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IDENTIFYING FITNESS AND OPTIMAL LIFE-HISTORY STRATEGIES FOR AN ASEXUAL FILAMENTOUS FUNGUS

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Abstract.—Filamentous fungi are ubiquitous and ecologically important organisms with rich and varied life histories, however, there is no consensus on how to identify or measure their fitness. In the first part of this study we adapt a general epidemiological model to identify the appropriate fitness metric for a saprophytic filamentous fungus. 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 life history model of the same fungus within a resource patch to show that a bang-bang resource allocation strategy maximizes the expected spore production, a critical fitness component. Unlike bang-bang strategies identified in other life-history studies, we find that the optimal allocation strategy for saprophytes does not entail the use of all of the resources within a patch.

Key words.—Bang-bang strategy, clonality, commensal, mycology, resource allocation, saprophyte.

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Fungi are ubiquitous organisms, often with complex life cycles, which influence the ecology and evolution of a wide range of taxa. Their ecological roles can range from mutualism to parasitism or even both depending on the environmental conditions (Pringle 2001). The fungal kingdom is diverse and, ironically, it is this diversity and the complexity of life cycles which has hindered the development of formal theory. For example, mycologists struggle to identify appropriate fitness metrics for filamentous fungi (Antonovics and Alexander 1989; Braiser 1999; Pringle and Taylor 2002). Moreover, there are few data to allow the comparison of one fitness estimate to another (but see Xu 1995; Pringle et al. 2003).

Without an understanding of what constitutes fitness, the selective forces shaping the evolution of different fungal life histories have been difficult to identify. The body of theory focused on fungal life histories is sparse. For example, an important study by Damgaard and Ostergard (1997) concentrates on a polycyclic fungal pathogen. The focus of this study is the within-patch resource use and spore production of a pathogenic fungus and, as a result, the authors do not explicitly derive the appropriate fitness metric of the fungus. In general, the conceptual foundation of these studies is varied, often incomplete, and less general than work done with other organisms.

In contrast, in both the plant and animal literature life-history theory has a long and rich tradition (Kozlowski 1992; Glazier 1999; Stearns 2000). Numerous life-history models have been developed to explore and describe the fitness advantages driving the evolution of various strategies. These efforts have yielded considerable insights into such areas as the trade-offs between itero 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). No parallel theoretical framework exists within the field of mycology.

This lack of a cohesive theoretical framework for fungi may stem from the fact that there is no standard fungal life cycle. Consequently, there may be no single fitness metric appropriate to all fungi because there is not a single life-history strategy common to all fungal species. Nonetheless, the appropriate fitness metric and optimal life-history strategy should be identifiable based on its particular lifestyle.

For example, models of plant life histories (for a recent review, see Iwasa (2000)) are likely to be directly applicable to fungi living in patches with renewable resources such as commensals or mutualists of root systems or endophytes of leaves. Fungi that negatively affect the ''life span'' of an occupied patch can be viewed as parasites and, consequently, one can draw on a wide range of life history models for such systems (Sasaki and Iwasa 1991; Antia et al. 1994; Ganusov et al. 2002; Coombs et al. 2003; Gilchrist et al. 2004).

However, many fungi are neither commensals, mutualists, or parasites, but instead saprobes. Hawksworth (2001) estimates the number of saprobic species of fungi to be in the hundreds of thousands. In addition to their great diversity, saprobic fungi are of great ecological importance, representing the primary decomposers of plant and animal tissues.

Saprobes differ from mutualists or parasites because saprobes do not directly influence the life span of resource patches, which are by definition dead. Saprobes differ from commensals because they do not inhabit renewable resource patches. As a result, the assumptions of previously developed life-history models are clearly violated. Consequently, our study is focused on elucidating appropriate fitness measures and the optimal life-history strategies of saprophytes.

More specifically, the first goal of our study is to illustrate how an idealized, primarily asexual saprobic fungi's natural history can be translated into a structured epidemiological

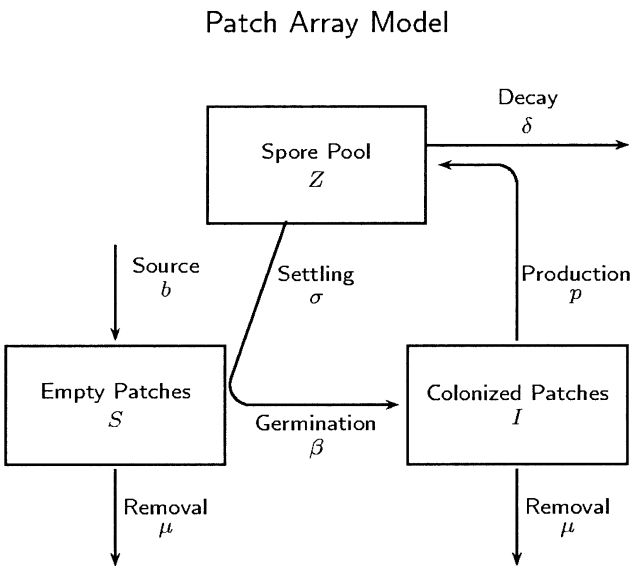

FIG. 1. Diagram of fungus and patch array processes. Uncolonized patches flow into the system at a steady rate. Uncolonized patches can become colonized via spore settlement from the spore pool. Colonized patches produce new spores which enter into the spore spool. Both uncolonized and colonized patches are removed from the system at a constant rate. This last assumption makes this resource patch array model directly applicable to both commensal and saprophytic fungi. The model can be applied to parasites or mutualists by modifing this assumption as noted below. Spores also decay at a constant rate. See text and Table 1 for more detailed model and parameter definitions.

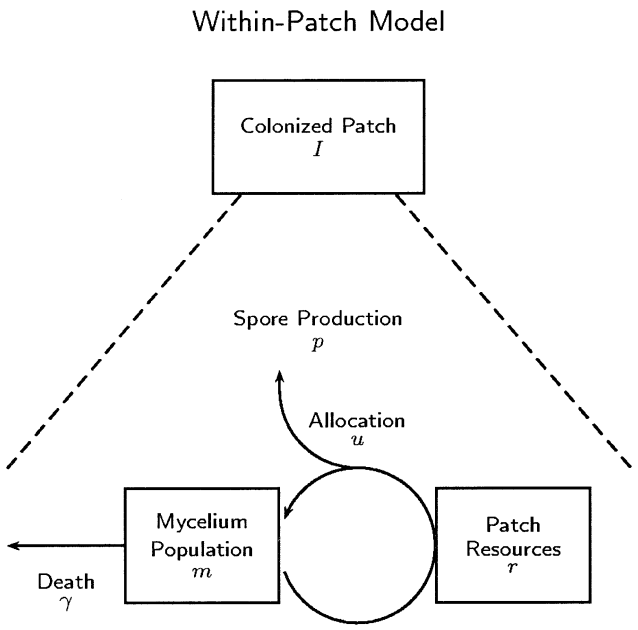

FIG. 2. Diagram of within-patch model which describes mycelium and resource dynamics inside a colonized patch. The fungus extracts resources from the patch at a rate proportional to the resource and mycelium densities within the patch. Extracted resources can then be used to produce either spores or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

model and how the tools of invasion analysis can be applied to derive the appropriate fitness term. In our model a fungal spore settles out of a spore pool onto a suitable resource patch, germinates, and then grows within the patch. As the fungus grows it can generate new asexual spores which are released from the patch back into the spore pool (Fig. 1). By formalizing this idealized description of a filamentous fungus' life cycle into an age-structured population model, we can identify the appropriate fitness metric using an invasion analysis. Our approach could be adapted to fungi with different ecological roles or more complicated life cycles by following these same steps of mathematical formalization and invasion analysis. We will refer to this model as our patch array model because it focuses on the dynamics of a fungus within an array (i.e., ''population'') of discrete resource patches.

Although not all saprobes colonize discrete resource patches, many do and the concept of a discrete resource patch has been used in other studies of both between-patch and within-patch fungal processes (Newton et al. 1998; Gourbiere et al. 1999; Gourbiere and Gourbiere 2002). Examples of saprobes that inhabit discrete resource patches include fungi on pine needles (Gourbiere et al. 1999, 2001) or fungi on individual trees such as *Neurospora spp*. (Jacobson et al. 2002), members of the Aphyllophorales (Alexopoulos et al. 1996), any saprobe restricted to rotting animals, or even water molds (Alexopoulos et al. 1996).

The second goal of this study is to illustrate how, having identified the appropriate fitness metric, one can begin to address simple life-history questions such as the allocation of resources to either mycelial growth or spore production. These allocation decisions occur at the scale of an individual fungus living within a resource patch. As a result, our life-history model is essentially a within-patch model of resource use and will be referred to as the within-patch model.

We note that our approach for coupling within-patch dynamics with a patch array model differs from the metapopulation approach developed by Gourbiere and Gourbiere (2002). Because of its metapopulation focus, in that study competitive interactions are modeled using classic Lotka-Volterra competition coefficients. Such an approach essentially reduces any within-patch processes to a ''black box'' and, as a result, can not address the life-history trade-offs that must underly such competitive interactions.

METHODS AND RESULTS

Deriving a Fitness Metric using a Patch Array Model

To model the population dynamics of fungi which inhabit discrete resource patches, we employ a mixture of coupled ordinary and partial differential equations that are derived from a structured epidemiological model (e.g., Murray 1993; Gilchrist and Sasaki 2002; Day and Proulx 2004). We keep track of three different components: uncolonized patches, colonized patches, and the fungal spore pool, S, I, and Z, respectively (see Fig. 1 and Table 1).

Our patch array model is for a single, asexual fungal strain that is either a saprophyte or commensal (hereafter referred to as the fungus or fungi). We assume that new, identical uncolonized patches, such as newly burned trees, flow into the system at a constant rate b. Uncolonized patches can be

TABLE 1. Parameters, their definitions, and units for the array model defined in equations (1)–(4).

Parameter	Definition	Units
Model of Fungus Population and Patch Array Dynamics		
$S(t)$	Number of uncolonized patches at time t	patch
$I(a, t)$	Density of colonized patches at time t with fungus age a	patch $\times$ time^{-1}
$Z(t)$	Number of spores in spore pool at time t	spores
$p(a)$	Spore production rate of a mycelium of age a	spores $\times$ time^{-1}
b	Uncolonized patch production rate	patch $\times$ time^{-1}
σ	Spore settling rate from the spore pool	spores^{-1} $\times$ time^{-1}
β	Probability of successful spore settlement & germination	
μ	Patch removal rate	time^{-1}
δ	Spore decay rate within the spore pool	time^{-1}
Φ	Expected spore production over the lifetime of a patch	spore/patch

transformed into colonized patches with the arrival and successful germination of a single fungal spore from the spore pool. 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).

Fungal spores either settle out of the spore pool or decay, becoming inviable. We will assume the spore settling rate from the spore pool, σ, and the spore decay rate within the spore pool, δ, are constants. The term β represents the probability a spore will land in a particular patch (i.e., the ratio of the area of a patch to the total area on which a spore could land) multiplied by the probability of successful germination given it lands in a patch. Either small patch sizes or low viability will lead to low values of β. We also explicitly assume that the germination rate of a spore arriving into an already colonized patch is zero. This assumption prevents any within-patch competition between individual fungi.

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 because it allows spore production to vary dynamically over the life span of the fungus. At this point we leave the exact form of $p(a)$ unspecified. Later we will assume it to be a function of the life-history strategy of a fungus within a resource patch. Finally, we note that patches have a background removal rate μ which represents the rate at which patches are destroyed by flood, burial, or other patch scale disturbance.

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

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

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

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

Equation (2) is a partial differential equation in which the left hand side indicates that colonized patches are structured by both time, t, and the age of the colonizing fungus, a. The right hand side of the equation indicates that colonized patches are removed at a constant per patch rate. Because both t and a have units of time, we will assume that $dt/da = 1$. The boundary condition for equation (2) is the influx of newly colonized patches into the age-structured system. Thus,

$$I(t,0) = \sigma\beta SZ. \tag{4}$$

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 our model to get the equilibrium densities of S, I, and Z. Using the superscript * to denote the equilibrium densities, the solutions are:

$$S^* = \frac{\sigma + \delta}{\sigma\beta\Phi} \tag{5}$$

$$I^*(a) = I_0^* \exp(-\mu a) \tag{6}$$

$$Z^* = \frac{1}{\beta\sigma}\left(\frac{b}{S^*} - \mu\right) \tag{7}$$

where,

$$I_0^* = b - \mu S^* \quad \text{and} \tag{8}$$

$$\Phi = \int_0^\infty p(a)\exp(-\mu a)\, da. \tag{9}$$

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, μ. Note that mutualists or parasites would influence the patch removal rate after colonization, and these changes could be incorporated into the exponential function in (9) if one wished to extend the models (e.g., Sasaki and Iwasa 1991).

In addition to the above solution, there is a second equilibrium, but at this equilibrium the fungus does not persist. In this second case, $S^* = b/\mu$, $I_0^* = 0$, and $Z^* = 0$. For the fungus to survive within the system the first equilibrium must

be stable and the second equilibrium must be unstable. If these conditions are to be met,

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

which implies that the density of uncolonized patches, S^*, under the first equilibrium when the fungus is present must be less than the density of uncolonized patches in the absence of the fungus, b/μ. From equation (5) it follows that there is a critical number of spores, Φ_c which must be produced for a fungus to be able 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 (May and Anderson 1979; Anderson and May 1991; Murray 1993; Jeger and van den Bosch 1994).

Invasion Analysis

In the previous section we found that equations (5) and (10) define the necessary conditions for a fungal strain to persist within the system. In this section we ask how the conditions for fungal persistence change when more than one fungal strain is competing for uncolonized patches. To determine when one fungal strain is more fit than another at the between-patch level, 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 absolute fitness, W, of a spore produced at time $t = 0$ from both the resident and novel strains.

From the perspective of a spore, absolute fitness is equal to the expected number of progeny spores. By virtue of the fact that the resident population is at equilibrium the absolute fitness of the resident strain, W_r, is equal to 1. Thus, when the absolute fitness of the novel strain, W_n, is greater than 1, then the novel strain will invade the resident population.

To calculate the absolute 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 $z_n(t) = \exp[-(\sigma_n + \delta_n)t]$.

At any given time point, the rate at which spores settle and successfully germinate is $\sigma\beta S_r^* z(t)$. Successfully settling and germinating spores leads to, on average, the production of Φ_n new spores.

Thus, the expected number of spores produced from a single spore is,

$$W_n = \Phi_n \int_0^\infty \sigma_n\beta_n S_r^* z_n(t)\, dt = S_r^* \frac{\sigma_n\beta_n\Phi_n}{\sigma_n + \delta_n} \tag{12}$$

$$= \frac{S_r^*}{S_n^*}. \tag{13}$$

Combining this result with the fact that $W_r = 1$ leads to the invasion criterion,

$$S_n^* < S_r^*. \tag{14}$$

Thus 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. Furthermore, minimizing S^* is equivalent to maximizing its inverse. Using Equation (5) we define relative fitness, w, as,

$$w = \frac{\sigma\beta\Phi}{\sigma + \delta}. \tag{15}$$

Thus we see that that in the absence of any trade-offs, the fitness of an asexual saprobe increases with the expected lifetime spore production of a patch, Φ, the rate at which its spores successfully settle into and germinate within a resource patch, β, and the ratio of spore settlement to spore decay, σ/δ. Furthermore, because all of the terms in w are for a single fungal strain (i.e., δ, σ, β, and Φ are not dependent on the competing strain), coexistence between two different fungal strains is in essence impossible.

Although it is easy to imagine trade-offs between any or all of the terms in equation (15), we will assume that the expected spore production Φ is independent of all other terms (c.f. Gilchrist et al. 2004). We now define and analyze a simple model of the growth of a fungus within a patch to identify optimal life-history strategies as they relate to the initial size of a fungus, the amount of resources contained in a patch, and the patch decay rate, μ.

Allocation Strategies for Saprophytic Fungi

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 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 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, Φ. To identify the optimal allocation strategy which maximizes Φ for a saprophytic filamentous fungus we define a simple model of mycelial dynamics within a non-renewable resource patch whose residence time is independent of the behavior of the colonizing fungus.

General Model of Fungal Growth within a Patch

We formulate the within-patch model by first assuming that every patch has the same initial density of resources, r_0, and that each spore germinates and leads to the same initial density of mycelial cells, m_0. These assumptions are consistent with our patch array model. In addition, we assume that the density of fungal mycelium m decays at a constant rate γ. 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.

Resources extracted from the patch by the fungus can be allocated to the production of either spores (Z in the patch

TABLE 2. Parameters, their definitions, and units for the within-patch model of mycelium dynamics. (a) Parameters in the dimensional version as defined in equations (16)–(18). (b) Parameters in the dimensionless version as defined in equations (19)–(21).

Parameter	Definition	Units
(a) Dimensional Model of Within-Patch Dynamics		
m	Density of mycelium within a patch	cells/patch
r	Density of resources within a patch	resources/patch
u	Proportion of resources allocated towards spore production	
m_0	Initial mycelium density	cells/patch
r_0	Initial resource density	resources/patch
γ	Mycelium cell background death rate	time^{-1}
ϵ	Resource extraction rate	cell^{-1} $\times$ time^{-1}
c_1	Conversion rate of resources into mycelium	cells/resource
c_2	Conversion rate of resources into spores	spores/resource.
(b) Dimensionless Model of Within-Patch Dynamics		
m'_0	Density of mycelium within a patch	γ/ϵ
r'_0	Density of resources within a patch	$\gamma/(c_1\ \epsilon)$
u	Proportion of resources allocated towards spore production	
m'_0	Initial mycelium density	γ/ϵ
r'_0	Initial resource density	$\gamma/(c_1\ \epsilon)$

array model) or mycelium cells m which form the hyphae within the patch. Whereas spore production leads to a direct contribution to the expected spore production of a patch, Φ, increasing mycelium density, m, can lead to an indirect contribution to Φ 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 $u(a)$ is a proportion it is constrained to be between zero and one. Our model assumptions lead to the following coupled equations:

$$\frac{dm}{da} = m[c_1\varepsilon r(1 - u) - \gamma], \tag{16}$$

$$\frac{dr}{da} = -\varepsilon mr, \tag{17}$$

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

Assuming that the spore production rate of the fungus, $p(a)$, is proportional to the amount of resources allocated to spore production by the fungus provides a link between this within-patch model and the expected spore production of a fungus, Φ, in the patch array model. It follows that,

$$p = c_2\varepsilon mru. \tag{18}$$

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 (for a more detailed discussion, see Edelstein-Keshet 1988). For our study, we can simplify our within-patch model by choosing our units of mycelial density m, resources r, spores Φ, mycelium age a, and patch removal rate μ by setting them equal to γ/ε, $\gamma/c_1\varepsilon$, $c_2\gamma/c_1\varepsilon$, $1/\gamma$, and $1/\gamma$, respectively. Doing so allows us to rewrite the within-patch model as,

$$\frac{dm'}{da'} = m'(r'(1 - u') - 1) \tag{19}$$

$$\frac{dr'}{da'} = -m'r' \tag{20}$$

with,

$$p' = m'r'u', \tag{21}$$

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 (19) and (20) can only be solved as an explicit function of a when $u(a) = 1$. Under this condition,

$$m(a) = m(a_s)\exp[(a - a_s)] \tag{22}$$

$$r(a) = r(a_s)\exp\{-[m(a_s) - m(a)]\}, \quad \text{if and only if } u = 1 \text{ from } a_s \text{ to } a, \tag{23}$$

where a_s represents the time at which $u(a)$ is set equal to 1.

Although 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 (19) and (20). For example, as long as m and r are nonzero, 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 $1/(1 - u)$ 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 (19) and (20) allows us to determine how the mycelial and resource densities within a patch change over time. These dynamics

are controlled by the life-history allocation strategy of the fungus, $u(a)$. Equation (21) allow us to relate the within-patch dynamics and the allocation strategy $u(a)$ of a fungus to its spore production rate $p(a)$.

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, Φ. Equation (21) 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 Φ given the initial resource and mycelium densities, m_0 and r_0, and u. Combining equations (9) and (21) leads to the expression,

$$\Phi = \int_0^\infty m(a)r(a)u(a)\exp(-\mu a)\,da, \tag{24}$$

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, μ. Equations (19) and (20) 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 (24) 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 Φ as a functional of u and, thus, employ the standard functional notation $\Phi[u]$.

To find an 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 A and B available online at: http://dx.doi.org/10.1554/05-261.1.s1. Here we will simply summarize our results.

A bang-bang strategy is defined as when all resources are first allocated towards vegetative growth and then, at a critical point, all resources are allocated towards reproduction (Vincent and Pulliam 1980). We find that, in general, the optimal allocation schedule will follow such a bang-bang strategy, switching from a 100% allocation to mycelial growth, $u(a) = 0$, to a 100% allocation to sporulation, $u(a) = 1$, at the critical time point a_s. (The notable exception to this statement is when $\mu = 0$. Under this restrictive condition, there exists an infinite family of optimal solutions that all result in the same expected spore production and a final resource level of $r = 1$ (Gilchrist and Sulsky, unpubl. data)). Thus we define the step function,

$$u(a; a_s) = \begin{cases} 0 & \text{if } a < a_s. \\ 1 & \text{else} \end{cases} \tag{25}$$

The temporal dynamics of m and r when a fungus follows a bang-bang strategy are illustrated in Figure 3.

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

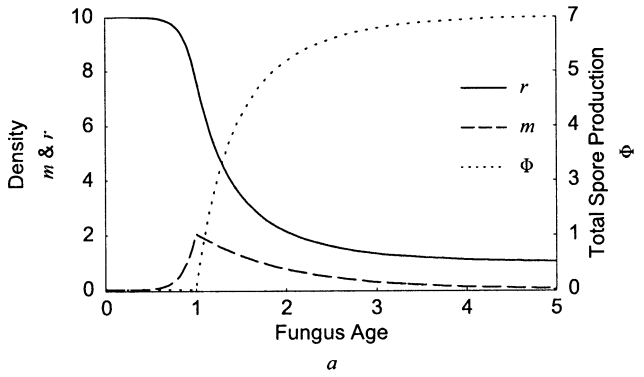

FIG. 3. Illustration of within-patch dynamics and spore production versus colony age a for a fungus following a bang-bang strategy. The terms m and r represent the density of mycelium and resources within the patch while Φ represents the cumulative number of spores produced. Prior to the switch point 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., $u = 1$).

$$r(a) = f[m(a),\mu], \tag{26}$$

where

$$f(m, \mu) = \frac{e^{-m}}{\displaystyle\int_0^1 [1 + m(x - 1)]x^\mu e^{mx}\,dx}. \tag{27}$$

Thus the optimal dynamic allocation schedule, $u(a; \hat{a}_s)$, is,

$$u(a; \hat{a}_s) = \begin{cases} 0 & \text{if } r(a) > f[m(a), \mu] \\ 1 & \text{else.} \end{cases} \tag{28}$$

The optimal allocation schedule defined in equation (28) 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' life span (Figs. 3 and 4).

The integral in $f(m, \mu)$ can be solved explicitly when μ is any nonnegative integer (i.e., $\mu = \{0,1,2, \ldots\}$), otherwise it can be evaluated numerically. In the special case where $\mu = 0$, $f(m, 0)$ simplifies to $\exp(m)$. Consequently, under this condition the optimal switch point satisfies the equality,

$$\ln(r) = m. \tag{29}$$

Working from this baseline, as μ increases, at low values of r the optimal switch curve decreases while at intermediate and high values of r the optimal switch curve increases. In the small region where it is advantageous to switch at a lower resource density, that is, $r(\hat{a}_s)|_{\mu>0} < r(\hat{a}_s)|_{\mu=0}$, the growth rate of the fungus is slow relative to the patch removal rate, μ, such that instead of growing larger in order to produce more spores in the future, it switches earlier to allocate all resources

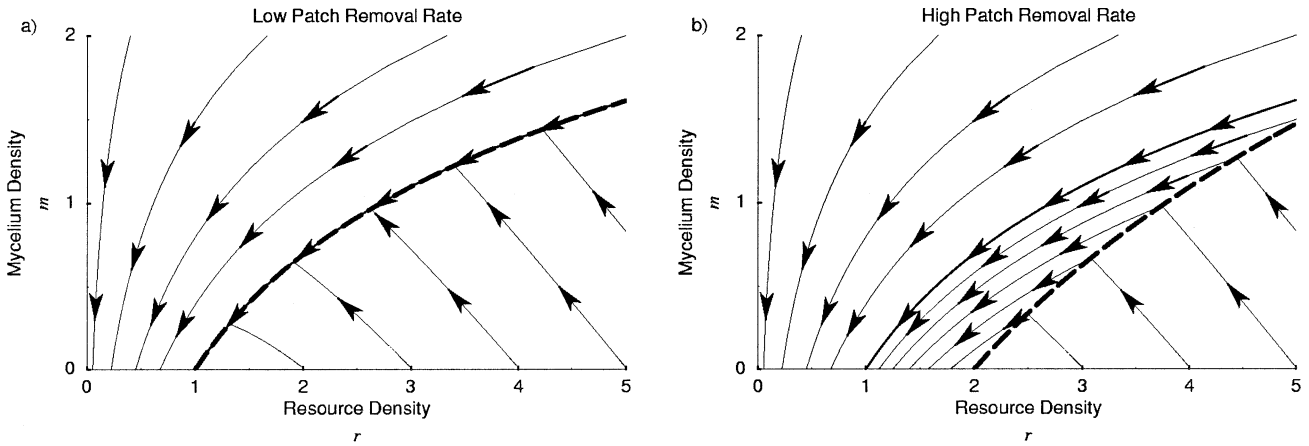

FIG. 4. Trajectories in the resource density r and mycelium density m phase plane for fungi following the optimal dynamic allocation strategies which maximizes expected spore production. Dashed line indicates optimal switch curve. Below the switch curve all resources are allocated towards mycelial growth ($u(a) = 0$). Upon reaching the switch curve and all resoucres are allocated towards spore production ($u(a) = 1$). (a) Optimal trajectories under a low patch removal rate, $\mu = 0$. Here the mycelium density declines along the curve $m(a) = \text{in}(r(a))$. (b)Optimal trajectories under a high patch removal rate, $\mu = 1$. 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.

to spore production. This is due to the slow fungal growth rate. As a result, the gain in spore production by growing larger is more than offset by the reduced value of these spores due to discounting (Fig. 6a).

In contrast, for most values of r_0 increasing patch removal rate leads to an increase in the critical resource density, that is, $r(\hat{a}_s)|_{\mu>0} > r(\hat{a}_s)|_{\mu=0}$. Because of the ample resource density the fungus can grow quickly within this region of the phase plane. 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. Because late spore production is heavily discounted this later reduction has little impact on Φ (see Fig. 6b).

Finally, we note that when $\mu = 0$, all strategies with initial conditions below the switch point curve (i.e., $r(0) > f(m(0),0)$ will eventually grow to this curve and then decay along it, approaching the final state of $m = 0$ and $r_f = 1$. However, when $\mu \neq 0$, the optimal switching curve no longer coincides with the optimal trajectories of mycelium decay and resource use (see Fig. 4b).

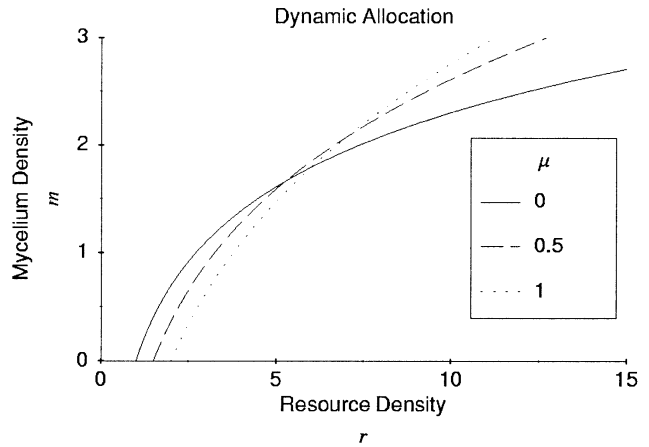

FIG. 5. The effect of the patch removal rate, μ on the behavior of the optimal dynamic resource allocation strategy $u(a; \hat{a}_s)$. Note how the effect of μ on the location of the optimal switch curve where u changes from 0 to 1.

DISCUSSION

Fungal Fitness

Experiments targeted at exploring natural selection require an understanding of how the various traits of an organism contribute to its fitness. The manner in which the specific traits of filamentous fungi combine to determine the fitness of an individual is not well understood, partly because the number and kind of traits involved have not been unambiguously defined. In this study we used an age-structured model of resource patch array dynamics to derive the relevant fitness metric for a diverse group of fungi, the saprophytes. This metric can be evaluated empirically and used to predict and test the fitnesses of individuals for a wide variety of species. The derived metric is specific to those fungi whose natural histories closely match our basic assumptions (e.g., a filamentous saprophyte that exploits discrete resource patches and reproduces asexually) as well as the assumptions of the patch array dynamics model (e.g., constant patch production rates, uniformity of patches, constant spore decay rate, etc.).

Because the patch array model is derived from the epidemiology literature we find a number of parallels between the spread and persistence of a saprophytic fungus within an array of resource patches and the spread and persistence of a disease within a population of hosts. In this model, there is a critical density of uncolonized patches required for a fungal strain to be able to establish itself within an array of resource patches. This also true for other organisms described using epidemiologically based models; for example, where a novel parasite can invade the host population if it can drive the equilibrium density of susceptible hosts below that of the resident strain (Frank 1992; Lenski and May 1994). It is this requirement which allows one fungal strain to competitively

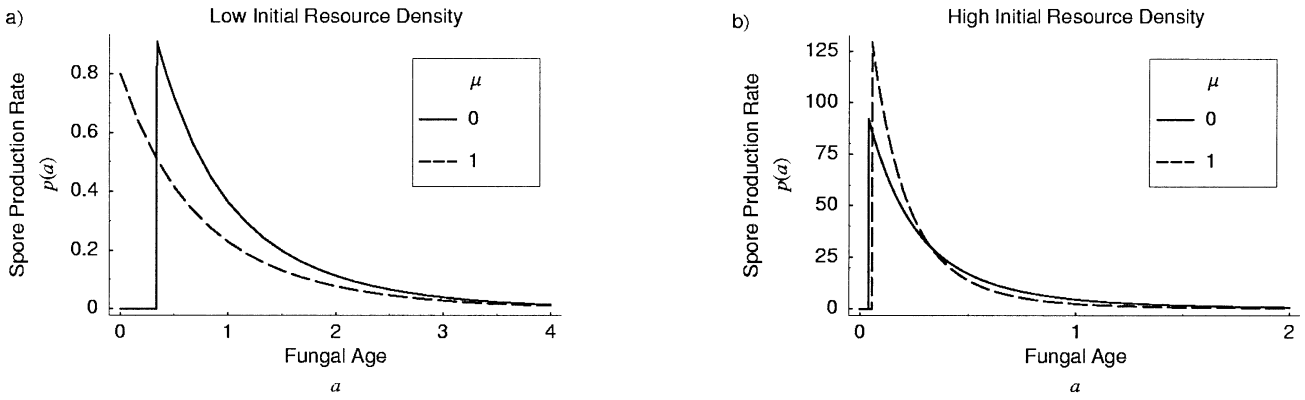

FIG. 6. A comparison of production schedules when a fungus uses the optimal allocation switch $\hat{a}_s$ for when $\mu = 0$ and $\mu = 1$ for two representative points in parameter space. (a) Low initial resource density where $r_0 = 2$ and $m_0 = 0.4$. Here the optimal switch time to spore porduction, $\hat{a}_s$, decreases with μ leading to an increase in spore production early in the fungus' lifespan at the cost of a decrease in spore production later. (b) High initial resource density where $r_0 = 30$ and $m_0 = 1$. Here the optimal switch time to spore production, $\hat{a}_s$, increases with μ leading to an decrease in early and late spore production but a large increase in spore production at intermediate time scales.

exclude another. In essence, a novel fungus can replace the resident strain at equilibrium if it is more effective at capturing the limited number of uncolonized patches flowing into the system. If this is the case then the novel strain will drive the density of uncolonized patches below the critical density necessary for the resident strain and, thus, result in its competitive exclusion.

Natural selection will favor strains which minimize the density of uncolonized patches, and for this reason it is possible to correctly identify the manner in which various fungal traits combine to form the appropriate fitness metric. In such a system, the fitness of a fungus is equal to its expected spore production weighted by the probability a spore lands in a patch and germinates before decaying. Expected spore production is a fungus' spore production rate, weighted by the probability a patch's persistence, summed over the residence time of a patch.

It is possible to expand our model such that the removal rate of a colonized patch is affected by the behavior of the colonizing fungus and so relate our model to the behavior of mutualists or parasites. Indeed, in terms of calculating the appropriate fitness term, the only difference between mutualist, commensal/saprophytic, or parasitic species that exploit discrete resource patches is how colonization affects the patch removal rate, μ. If the colonized patch removal rate is greater than the background patch removal rate then the fungus is essentially acting as a parasite. If the colonized patch removal rate is less than the background patch removal rate then the fungus is essentially acting as mutualist. Such a modification will only affect how we weight spore production over the lifetime of a resource patch.

In general, it should be possible to measure each of the traits that contribute to fungal fitness. For example, the total spore production of an individual has been estimated in a wide range of saprobes including *Ganoderma applanatus*, and *Calvatia gigantea* (Buller 1958). However, the total number of spores which can be produced by a fungus in a patch is not all that matters. For example, the probability that a resource patch will last long enough to allow a fungus to sporulate is another important component of fitness. If spore production occurs 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. It seems plausible that for some fungi this survivorship probability could be estimated in both the laboratory and/or field. In addition, other important components of fungal fitness, including spore germination or settlement rates, can be estimated (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 (e.g., see Gourbiere et al. 1999). Our work suggests that this term may provide a tractable measure of fungal fitness and one that can be usefully exploited for fungi which inhabit clearly discretized patches.

It is likely that the different terms in the fitness metric we identify are related and understanding their mutual influence may lead to additional insights into fungal biology and life-history evolution. For example, a fungus may increase the expected number of spores it produces by decreasing the size of each spore. However, if a trade-off between spore size and spore germination exists, then decreasing spore size may ultimately not be advantageous. Similar trade-offs have been explored in the plant, animal, and parasite literature (Smith and Fretwell 1974; Lloyd 1987; Elgar 1990; Carriere and Roff 1995; Einum and Fleming 2000; Gilchrist et al. 2004). 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?

Maximizing Expected Spore Production

In the second part of this study, we identified the resource allocation strategy which maximizes the expected spore pro-

duction of a fungus. Our model differs from previous fungal life-history models in a number of ways. Most importantly, our approach does not place any external or a priori restrictions on the dynamical growth or allocation behavior of the fungus (c.f. Damgaard and Ostergard 1997). We also avoid making additional assumptions such as a fixed levels of resource use (Newton et al. 1998) or spore production (Gourbiere et al. 1999; Gourbiere and Gourbiere 2002). Instead, limitations to the growth and allocation behavior of the fungus result only from the underlying model assumptions.

Other models of life-history evolution for organisms inhabiting discrete patches focus on either parasites or plants. It is likely that insights from these models can be directly translated to parasitic, mutualist, or commensalist fungi. However, the assumptions underlying our within-patch model represent a fourth and previously ignored category—that of a saprophyte. Saprophytes differ from parasites and mutualists in how they affect the persistence of a patch (a between-patch model process). In addition to these between patch differences, at a within-patch level saprobes differ from parasites, mutualists, commensalists, and plants in that the resources within a patch are nonrenewing. As a result, it is unclear what type of optimal within-patch life-history strategy to expect from saprobes.

For example, in the simplest plant life-history models resources (i.e., light) flow into the system at a constant rate over a fixed growing season (Cohen 1971; Vincent and Pulliam 1980; Iwasa and Roughgarden 1984). In these models the resource, sunlight during the growing season, is renewable and as a result a plant's use of the resource has no affect on the persistence of the patch. The optimal plant life-history strategy in these cases is a dynamic, bang-bang strategy. In contrast, in parasite life-history models resources are essentially self-renewing but a parasite's use of them affects the persistence of the patch (i.e., a virus kills an infected host or cell) (Anderson and May 1991). The optimal parasite life-history strategy under these conditions is a fixed, rather than a dynamic, within-host or cell replication rate (Sasaki and Iwasa 1991; Coombs et al. 2003).

Interestingly, we find that in the case where allocation levels are allowed to vary dynamically the optimal life-history strategy of a saprophytic fungus is the same as that for annual plants, that is, a bang-bang strategy. The details of the optimal timing of this bang-bang strategy vary with the resource levels and the patch background removal rate of the system. This suggests that the fixed resource level of a patch for a saprophytic fungus is analogous to the fixed growing season of an annual plant. If this analogy is correct then fungi in patches with seasonal removal rates might develop an iteroparous strategy (e.g., see Iwasa and Cohen 1989; Kozlowski and Teriokhin 1999). This analogy also suggests that if there is sufficient variation in the removal rate of a patch across generations, natural selection may favor a mixed allocation strategy, as opposed to a bang-bang one (King and Roughgarden 1982; Amir and Cohen 1990). However, it is important to test these predictions explicitly as a finite season length and a finite initial resource level are analogous, but not equivalent. The differences between season length and resources are highlighted by the fact that a plant following an optimal growth schedule utilizes the entire growing season whereas, in contrast, a saprophytic fungus following an optimal resource allocation schedule does not utilize all of the resources in a patch.

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. In addition, anecdotal evidence suggests that other species may follow a bang-bang strategy in nature. Zygomycete 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).

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 the use of a formal description of a fungal life cycle allows one to identify the appropriate fitness metric. Although the exact relationship between fitness and expected spore production, spore decay, spore settlement, and spore germination may vary with different life cycles, we suspect that each of these terms will be an important fitness component for a wide array of fungi. In the future it will be important to understand how within-patch competition and trade-offs between different fitness components interact.

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