both decompose wood or litter, and exist as an endophyte in a different, living host (Lodge 1997), suggesting there are benefits to the lifestyle.

Carroll (1999) proposed that some endophyte-competent fungi may utilize an endophytic phase to increase dispersal, a concept known as the Foraging Ascomycete hypothesis (Fig. 1). Thomas and Vandegrift et al. (2015) expanded this concept, proposing that some endophytic fungi utilize the endophytic phase to bridge spatial and temporal gaps in substrates and suitable environmental conditions. We use the term viaphytic, recently proposed by Nelson (2016), to describe endophytic fungi that are observed to transfer from endophytic infections to woody substrates. This term is distinct from "endophyte competence" (Hardoim 2008), which denotes the ability of a microorganism to endophytically infect a host, but does not inform the ability to disperse beyond this endophytic state.

Endophytes provide important services to forests, through their hosts. Some endophyte species have been shown to increase increase drought tolerance or even disease resistance, often in the form of local "adaptation" (Rodriguez 2009, Giaque 2013). Presumably, many more important plant symbionts remain to be discovered (Gazis 2012, Suryanarayanan 2009). Even if not directly contributing to plant fitness, the community at large of plant-associated, commensal microbes may be important to preventing disease (Herre 2007). Microbial partners to plants may become more important in the current context of climate-change associated stresses (Woodward 2012). Land use changes have been shown to induce changes in microbial population dynamics (Arnold 2003b, Rodrigues 2013). In the status quo of rapid change, models of effects of environmental change of plant-microbial communities are increasingly pertinent.

Attempts to model microbiome community assembly and dynamics are in their infancy (Nemergut 2013). The astounding diversity of microbiomes, the complexity of real-world environmental systems, and the particular difficulties of quantifying fungal individuals, all appear to have stunted the development of robust and useful ecological models for fungi. Here an Agent-Based Model (ABM) approach (Grimm 2005) is employed to examine the Foraging Ascomycete hypothesis, as set of competition "experiments" among viaphytic and non-viaphytic fungi. Agent-based models take a "bottom-up" approach to understanding systems of many interacting actors, often including an explicitly spatial and stochastic behaviours that can prove difficult to realistically model with traditional population and community ecology mathematical models. For these reasons, ABMs may prove increasingly useful in future ecological modeling of fungi and other microbes.

The Foraging Ascomycete agent-based-model is presented here using the standard 'ODD' (Overview, Design concepts, and Details) protocol for describing agent-based models (Grimm 2006, Grimm 2010). Following this several sets of simulations are reviewed, which explore the theoretical benefits and limits of viaphytism as part of a fungal life-history strategy. In addition, several simple scenarios of deforestation are simulated, to highlight the potential for ABMs to

help in the understanding of microbial ecology in the context of current environmental challenges.

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 new substrates.

Methods

Methods I. ODD protocol

Purpose

The purpose of this model is explore the feasibility of Viaphytism (Carroll 1999, Thomas and Vandgrift 2015, Nelson 2017), as part of a fungal life history and dispersal strategy. An ABM approach is used here to explore the possible advantages to fitness and dispersal conferred by endophytism in fungi, by enacting competition-type scenarios among fungi with and without endophyte-competence.

Entities, state variables, and scales

Three agent types are placed on a spatial grid: trees, fungi, and woody debris.

Tree-agents represent individual adult trees with diameter-at-breast height greater than 10 cm. State variables of trees include position, leaf dispersal ability, state of endophyte infection (positive or not), and rate of endophyte loss. Leaf dispersal ability is a positive integer, where larger values represent longer-range and more plentiful leaf deposition (see submodels). State of endophyte infection denotes whether a tree carries the endophyte stage of an endophyte-competent fungus in its leaves. Successful infection from fungal spores changes a tree-agent's infection state to positive. Infections can be lost, and this loss is controlled by the endophyte-loss state variable, a number between 0 and 1, representing the probability that an infection is lost at each timestep.

A fungus agent represents a mycelium, resulting from a single reproductive event, either a spore- or leaf-vectored inoculation of wood. State variables of fungi include: position, spore dispersal ability, stored energy (biomass), and endophyte-competence. Like leaf dispersal in trees, spore dispersal ability is a positive integer, with larger values representing longer-range and more plentiful spore deposition across the landscape when sporulation occurs (see submodels). Energy is representative of biomass and potential energy gain from decomposition of woody debris. Sufficient energy stores allows for a sporulation event. Endophyte-competence denotes the ability of a fungus to reside as an endophyte in leaves after infection of leaves from fungal spores. In terms of the model, endophyte competences indicates whether a fungus can change the endophyte infection status of a tree during a sporulation event, and then disperse through leaves (viaphytism).

Woody debris agents represent the biomass deposited on the forest floor from the canopy. State variables of woody debris are position and stored energy (biomass). New wood are given a starting amount of energy, and this wood biomass is converted incrementally to fungal biomass if fungi are present in the cell.

Grid cells are not given attributes, except for the agents they hold, and their location, in the form of x and y coordinates. For all the scenarios examined here, the grid spans one square hectare (100m by 100m), wherein each grid cell represents one square meter. Grid is toroidal, and agents of all types can occur at all grids, though fungi will not persist for long periods without woody debris also present because of energy constraints.

Model-wide, environmental state variables include the rate of deposition of new woody debris, number and spatial clustering parameters. Trees can be removed at any time during a simulation to model effects of deforestation.

Process overview and scheduling

Time steps begin with the placement of new woody debris on the landscape. Following this, agents are chosen randomly to act, regardless of type. See figure 1 for a summary schematic of model processes for one time step.

Fungus agents begin with a test of their biomass (energy) reserves. If energy is high enough, sporulation occurs, possibly instantiating new fungus agents on woody debris. If the sporulating fungus is endophyte-competent, the spores can also change the endophyte infection status of trees on the landscape to positive. Sporulation results in a loss of energy for the parent fungus agent. Following this, fungus agents decompose the woody debris available in their grid cell, resulting in a gain of energy for each fungus agent present and a loss of stored energy in the woody debris. If the woody debris at a grid cell has died, fungus agents continue to respire, subtracting from their energy each turn until they have energy < 1, upon which they die.

Tree agents begin by dropping leaves. If a tree has a positive endophyte infection state, these leaves disperse to the landscape and can inoculate woody debris, instantiating a new fungus agent. Trees can also be removed from the landscape, which if requested occurs at the very beginning of a step, before deposition of woody debris.

Woody debris agents are placed at the beginning of each time step, in multiple random locations at the start of each step. The exact number of woody debris agents laid down each step is random, but the energy in each varies and the total energy represented by all the new woody debris will approximately equal the New Wood Energy state variable set by model user. Woody debris agents then test their biomass (energy) state variable: when energy < 1, the agent is removed from the landscape.

After all agents present on the landscape act, data collection takes place, and the time step is complete. Under model default settings, each time step is intended to represent approximately 3 months.

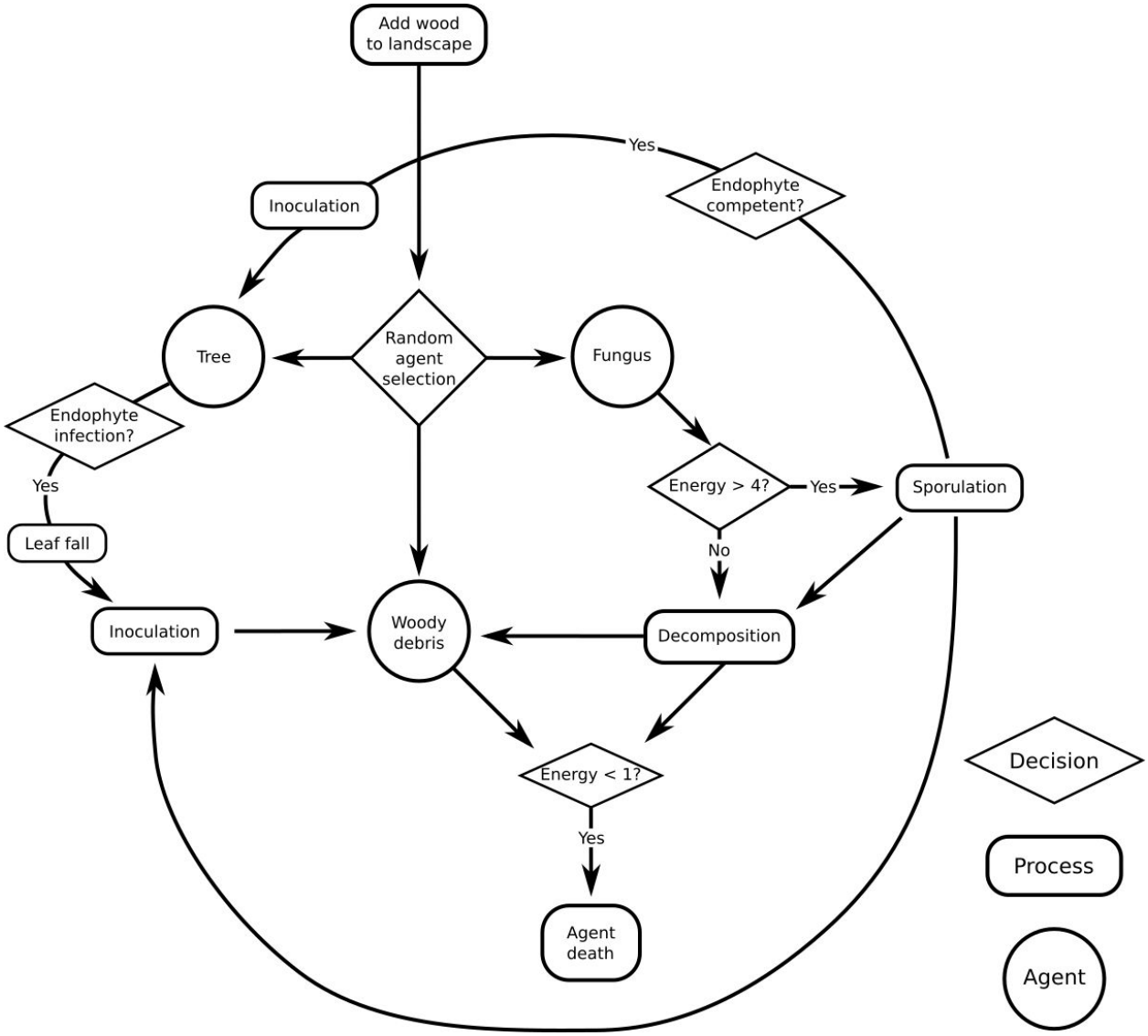

Figure 2. Schematic of processes possible during one timestep of the model. [For a higher resolution image click here](#).

Design concepts

Basic principles

This ABM is primarily a model of dispersal and competition among fungi. Patterns of spore dispersal at various scales are measured in Galante et al (2011), Norris et al. (2012), Peay et al (2012), and others. These studies show that the negative exponential family of functions can be parameterized to fit abundances and probabilities of spore-dispersal in nature. Leaf fall has also

been shown to be well described by exponential decay functions (Ferrari and Sugita 1996). These well-established patterns of dispersal serve as first principles in this model, guiding the behavior of both tree and fungus agents.

However, the purpose of the model is to explore the hypothesis that some fungi utilize an endophytic life stage to enhance dispersal and to persist on the landscape during times of scarcity, intense competition, or environmental stress (Carroll 1999, Thomas and Vandegrift 2015). This viaphyte life history strategy, where some fungi alternate endophytic and free-living phases, is a basic principle of the model, and the focus of the simulations presented below.

Emergence

Emergent properties of interest are: (1) emergence of endophytism is beneficial life history strategy despite its costs, (2) differential responses of viaphytic fungi to changes in substrate (woody debris), as compared to non-viaphytic fungi, (3) changes in abundances of endophyte-competent fungi that result from changes among spatial relationships of trees, including deforestation, that aren't well modeled as a function of simple abundances of trees.

Adaptation, Objectives, Learning, and Prediction

Fungus agents are intended to seek reproductive success, which can be measured either by number of substrates occupied or sporulation events. However, fungus agents are not given the ability to modify their behaviors to increase fitness. As such, they do not take any measure of success, memory of past events, or predictions of future conditions, into account during their actions.

Sensing

Fungus agents' decisions are based primarily on internal sensing of biomass (stored energy) to decide when to initiate sporulation and external sensing of distance woody debris and trees when sporulating, to determine the probability of infection. Inoculation of woody debris by endophyte infected trees also senses the distance to woody debris to calculate probabilities of infection.

Interaction

Interactions among fungi are indirectly competitive, mediated through wood debris agents. Woody debris agents are consumed by fungal agents as a source of energy, and the presence of existing fungus agents associated with a woody debris agent reduces the likelihood of establishing new fungus agents on a woody debris agent.

Stochasticity

Several stochastic processes are used in the model to emulate the variable environment of forest ecosystems. Amount of wood deposition per step, number of successes in sporulation/inoculation, initial placement of trees and woody debris, and methods of tree

selection in deforestation all involve stochastic selections of agents and locations. These are described in the sub models.

Observation

At the end of each step in the model the following are recorded: total numbers of fungus agents, woody debris agents occupied by fungus agents of both endophyte-competent and non-competent fungi, total sporulation events by both types of fungi, percent of trees infected by endophytes, and for deforestation scenarios, total number of trees on the landscape.

Initilization

Model default density of ~600 trees in a 1 ha plot are intended to approximate that of wet tropical forests (Crowther et al 2015). Initial conditions of the model are intended to emulate a recent small disturbance in a forest landscape, where a larger than usual amount of uncolonized woody debris has been randomly deposited. Unless otherwise specified, all model runs begin with one fungus agent of each type, randomly associated with a woody debris agent. These initial fungus agents are assumed to have established themselves and begin the model with a starting energy sufficient to sporulate 2 or three times. Endophytism in the model can be disabled, allowing competition experiments between two non-viaphytic fungi. Dispersal coefficients are assigned to both types of fungi, and to trees for dropping leaves, though this last setting is typically held at a default value from leaf fall data (see submodels). Default initial Woody debris agents have a total biomass/energy of 30 (this can be changed by the user). Rate of new woody debris deposition on the landscape can also be set prior to initialization, though this was typically held a default value found to allow aggressive, non-viaphytic fungi to persist on the landscape. Initialization states are intended vary among model runs, to explore the benefits and limits of a viaphyte-style life history strategy.

Input

Deforestation scenarios require time-series input data, in the form of timing, intensity, and spatial nature of tree removal. Otherwise the model does not require input data.

Submodels

Submodels are listed in figure two schematically as processes. In addition, we describe procedures for initial placement of trees, and two deforestation submodels.

Wood deposition

Wood deposition (fig. 3) is given total energy budget per timestep (A), that is defined by the user/defaults before initiating a model run. To simulate the variety of sizes of woody debris that occur in forest settings, however, each new woody debris agent (W) is given variable (random) initial energy (e), taken from the iteratively smaller range of energy remaining. As agents are added, a tally of energy used ("a") is maintained. This tally "a" will ultimately approximately equal the wood deposition rate given by the user/default, and the submodel exits.

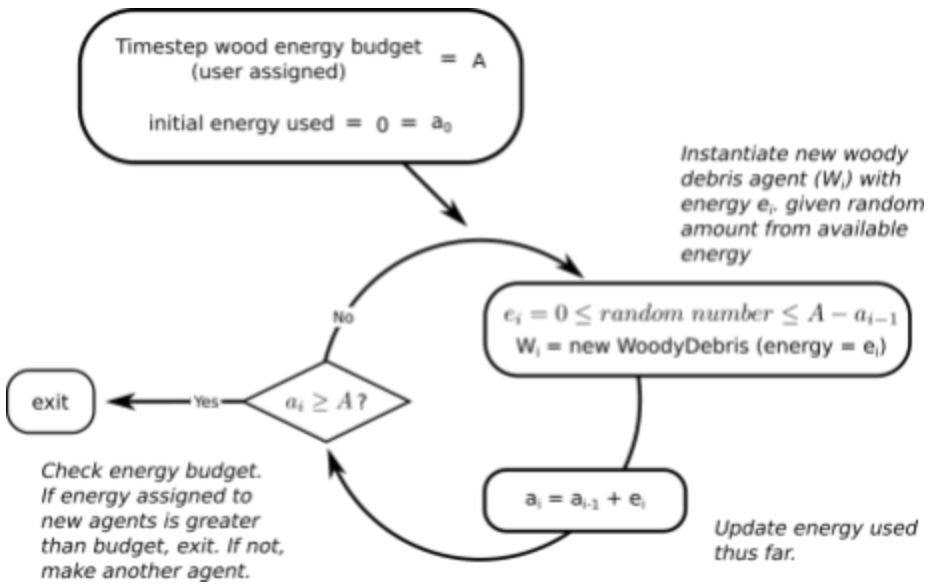

Figure 3. Wood deposition submodel. [For a higher resolution image click here](#).

Sporulation and inoculation

Calculation of probability of infection of a woody debris or tree agent from spores is an exponential decay function of distance ("x") from self (fungus agent), multiplied by a dispersal ability coefficient ("D") assigned by the user (figure 4). Viaphytic and non-viaphytic fungi can be - and usually are - assigned distinct dispersal abilities. Probability of Inoculation of woody debris agent is furthered multiplied by the fraction of current, remaining energy ("E_c") over starting energy ("E_i"), to give a handicap to colonization of woody debris agents by new fungi, if the wood is already inhabited by other fungi.

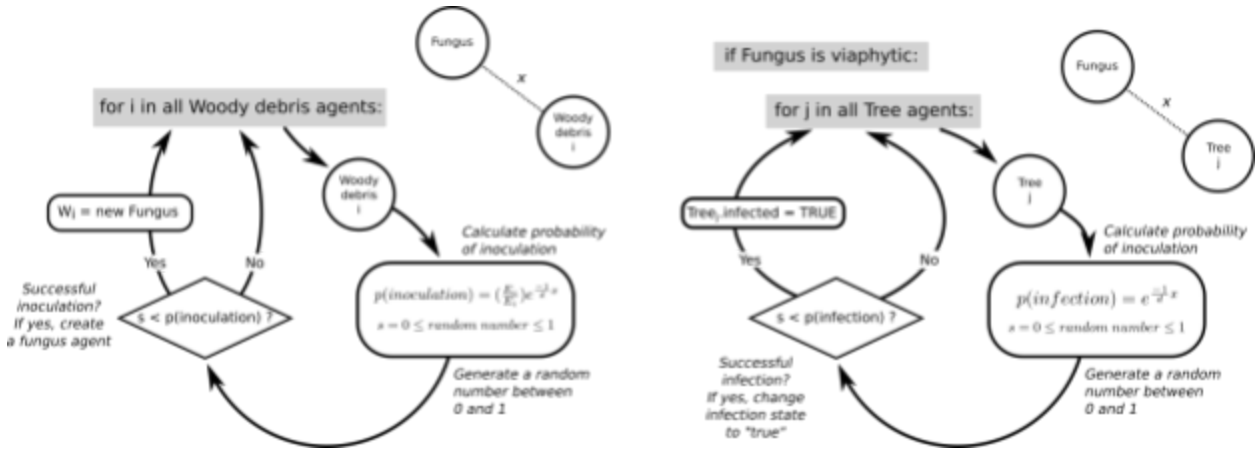

Figure 4. Sporulation submodel, for both woody debris inoculation and endophyte infection of trees. [For a higher resolution image click here](#).

Leaf fall and leaf-vectored wood inoculation

Leaf fall is treated similarly to sporulation (fig. 4), except that it occurs at every time step, as an action of all Tree agents, without any energy budgeting. For the purposes of this study, leaf fall for all tree agents was calibrated at d=4. The equation for determining the probability of inoculation of a Woody debris agent is identical:

$$p(inoculation) = (\frac{E_c}{E_i})e^{\frac{-1}{d}x}$$

Where "E_c" and "E_i" are current and initial energy, "x" is the distance between Tree agent and Woody debris agent, and "d" is the dispersal ability coefficient for trees, usually held at d=4.

Decomposition

Decomposition is modeled here as a simple one-way transferral of energy from Woody debris agents to their associated Fungus agents. Every time-step, each Fungus agent on a grid cell with a Woody debris agent gains one energy, and causes the Woody debris agent to lose one energy. Thus, a cell with numerous Fungus agents will show rapid decomposition of the resident Woody debris agent, and becomes increasingly difficult to for new Fungus agents to access. After a Woody debris agent drops below one energy in a turn, it is removed from the model. Fungus agents will then respire away stored energy at a rate of one per step until dropping below one unit of energy, then removal from the model, unless a new Woody debris agent is placed on the cell.

Tree placement

Initial tree placement on the model landscape follows a “Thomas” process (Thomas 1949), controlled by three, user-defined parameters: the poisson-process rate of parent points that will become centers of tree clusters (“kappa” or κ), a secondary poisson-process rate for child points that will become Tree agents (“mu” or μ) the spread (variance) of child points(“sigma” or **σ**). Default settings are intended to create approximately 600 trees per hectare (Crowther et al 2015). See supplementary materials for full details on tree placement algorithms.

Tree removal

Tree removal can be programmed into model runs at any time. Two types of tree removal have been included as functions in the model, to emulate two broad categories of deforestation: (1) thinning, or selective logging, where trees are removed at +/- the same rate, throughout the landscape, interspersed among leave trees, or (2) fragmenting, where contiguous blocks of forest are removed. The first attempts to emulate the results of selective logging, often in the form of "highgrading.” The second is intended to model land use conversions - homesteading, conversion to agriculture, etc. (Kettle and Koh 2014).

Thinning of trees requires one argument from the user, the intensity of the thin. This number is between 0 and 1, indicating the proportion of trees to be removed, each of which are randomly, independently selected from the pool of the entire set of trees on the landscape.

Fragmentation of forest accepts two arguments, the number and radius of fragments. Fragment center locations are assigned randomly, then all trees within the user-assigned radius from each center are protected, and the remaining trees are removed from the model (fig 4).

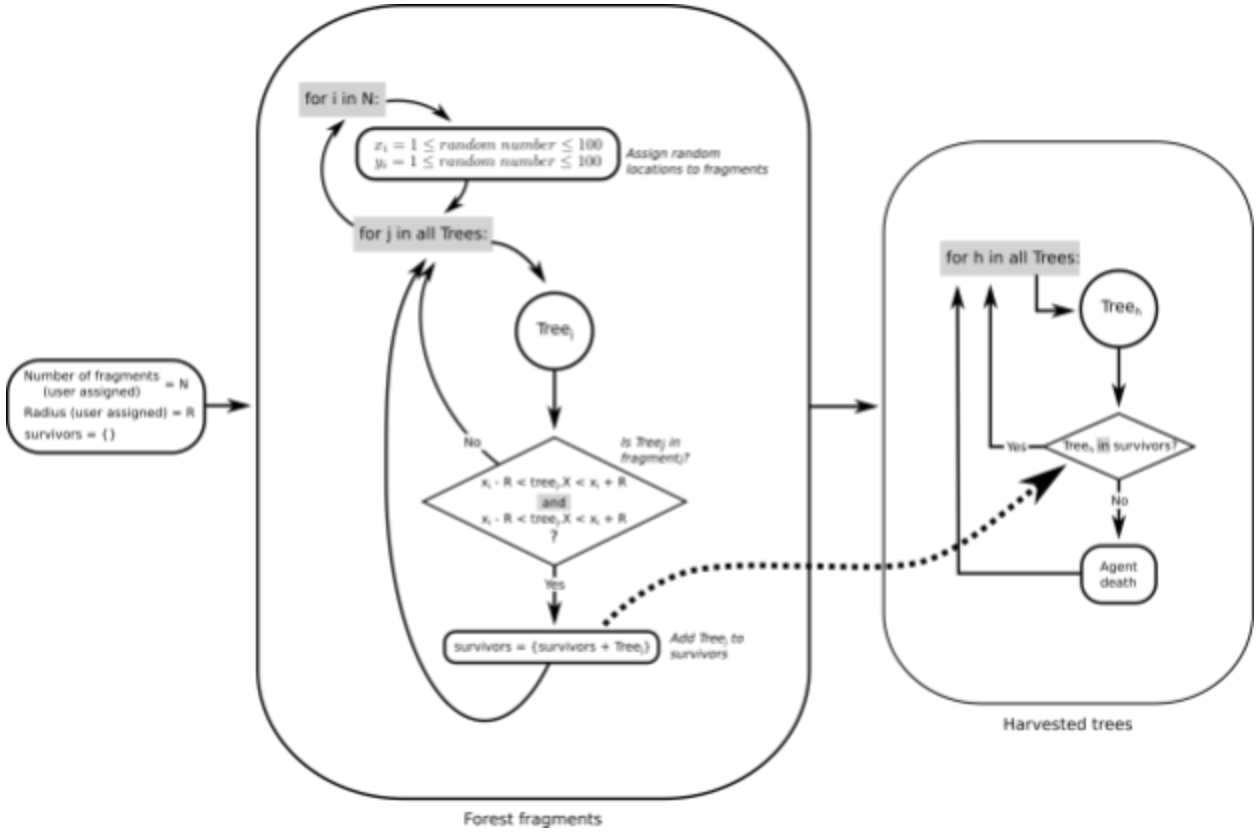

Figure 4. Forest fragmentation submodel. For a higher resolution image click here.

Methods II: Simulations

Basic behaviour of the model was characterized by first defining a non-viaphytic, “typical” fungus. Negative exponential models with various dispersal coefficient settings were visualized (supp. fig. 1) and compared with estimates of spore dispersal from empirical studies (Norros 2012, Peay 2012, Galante 2011) to characterize a well-dispersed fungus. This well-dispersed fungus was then tested on the model landscape using a parameter sweep of dispersal coefficients in the “tropical forest” of default model settings. Next, a model viaphytic fungus was defined as the lowest-dispersing viaphytic fungus that could cooccur and compete successfully with the model non-viaphytic fungus. See supplemental material for full details of the calibration process of default Fungus agent dispersal abilities. Once defined, these model viaphyte (d=2) and non-viaphyte (d=10) fungi were used as default settings for Fungus agents in subsequent simulations to explore properties of the model.

Additional tests included:

- Sensitivity of fungus agents to initial amounts of wood on the landscape, and to regular rates of wood deposition after initialization.
- Sensitivity of viaphytic fungi to residence times of endophytic infection in host-trees.
- Sensitivity of viaphytic fungi to deforestation, using three deforestation scenarios: (1) one-time thinning of various intensities, (2) serial thinning, and (3) fragmentation of the 1 ha forest plot into 15 m-diameter clusters.

In most parameter sweeps, 100 simulations of 50 timesteps were run for each level of the variable of interest. In deforestation simulations, which were run for 100 timesteps, with "harvests" introduced at timestep 51. Examples of exact code for each sweep are available in supplemental scripts.

Results

Model fungus agent calibrations

A non-viaphyte fungus with a dispersal coefficient of d=10 was found to fit expectations from empirical data and to persist reliably on model landscapes (fig. 5). At lower dispersal abilities, populations often went to zero, or had not finished decomposing initial wood deposits within 50 steps. At d=10, Fungus agents were able to fully colonize initial deposits wood on the landscape, then maintain a lower, steady population where woody debris agents inoculated by fungi were approximately equal to the amount of new woody debris energy deposited on the landscape each turn.

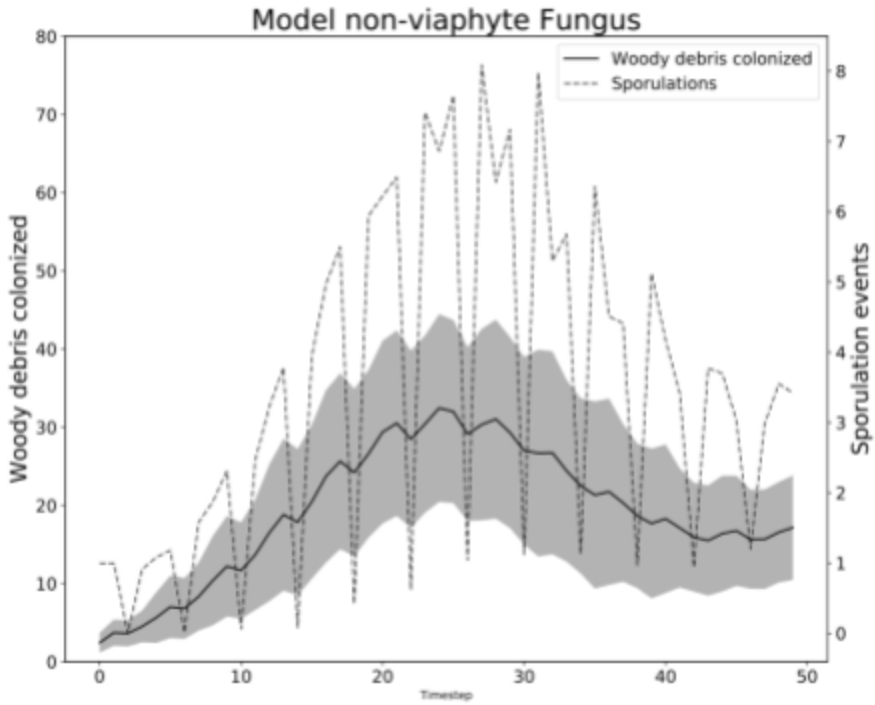

Figure 5. Behavior of model non-viaphytic fungi on the default model landscape. Error lines are one standard deviation from the mean. [For a higher resolution image click here](#).

A viaphyte fungus with a dispersal coefficient of d=2 was the lowest-dispersing fungus that maintained a balanced competition with our model non-viaphytic fungus (fig 6). Below this dispersal level (d<2) for viaphytes the model non-viaphyte fungus agents clearly outcompeted the viaphytes, keeping infected trees and inoculated substrates to near zero levels. The reverse was true above (d>2) this dispersal level.

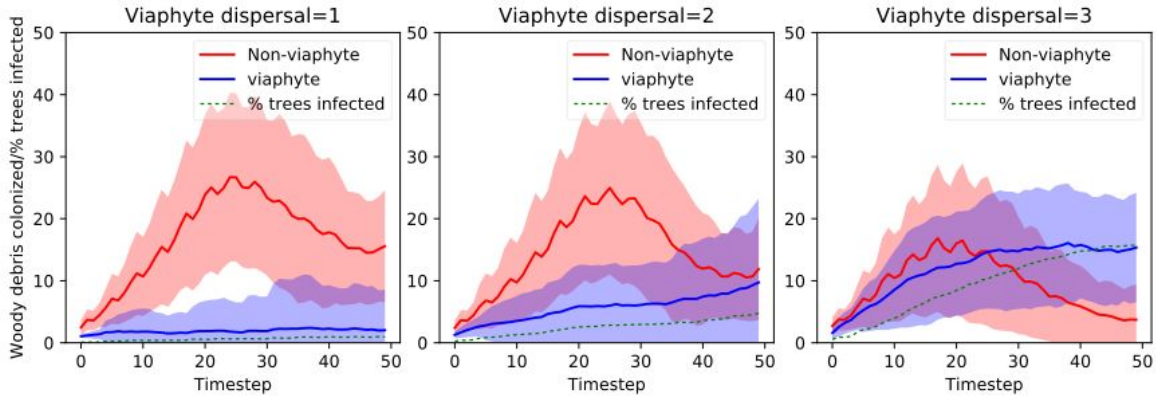

Figure 6. Competition of viaphytic fungi with various dispersal abilities against a model non-viaphytic

fungus. For a higher resolution image click here.

Importance of initial wood deposition and subsequent rates of wood deposition

Model, non-viaphytic Fungus agents increased their populations rapidly when presented with large abundances of woody debris (fig 7). Larger initial deposits of wood on the landscape were often consumed as or more quickly than small abundances. Higher initial abundance of wood was equivalent to more continuous distributions of woody debris, with fewer gaps in substrate, making all woody debris on the landscape generally more available. These conditions allow exponential population growth of fungi and quicker consumption of wood, despite absolute wood biomass being much greater.

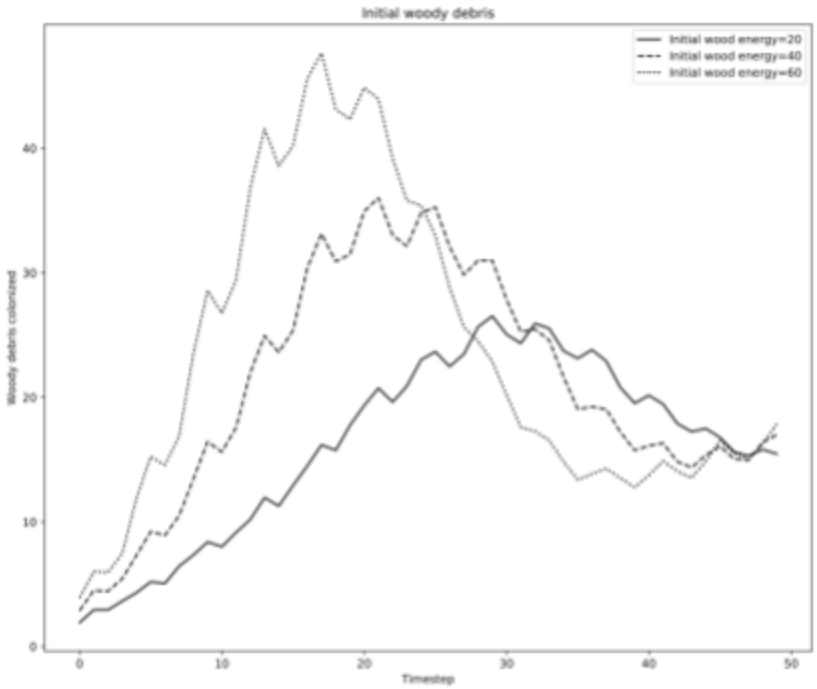

Figure 7. Response by fungi to varying amounts of substrate on the landscape.

Figure 7. Response by fungi to varying amounts of substrate on the landscape. For a higher resolution image click here.

Subsequent, per-step wood deposition was important for this reason also (fig. 8), as sufficient wood is required to sustain fungus agents in the long-term, but also to enable the initial explosive exploitation of wood on the landscape by bridging gaps between islands of existing substrate reserves on the landscape. Less-aggressively-dispersed model viaphytes respond less dramatically to abundances of woody debris on the landscape, taking longer to reach peak abundances. With viaphytic fungi, abundances was also highly influenced by the increasing number of endophytically-infected trees

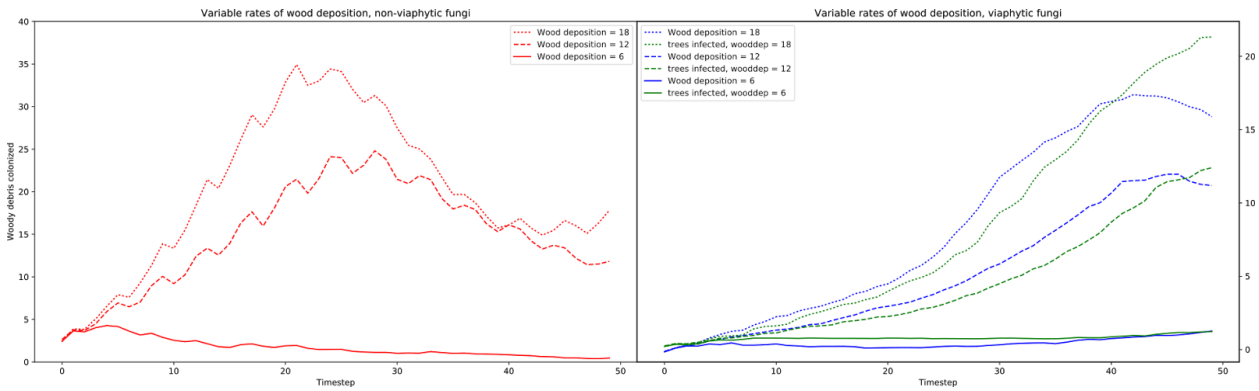

Figure 8. Differential response by model non-viaphyte and viaphytes to per-step wood deposition rates. [For a higher resolution image click here](#).

Importance of residence times of endophytic infection in host-trees

All benefits conferred by the endophytic phase are contingent upon a low rate of loss by trees of their endophyte infection. Under model defaults, endophyte loss greater than 5% per time-step caused loss of all competitive advantage by model viaphytes (fig 9.).

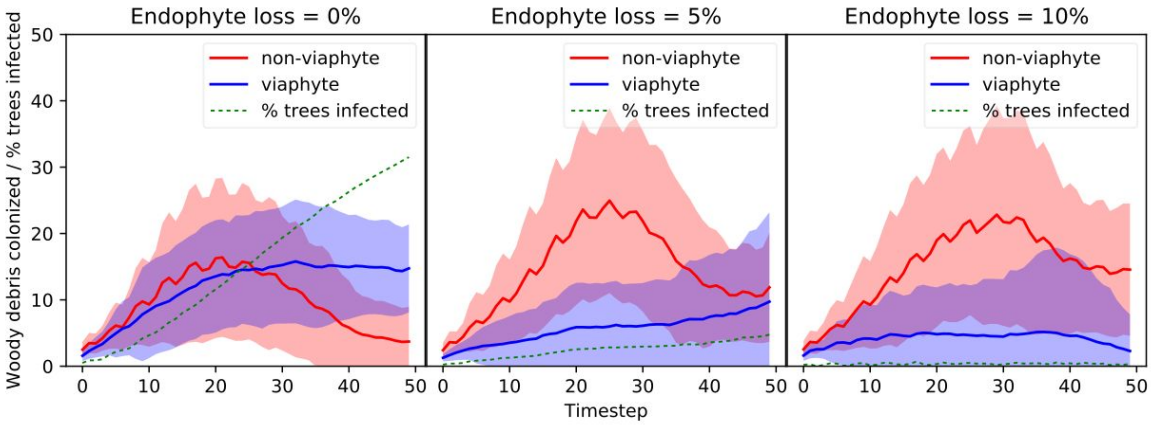

Figure 9. Effect of endophyte infection loss rates on viaphyte success. [For a higher resolution image click here](#).

Deforestation and its ecological consequences

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 (fig. 10a) Drastic thins (70-100%) reduce this stability (figure 10b). Lighter thins (10-30%) appear to affect established populations of endophytes minimally. Serial thinning, or 10% removal of trees every 10 steps, beginning at step 51, has less impact on viaphyte populations than the comparable event of thinning 40% of trees at once (fig 10c). As modeled here, fragmentation of forest has similar effect to comparable thins, but endophyte populations remain stable at higher rates of removal, with viaphytic fungi recovering to competitive abundances even at 70% removal of trees (fig 10d).

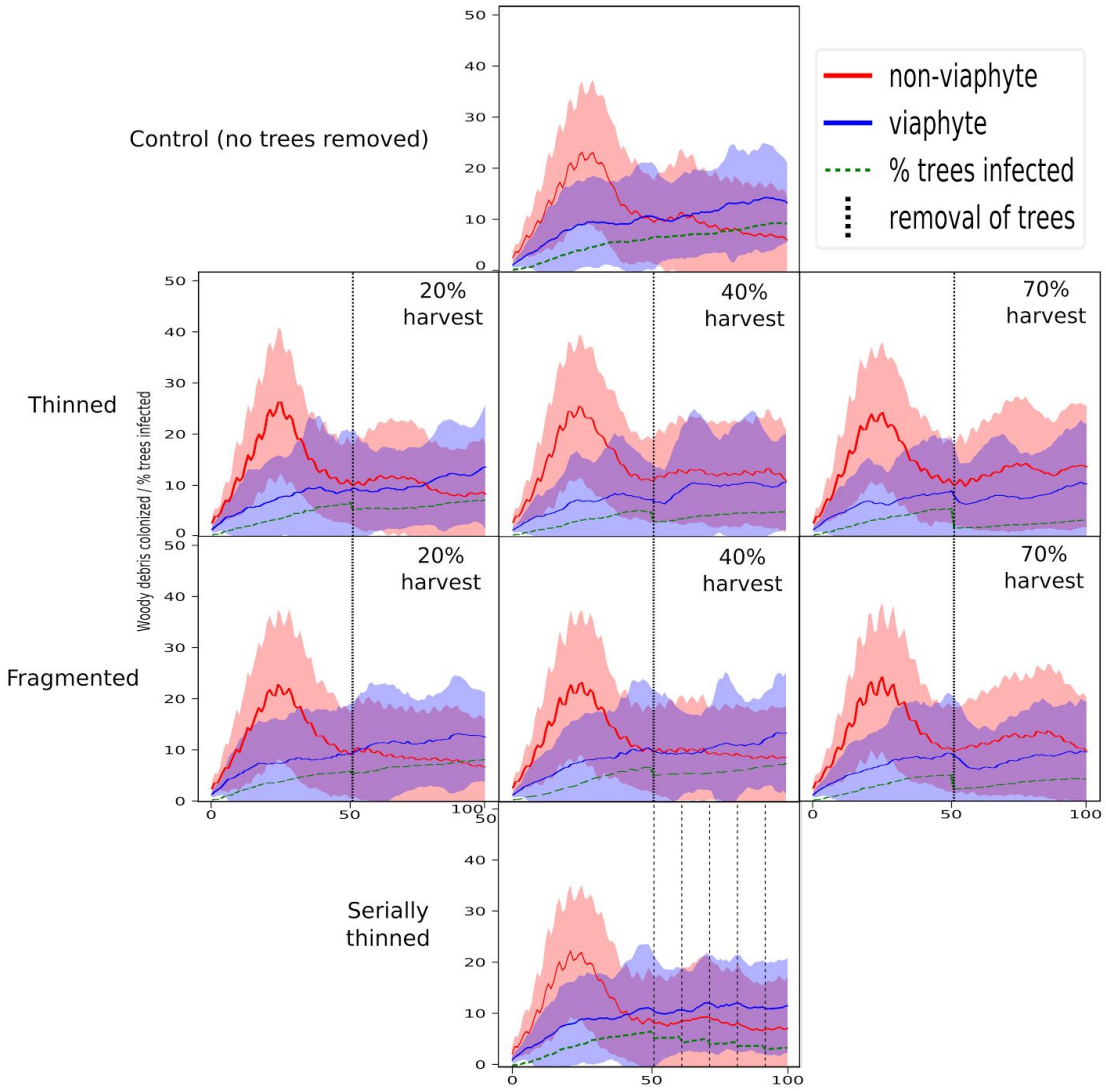

Fig 10. Deforestation scenarios - thinning, fragmentation, and serial thinning. [For a higher resolution image click here](#).

Discussion

The model presented predicts that fungi in a wet tropical forest 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 fungus to persist and compete on a landscape of other, far-better dispersed fungi.

Persistence is due, in large part, to the highly spatially and temporally autocorrelated pattern of colonization that results from spore dispersal - fungus agents must be able to bridge gaps in woody debris over distance and time to persist on the landscape. Fungi without endophyte-competence must overcome this limitation simply by increasing dispersal (or other strategies not examined in this model). This creates a feedback, since most spores must fall locally in order for some percent to reach farther distances, meaning that 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 are not found, local extinction is very possible. In addition, offspring of a sporulating fungus are often 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 or 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 woody agents across the landscape, regardless of the presence of canopy.

Certain types of deforestation are implicated here as more problematic than others for allowing endophytes to persist on the landscape. Small scale, regular disturbances were more sustainable in terms of endophyte populations than large single harvesting events, reducing the chance of stochastic removal of a species from the landscape and enabling populations of endophytes to regenerate into other trees from remnant trees. Host preferences are not modeled here, and would exacerbate any negative effects of selective thinning. Fragmentation as modeled here was less impactful on endophyte populations than comparable dispersed thinning, as it left large blocks of contiguous forest to remain on much of the landscape. Fragmentation as modeled here is of small scale, and does not necessarily reflect larger scale fragmentation such as is occurring throughout much of the tropics (Kettle and Koh 2014), however.

This study and other studies (Boswell 2012) have demonstrated just some of potential uses for simulation-based models in mycology. Effort must be made to find realistic and useful modeling solutions for mycology, as understanding the bewildering diversity and complexity of ecology of fungi becomes ever more urgent in a changing world.

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