Fitness and Optimal Life-History Strategies in Filamentous Fungi

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Submitted to Evolution on January 21, 2004

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Key words and phrases. Filamentous Fungi, Fitness, Life History Evolution, Bang-Bang Strategy, Resource Allocation

Running title. Fungal Fitness & Life History Strategies
Abstract

Filamentous fungi are ubiquitous and ecologically important organisms with rich and varied life-histories. Yet the fitness of these fungi is poorly understood and there is no consensus on what constitutes an appropriate fitness measure. In the first part of this study we use an idealized model of a fungal life cycle to identify an appropriate fitness term. We find that fungal fitness is inversely proportional to the equilibrium density of uncolonized fungal resource patches which, in turn, is a function of the expected spore production of a fungus. In the second part of this study we use a simple model of fungal life history dynamics within a resource patch to identify the optimal resource allocation strategy for a filamentous fungus under both static and dynamic allocation strategies. In both the static and dynamic scenarios, the optimal allocation strategy varies with the initial conditions of the system. In the case of dynamic allocation we find that a bang-bang strategy is generally optimal. Our work also suggests possible trade-offs between the different terms which define fungal fitness and provides a framework to identify the appropriate fitness measure for fungi with life cycles different from the one considered here.
Introduction

Life-history theory has a long and rich tradition in both the plant and animal literature. Numerous models have been developed to explore and describe the fitness advantages driving the evolution of various life-history strategies. These efforts have yielded considerable insights into such areas as the trade-offs between iteroparity and semelparity (Cole, 1954; Charnov and Schaffer, 1973), offspring size and number (Smith and Fretwell, 1974; Lloyd, 1987; Hendry et al., 2001), and the timing of breeding (Iwasa and Levin, 1995). These and other life-history studies have deepened our understanding of plant and animal evolution. It is striking that no parallel theoretical framework exists for the field of mycology. The almost total absence of life-history theory related to fungi is particularly startling given the ubiquitous influence of pathogenic and mutualist fungi on the ecology and evolution of both plants and animals, including humans.

Fungi are devastating agricultural and human pathogens, exacting great social and economic costs. Examples include the rust fungi (e.g. *Puccinia graminis*) which attack grain crops and cause economic hardship and even famine (Agrios, 1997), the filamentous fungus *Aspergillus fumigatus* which is responsible for the death of many immunocompromised individuals such as AIDS and leukemia patients (Latge, 1999). More generally, fungal species influence the ecology and evolution of a variety of organisms from plant seedlings (e.g., the oomycetes *Pythium spp.*) to insects (e.g., members of the order Entomophthorales). Ecologically, fungi are mutualists as well as pathogens. Mycorrhizal fungi may facilitate the exchange of nutrients between plants (Simard et al. 1997, but see Robinson and Fitter 1999; Simard et al. 2002) and are also thought to have facilitated plants’ invasion of the terrestrial environment (Simon et al., 1993). Other fungal groups are important food sources for a wide array of animals (Maser et al., 1978; Lebel and Claridge, 2002). Moreover, fungi can be used to explore a variety of ecological and evolutionary questions, including questions related to
transmission-ratio distortion (Turner and Perkins, 1991), costs of resistance (Cowen et al., 2001), and speciation (Dettman et al., 2003).

Fungi seem unusual and complex when compared to plants or animals. As a result, it is not immediately clear when insights garnered from models developed for plants and animals will translate to fungi. In the life-history literature, plants are generally modeled as sessile autotrophs, and animals are generally modeled as mobile heterotrophs. Most fungi are sessile heterotrophs, i.e., they spend most of their life cycle in a sessile stage, and yet are dependent on local, external carbon sources for energy.

Ironically, it is the very diversity and complexity of fungal natural histories, which reflect and contribute to their ecological and evolutionary importance, which hinder the development of fungal life-history theory. Mycologists struggle to identify an appropriate fitness metric for filamentous fungi (Antonovics and Alexander, 1989; Braiser, 1999; Pringle and Taylor, 2002). There is no standard measure of fungal fitness, no analogy to pollen flow and seed set in an annual plant, or number of progeny in an animal. One result of this lack of standards is that there are little data to correlate one fitness estimate to another (but see Xu, 1995; Pringle et al., 2003). Without an understanding of what constitutes fitness, it is difficult to identify the selective forces driving the evolution of different life-history strategies. It seems reasonable to suggest that there is no standard fitness metric because there is no standard fungal life cycle and, consequently, the appropriate fitness metric can vary from system to system.

Therefore, a necessary step in developing evolutionary explanations for different fungal life histories is a general approach for identifying the appropriate fitness metric for a given life cycle. Towards this end, in this study we illustrate how the tools of invasion analysis can be applied to a simple model of an idealize filamentous fungus’ life cycle to derive the appropriate fitness term. In the model we develop and analyze here, a fungal spore settles out of a spore pool into a suitable resource patch, germinates, and then grows within the patch. The
resource patch in this model is defined very generally and, as a consequence, can represent a wide range of patch types including: an individual animal, as would be the case for a fungal pathogen, for example *Coccidiodes immitis*; an individual or population of plants, as would be likely for numerous species of arbuscular mycorrhizal fungi; or the habitat of a saprophytic fungus, for example burned trees colonized by individuals of *Neurospora crassa* (Jacobson et al., 2002). As the fungus grows within the patch it can generate new asexual spores which are released into the spore pool (Figure 1). By formalizing this idealized description of a filamentous fungus’ life cycle into an age-structured population model, we can identify the appropriate fitness term using an invasion analysis. Our approach could be adapted to fungi with more complicated life cycles by following these same steps of mathematical formalization and an invasion analysis.

The second goal of this study is to illustrate how, having defined the appropriate fitness term for a specific fungal system, one can begin to address simple life-history questions such as the allocation of resources to either mycelial growth or reproduction via spores. One of the important components in the fitness measure we identify is the expected lifetime spore production of a fungus within a resource patch. Previous plant and parasite life-history models for fungi living in patches with renewable resources are likely to be directly applicable to commensal fungi. However, saprophytic fungi inhabit non-renewable resource patches and previously studied life-history models cannot be applied to such organisms. Thus to better understand the trade-offs faced by this group of fungi, we develop a second model at the scale of the resource patch. In this within-patch model, we assume that the patch resources are finite and non-renewing and that fungi are faced with the choice of allocating patch resources to either growth within the patch or spore production. We identify the allocation strategies which maximize a fungus’ expected lifetime spore production using Pontryagin’s maximum principle (Pontryagin et al., 1964). In spite of the fact that the underlying assumptions of this within-patch model differ from other life-history models, the optimal life-history strategies
we identify are strikingly reminiscent of life-history studies in the plant, animal, and viral literature.

[Figure 1 about here.]

**Population Model**

In order to model the population dynamics of a fungal life cycle at the level of a resource patch, we employ a mixture of coupled ordinary and partial differential equations. Our model is similar in form to a structured epidemiological model (e.g. Murray, 1993; Gilchrist and Sasaki, 2002) and, therefore, we employ similar notation. Specifically, we keep track of three different components: uncolonized patches, colonized patches, and the fungal spore pool, $S$, $I$, and $Z$ respectively (see Figure 1). In contrast, the colonized patches are structured by both time $t$ and the age of the fungus within the patch $a$ (i.e., the time since the arrival and successful germination of a fungal spore). As a consequence, the colonized patches are modeled using a partial, rather than an ordinary, differential equation.

Our population model is for a single, asexual fungal strain. We begin by assuming that new, uncolonized patches, such as newly burned trees, flow into the system at some constant rate $b$. These uncolonized patches can be transformed into colonized patches with the arrival and successful germination of a fungal spore from the spore pool.

In this model we explicitly assume that the germination rate of a spore arriving into an already colonized patch is zero. This assumption prevents any competition between individual fungi within a patch. While this assumption is clearly unrealistic, it is a logical starting point for modeling and understanding which aspects of a fungus’s life-history are important for determining its fitness. We are currently working to expand our approach to include within-patch competition and will describe its effect in a later study.
If the spore successfully germinates it forms a fungal mycelium and may begin to produce mitotic spores which are released into the well mixed spore pool. In our model we represent the spore production rate, \( p \), as a function of fungal age, \( a \). Describing spore production rate with the function \( p(a) \) makes our model more realistic and general than simply representing spore production rate with a fixed value because it allows spore production to vary dynamically over the lifespan of the fungus. In a later section we will assume that the spore production rate \( p(a) \) is a function of the life-history strategy of the fungus within a patch.

Fungal spores in the spore pool can either settle out of the pool onto an uncolonized patch or decay, becoming inviable. We will assume the spore settling rate from the spore pool, \( \sigma \), and the spore decay rate within the spore pool, \( \delta \), to both be constants. The probability, per unoccupied patch, that a settling spore lands in a patch and successfully germinates is \( \beta \). Finally, all patches are assumed to have a background removal rate \( \mu \) which represents the rate at which patches are destroyed by flood, fire, burial, or other patch scale disturbance (see Table 1 for a list of definitions of parameters used in the population model).

[Table 1 about here.]

This patch-fungal system can be described by the following coupled differential equations,

\[
\frac{dS}{dt} = b - S (\sigma \beta Z + \mu) \tag{1}
\]

\[
\frac{\partial I}{\partial t} + \frac{\partial I}{\partial a} = -\mu I \tag{2}
\]

\[
\frac{dZ}{dt} = \int_0^\infty p(a) I(a, t) \, da - (\sigma + \delta) Z. \tag{3}
\]

Equation (2) is a partial differential equation in which colonized patches are structured by both time, \( t \), and the age of the colonizing fungus. Because both \( t \) and \( a \) have units of time, we will assume that \( dt/da = 1 \). The equation simply states that colonized patches are removed at a constant per patch rate as time progresses Sinko and Streifer (1967).
Because equation (2) is a partial differential equation, it requires a boundary condition in order to ensure a unique solution. The boundary condition for equation (2) describes the influx of newly colonized patches into the age-structured system and is defined as,

\[ I(t, 0) = \sigma \beta S Z. \]  

(4)

It should be noted that the above model implicitly assumes that all patches have the same initial resource densities. This assumption can be relaxed by indexing the colonized and uncolonized patches by their initial resource level. We discuss the effects of relaxing this assumption later.

**Equilibrium Solutions**

If we assume that the fungal-patch system has come to an equilibrium (i.e. \(dS/dt = \partial I/\partial t = dZ/dt = 0\)), we can solve the above equations to get the equilibrium densities of \(S\), \(I\), and \(Z\). Using the superscript * to denote the equilibrium densities, the solutions are:

\[ S^* = \frac{\sigma + \delta}{\sigma \beta \Phi} \]  

(5)

\[ I^*(a) = I_0^* \exp[-\mu a] \]  

(6)

\[ Z^* = \frac{1}{\beta \sigma} \left( \frac{b}{S^*} - \mu \right) \]  

(7)

where,

\[ I_0^* = b - \mu S^* \]  

(8)

and,

\[ \Phi = \int_0^\infty p(a) \exp[-\mu a] da \]  

(9)

The term \(I_0^*\) is equal to the boundary condition described in equation (4) when the system is at equilibrium. Thus, \(I_0^*\) represents the equilibrium patch colonization rate. The scalar
Φ represents the expected number of spores produced over the lifetime of a fungus within a patch (expected spore production, for short). The expected spore production, Φ, is equal to the sum of spore production, \( p(a) \), over the lifetime of a fungus weighted by the probability the patch has not been removed by a disturbance event, \( e^{-\mu a} \). Thus, Φ is a function of both the spore production schedule (i.e., the behavior of \( p(a) \) over all \( a \)) and the background patch removal rate, \( \mu \).

In addition to the above solution, there is a second equilibrium in which the fungus cannot persist. In this second case, \( S^* = b/\mu, I_0^* = 0, \) and \( Z^* = 0. \) In order for the fungus to persist within the system the first equilibrium must be stable and the second equilibrium must be unstable. In order for these conditions to be met,

\[
S^* < \frac{b}{\mu} \tag{10}
\]

which implies that the density of uncolonized patches, \( S^* \), under the first equilibrium must be less than the density of uncolonized patches in the absence of the fungus, \( b/\mu \). From equation (5) it follows that there is a critical number of spores, \( \Phi_c \) which must be produced or else the fungus will be unable to replace itself within the population. This critical value is,

\[
\Phi_c = \frac{\mu}{\beta b} \left( 1 + \frac{\delta}{\sigma} \right). \tag{11}
\]

Similar thresholds are well known for epidemiological systems (Anderson and May, 1978; May and Anderson, 1979; Anderson and May, 1982).

**Invasion Analysis**

Having determined the necessary conditions for a fungal strain to persist within the system, we ask how the conditions for fungal persistence change when more than one fungal strain is competing for uncolonized patches. In order to determine when a fungal strain is more
fit than another, we conduct an invasion analysis to determine the necessary conditions for a novel fungal strain to invade a resident fungal population. We begin our analysis by first assuming that the resident fungal strain is at its equilibrium density and distribution as described in equations (5)-(9). Employing the subscripts \( r \) and \( n \) to identify resident and novel strain specific terms, respectively, our next step is to calculate the fitness, \( W \), of a spore produced at time \( t = 0 \) for the resident and novel strains.

In our model system, new patches can only be colonized via spore dispersal. From the perspective of a spore, its fitness is equal to the expected number of progeny spores it can produce. By virtue of the fact that the resident population is at equilibrium the fitness of the resident strain, \( W_r \), is equal to 1. Thus when the fitness of the novel strain, \( W_n \), is greater than 1, then the novel strain will invade the resident population.

In order to calculate the fitness of a novel spore, let \( z_n(t) \) represent the probability that the novel spore is alive at time \( t \). Thus,

\[
\frac{dz_n}{dt} = - (\sigma_n + \delta_n) z_n
\]

which can be solved, yielding

\[
z_n(t) = \exp[-(\sigma_n + \delta_n)t].
\]

The probability that the spore settles and successfully germinates at any given time point is \( \sigma \beta S^*_r z(t) \). Successfully settling and germinating spores lead to, on average, the production of \( \Phi_n \) new spores. Thus, the expected number of spores produced from a single spore is,

\[
W_n = \Phi_n \int_0^\infty \sigma_n \beta_n S^*_r z_n(t) dt
\]

\[
= S_r^* \frac{\sigma_n \beta_n \Phi_n}{\sigma_n + \delta_n}
\]

which can be rewritten using equation (5) as

\[
W_n = \frac{S^*_r}{S^*_n}
\]
As previously stated, the invasion criteria for the novel strain is $W_n > 1$. Thus from equation (16) it follows that the equilibrium density of uncolonized patches for the novel strain must be less than that of the resident strain. More simply put, our invasion criterion is,

\[ S_n^* < S_r^*. \]  

(17)

Equation (17) indicates that under the assumptions made in our population model, coexistence of two fungal strains $i$ and $j$ can occur only if $S_i^* = S_j^*$.

Mechanistically, our results demonstrate that a novel fungal strain will successfully displace the resident strain when it can drive the density of the uncolonized patches below the density necessary for the persistence of the resident strain. In other words, a successfully invading strain drives the system to a state in which the density of uncolonized patches is so low that the resident strain is, on average, unable to replace itself. This result is very similar to the results found in the epidemiology literature indicating that a novel parasite can invade the host population if it can drive the equilibrium density of susceptible hosts below that of the resident strain (Lenski and May, 1994).

Our invasion criterion indicates that natural selection will favor fungal strains which minimize the equilibrium density of uncolonized patches. Minimizing $S^*$ is equivalent to maximizing the fractional term in equation (15) and so we can define relative fitness, $w$, as,

\[ w = \frac{\sigma \beta \Phi}{\sigma + \delta}. \]  

(18)

The $\sigma \beta$ term in the numerator of $w$ can be interpreted as the rate at which spores encounter and colonize empty patches per unit density of patches, and $\Phi$ is simply the number of spores produced per colonized patch; the denominator is the total rate at which spores leave the spore pool (either through settlement or decay).

Because all of the terms in $w$ are for a single fungal strain (i.e., $\delta$, $\sigma$, $\beta$, and $\Phi$ are not dependent on the competing strain), coexistence between two different fungal strains is only
possible if they have the same fitness values. Thus coexistence in this model is essentially non-existent. However, we believe that including within-patch competition between strains could allow for the coexistence of multiple strains because, total spore production would then also be a function of the the competing strain’s production strategy. Equation (18) also indicates that in the absence of any trade-offs, the fitness of an asexual fungal strain increases with the expected lifetime spore production of a patch, \( \Phi \), the rate at which it successfully settles into and germinates within a resource patch, \( \beta \), and the ratio of spore settlement to spore decay, \( \sigma/\delta \).

Although it is easy to imagine trade-offs between any or all of these terms, for our purposes we will assume that the expected spore production \( \Phi \) is independent of all other terms in equation (18). Consequently, in the following section we define and analyze a simple model of the growth of a fungus within a patch to identify optimal life-history strategies as a function of the size of a fungal spore, the amount of resources contained in a patch, and the patch decay rate, \( \mu \).

**Within-Patch Model**

Because resources within a patch are limited, when a fungal spore lands in a resource patch a natural question arises: “If the fungus has the choice of investing resources into either mycelium composed of hyphae or spores, what is the optimal resource allocation strategy?” If we assume that the spore decay, settling, and germination rates are independent of one another and, for simplicity, fixed, then the optimal resource allocation strategy will be the one which maximizes the expected number of spores produced over the lifetime of a patch, \( \Phi \). Consequently, we use \( \Phi \) as a proxy measure of relative fungal fitness \( w \), as defined in equation (18).

As mentioned earlier, the sessile yet heterotrophic nature of most fungi makes it unclear
which insights from the life-history literature are relevant for fungi. If the resource within a patch are self-renewing, as with commensal fungi, then direct analogies to plant life-history models or parasite life-history models in which the plant or parasite’s goal is to maximize its number of offspring are likely to exist for many of these systems (for example see Sasaki and Iwasa, 1991; Iwasa, 2000; Coombs et al., 2003). However, possible analogies disappear when the resources within a patch are non-renewing, as with saprophytic fungi. Therefore, in order to identify the optimal allocation strategy which maximizes $\Phi$, for a saprophytic filamentous fungus we define a simple model of fungal mycelium dynamics within a patch.

The dynamics of this simple mechanistic model are driven, in part, by how the fungus chooses to allocate the resources it extracts from its patch. We identify the optimal allocation strategy under two different life-history scenarios. The first and more restrictive scenario assumes that the resource allocation strategy is fixed for the entire lifespan of the fungus. The second and more general scenario allows the resource allocation strategy to vary over the lifespan of the fungus. While the nature of the allocation strategy varies between these two scenarios, the underlying model of within-patch dynamics does not.

**Model Definition**

Here we define a model of fungal growth dynamics within a patch. We use this model to explore how spore production, $\Phi$, changes with the life-history strategy of the fungus. The goal of the model is to provide a description of how spore production varies with both the age of a fungus and its life-history strategy.

We begin our description of the within-patch model by first assuming that each patch has some initial density of resources, $r_0$, and that each spore germinates and leads to the same initial density of mycelial cells, $m_0$. In addition, we assume that the density of fungal mycelium $m$ decays at a constant rate $\gamma$. We also assume that the fungus extracts resources
from the patch at a rate proportional to its own size, $m$, and the resource density of the patch, $r$. Biologically this implies that the rate of resource extraction increases with both the amount of mycelium and resources within a patch, $m$ and $r$, respectively.

[Figure 2 about here.]

Once resources have been extracted from the patch by the fungus, they can be allocated to either the production of spores or mycelium cells $m$ which forms the hyphae within the patch. While spore production leads to a direct contribution to the expected spore production of a patch, $\Phi$, increasing mycelium density, $m$, can lead to an indirect contribution to $\Phi$ via greater future resource extraction and, subsequently, greater spore production.

The resource allocation level, $u(a)$, describes the proportion of extracted resources which are allocated to spore production. Because the resource allocation level, $u(a)$, is a proportion, it is constrained to be between zero and one. The resource allocation schedule of a fungus, $u$, is the behavior of its resource allocation function, $u(a)$, over all $a$. The assumptions we have just outlined lead to the following coupled equations:

$$\frac{dm}{da} = m(c_1 \varepsilon r(1 - u) - \gamma), \quad (19)$$
$$\frac{dr}{da} = -\varepsilon m r, \quad (20)$$

where $\varepsilon$ is the resource extraction rate and $c_1$ is the conversion rate for resources into mycelial biomass. Further, by definition, $m(0) = m_0$ and $r(0) = r_0$. See Table 2(a) for a list of parameters and units of this within-patch model.

[Table 2 about here.]

If we assume the spore production rate of the fungus, $p(a)$, is proportional to the amount of resources allocated to spore production by fungus we provide a link between this model
and the expected spore production of a fungus, $\Phi$, in the population model. It follows that,

$$p = c_2 \varepsilon \ m \ r \ u. \quad (21)$$

Non-dimensionalization is a standard technique to simplify a model and allows one to reduce the overall number of model parameters. For example, instead of measuring time in units of days or weeks, it is often simpler to measure time in terms of the reciprocal of an organism’s death rate and thus in the dimensionless formulation of the model, the death rate is scaled to one (see Edelstein-Keshet (1988) for a more detailed discussion). For our study, we can simplify our within-patch model by choosing our units of mycelial density $m$, resources $r$, spores $\Phi$, mycelium age $a$, and patch removal rate $\mu$ by setting them equal to $\frac{\gamma}{e}$, $\frac{\gamma}{c_1 e}$, $\frac{c_2 \gamma}{c_1 e}$, $\frac{1}{\gamma}$, and $\frac{1}{\gamma}$, respectively. Doing so allows us to rewrite the within-patch model as,

$$\frac{dm'}{da'} = m'(r'(1 - u') - 1) \quad (22)$$

$$\frac{dr'}{da'} = -m'r' \quad (23)$$

with,

$$p' = m' r' u', \quad (25)$$

where here the prime (') denotes dimensionless quantities. Unless otherwise noted, all future terms will be in dimensionless form. Thus we will drop the prime for notational simplicity.

We note that equations (22) and (23) can only be solved as an explicit function of $a$ when $u(a) = 1$. Under this condition,

$$m(a) = m(a_s) \ exp \ [(a - a_s)] \quad (26)$$

$$r(a) = r(a_s) \ exp \ [- (m(a_s) - m(a))] \quad \text{if and only if } u = 1 \text{ from } a_s \text{ to } a, \quad (27)$$

where $a_s$ represents the time at which $u(a)$ is set equal to 1.
While our ability to explicitly solve for $m(a)$ and $r(a)$ is limited, we can gain some insight into the dynamics of the within-patch system from equations (22) and (23). For example, as long as $m$ and $r$ are non-zero, the resource density is always declining (although not necessarily to zero). In addition, there is a critical resource density above which the mycelium is growing and below which it is declining with age $a$. This critical resource density is equal to $\frac{1}{1-u}$ and reflects the fact that below a certain resource level the amount of resources allocated towards mycelial growth, $r m(1 - u)$, is not enough to balance the mycelial background death rate.

The within-patch model described by equations (22) and (23) allows us to determine how the mycelial and resource densities within a patch change over time. These dynamics are driven, in part, by the life-history allocation strategy of the fungus, $u(a)$. Equation (25) allow us to relate the within-patch dynamics and the allocation strategy $u(a)$ of a fungus to its spore production rate, $p(a)$. In the following section we use this within-patch model to determine how the expected spore production of a patch, $\Phi$, is affected by a fungus’ allocation strategy.

**Spore Production and Allocation Schedule**

The dynamics of mycelial growth and spore production within a patch are determined by the fungus’ allocation schedule, $u$, and we are specifically interested in understanding how $u$ affects fungal fitness via expected spore production, $\Phi$. Equation (25) allows us to calculate the spore production rate, $p(a)$, for any age, $a$, given the mycelium density, the resource density, and the allocation rate, $m$, $r$, and $u$, respectively. Having an explicit formula for $p(a)$ allows us to use equation (9) to calculate the expected spore production, $\Phi$, given the initial resource and mycelium densities, $m_0$ and $r_0$, and the production schedule, $u$. 

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Combining equations (9) and (25) leads to the expression,

$$\Phi = \int_0^\infty m(a) r(a) u(a) \exp[-\mu a] \, da. \quad (28)$$

where the product of the terms $m$, $r$, and $u$ represents the spore production rate, $p(a)$, and $\exp[-\mu a]$ represents the probability a patch will persist until time $a$ given the background patch removal rate, $\mu$. Equations (22) and (23) define how a fungus’ allocation schedule, $u$, affects the dynamics of $r$ and $m$ within a patch. Because $r$ and $m$ are affected by $u$, from equation (28) it follows that a fungus’ expected spore production is both a direct and indirect function of $u$. Henceforth, we will view the expected spore production of a patch $\Phi$ as a functional of $u$ and, thus, employ the standard functional notation $\Phi[u]$. Below we identify the optimal static and dynamic allocation schedules which maximize the expected spore production of a patch.

**Static Allocation Schedules**

In this section we identify the optimal allocation schedules under the assumption that a fungus’ allocation schedule is fixed over its lifetime. When resource allocation is static, the allocation schedule $u(a)$ is equal to the constant $u_S$. Thus, in the static case, we are looking for the allocation level $u_S$ which maximizes the functional $\Phi[u = u_S]$ (which we abbreviate as $\Phi[u_S]$).

We begin by identifying the optimal allocation schedule, $\hat{u}_S$, under the simplifying assumption that the patch removal rate, $\mu$, is very small and, therefore, can be ignored. This simplifying assumption allows us to derive explicit, analytic solutions for $\hat{u}_S$ as a function of the initial conditions of a patch. We then relax this simplifying assumption and identify the optimal static allocation schedule, $\hat{u}_S$, when $\mu$ is (effectively) greater than zero using a numerical analysis.
Optimal Allocation Schedules for $\mu \approx 0$: Equation (28) indicates that the expected lifetime spore production of a fungus, $\Phi$, is equal to the spore production rate at each point in time $a$ weighted by the probability a patch will persist until $a$, summed across all time. If we assume that the resource and mycelium dynamics within a patch occur on a much faster time scale than the background patch removal rate $\mu$ (which we remind the reader is now scaled by the mycelial background decay rate $\gamma$), we can approximate equation (28) as,

$$\Phi[u_S] = \int_0^\infty m r u_S da,$$

(29)

thus removing any direct dependence of $\Phi$ on $a$. Although the difference between equations (28) and (29) may seem slight, because $\Phi$ is no longer explicitly dependent on $a$, our ability to evaluate equation (29) analytically is greatly increased.

As previously stated, we can only solve for $m$ and $r$ as an explicit function of $a$ when $u_S = 1$. However, when $u_S < 1$ we can get a time independent solution for mycelial density $m$ as a function of resource density $r$ by dividing equation (22) by equation (23). Doing so yields,

$$\frac{dm}{dr} = -(1 - u_S) + \frac{1}{r}.$$  
(30)

which can be solved, yielding:

$$m(r) = m_0 + \ln \left( \frac{r}{r_0} \right) + (r_0 - r) (1 - u_S).$$

(31)

Differentiating equation (30) with respect to $r$ indicates that $m$ is a decelerating function of $r$. Furthermore, no matter what the allocation strategy, the resource level in a patch, $r$, declines over time. Once the resource level drops below the critical resource level $1/(1 - u_S)$, the mycelial density begins to decline towards zero while the resource density declines towards a non-zero final resource density $r_f$. The final resource density, $r_f$, is a function of the fungus’ allocation level, $u_S$ and is defined implicitly by the equation,

$$m_0 + \ln \left( \frac{r_f}{r_0} \right) + (r_0 - r_f) (1 - u_S) = 0,$$

(32)
From equations (32) and (A.2) it can be shown that \( r_f(u_S) \) is an increasing function of \( u_S \), that is, less allocation to mycelium leads to a greater amount of resources remaining in the patch. Figure 3(a) provides an illustration of how \( u_S \) affects the system’s trajectory through the \( r \) and \( m \) phase plane and, ultimately, \( r_f \).

[Figure 3 about here.]

From equation (23), we have the relationship \( mr da = -dr \) which allows us to employ a substitution of variables in the integral in equation (29), giving us

\[
\Phi[u_S] = -u_S \int_{r_0}^{r_f(u_S)} dr 
= u_S(r_0 - r_f(u_S)).
\]

Note that this substitution of variables is only possible because there is no direct dependence of \( \Phi \) on \( a \) in equation (29) (c.f. equation (28)).

In Appendix A we show that the optimal allocation strategy, \( \hat{u}_S \), ultimately depends on the initial conditions of the within-patch model. If the initial mycelium density is large relative to the initial resource density, i.e., \( m_0 > \ln(r_0) \) then the optimal allocation strategy is to allocate all resources into spore production, i.e., \( \hat{u}_S = 1 \). Increasing mycelial density, \( m \), can sometimes lead to an indirect contribution to \( \Phi \) via greater future resource extraction. However, under these conditions it does not pay for the fungus to invest any resources into increasing its mycelium density, because there is so little resource to extract.

On the other hand, if the initial mycelial density is low relative to the resource density, then the optimal allocation strategy is to direct some of the resources (but never all) to mycelium growth, i.e., \( 0 < \hat{u}_S < 1 \). In this scenario, the initial amount of resources within the patch is great enough that the indirect benefit of investing in mycelium, which in turn allows for greater resource extraction in the future, outweighs the immediate reduction in spore production.
While resource extraction is important, the strategy which maximizes expected spore production, $\Phi$, does not entail extracting all of the resources within a patch. Indeed, if $m_0 \leq \ln(r_0)$, then optimal allocation strategy, $\hat{u}_S$, is such that $r_f(\hat{u}_S)$ equals 1. See Figure 3(b) for an illustration of this behavior.

More explicitly, we find that,

$$\hat{u}_S(r_0, m_0) = \begin{cases} 
1 - \frac{m_0 - \ln(r_0)}{1 - r_0} & \text{if } m_0 < \ln(r_0) \\
1 & \text{else} 
\end{cases}$$

Equation (35) indicates that there is a simple curve running through the initial condition parameter space which satisfies the equality $m_0 = \ln(r_0)$. Above this curve $\hat{u}_S = 1$ while below this curve $0 < \hat{u}_S < 1$ (see Figure 4).

[Figure 4 about here.]

Optimizing allocation when $\mu > 0$: If we relax the assumption that the background patch removal rate, $\mu$, is effectively zero, then we cannot carry out the substitution of variables we used in equation (33) to simplify our expression for $\Phi$. This is because a non-zero value of $\mu$ implies that it is not only the trajectory through $m$ and $r$ space and the resultant cumulative production that matters, but the timing of such production as well. Equation (28) implies that any contribution to $\Phi$ made by spore production at age $a$ must be weighted by the probability that the patch will survive until that age, $\exp(-\mu a)$. When $\mu > 0$, any future spore production is discounted relative to current spore production. Late sporulation contributes less to $\Phi$ than early sporulation because there is a chance the patch will be removed from the system by a disturbance event before this sporulation occurs. Because the actual timing of production must be known in order to calculate $\Phi$, it is necessary for us to know $p(a)$ strictly as a function of $a$. As a consequence, in order to calculate $\Phi$ when $\mu > 0$ we must rely on purely numerical methods to solve $m$ and $r$ as a function of $a$. 

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Fortunately, the equations describing the within-patch dynamics, (22) - (25) are generally well behaved and can be solved for any value of $u$ using standard numerical methods. Finding the optimal allocation value given the initial conditions $(r_0, m_0)$ and $\mu$ simply entails searching for the $u_S$ value which maximizes $\Phi$. Our numerical analysis indicates that when $\mu > 0$ the qualitative behavior of $\hat{u}_S$ as a function of $r_0$ and $m_0$ is similar to the case when $\mu = 0$. As before we find that there is a curve running through the initial condition parameter space, $(r_0, m_0)$, above which $\hat{u}_S = 1$ and below which $0 < \hat{u}_S < 1$.

Relative to the case of $\mu = 0$, increasing $\mu$ has the effect of shifting the curve dividing the two regions where $\hat{u}_S = 1$ and $0 < \hat{u}_S < 1$. At low values of $r_0$ and $m_0$, increasing $\mu$ leads to greater values of $\hat{u}_S$ relative to when $\mu = 0$. Figure 5(a) illustrates that when $r_0$ and $m_0$ are small the increase in spore production resulting from resource investment in mycelium occurs late in the lifespan of the fungus. When $\mu = 0$ there is no discounting of these spores, despite their late production, and consequently investing more resources in mycelium leads to an increase in expected spore production, $\Phi$. However, when $\mu > 0$, the contribution to $\Phi$ of these late spores is greatly diminished. Consequently, instead of investing resources in mycelium it is better to direct these resources directly towards spore production. One consequence of this behavior is that the dividing curve shifts to the right at low values of $r_0$ (see Figure 6(a)).

In contrast, outside of this region where $r_0$ and $m_0$ are small, increasing $\mu$ leads to lower values of $\hat{u}_S$. Figure 5(b) illustrates that in this region the fungus can grow relatively quickly and, as a result, the short term reduction in spore production due to investing more resources into mycelium (i.e., decreasing $u$) is more than offset by a large increase in spore production rate at intermediate timescales. This increased investment in mycelium will also lead to a reduction in spore production late in the fungus’ lifespan. However, this reduction has little impact on $\Phi$ because late spore production is heavily discounted. One consequence of this behavior is that the dividing curve shifts upward at higher values of $r_0$ (again see Figure
Dynamic Allocation Schedules

In the previous section we examined the case where the resource allocation schedule \( u \) was assumed to be fixed over the lifetime of a fungus. In this section we relax this assumption and allow \( u \) to vary dynamically with fungus age \( a \). In order to find the optimal dynamic production schedule, we use Pontryagin’s maximum principle (Pontryagin et al., 1964) which has a long and rich history in the field of life-history studies (Perrin and Sibly, 1993). The full details of our analysis are presented in Appendix B. Here we will simply summarize our results.

We find that, in general, the optimal allocation schedule will follow a bang-bang strategy, switching from \( u(a) = 0 \) to \( u(a) = 1 \) at the critical time point \( a_s \). Thus we define the step function,

\[
u_D(a; a_s) = \begin{cases} 
0 & \text{if } a < a_s \\
1 & \text{else}
\end{cases}.
\]

The temporal dynamics of \( m \) and \( r \) when a fungus follows a bang-bang strategy are illustrated in Figure 7.

The switching time which maximizes the functional \( \Phi[u = u_D(a; a_s)] \) (which we abbreviate as \( \Phi[u_D(a; a_s)] \)) is defined as the optimal switch time \( \hat{a}_s \) and satisfies the equality

\[
r(a) = f(m(a), \mu),
\]

where,

\[
f(m, \mu) = \frac{e^{-m}}{\int_0^1 (1 + m(x - 1))x^\mu e^{mx}dx}.
\]
Thus the optimal dynamic allocation schedule, $u_D(a; \hat{a}_s)$, is,

$$u_D(a; \hat{a}_s) = \begin{cases} 
0 & \text{if } r(a) > f(m(a), \mu) \\
1 & \text{else}
\end{cases}$$

The optimal allocation schedule defined in equation (39) simply states that as long as the resource density $r$ is above $f(m, \mu)$, then the optimal allocation strategy is to allocate all resources towards mycelium growth. As the fungus pursues this optimal allocation strategy the mycelium density will increase and, concomitantly, the resource density will decrease. Eventually $f(m, \mu)$ will equal the current resource density $r$. At this point the optimal strategy switches from allocating all resources towards mycelium growth to allocating all resources towards spore production. This allocation strategy is then pursued for the remainder of the fungus’ lifespan (Figures 7 and 8).

The integral in $f(m, \mu)$ can be solved explicitly when $\mu$ is any non-negative integer (i.e., $\mu = \{0, 1, 2, \ldots\}$), otherwise it can be evaluated numerically. For example, in the special case where $\mu = 0$, $f(m, 0)$ simplifies to $\exp(m)$ and, consequently, the optimal switch point satisfies the equality $\ln(r) = m$. Thus we find an interesting parallel between the optimal static and dynamic cases when $\mu \approx 0$. In the case of a fixed allocation schedule, the equality $m_0 = \ln(r_0)$ represents the dividing line between $\hat{u}_S = 1$ and $0 < \hat{u}_S < 1$. In the case of a dynamic allocation schedule, the equality $m = \ln(r)$ represents the switch point where the fungus switches from allocating resources towards within-patch growth to sporulation. In addition, when $\mu = 0$, the optimal switch curve and the mycelium-resource trajectory after switching are equivalent. Consequently, any optimal trajectory which begins below the
switch curve (i.e., \( r(0) > f(m(0), 0) \)), will eventually approach the final state of \( m = 0 \) and \( r_f = 1 \).

The optimal switch curves change with \( \mu \) in a manner reminiscent of the dividing curves in the static case (c.f. Figure 6 (b) and (a)). For \( \mu > 0 \), at low values of \( r \) the optimal switch curve decreases while at intermediate and high values of \( r \) the optimal switch curve increases relative to \( \mu = 0 \). Our explanation of these changes is also reminiscent of the static case. In the small region where \( r(\hat{a}_s)|_{\mu>0} < r(\hat{a}_s)|_{\mu=0} \), the growth rate of the fungus is so slow that instead of growing larger in order to produce more spores in the future, it switches earlier to allocate all resources to spore production. This is because, due to the slow fungal growth rate, the gain in spore production by growing larger is more than offset by the reduced value of these spores due to discounting (Figure 9(a)). However, for most values of \( r \), \( r(\hat{a}_s)|_{\mu>0} > r(\hat{a}_s)|_{\mu=0} \). In this region of the phase plane the fungus can grow quickly. Thus even though a fungus pays an immediate direct cost for delaying spore production, this delay is offset by the fact that when it does switch to spore production the initial spike of production will be larger. In addition, this delaying tactic also leads to a reduction in late spore production, but as with the static case, this later reduction has little impact on \( \Phi \) because late spore production is heavily discounted (see Figure 9 (b)). In the case where \( \mu = 0 \), after switching \( u \) to one the fungi decay along the curve \( r = \ln(m) \) in \((r, m)\) space. However, when \( \mu \neq 0 \), the optimal switching curve no longer coincides with these decay trajectories. As a result the final resource levels vary with the initial conditions of the system (see Figure 8(b))

[Figure 9 about here.]
Comparing Static and Dynamic Spore Production

In Appendix C we show how it is possible to calculate the optimal spore production rate for both the optimal dynamic and static production schedules when $\mu = 0$. Surprisingly, equations (C.2) and (C.6) indicate that the optimal expected fungal spore production in the dynamic scenario, $\Phi[u_D(a; \hat{a}_s)]$, is equivalent to the expected spore production in the static scenario, $\Phi[\hat{u}_S]$. Indeed, we can show that under the condition $\mu = 0$, there is actually a family of optimal solutions of which the optimal static schedule and optimal dynamic schedule are actually two special cases. In the portion of the $r$ and $m$ phase plane where $m \geq \ln(r)$, $\hat{u}_S = 1 = u_D(a; \hat{a}_s)$. When $m < \ln(r)$, at each age $a$ along a trajectory in $r$ and $m$ space, we can pick $u(a)$ either to be $\hat{u}_S(r, m)$ or zero. The value $\hat{u}_S(r, m)$ corresponds to the optimal static allocation strategy in this region while the value of zero corresponds to the optimal dynamic allocation strategy in this region. Essentially at every point we can pick between the static or dynamic strategy and a different set of choices will lead to a different trajectory for $r$ and $m$ through this region. However, all trajectories will give the same expected spore production, $\Phi$. Thus we see that under the special assumption that $\mu = 0$ there are uncountably many dynamic allocation schedules which can maximize spore production $\Phi$.

When comparing the fitnesses of the optimal dynamic and static schedules when $\mu$ is non-zero, the general family of optimal solutions we observe when $\mu = 0$ disappears. Nonetheless, there is a substantial region of parameter space where both $\hat{u}_S$ and $u_D(a; \hat{a}_s)$ are equivalent (i.e., $\hat{u}_S = 1$ and $\hat{a}_s = 0$) and, consequently, so are their spore production values (i.e., $\Phi[u_D(a; \hat{a}_s)] = \Phi[\hat{u}_S]$). However, outside this region where $\hat{u}_S = 1$ and $\hat{a}_s = 0$, when $\mu$ is non-zero we find that the optimal dynamic schedule leads to a greater expected number of spores than the optimal static schedule (i.e., $\Phi[u_D(a; \hat{a}_s)] > \Phi[\hat{u}_S]$). The relative difference between $\Phi[\hat{u}_S]$ and $\Phi[u_D(a; \hat{a}_s)]$ increases with decreasing values of $m_0$ and increasing values
Note on Patch Heterogeneity

The models used in this study were intentionally chosen to be simple for two reasons. The first reason is to facilitate their analysis and interpretation. The second reason is to provide a basic reference point for more elaborate models. For example, in the population model we assumed that resource patches are uniform, i.e., they all have the same initial resource level $r_0$. Here we briefly note that it is possible to relax this assumption by assuming that uncolonized patches are produced according to some continuous distribution such that $b(r_0)$ represents the production rate of patches with initial resource density equal to $r_0$. If we assume that spore quality and patch removal rates are independent of the patch’s initial resource level then allowing for heterogeneity in initial patch resource levels requires that we modify equations (1)-(4) in the following way. First, the density of uncolonized and colonized patches, $S$ and $I$, must now be indexed $r_0$ and now each represents a family of equations. Indexing $I$ by $r_0$ implies that the right-hand side of equation (3) must also be integrated across the distribution of $r_0$ values. A similar integration must also be carried out when calculating fungal fitness. Making the relevant parameters a function of $r_0$ and using $\tilde{w}$ to represent the expected fitness of a fungal strain across all habitat types, we see that if $r_0$ has a continuous distribution then

$$\tilde{w} = \int_{r_0} w(r_0) dr_0$$

$$= \frac{\sigma}{\sigma + \delta} \int_{r_0} \beta(r_0) \Phi(r_0) dr_0.$$  

It is clear that in the absence of any additional trade-offs, maximizing $\tilde{w}$ is equivalent to maximizing $w(r_0)$ at each initial resource value $r_0$. Thus the life-history strategies we identi-
fied for maximizing $\Phi$ in the within-host models apply to both the uniform and non-uniform patch models.

**Discussion**

A major goal of life-history theory is an understanding of the resource allocation strategies evolved by organisms. As a first step towards developing life-history theory for fungi, we developed a model of fungal population dynamics in which spores settle onto a resource patch, germinate, and, subsequently, create new spores. Because our population model is derived from the epidemiology literature we find a number of parallels between the spread and persistence of a disease within a host population and the spread and persistence of a fungus within a population of resource patches. For example, a disease will persist in a host population if the density of hosts is above a critical level (Anderson and May, 1979). Similarly, a fungus will persist in a patch system if the density of uncolonized patches is above a critical level. The value of this critical density will depend on the value of various fungal parameters such as the spore germination rate. One consequence of the existence of a critical density is that a novel fungal strain can replace the resident strain only if the novel strain can drive the density of uncolonized patches below the critical density of the resident strain. In essence, the novel fungus can replace the resident strain if it is more effective at capturing the limited number of uncolonized patches. By favoring strains which minimize the density of uncolonized patches, natural selection will, equivalently, maximize the product of the spore settlement rate, the germination probability, and the expected spore production of a patch divided by the sum of the spore settlement rate and the spore decay rate. It is this term which we identify as the appropriate measure of relative fitness for fungi whose life cycle is consistent with our population model. Fungi with different life cycles will require a similar formulation and analysis to identify the relevant fitness term, and these models can
be developed from the simple model we describe. The population model we used to identify fungal fitness precludes multiple colonizations of a single resource patch and, for this reason, does not permit for competition for resources within a patch. However, our current model and analysis suggests how the evolutionary behavior of the system may change if within-patch competition is allowed. We expect that within-patch competition will result in a set of patches structured by their resource levels. This set of structured resource patches should lead to different fungal species exploiting the different resource levels. We imagine that this resource partitioning will, in turn, allow for the co-existence of multiple fungal strains in a manner similar to competing digger and grazer snail species which are able to co-exist due to inherent trade-offs between resource acquisition and movement (Richards et al., 2000; Wilson and Richards, 2000) or multiple strains of parasites as have been suggested for host-parasite systems Nowak and May (1994); Mosquera and Adler (1998).

It is conceivable that each of the parameters in the fungal fitness term can be measured. For example, the total spore production of an individual has been estimated in a wide range of species such as *Ganoderma applanatus* (Buller, 1958), *Calvatia gigantea* (Buller, 1958), *Rhizopogon evadens* (T.D. Bruns, pers. comm.), and *Gigaspora gigantea* (Pringle, 2001). However, as our definition of expected spore production indicates, the total number of spores which can be produced by a patch is not all that matters. The timing of this production, weighted by the probability that the resource patch a fungus inhabits will persist to a given time, must be understood in order to accurately estimate the expected spore production of a fungus. For fungi in which spore production occurs in a large burst of sporulation over a relatively short period of time, the expected spore production can be estimated by weighting total spore production by the probability that a patch will persist until a fungus sporulates. Other fitness terms, such as spore germination or settlement rates, can also be estimated. For example, spore germination is easily measured in a wide variety of fungi including *Neurospora crassa*, and various species of arbuscular mycorrhizal fungi (Davis
and de Serres, 1970; Siqueira et al., 1982; Maia and Yano-Melo, 2001). In cases where the individual fitness terms are more difficult to measure it may be possible to estimate fitness indirectly by assuming the system is at equilibrium and measuring the density of uncolonized patches. Indeed our work suggests that this term may provide a tractable and, at this point, unexploited measure of fungal fitness. Such an approach may be most easily executed using fungi which infect clearly discretized habitats such as individual plants or animals.

Because it is likely that the different terms in the fitness measure we identify are interlinked, understanding how they are linked may lead to additional insights into fungal biology and life-history evolution. For example, one possible way a fungus could increase the expected number of spores it produces is by decreasing the size of each spore. However, if a trade-off between spore size and spore germination rate exists, then decreasing spore size may, ultimately, not be advantageous. Similar trade-offs have been explored in both the plant and animal literature (Smith and Fretwell, 1974; Lloyd, 1987; Elgar, 1990; Carriere and Roff, 1995; Einum and Fleming, 2000). These trades-offs are relatively well understood in a number of cases. Unfortunately, trade-offs between spore number, spore size, and germination rates have not received much attention in the mycological literature and, consequently, are poorly understood (Pringle and Taylor, 2002). Exploring the nature of these trade-offs in the lab or field might provide an understanding of a variety of questions, including, what is an optimal spore size? How does the optimum change with environmental conditions?

Furthermore, previous life-history models focused on maximizing the number of progeny where resources are self-renewing should apply to parasitic and mutualist fungi depending on the underlying model assumptions. However, these life-history models do not translate to saprophytic fungi growing on non-renewing resource patches. Consequently, in the second part of this study we examined how the spore production of such a fungus is influenced by its resource allocation strategy. We used a simple model of within-patch dynamics and identified the optimal resource allocation strategies under the assumptions that the allocation strategy
is either fixed or dynamic over the lifetime of the fungus. Our results suggest that when resources are limited relative to the size of the germinating spore, both the optimal static and dynamic strategies are to allocate all resources towards spore production, for the entire lifetime of the saprophytic fungus. When resource levels are high relative to the size of the germinating spore, the optimal static allocation strategy is a mixed one in which some resources are allocated towards mycelium production, while the rest are allocated towards spore production. The optimal proportion of resources allocated to mycelium vs. spores varies with the initial densities of resources and mycelium. In the more general case where the allocation strategy can vary dynamically over the lifetime of a fungus, the optimal strategy is a bang-bang strategy. In a bang-bang strategy all resources are first allocated towards mycelial growth and then, at a critical size, all resources are allocated towards sporulation. The critical size for switching between growth and sporulation is a function of the resource level and, consequently, changes with initial conditions of the system. When comparing the expected spore production of the optimal static and dynamic schedules, we found that except when the patch removal rate was zero, the dynamic schedule led to greater spore production than the static case.

In addition to the initial conditions of the system, we found that optimal resource allocation strategies are also sensitive to the background patch removal rate. When the initial resource levels are high, as the patch removal rate increases, the optimal static allocation strategy is to allocate less resources towards spore production and more resources towards mycelial growth. This shift in allocation level leads to an increase in the spore production rate at intermediate fungal ages at the cost of a slight decrease in spore production early in the fungus’ lifespan and a larger decrease in spore production late in the fungus’ lifespan. This large decrease in spore production late in life has little impact on expected spore production of a patch, because the probability a patch will persist to these late times is low.

In the case of the dynamic schedule, as the patch removal rate increases, the optimal
dynamic allocation strategy is to delay switching to sporulation so that the fungus can grow larger. Because delaying sporulation increases the probability that a patch will be removed before any spore production occurs, this change in strategy may seem paradoxical at first glance. In fact, because the fungus can grow quickly, the short delay in spore production is more than offset by a large increase in spore production at intermediate fungal ages. Furthermore, as in the static case, the decrease in late spore production is of little consequence because it is unlikely the patch will still be present at such times. In contrast, when the initial resource densities are low, the fungus’ growth rate is also low and it is generally more advantageous for the fungus to allocate more resources to spore production in the static case or switch to sporulation earlier in dynamic case. It is worth noting that we also show that variation in the patch resources does not affect the optimality of a particular allocation strategy for a given initial resource level.

How often saprophytic fungi actually pursue a dynamically optimal bang-bang strategy is uncertain. Instances where such strategies are observed may be viewed as weak evidence for the validity of our model. For example, fungi grown on a petri dish often display exactly this behavior. Anecdotal evidence suggests that other species may follow a bang-bang strategy in nature. Zygomycte taxa restricted to discrete habitats, including species of Pilobolus on dung or Rhizopus on fruit, will grow to cover the substrate and subsequently sporulate; so too will Ascomycete species of the genus Penicillium (Alexopoulos et al., 1996). It is also worth noting that bang-bang strategies have also been predicted in plant life-history studies (Iwasa and Roughgarden, 1984). This parallel suggests that fungi in patches with seasonal removal rates might develop an interoparous strategy (e.g. see Iwasa and Cohen, 1989). It is surprising to find that bang-bang allocation strategies may be useful for a disparate array of taxa under various resource conditions.

Given the evolutionary and ecological importance of fungi, it is clear that a better understanding of fungal fitness is needed. In this study we illustrate how, using a formal
description of a fungus’ life cycle, the appropriate fitness measure can be identified. While
the exact relationship between fitness and expected spore production, spore decay, spore set-
tlement, and spore germination may vary with different life cycles, we suspect that each of
these terms will be important fitness components for a wide array of fungi. Yet how exactly
such factors combine to shape an organisms fitness should be explicitly derived from explicit
models tailored for a particular fungal life cycle. In addition to such studies in the future it
will also be important to understand how within-patch competition and trade-offs between
different fitness components interact. These types of studies, ideally combined with empiri-
cal field and laboratory data, will provide important insights into how natural selection can
shape fungal life-history evolution.

Acknowledgments

M.G. gratefully acknowledges A. Wagner for support through NIH grant GM63882. A.P. ac-
knowledges support through the Miller Institute for Basic Research in Science and J.W. Tay-
lor for advice.

Appendices

A Optimal Allocation: Static Schedule when $\mu = 0$

We begin our maximization of expected spore production under the assumption of a static
allocation schedule, $\Phi[u_S]$, and with $\mu = 0$, by differentiating $\Phi[u_S]$ in equation (34) with
respect to $u_S$. Doing so yields,

$$\Phi'[u_S] = r_0 - r_f(u_S) - u_S r'_f(u_S).$$

(A.1)
where the prime indicates differentiation with respect to \( u_S \). In order to calculate the term 
\( r_0'(u_S) \), we differentiate our implicit definition of \( r_f \) from equation (32),

\[
r_0'(u_S) = r_f(u_S) \frac{r_0 - r_f(u_S)}{1 - (1 - u_S)r_f(u_S)}.
\] (A.2)

Substituting this expression into equation (A.1) yields,

\[
\Phi'[u_S] = \frac{(r_0 - r_f(u_S))(1 - r_f(u_S))}{1 - (1 - u_S)r_f(u_S)},
\] (A.3)

We will show below that the denominator of (A.3) is never zero; therefore the allocation strategy \( u_S \) which maximizes expected spore production \( \Phi[u_S] \) may either be an interior optimum or a boundary optimum. An interior optimum satisfies the following two conditions:

\[
\Phi'(u_S) = 0 \quad \text{and} \quad \Phi''(u_S) < 0;
\]

and a boundary optimum, satisfies either \( \Phi'[u_S] < 0 \) or \( \Phi'[u_S] > 0 \) for all \( u_S \), indicating a boundary optimum at \( u_S = 0 \) or \( u_S = 1 \), respectively.

To find the optimum \( u_S \), we show that the sign of (A.3) is determined by the sign of 
\( 1 - r_f(u_S) \). We begin by noting that because \( r \) is a decreasing function of \( a \), \( r_0 - r_f \) will, therefore, always be positive. Further, as we will now show, \( 1 - (1 - u_S)r_f(u_S) \) is also always positive. We show this by demonstrating that it is impossible for \( r_f \) to equal \( 1/(1 - u_S) \). If \( r_f \) was equal to \( 1/(1 - u_S) \) then from equation (32) we would conclude that

\[
r_0(1 - u_S) - \ln(r_0(1 - u_S)) = 1 - m_0.
\] (A.4)

However, for any positive variable \( x \), the general function \( x - \ln x \) is always greater than or equal to one, and, therefore, it follows that the left-hand side of (A.4) will always be greater than or equal to one. In contrast, because \( m_0 > 0 \), the right-hand side of (A.4) is always less than one. Thus, the equality in (A.4) can not be satisfied. Therefore, since \( r_f \) cannot equal \( 1/(1 - u_S) \), the denominator in equation (A.3) cannot change sign with \( u_S \). Further, because
\[ 1 - (1 - u_S)r_f(u_S) \] is positive when \( u_S \) is equal to one, we conclude that the denominator in equation (A.3) is positive for all \( u_S \) and, consequently, the sign of \( \Phi'[u_S] \) is equivalent to the sign of \( 1 - r_f(u_S) \).

As a result, in order for a valid interior optimum to exist \( r_f(\hat{u}_S) \) must be equal to 1 and \( \hat{u}_S \) must be between 0 and 1. Substituting the identity \( r_f = 1 \) into equation (32), implies that the unique solution for \( \hat{u}_S \) is,

\[ \hat{u}_S = \frac{r_0 - \ln(r_0) - 1 + m_0}{1 - r_0}. \] (A.5)

This is a valid solution provided \( 0 \leq u_S \leq 1 \); that is, provided

\[ 0 \leq r_0 - \ln r_0 - 1 + m_0 \quad \text{and} \quad m_0 \leq \ln r_0. \] (A.6)

The first inequality in (A.6) always holds \( (m_0 > 0 \text{ and } r_0 - \ln r_0 \geq 1) \); so only the second inequality needs to be satisfied. Finally, we note that when \( u_S \) is given by (A.5), it can be shown that

\[ \Phi''(\hat{u}_S) = - \left( \frac{(1 - r_0)^2}{1 - m_0 - r_0 + \ln(r_0)} \right)^2 < 0, \] (A.7)

thus proving that \( \hat{u}_S \) given by (A.5) is a unique interior optimum when \( m_0 \leq \ln r_0 \). The value of the optimal reproductive allocation strategy, \( \hat{u}_S \), is dependent on the initial conditions, \( m_0 \) and \( r_0 \), of the within-patch system. Also note for use in Appendix C that \( r_f(\hat{u}_S) = 1 \) in this case.

When \( m_0 > \ln r_0 \), (A.5) does not provide a valid optimum since the value of \( u_S \) is above the permissible range. As we now show, under these conditions \( \Phi \) is maximized at the boundary \( u_S = 1 \). In this case, we show that \( r_f(u_S) < 1 \) so that (A.1) implies \( \Phi'[u_S] > 0 \) for all \( u_S \). Therefore, \( \Phi[u_S] \) is an increasing function of \( u_S \), and the expected spore production is maximized at the boundary value \( u_S = 1 \). The proof that \( r_f(u_S) < 1 \) follows from examining
equation (32)

\[ \ln(r_f(u_S)) + (r_0 - r_f(u_S))(1 - u_S) = \ln(r_0) - m_0 < 0 \quad \text{therefore} \]

\[ \ln(r_f(u_S)) < (r_f(u_S) - r_0)(1 - u_S) < 0. \]

The above inequalities show \( \ln(r_f(u_S)) < 0 \), or \( r_f(u_S) < 1 \), as required.

To summarize, we have shown that the optimal reproductive strategy for a static allocation schedule when \( \mu = 0 \) depends on the initial conditions of the within patch model and is given explicitly by

\[ \hat{u}_S = \begin{cases} 
(r_0 - 1 - \ln(r_0) + m_0)/(1 - r_0) & \text{if } m_0 \leq \ln(r_0) \\
1 & \text{else} 
\end{cases} \]  

(A.8)

**B Optimal Allocation: Dynamic Schedule**

We wish to optimize the expected spore production, \( \Phi \). In the language of standard optimal control theory (Brogan, 1985), the goal is to optimize the total cost function which is the integral of the cost function or Lagrangian, \( L \) over a given time period. In our specific case, the Lagrangian is equal to the spore production rate weighted by patch survivorship (i.e., \( L(m, r, u, a) = u(a)m(a)r(a)e^{-\mu a} \)), and our time period is from from the initial age, \( a = 0 \) to the final age, \( a = a_f \).

The total cost function is \( \Phi \); explicitly,

\[ \Phi = \int_0^{a_f} L(m(a), r(a), u(a), a)da = \int_0^{a_f} u(a)m(a)r(a)e^{-\mu a}da. \]

(B.1)

The optimal control problem is to find the allocation strategy (i.e. control) \( \hat{u}(a) \) that maximizes \( \Phi \) subject to the dynamic constraints that \( m(a) \) and \( r(a) \) satisfy the equations (22)-(23). Because the function \( u(a) \) is a proportion, by definition it must be between zero and one. We call the set of functions whose range is between zero and one, admissible, and require that \( u(a) \) be in this admissible set. When the set of admissible controls is unrestricted,
the calculus of variations can be used to derive necessary conditions that characterize the optimal solution. In our case, the control, $u(a)$ is restricted to the interval $[0, 1]$; therefore unrestricted variations in $u(a)$ are not allowed. Pontryagin’s maximum principle (Pontryagin et al., 1964) provides a set of necessary conditions for optimality in the case of restricted controls. When these necessary conditions are satisfied, the solution must be a maximum. However, because these conditions are not sufficient, other solutions which maximize $\Phi$ may also exist.

The maximum principle states that the optimal allocation strategy $\hat{u}(a)$ is that member of the admissible set which maximizes the so-called Hamiltonian, $H$, at each age $a$. For a system with two state variables, the Hamiltonian is defined as

\[ H = L + \psi^1 f^1 + \psi^2 f^2 \]  

(B.2)

where $L$ is the Lagrangian. The functions $f^1$ and $f^2$ describe the dynamics of the two model variables (also called state variables) $m$ and $r$, (i.e., $f^1 = dm/da$ and $f^2 = dr/da$). The Hamiltonian also contains two new variables, $\psi^1(a)$ and $\psi^2(a)$, called co-state variables, which we describe next.

The co-state variables are Lagrange multipliers and, in our example, act to ensure that $m(a)$ and $r(a)$ satisfy equations (22)-(23). These co-state variables can be interpreted as describing the marginal value of mycelium and resources at each age $a$; respectively (Iwasa and Roughgarden, 1984). For the fungal-patch system, equation (B.2) can be rewritten as,

\[ H(m, r, u, \psi^1, \psi^2, a) = u m r e^{-\mu a} + \psi^1 m(r(1 - u) - 1) - \psi^2 r m \]  

(B.3)

As we show below, the co-state variables are the solutions to the following linear, ordinary
differential equations

\[
\frac{d\psi^1}{da} = -\left( \frac{\partial f^1}{\partial m} \psi^1 + \frac{\partial f^2}{\partial m} \psi^2 + \frac{\partial L}{\partial m} \right)
\]

\[
= - \left( (r(1-u) - 1)\psi^1 - r \psi^2 + u r e^{-\mu a} \right) \quad \text{(B.4)}
\]

\[
\frac{\partial \psi^2}{\partial a} = -\left( \frac{\partial f^1}{\partial r} \psi^1 + \frac{\partial f^2}{\partial r} \psi^2 + \frac{\partial L}{\partial r} \right)
\]

\[
= - \left( m(1-u)\psi^1 - m \psi^2 + u m e^{-\mu a} \right) \quad \text{(B.5)}
\]

with the boundary conditions \( \psi^1(a_f) = 0 \) and \( \psi^2(a_f) = 0 \).

Before we apply the maximum principle, we hope to provide some insight by digressing for a moment to explain the origin of the equations for the co-state variables \( \psi^1 \) and \( \psi^2 \), as well as the connection between maximizing the Hamiltonian for the system, \( H \), and our cost function, \( \Phi \). Readers who are not interested in this digression may skip to the paragraph containing equation (B.11).

To simplify the notation in this digression as well as emphasize its generality we will use vector notation. Let \( \vec{x}(a) \) be the age-dependent vector of state variables of the system. The dynamics of the state variables are determined by the set of equations defined by the vector \( \vec{f}(\vec{x}, u) \), thus, by definition,

\[
\frac{d\vec{x}}{da} = \vec{f}(\vec{x}(a), u(a)). \quad \text{(B.6)}
\]

In our specific case, \( \vec{x} = (m, r)^T \) and \( \vec{f}(\vec{x}, u) = (f^1, f^2)^T \).

Let the vector \( \vec{\psi} \) be a vector of our co-state variables which are also age dependent, e.g., \( \vec{\psi} = (\psi^1, \psi^2)^T \) in our specific case. Next let \( \vec{x}(a) \) and \( \hat{u}(a) \) be the optimal quantities and let \( \vec{x}(a) \) be an arbitrary set of state variables and let \( u(a) \) be an arbitrary but admissible allocation function. Because the final age is not fixed in advance, we also want to determine the optimal final age, \( \hat{a}_f \).

In this notation, the optimal control problem is to find \( \vec{x}(a), \hat{u}(a) \) and \( \hat{a}_f \) to maximize \( \Phi \), with \( \hat{u}(a) \) in the admissible set of functions. In order to do this, we define the function \( \vec{\Phi} \) as
the sum of the total cost, $\Phi$, and the Lagrange multipliers times the constraints,

$$
\Phi = \int_0^{a_f} \left\{ L(\tilde{x}, u, a) + \psi^T(a) \left[ f(\tilde{x}, u) - \frac{d\tilde{x}}{da} \right] \right\} da.
$$

As mentioned previously, the co-state variables $\psi$ are Lagrange multipliers and function to to ensure that $\tilde{x}$ will satisfy equation (B.6). If $\tilde{x}(a)$ satisfies equation (B.6) then the additional term in the last equation is zero and $\Phi$ and $\Phi$ have the same maximum. Our goal becomes to find $\hat{u}(a), \tilde{x}(a)$, and $a_f$ by maximizing the function $\Phi$.

A maximum of $\Phi$ is characterized by the property that the difference between $\Phi$ at the optimal value and $\Phi$ at any other value is non-negative. Thus, we define $\Delta \Phi = \Phi(\tilde{x}, \hat{u}, \hat{a}_f) - \Phi(\tilde{x}, u, a_f)$ and note that $\Delta \Phi \geq 0$ for any arbitrary set of $\tilde{x}$ and $a_f$ values and any arbitrary, but admissible, control function $u$.

Now consider slight perturbations from the optimal state, such that $\tilde{x}(a) = \hat{x}(a) + \delta \tilde{x}(a)$ and $a_f = \hat{a}_f + \delta a_f$, where $\delta \tilde{x}$ and $\delta a_f$ represent slight, but arbitrary changes in $\tilde{x}$ and $a_f$. A Taylor series expansion of $\Phi(\tilde{x}(a) + \delta \tilde{x}(a), u(a), \hat{a}_f + \delta a_f)$ shows that $\Delta \Phi$ is the first variation of $\Phi$, $\delta \Phi$, plus second and higher order terms in the perturbations. The optimality condition is $\Delta \Phi \geq 0$, but if $\tilde{x}, u$ and $a_f$ are close enough to $\hat{x}, \hat{u}$ and $\hat{a}_f$, then the second order and higher terms of the Taylor expansion can be ignored and the sign of $\Delta \Phi$ will be the same as the sign of $\delta \Phi$.

After performing the Taylor series expansion, integrating by parts, and collecting terms, the first variation of $\Phi$ can be written

$$
\delta \Phi = - \int_0^{a_f} \left\{ \left[ \nabla_x L(\tilde{x}, u, a) \right]^T + \psi^T \left( \frac{df}{d\tilde{x}} \right) + \frac{d\psi^T}{da} \right\} \delta \tilde{x} \right\} da + \psi^T(\hat{a}_f) \delta \tilde{x}(\hat{a}_f)
$$

$\quad - H(\tilde{x}(\hat{a}_f), u(\hat{a}_f), \psi(\hat{a}_f), \hat{a}_f) \delta a_f + \int_0^{a_f} \left[ H(\hat{x}, \hat{u}, \psi, a) - H(\hat{x}, u, \psi, a) \right] da,
$$

where the Hamiltonian of the system, $H$, defined to be $H(\hat{x}, \hat{u}, \psi, a) = L(\hat{x}, \hat{u}, a) + \psi(a)^T \hat{f}(\hat{x}, \hat{u})$, is the same as (B.2) or (B.3), but using the vector notation for the variables.
From the reasoning presented above, when $\delta \Phi$ is non-negative the system is optimized. Thus we wish to determine the necessary conditions under which $\delta \Phi \geq 0$ for any arbitrary set of perturbations, $\delta x$ and $\delta a_f$. One way to ensure this condition is for each of the terms in $\delta \Phi$ to be greater than or equal to zero. For example, if we examine the first term on the right-hand side of (B.8), because the term $\delta x(a)$ is arbitrary (and, therefore, its terms may be any sign), its coefficient must vanish for all $a$ on the optimal trajectory. Otherwise, if there is any interval in age, no matter how small, where this coefficient is positive (or negative), we can choose $\delta x(a)$ to be zero outside this interval and negative (or positive) inside this interval, and the integral of the product will be negative. Therefore, setting the coefficient of $\delta x(a)$ to zero, shows the Lagrange multipliers, $\bar{\psi}$, must evolve according to

$$\frac{d\bar{\psi}}{da} = -\left(\frac{df}{dx}\right)^T \bar{\psi} - \nabla_x L.$$  \hspace{1cm} (B.9)

This equation is the vector version of equations (B.4)-(B.5).

The boundary conditions for $\bar{\psi}$ arise from the term involving $\delta x(\hat{a}_f)$ in (B.8) which must also be nonnegative. If $a_f$ is not fixed, then $\delta x(\hat{a}_f)$ is arbitrary, so, using the same reasoning as above, its coefficient, $\bar{\psi}_T$ must vanish. This condition supplies the boundary condition that $\bar{\psi}(\hat{a}_f) = 0$. The second to last term in (B.8) gives the condition that the Hamiltonian must be zero at the final age, $H(\hat{x}(\hat{a}_f), u(\hat{a}_f), \bar{\psi}(\hat{a}_f), \hat{a}_f) = 0$, since $\delta a_f$ is arbitrary.

In addition, the integral containing the Hamiltonian in (B.8) must be non-negative for any admissible $u$, including a $u$ that equals $\hat{u}$ for all except an infinitesimal interval in $a$. Therefore, we must conclude that

$$H(\hat{x}, \hat{u}, \bar{\psi}, a) \geq H(\hat{x}, u, \bar{\psi}, a)$$ \hspace{1cm} (B.10)

for all $a$ and all admissible $u$. This equation constitutes a version of the Pontryagin maximum principle where $\hat{u}(a)$ is determined to maximize $H$ and thus ends our digression.
To apply the maximum principle, we examine the behavior of the Hamiltonian for our system, equation (B.3), by differentiating it with respect to $u$. Doing so gives us the condition,

$$\frac{\partial H}{\partial u} = mr(e^{-\mu a} - \psi^1).$$

(B.11)

Equation (B.11) indicates that when $\psi^1 > e^{-\mu a}$, the Hamiltonian, $H$, is a strictly decreasing function of $u$ (i.e., $\partial H/\partial u < 0$). Consequently, under this condition $H$ is maximized at $u = 0$. Conversely, when $\psi^1 < e^{-\mu a}$, we see that $H$ is a strictly increasing function of $u$ (i.e., $\partial H/\partial u > 0$). Under this condition $H$ is maximized at $u = 1$. Thus, the value of $u$ that maximizes $H$ depends on how $\psi^1$ changes with age.

As we demonstrated earlier, the dynamics of $\psi^1$ and $\psi^2$ are governed by equations (B.4)-(B.5), with the boundary conditions, $\psi^1(\hat{a}_f) = \psi^2(\hat{a}_f) = 0$. These boundary conditions are given at an arbitrary final age after which spore production and growth ceases (eventually we will look at the limit as $\hat{a}_f$ goes to infinity). Since $\psi^1(\hat{a}_f) = 0$ we conclude that $u(\hat{a}_f) = 1$ because $e^{-\mu \hat{a}_f} > 0$. Solving for $\psi^1$ and $\psi^2$ going backward in age from $\hat{a}_f$, either $u(a)$ stays 1, or there is an age, $\hat{a}_s$ where $u$ switches to zero. We assume there is at most one switch and it occurs if $\psi^1(\hat{a}_s) = e^{-\mu \hat{a}_s}$. Thus if $u_D(a; \hat{a}_s)$ is the optimal allocation level at age $a$, we conclude,

$$u_D(a; \hat{a}_s) = \begin{cases} 
0 & \text{if } \psi^1(a) > e^{-\mu a} \\
1 & \text{else} 
\end{cases}.$$  

(B.12)

In general, the optimal allocation schedule follows what is often referred to as a bang-bang strategy where the fungus switches from allocating all of its resources towards mycelium growth (i.e., $u = 0$) to allocating all of its resources towards spore production (i.e., $u = 1$). The optimal switch time $\hat{a}_s$ is defined by the relation,

$$e^{-\mu \hat{a}_s} = \psi^1(\hat{a}_s).$$

(B.13)
In order to obtain the conditions for the switch point we must solve for the functions $\psi^1$ and $\psi^2$. We begin by solving for $m$ and $r$ after the optimal switch point. Because $u$ is 1 for all $\hat{a}_s \leq a \leq \hat{a}_f$, we can explicitly solve for the mycelium and resource dynamics during this period. Doing so gives,

$$m(a) = m(\hat{a}_s) e^{-(a-\hat{a}_s)} \quad \text{(B.14)}$$

$$r(a) = r(\hat{a}_s) \exp \left[ - (m(\hat{a}_s) - m(a)) \right] \quad \text{if and only if } a > \hat{a}_s. \quad \text{(B.15)}$$

where $m(\hat{a}_s)$ and $r(\hat{a}_s)$ are equal to the mycelium and resource density at the optimal switch point $\hat{a}_s$.

Combining our solutions for $m$ and $r$ with the differential equations for $\psi^1$ and $\psi^2$ in (B.4)-(B.5) and their boundary conditions, it follows (after a fair amount of algebra) that

$$\psi^1(a) = r(\hat{a}_s) e^{-m(\hat{a}_s)+a} \int_{a}^{\hat{a}_f} (1 + m(\hat{a}_s) e^{\hat{a}_s(1+y-a)} \exp \left[ -y(1+\mu) + m(\hat{a}_s) e^{\hat{a}_s-a} \right] dy$$

Putting this expression for $\psi^1(a)$ into equation (B.13) we see that the optimal switch time, $\hat{a}_s$, satisfies the relation,

$$r(\hat{a}_s) = \frac{e^{m(\hat{a}_s)}}{\int_{\hat{a}_s}^{\hat{a}_f} (1 + m(\hat{a}_s) (e^{\hat{a}_s-y} - 1)) \exp \left[ -y(1+\mu) + m(\hat{a}_s) e^{\hat{a}_s-y} \right] dy. \quad \text{(B.17)}$$

Using the substitution $x = e^{\hat{a}_s-y}$ and taking the limit as $a_f \to \infty$ allows us to rewrite equation (B.17) as,

$$r(\hat{a}_s) = \frac{e^{-m(\hat{a}_s)}}{\int_{0}^{1} (1 + m(\hat{a}_s) (x - 1)) x^\mu e^{m(\hat{a}_s)x} dx. \quad \text{(B.18)}$$

We note that $m$ goes to zero as the final age goes to infinity, so the Hamiltonian will also go to zero, as required by the variational equation (B.8). The integral in equation (B.18) can be evaluated explicitly when $\mu = \{0, 1, 2, \ldots \}$, otherwise it can be evaluated numerically.
C Calculating Maximum Spore Production when \( \mu = 0 \)

Static Case

Here we show how it is possible to calculate the lifetime spore production of a fungus following the optimal fixed allocation schedule, \( \hat{u}_S \), solely in terms of the initial conditions of the system. To calculate \( \Phi[\hat{u}_S] \) we begin with equation (34) which states,

\[
\Phi[\hat{u}_S] = u(r_0 - r_f(\hat{u}_S)).
\]  

(C.1)

From Appendix A we know that when \( m_0 \leq \ln(r_0) \), \( r_f(\hat{u}_S) = 1 \) and \( \hat{u}_S \) is equal to \((r_0 - 1 - \ln r_0 + m_0)/(r_0 - 1)\). Thus, for \( m_0 \leq \ln(r_0) \),

\[
\hat{u}_S(r_0 - r_f(\hat{u}_S)) = r_0 - 1 - \ln r_0 + m_0.
\]

In the case where \( m_0 > \ln(r_0) \), \( \hat{u}_S = 1 \). Consequently, putting \( u = 1 \) in (32) and solving for \( r_f(1) \) shows \( r_f(1) = r_0 e^{-m_0} \). Thus,

\[
\Phi[\hat{u}_S] = \begin{cases} 
  r_0 - 1 - \ln r_0 + m_0 & \text{if } m_0 \leq \ln(r_0) \\
  r_0(1 - e^{-m_0}) & \text{else.}
\end{cases}
\]  

(C.2)

Dynamic Case

Here we show how it is possible to calculate the lifetime spore production of a fungus following the optimal dynamic schedule solely in terms of the initial conditions of the system. To calculate \( \Phi[u_D(a; \hat{a}_s)] \), we first recognize that because the spore production rate is zero prior to the switching time \( a_s \), we can rewrite the integral in equation (28) as,

\[
\Phi[u_D(a; \hat{a}_s)] = \int_{a_s}^{\infty} m(a) r(a) \, da.
\]  

(C.3)

Furthermore, because \( u_D(a; a_s) = 1 \) for all \( a > a_s \), we can use equations (26) and (27) to solve for \( m \) and \( r \) explicitly during this period. Doing so gives us the following definition of
\( \Phi \) as a function of \( m_s \) and \( r_s \),

\[
\Phi[u_D(a; a_s)] = r(a_s) \left( 1 - e^{-m(a_s)} \right). \tag{C.4}
\]

As previously mentioned at the optimal switch time \( \hat{a}_s \), the equality \( m(a_s) = \ln(r(a_s)) \) holds and, consequently, equation (C.4) can be rewritten as,

\[
\Phi[u_D(a; a_s)] = r(a_s) \left( 1 - \frac{1}{r(a_s)} \right). \tag{C.5}
\]

From equation (31) it can be shown that \( \hat{r}_s = m_0 + r_0 - \ln(r_0) \). Thus it follows that

\[
\Phi[u_D(a; \hat{a}_s)] = \begin{cases} 
    r_0 - 1 - \ln r_0 + m_0 & \text{if } m_0 \leq \ln(r_0) \\
    r_0 (1 - e^{-m_0}) & \text{else.}
\end{cases} \tag{C.6}
\]

Equations (C.2) and (C.6) indicate that the optimal static and dynamic schedules lead to the same expected spore production value under the condition that \( \mu = 0 \).
References


Elgar, M. A. 1990. Evolutionary compromise between a few large and many small eggs - comparative evidence in teleost fish. Oikos 59:283 – 287.


## Tables

### Population Model of Fungus & Patch Dynamics

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S(t)$</td>
<td>Number of uncolonized patches at time $t$</td>
<td>patch</td>
</tr>
<tr>
<td>$I(a,t)$</td>
<td>Density of colonized patches at time $t$ with fungal population age $a$</td>
<td>patch $\times$ time$^{-1}$</td>
</tr>
<tr>
<td>$Z(t)$</td>
<td>Number of spores in spore pool at time $t$</td>
<td>spores</td>
</tr>
<tr>
<td>$p(a)$</td>
<td>Spore production rate of a mycelium of age $a$</td>
<td>spores $\times$ time$^{-1}$</td>
</tr>
<tr>
<td>$b$</td>
<td>Uncolonized patch production rate</td>
<td>patch $\times$ time$^{-1}$</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>Spore settling rate from the spore pool</td>
<td>spore$^{-1} \times$ time$^{-1}$</td>
</tr>
<tr>
<td>$\beta$</td>
<td>Probability of successful spore germination</td>
<td></td>
</tr>
<tr>
<td>$\mu$</td>
<td>Patch removal rate</td>
<td>time$^{-1}$</td>
</tr>
<tr>
<td>$\delta$</td>
<td>Spore decay rate within the spore pool</td>
<td>time$^{-1}$</td>
</tr>
<tr>
<td>$\Phi$</td>
<td>Expected spore production over the lifetime of a patch</td>
<td>spore/patch</td>
</tr>
</tbody>
</table>

Table 1: Table of parameters, their definitions, and units for the population model defined in equations (1)-(4).
(a)

**Dimensional Model of Within-Patch Dynamics**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$m$</td>
<td>Density of mycelium within a patch</td>
<td>cells/patch</td>
</tr>
<tr>
<td>$r$</td>
<td>Density of resources within a patch</td>
<td>resources/patch</td>
</tr>
<tr>
<td>$u$</td>
<td>Proportion of resources allocated towards spore production</td>
<td></td>
</tr>
<tr>
<td>$m_0$</td>
<td>Initial mycelium density</td>
<td>cells/patch</td>
</tr>
<tr>
<td>$r_0$</td>
<td>Initial resource density</td>
<td>resources/patch</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>Mycelium cell background death rate</td>
<td>time$^{-1}$</td>
</tr>
<tr>
<td>$\varepsilon$</td>
<td>Resource extraction rate</td>
<td>cell$^{-1} \times$ time$^{-1}$</td>
</tr>
<tr>
<td>$c_1$</td>
<td>Conversion rate of resources into mycelium</td>
<td>cells/resource</td>
</tr>
<tr>
<td>$c_2$</td>
<td>Conversion rate of resources into spores</td>
<td>spores/resource</td>
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</table>

(b)

**Dimensionless Model of Within-Patch Dynamics**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$m'$</td>
<td>Density of mycelium within a patch</td>
<td>$\gamma/\varepsilon$</td>
</tr>
<tr>
<td>$r'$</td>
<td>Density of resources within a patch</td>
<td>$\gamma/(c_1 \varepsilon)$</td>
</tr>
<tr>
<td>$u$</td>
<td>Proportion of resources allocated towards spore production</td>
<td></td>
</tr>
<tr>
<td>$m'_0$</td>
<td>Initial mycelium density</td>
<td>$\gamma/\varepsilon$</td>
</tr>
<tr>
<td>$r'_0$</td>
<td>Initial resource density</td>
<td>$\gamma/(c_1 \varepsilon)$</td>
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</table>

Table 2: Table of parameters, their definitions, and units for the within-patch model of mycelium dynamics. (a) Parameters in the dimensional version as defined in equations (19)-(21). (b) Parameters in the dimensionless version as defined in equations (22)-(25).
List of Figures

Figure 1  Diagram of fungus and patch population processes. Uncolonized patches flow into the system at a steady rate. Uncolonized patches can become colonized via spore settlement from the spore pool. Colonized patches produce new spores which enter into the spore pool. Both uncolonized and colonized patches are removed from the system at a constant rate. Spores also decay at a constant rate. See text and Table 1 for more detailed model and parameter definitions.

Figure 2  Diagram of within patch mycelium and resource processes within a colonized patch. The fungus extracts resources from the patch at a rate proportional to the resource and mycelium densities within the patch. Extracted resources can then be used to produce either spores or mycelium cells based on the resource allocation schedule of the fungus. See text and Table 2 for more detailed model and parameter definitions.

Figure 3  (a) Within-patch model phase plane dynamics of mycelial density $m$ and resource density $r$ for fungal patches starting with the same initial conditions $(r_0, m_0) = (5, 0.3)$ but under different fixed allocation strategies $u_S$. (b) Within-patch phase plane dynamics of mycelium density $m$ and resource density $r$ when the allocation strategy $u_S$ is optimized according to equation (35). The thick line delineates the regions where $\hat{u}_S = 1$ and $0 < \hat{u}_S < 1$ is defined by the equation $m_0 = \ln(r_0)$.

Figure 4  Contour plots of the optimal resource allocation parameter value $\hat{u}_S$ as a function of the initial conditions of the within-host system. Plots differ by patch removal rates. (a) low patch removal rate, $\mu \approx 0$ and (b) high patch removal rate, $\mu = 1$. The thick line delineates regions where $\hat{u}_S = 1$ and $0 < \hat{u}_S < 1$ is defined by equation (37).
Figure 5  Plots comparing spore production rates, $p$, vs. fungus age, $a$, when the fungus follows the optimal static production schedule, $\hat{u}_S$, for two different patch removal rates, $\mu \approx 0$ and $\mu = 1$. Plots (a) and (b) differ by initial mycelium and resource levels, $m_0$ and $r_0$, respectively. (a) Low $r_0$ and $m_0$ values ($r_0 = 2, m_0 = 0.4$). Here the optimal allocation level to spore production, $\hat{u}_S$, increases with $\mu$ leading to an increase in spore production early in the fungus’ lifespan at the cost of a decrease in spore production later. (b) High $r_0$ and $m_0$ values ($r_0 = 30, m_0 = 1$). Here the optimal allocation level to spore production, $\hat{u}_S$, decreases with $\mu$ leading to a decrease in early and late spore production but a large increase in spore production at intermediate time scales.

Figure 6  Comparison of the effect of the patch removal rate, $\mu$, on the behavior of the optimal static and dynamic resource allocation strategies, $\hat{u}_S$ and $u_D(a; \hat{a}_s)$ respectively. (a) Static case: the effect of $\mu$ on the curve dividing the regions where $\hat{u}_S = 1$ and $0 < \hat{u}_S < 1$. (b) Dynamic case: the effect of $\mu$ on the location of the optimal switch curve defined by equation (37).

Figure 7  Illustration of patch dynamics and spore production vs. colony age $a$ for a fungus following a bang-bang strategy. The terms $m$ and $r$ represent the density of mycelium and resources within the patch while $\phi$ represents the cumulative number of spores produced. Prior to the switch point at $a = 1$, all resources are allocated towards mycelial growth (i.e., $u = 0$). After the switch point, all resource are allocated towards spore production (i.e., $u = 1$).

Figure 8  Various within-patch model trajectories in the resource density $r$ and mycelium density $m$ phase plane where the dynamic resource allocation parameter $u(a)$ is chosen to maximize spore production, $\Phi$, based on the initial conditions of the system $(r_0, m_0)$. Dashed
line indicates optimal switch curve. Below the switch curve all resources are allocated towards mycelial growth \((u(a) = 0)\). Upon reaching the switch curve and all resources are allocated towards spore production \((u(a) = 1)\). (a) Optimal trajectories for when \(\mu = 0\). The mycelium density declines along the curve \(m(a) = \ln(r(a))\). (b) Optimal trajectories when \(\mu = 1\). The mycelium density no longer declines along the switch curve and, consequently, the amount of resources left in the patch varies with the initial conditions.

Figure 9  A comparison of production schedules when a fungus uses the optimal allocation switch \(\hat{a}_s\) for when \(\mu = 0\) and \(\mu = 1\) for two representative points in parameter space. (a) Low \(r\) values \((r_0 = 2, \ m_0 = 0.4)\). Here the optimal switch time to spore production, \(\hat{a}_s\), decreases with \(\mu\) leading to an increase in spore production early in the fungus’ lifespan at the cost of a decrease in spore production later. (b) High \(r\) values \((r_0 = 30, \ m_0 = 1)\). Here the optimal switch time to spore production, \(\hat{u}_S\), increases with \(\mu\) leading to an decrease in early and late spore production but a large increase in spore production at intermediate time scales.

Figure 10  Contour plot illustrating relative differences in expected spore production under the optimal static and dynamic allocation strategies, \(\Phi_S\) and \(\Phi_D\), respectively, when \(\mu = 1\).
Figures

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