

# The persistence of vertically transmitted fungi in grass metapopulations

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Theory predicts that (i) vertical transmission of parasites (i.e. when they are passed directly from a host to its offspring) selects for benign association with the host and that (ii) vertically transmitted parasites that lower their hosts' fitness cannot persist if they are not able to infect horizontally (i.e. contagiously) other host individuals in the population. In this paper, we develop a mathematical model to examine whether mutualism is a prerequisite for persistence of exclusively vertically transmitted (from maternal plant to offspring via seeds) fungal endophytes in structured grass metapopulations. Interestingly, endophyte survival does not require plant mutualism, even in a metapopulation consisting of qualitatively identical patches, if vertical transmission of the fungus is perfect, i.e. if all established seedlings in offspring of the endophyte-infected plant are infected. In more realistic situations, when the metapopulation consists of qualitatively different patches, endophyte-infected plants may persist at the metapopulation level even if the vertical transmission is imperfect (due to hyphae inviability or failure to grow into all seeds) and the endophyte decreases the host grass fitness in certain environments. These results have biological importance because they (i) question the requirement of a mutualistic nature in exclusively vertically transmitted symbionts and (ii) emphasize the importance of habitat diversity in relation to symbiont success in vertical transmission.

**Keywords:** mutualism; parasitism; horizontal and vertical transmission; metapopulation; grasses; endophytes

## 1. INTRODUCTION

Grass endophytes have been considered plant mutualists because they receive nutrition and protection from the host and asexual dispersion by growing into the host's seeds, while the host receives benefits through increased resistance to herbivores, pathogens and drought and flooding stress and enhanced competitive abilities (Clay 1990; Breen 1994; Clay & Holah 1999). The association is highly integrated and fungal survival and distribution largely depend on host fitness, particularly when the fungus has entirely lost contagious transmission by spores. In these grass–endophyte associations, only one fungal genotype is transmitted vertically to seed progeny, promoting stable interaction between the fungal genotype and the host lineage. A fungus usually produces considerable mycelial biomass within the host, sometimes throughout the entire plant, and is considered always to grow along the stem to developing flowerheads and seeds. The generation time of grass endophytes is relatively long, exceeding the lifespan of the host, and the reproductive success of the host plant largely determines the distribution of endophyte-infected grasses. Thus, vertical transmission should align the interests of partners so that the fungus–host association should evolve toward mutualism. Accordingly, the endophyte's interest to maximize the fitness of its host is expected to be strongest in systems dominated by strict vertical transmission, i.e. in systems such as *Neotyphodium* endophytes in cool-season grasses, on which most of the conceptual framework of endophyte–plant

associations has been based (Saikonen *et al.* 1998; Saikonen 2000).

Because the fitness of vertically transmitted fungi and their host plants is closely linked, frequencies of infected grasses should increase over time in plant populations if endophytes increase the fitness of their host (e.g. Leuchtman & Clay 1997). Evidence from agricultural grasses generally support this prediction (Clay 1996; Leuchtman & Clay 1997; Saikonen *et al.* 1998), whereas recent studies on semi-natural and natural grass systems indicate that infection frequencies are more variable in wild grass populations (Lewis *et al.* 1997; Schulthess & Faeth 1998; Saikonen *et al.* 2000). Although infections are widespread in native grass species, infection levels are generally relatively low within species and variation in infection frequencies among local populations can be very high (Saikonen *et al.* 2000). Recent literature has suggested four possible explanations for the observed intermediate endophyte infection rates in natural grass populations (Clay 1993; Ravel *et al.* 1997; Saikonen *et al.* 1998).

- (i) Infection has not yet reached equilibrium (Clay 1993).
- (ii) Uninfected and infected grasses may coexist as interconnected populations or metapopulations, even when subpopulations of infected hosts become extinct, or if non-infected plants are locally at a selective disadvantage relative to infected plants (Saikonen *et al.* 1998).
- (iii) Mathematical models predict that uninfected grasses could be persistent in a population assuming that loss of infection from seeds from infected plants, due

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to either hyphae inviability or failure to propagate into seeds, is greater than 10% (Ravel *et al.* 1997).

- (iv) The costs and benefits of endophyte infections to host plants may vary spatially and temporally in natural populations and thus selection and frequency of infected and uninfected grasses should vary accordingly (Saikkonen *et al.* 1998).

The first explanation describes the current frequency of endophyte-infected grasses in a population, whereas the others elucidate an actual mechanism driving the intermediate endophyte infection rates. Furthermore, these explanations operate at different time scales (ecological or evolutionary), are not mutually exclusive and can possibly be confounded with occasional horizontal transmission of fungi (Saikkonen *et al.* 1998).

In this paper, we develop a mathematical model to explain co-occurrence of endophyte-infected and endophyte-free plants in grass metapopulations. According to current theory of mutualism, we model endophyte–plant associations as a situation where the reciprocal exploitations provide net benefits to both partners (Nowak *et al.* 1994; Leimar 1997; Doebeli & Knowlton 1998; Herre *et al.* 1999; Gyllenberg *et al.* 2002). By this view, although endophytes inevitably benefit host plants in many environments, these benefits would not come without associated costs. Endophytes require energy from the host plant and these costs may occasionally outweigh the benefits, particularly under poor resource conditions, and as such may limit resources available to competing plant activities such as growth or reproduction in the host plant. Under such conditions, endophytic fungi should be considered parasites. This provides an opportunity to work apart from the unnecessary and potentially misleading dichotomy between current theory of the ecology and evolution of plant–endophyte symbiosis and plant pathogen and parasite interactions (see, for example, Clay 1990; Kover *et al.* 1997; Kover & Clay 1998). Using mathematical models, we focus primarily on two questions: (i) is mutualism a prerequisite for the survival of a strictly vertically transmitted endophytic fungus in structured grass metapopulations and (ii) what are the ecological conditions under which coexistence of infected and uninfected plants is possible? In the first step, we assume that the metapopulation consists of qualitatively identical patches. Because this is generally not the case in nature, we extend the model by assuming that patches have different qualities.

## 2. STRUCTURED METAPOPOPULATION DYNAMICS OF MATERNAL VERTICALLY TRANSMITTED ENDOPHYTES

Grasses, like most organisms, have a hierarchical spatial metapopulation structure of several local populations, which are connected by dispersal (e.g. Hanski 1999). Thus, persistence of fungal grass endophytes can most conveniently be modelled in the framework of metapopulation dynamics. In our case, local populations are structured by the number of endophyte-infected and uninfected grass individuals and therefore we have to use structured metapopulation models (Gyllenberg & Hanski 1992; Gyllenberg *et al.* 1997; Gyllenberg & Metz 2001;

Metz & Gyllenberg 2001). In the model, we consider a metapopulation with a sufficiently large number of habitable patches so that it could be approximated well with infinitely many patches. We regard the metapopulation as a population of basic entities that can be local populations or dispersers (grass seeds). Thus, the local dynamics has two components: one describing the dynamics of a local grass population and the other dynamics within the disperser pool. Endophyte-free ( $E^-$ ) and endophyte-infected ( $E^+$ ) grasses may coexist both in patches as established plants and in the disperser pool as grass seeds. Because current understanding of the ecological and economic importance of endophytes is largely based on research of tall fescue, *Festuca arundinacea*, hosting the *Neotyphodium* endophyte (Hoveland 1993; Saikkonen *et al.* 1998; Clay & Holah 1999; Saikkonen 2000), which is assumed to be only vertically transmitted via seeds of infected plants to offspring, we also assume only vertical transmission of infection in the model. However, because endophyte infection cannot be gained by contagious spreading, but vertical transmission of endophytes can be imperfect (Ravel *et al.* 1997; Saikkonen *et al.* 1998; Clay & Holah 1999), we assume that endophyte-free plants produce uninfected seeds, whereas endophyte-infected plants produce both infected and uninfected seeds with probabilities  $p$  and  $(1-p)$ , respectively.

The state of the local population is represented by three vectors ( $E^-, E^+, \mathbf{x}$ ), where  $E^-$  and  $E^+$  are the local densities of endophyte-free and endophyte-infected individuals and  $\mathbf{x}$  is the quality of the patch. The metapopulation state is then described by the distribution  $n(t, E^-, E^+, \mathbf{x})$  of local population states. The patches are equally coupled by dispersal. Each seed in a local population immediately enters the disperser pool, where it experiences mortality at a per disperser rate  $\nu$ ; the seeds leave the disperser pool by immigrating (at a per capita rate  $\alpha$ ) and germinating into a patch with state ( $E^-, E^+, \mathbf{x}$ ) at per capita rates of  $q_{E^-}(E^- + E^+, \mathbf{x})$  if they are endophyte-free and  $q_{E^+}(E^- + E^+, \mathbf{x})$  if they are endophyte-infected, respectively.

Local catastrophes that wipe out the local grass population may occur with rate  $\varepsilon(\mathbf{x})$ . After a local catastrophe, the patch is immediately recolonized due to the continuous inflow of seeds from the dispersal pool. We assume that the densities ( $D_{E^-}$ ,  $D_{E^+}$ ) of the endophyte-free and infected seeds in the dispersal pool are the only components of the environmental interaction. As we are interested in steady states, we assume that this environment is constant, characterized by the constant immigration rates per patch  $I_{E^-} = \alpha D_{E^-}$ ,  $I_{E^+} = \alpha D_{E^+}$  (Diekmann *et al.* 2002).

The local population growth is a consequence of seed germination and death of plants at per capita rates of  $\mu_{E^-}$ ,  $\mu_{E^+}$ . Once the local densities ( $E^-, E^+$ ) of uninfected and infected individuals within a patch are acquired, they can be substituted into the steady-state equations for the dispersal pool. For a more detailed description of the model, see Gyllenberg *et al.* (2002) and Appendix A. Subsequently, we solve this equation and obtain the three possible equilibria of the dispersal pool that predict persistence of the endophytes if  $I_{E^+} > 0$ , extinction of the endophytes if  $I_{E^+} = 0$ , or even extinction of the entire metapopulation if  $I_{E^-} = I_{E^+} = 0$ , depending on the parameters.

### 3. METAPOPULATION CONSISTING OF IDENTICAL PATCHES

To begin with, we assume that the metapopulation consists of qualitatively identical patches. In this case, the variable  $x$  (the quality of the patch) is superfluous and all of the model ingredients become constants. In order to determine conditions for the metapopulation to invade a virgin environment, we calculate the numbers  $R_{uv}$ , defined as the expected number of seedlings of type  $u$  produced by grass clone of type  $v$  (here,  $u$  and  $v$  stand for either infected ( $E^+$ ) or uninfected ( $E^-$ ) in an otherwise population-free (i.e. virgin) environment:

$$R_{E^-E^-} = \frac{\pi\gamma_{E^-}A}{\mu_{E^-} + \varepsilon}, \tag{3.1}$$

$$R_{E^-E^+} = (1 - p)\frac{\pi\gamma_{E^+}B}{\mu_{E^+} + \varepsilon}, \tag{3.2}$$

$$R_{E^+E^-} = 0, \tag{3.3}$$

$$R_{E^+E^+} = p\frac{\pi\gamma_{E^+}B}{\mu_{E^+} + \varepsilon}, \tag{3.4}$$

where  $\pi$  is the probability that a disperser survives migration,  $A$  and  $B$  are probabilities for an uninfected and infected seed to germinate in an empty patch, respectively, and  $\gamma_{E^-}$  and  $\gamma_{E^+}$  are per capita fertility rates of uninfected and infected plants, respectively. The numbers defined by equations (3.1)–(3.4) form the next generation operator:

$$L = \begin{pmatrix} R_{E^-E^-} & R_{E^-E^+} \\ R_{E^+E^-} & R_{E^+E^+} \end{pmatrix}, \tag{3.5}$$

giving the contribution to the next generation. The growth or decline of the metapopulation is determined by the largest eigenvalue  $R_0$  of  $L$  (Gyllenberg *et al.* 2002; Diekmann *et al.* 2002). Because  $R_{E^+E^-} = 0$ , we have  $R_0 = \max\{R_{E^-}, R_{E^+}\}$  where we have for simplicity replaced  $R_{E^+E^+}$  by  $R_{E^+}$  and  $R_{E^-E^-}$  by  $R_{E^-}$ . The grass metapopulation can invade a virgin environment if and only if  $R_0 > 1$ , that is, if every grass clone, on average, produces more than one seedling.

We can distinguish four possible cases: one case in which the metapopulation will go extinct and three cases maintaining the structured metapopulation consisting of local grass populations. The grass metapopulation becomes extinct in the first case because neither endophyte-free nor endophyte-infected plants produce enough offspring, i.e. when  $R_{E^-} < 1$  and  $R_{E^+} < 1$ . In nature, such an unfavourable environment for plants is out of the tolerance and distribution range of the species. In the three other cases, grass metapopulation is maintained but endophyte–host plant interactions range from antagonistic to mutualistic (figure 1) and frequencies of endophyte-infected plants in local grass populations vary accordingly.

First, the grass metapopulation will become endophyte-free if the fungus is clearly a strong parasite or a pathogen having negative fitness consequences to the host plant, i.e. when  $R_{E^-} > 1$  and  $R_{E^+} < 1$ . Because the endophyte in this case decreases survival and/or the lifetime reproductive success of the host, endophyte-infected grasses in the grass metapopulation will become extinct.

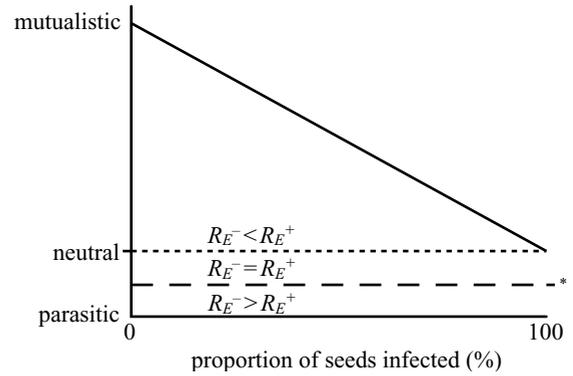


Figure 1. Endophyte–plant association along the continuum from parasitic to mutualistic in relation to fungal transmission success via seeds. Asterisk, threshold for negative fitness consequences for the host plant.

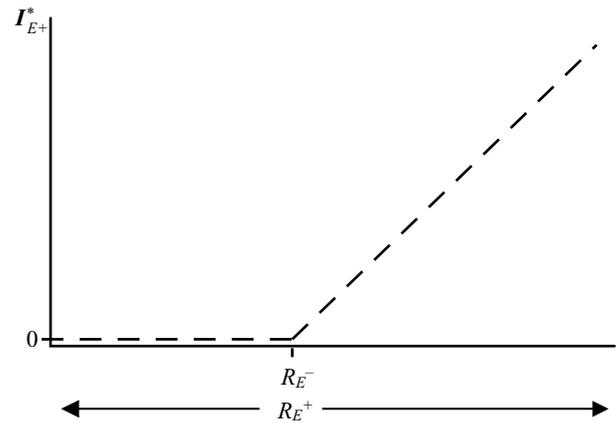


Figure 2. The inflow of endophyte-infected seeds ( $I_{E^+}^*$ ) in relation to relative reproduction ratio of uninfected ( $R_{E^-}$ ) and infected ( $R_{E^+}$ ) plants.

Second, both endophyte-infected and uninfected plants can survive (i.e.  $R_{E^-} > 1$  and  $R_{E^+} > 1$ ). However, the frequency of endophyte-infected plants may vary from 0 to 100%, depending on the success of vertical transmission of the fungus and the relative fitness and distribution ability of infected and uninfected plants. If the reproduction ratio of infected plants is lower compared with endophyte-free plants ( $R_{E^-} > R_{E^+}$ ), the infected part of the metapopulation becomes extinct over time because inflow of infected seeds into local populations stops (figure 2). Of particular interest is that coexistence of endophyte infection does not necessarily require endophyte–plant mutualism, i.e. that  $R_{E^-} < R_{E^+}$ . Non-mutualistic endophyte association ( $R_{E^-} = R_{E^+}$ ) is indeed possible, but only if vertical transmission is perfect ( $p = 1$ ), i.e. all grass seeds contain a viable endophyte, and furthermore that all established seedlings in offspring are endophyte-infected. In such a case, the proportional inflow of endophyte-infected plants in the metapopulation may vary from 0 to 1, depending on the initial proportion in the dispersal pool (figure 3). Although not predicted by the model, we may assume that commensalistic endophyte–plant associations are possible until the endophyte lowers the fitness of the host plant, i.e. the survival or lifetime reproductive success of the host (in figure 1; see also Lipsitch *et al.* 1995). Furthermore, the linear relationship between strength of mut-

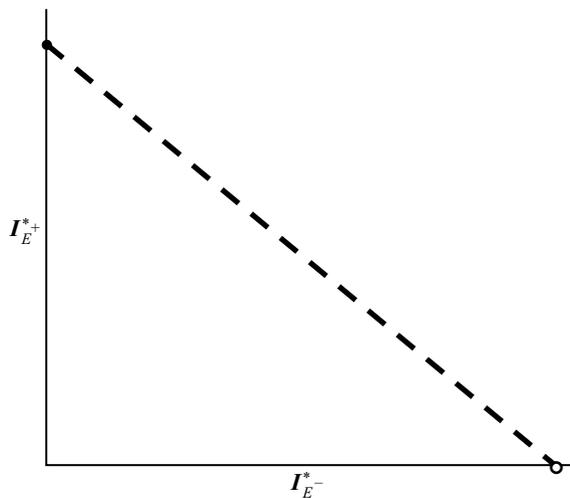


Figure 3. Relationship between the inflow of endophyte-free ( $I_E^-$ ) and endophyte-infected ( $I_E^{*+}$ ) seeds into a local population when vertical transmission is perfect ( $p = 1$ ). Filled circle,  $R_E^- < 1 < R_E^+$ ; open circle,  $R_E^- > 1 > R_E^+$ .

ualism and fungal transmission success (figure 1) suggests that the maintenance of endophyte-infected plants in grass metapopulations does not presuppose strong fungal mutualism, if the endophyte is successfully transmitted into nearly all developing seeds in infected plants. This is a reasonable assumption if developing seeds germinate during the autumn or subsequent season, but focuses attention on the importance of seed banks and the long-term storage of seeds in agronomy because seed endophyte viability gradually declines over time (e.g. Clay & Holah 1999).

Third, if  $R_E^- < 1$  and  $R_E^+ > 1$ , then the endophyte is clearly mutualistic, increasing plant fitness either by increasing survival or reproduction of the host. Because endophyte-free plants do not produce enough offspring ( $R_E^- < 1$ ), endophytes are indeed a prerequisite for metapopulation persistence, as it will become extinct in the absence of endophyte-infected plants. However, endophyte-free plants will not become extinct because of imperfect transmission (see also Ravel *et al.* 1997). Thus, the metapopulation will be ‘fed’ all the time with new endophyte-free seeds produced by infected plants due to failure of fungal hyphae to grow into seeds or loss of viability of hyphae in infected seeds.

In short, in the special case of identical patches, the model suggests the following:

- (i) A strictly vertically transmitted (endophyte/) parasite/pathogen, having negative fitness consequences to the host, cannot survive without contagious infections if the metapopulation consists of identical patches.
- (ii) Endophyte-infected and uninfected plants may coexist, although the endophyte–plant association is not mutualistic, but only if vertical transmission of the fungus is perfect.
- (iii) Endophyte-free plants persist in a metapopulation although endophyte–plant association is clearly mutualistic if the vertical transmission of the fungus is imperfect.
- (iv) This model also emphasizes the urgent need for

studies examining the success of vertical transmission in nature.

#### 4. METAPOPULATION CONSISTING OF QUALITATIVELY DIFFERENT PATCHES

Next, we consider the case in which patches are of different quality. We consider both the continuous and discrete cases and ask whether endophyte-infected and uninfected plants are able to coexist if the grass metapopulation consists of patches unfavourable and favourable to endophyte association. In these cases, the attempt to solve the steady-state equations analytically leads, even in the simplest case, to a fourth degree polynomial equation with 14 parameters (see Gyllenberg *et al.* 2002). Although we are not able to derive conditions for persistence of endophyte-infected grasses at equilibrium, we can find conditions for invasion of endophyte-infected and uninfected grasses in a virgin environment. These conditions are very similar to the above-mentioned four scenarios distinguished in the case of identical patches, because regardless of the qualitative structure of the patches, the necessary condition for invasion in a virgin environment is a sufficient number of offspring, i.e.  $R_0 > 1$ .

$$R_0 = \max\{R_E^-, R_E^+\} > 1.$$

- (i)  $R_E^-(\mathbf{x}) < 1, R_E^+(\mathbf{x}) < 1 \Rightarrow$  no invasion.
- (ii)  $R_E^-(\mathbf{x}) > 1, R_E^+(\mathbf{x}) < 1 \Rightarrow$  only endophyte-free plants can invade the virgin habitat leading to extinction of infected grasses in metapopulation.
- (iii)  $R_E^-(\mathbf{x}) > 1, R_E^+(\mathbf{x}) > 1 \Rightarrow$  both infected and uninfected plants can invade the virgin environment.
- (iv)  $R_E^-(\mathbf{x}) < 1, R_E^+(\mathbf{x}) > 1 \Rightarrow$  endophyte-free plants do not produce enough offspring and thus endophyte-free plants persist in a grass metapopulation only if vertical transmission ( $p$ ) is imperfect (due to either hyphae inviability or failure to grow into all seeds).

Thus, maintenance of endophyte-infected and uninfected grasses in a metapopulation can be approached by examining the expected number of seeds produced during the lifetime of endophyte-free and infected grass individuals. For instance, in the discrete case of  $n$  types of patches, the expected number of seeds produced by endophyte-free and infected grass individuals are, respectively

$$R_E^- = \sum_{k=1}^n f_k \frac{\pi \gamma_E^{k-} A_k}{\mu_E^{k-} + \varepsilon_k} = \sum_{k=1}^n f_k R_E^{k-}, \tag{4.1}$$

$$R_E^+ = \sum_{k=1}^n f_k \frac{p \pi \gamma_E^{k+} B_k}{\mu_E^{k+} + \varepsilon_k} = \sum_{k=1}^n f_k R_E^{k+}, \tag{4.2}$$

where  $f_k$  is the fraction of patches with quality  $x_k$  and the subscript  $k$  denotes the corresponding local parameters.

Due to the heterogeneous structure of the environment, endophyte-infected plants may produce a sufficient number of offspring to invade virgin environments at the metapopulation level ( $R_E^+ > R_E^- > 1$  or  $R_E^+ > 1 > R_E^-$ ), even if the vertical transmission is imperfect and the endophyte decreases host grass fitness in certain environments.

If we consider, for instance, that we have  $f_1 = 0.2$  endophyte-unfavourable patches and  $f_2 = 0.8$  endophyte-favourable patches, such that the basic reproduction ratios are:

$$R_{E^-}^1 = 5, R_{E^-}^2 = 0.5, R_{E^+}^1 = 0.5, R_{E^+}^2 = 20 \text{ or}$$

$$R_{E^-}^1 = 1.2, R_{E^-}^2 = 0.8, R_{E^+}^1 = 0.9, R_{E^+}^2 = 1.5;$$

we then get  $R_{E^-} = 1.4, R_{E^+} = 16.1 \Rightarrow R_{E^+} \gg R_{E^-} > 1$ , in the first case, and  $R_{E^-} = 0.88, R_{E^+} = 1.38 \Rightarrow R_{E^+} > 1 > R_{E^-}$ , in the second case.

Indeed, this demonstrates that a structured metapopulation of interconnected local grass populations provides a comprehensive framework to understand how exclusively vertically transmitted fungal endophytes can be observed, even if they locally lower the survival or reproductive success of plants.

## 5. AVENUES OF FUNGAL ENDOPHYTE PERSISTENCE IN NATURAL GRASS POPULATIONS

Our model incorporates the framework of metapopulation dynamics emphasizing the importance of spatial structure and dispersal of host plants to persistence of endophytes in grass populations. The model demonstrates that mutualism is not required for the survival of endophytes in grass populations, even if the endophyte spreads only via seeds of infected plants. Indeed, non-mutualistic endophyte association is possible even in grass metapopulations that consist of homogenous patches, but only if vertical transmission of the endophyte is perfect. Questioning the necessity of mutualism, our model addresses the importance of more comprehensive insights into the endophyte-plant interaction. Mutualistic association of the fungus with the host plant indisputably provides the best-established explanation in ecological literature for high endophyte frequencies in grass populations. However, considering how widespread seed-borne endophytes are in native grass species and, on the other hand, how variable endophyte frequencies can be among grass populations (White & Cole 1985; Lewis & Clements 1986; White & Cole 1986; Latch *et al.* 1987; Clay & Leuchtman 1989; Lewis *et al.* 1997; Oliveira *et al.* 1997; Schulthess & Faeth 1998; Saikkonen *et al.* 2000), it would be premature or even naive to assume all grass endophytes to be either non-mutualistic 'hitchhikers' or ubiquitous mutualists.

First, an increasing number of recent studies suggests that endophyte-grass interactions range from antagonistic to mutualistic depending on prevailing environmental conditions and the genotypes of the fungus or host plant (Cheplick *et al.* 1989; Agee & Hill 1994; Saikkonen *et al.* 1998, 1999; Clay & Holah 1999; Saikkonen 2000). Costs may occasionally outweigh the benefits of endophytes, particularly under poor resource conditions when resources are insufficient for competing plant activities such as growth or reproduction. Poor resource conditions may also constrain defence against herbivores, purportedly the primary driving selective force behind endophyte-plant mutualism (Clay 1990; Saikkonen *et al.* 1998) because plant defences rely on nitrogen alkaloid mycotoxins (Siegel & Bush 1997). Thus, endophytes may become selectively disadvantageous to the plant under limited resource conditions (e.g. Cheplick *et al.* 1989). However,

the second part of our model, a structured metapopulation consisting of qualitatively different patches, reveals that strictly vertically transmitted endophytes can persist even if they lower the survival or lifetime reproductive success of their hosts locally. Analogously to qualitatively different patches, maintenance of endophyte-infected and uninfected grasses in a metapopulation can be assumed to be promoted by genetic differences in endophytes and host grasses in their environmental tolerance.

Second, the epidemiological importance of vertical transmission may be overemphasized, although inevitably it is the primary mode of transmission and provides an opportunity for extensive establishment of an endophyte within an environment favouring infected plants. Indeed, even scarce sporadic horizontal transmission of an endophyte may be of critical importance for the survival and distribution of the fungus. Asexual *Neotyphodium* endophytes are automatically assumed to be 'trapped' in the host plant (see, for example, Clay & Holah 1999), although very little is known about the prevalence of their horizontal transmission (by either asexual or sexual spores) in nature. However, contagious spread should not be ruled out even in *Neotyphodium* endophytes because they produce asexual conidia on growth media (Glenn *et al.* 1996) and on living plants (White *et al.* 1996).

It is noteworthy that the presented explanations for co-occurrence of endophyte-infected and uninfected grasses are not mutually exclusive (Saikkonen *et al.* 1998) and performance of plants and heterotrophic organisms is modified by the sum of interactions occurring in nature at all trophic levels. In other words, numerous forces act simultaneously or in an integrated fashion. For example, metapopulation processes, varying selective pressures and imperfect vertical transmission may combine to maintain infected and uninfected hosts in natural populations. Furthermore, most natural populations may be mosaics of unique endophyte-host plant genotypic combinations that are adapted to local biotic and abiotic environments. Consideration of metapopulation processes, spatially and temporally varying selective pressures and endophyte-host genotypic combinations, will become increasingly important in unravelling interactions between endophytes, host plants and other interacting species.

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## APPENDIX A

The local population dynamics is given by

$$\begin{cases} \frac{dE^-}{dt} = I_{E^-} q_{E^-} (E^- + E^+, \mathbf{x}) - \mu_{E^-} (E^- + E^+, \mathbf{x}) E^-, \\ \frac{dE^+}{dt} = I_{E^+} q_{E^+} (E^- + E^+, \mathbf{x}) - \mu_{E^+} (E^- + E^+, \mathbf{x}) E^+, \end{cases} \quad (\text{A } 1)$$

where  $\mathbf{x}$  is patch quality, and  $I$ ,  $q$  and  $\mu$  are immigration rates per patch, germination probability and death rate of endophyte-free ( $E^-$ ) and endophyte-infected ( $E^+$ ) grasses, respectively.

We are interested in the steady states at the metapopulation level. Therefore we solve (A 1) and substitute the solution ( $E^-$ ,  $E^+$ ) into the equations describing the equilibrium condition within the disperser pool. We denote the solution of (A 1) with initial conditions  $E^-(0) = 0$ ;  $E^+(0) = 0$  (corresponding to recolonization) by ( $E_I^-(t, \mathbf{x})$ ,  $E_I^+(t, \mathbf{x})$ ). Note that this solution depends on  $I$ . Substitution of ( $E_I^-$ ,  $E_I^+$ ) into the steady-state condition for the dispersal pool yields:

$$\left\{ \begin{array}{l} I_{E^-} = \pi \int_0^{+\infty} \int_X \gamma_{E^-}(\mathbf{x}) E_I^-(t, \mathbf{x}) \psi(\mathbf{x}) \varepsilon(\mathbf{x}) e^{-\varepsilon(\mathbf{x})t} d\mathbf{x} dt \\ \quad + (1-p) \pi \int_0^{+\infty} \int_X \gamma_{E^+}(\mathbf{x}) E_I^+(t, \mathbf{x}) \psi(\mathbf{x}) \varepsilon(\mathbf{x}) e^{-\varepsilon(\mathbf{x})t} d\mathbf{x} dt, \\ I_{E^+} = p \pi \int_0^{+\infty} \int_X \gamma_{E^+}(\mathbf{x}) E_I^+(t, \mathbf{x}) \psi(\mathbf{x}) \varepsilon(\mathbf{x}) e^{-\varepsilon(\mathbf{x})t} d\mathbf{x} dt, \end{array} \right. \quad (\text{A } 2)$$

where  $\pi$  is the probability that a disperser survives migration,  $\varepsilon$  is the local catastrophe rate,  $\gamma_{E^-}(\mathbf{x})$ ,  $\gamma_{E^+}(\mathbf{x})$  are the per capita fertility rates,  $\psi(\mathbf{x})$  is the distribution of the patch quality  $x$  and  $p$  is the infection transmission probability. The solution ( $I_{E^-}$ ,  $I_{E^+}$ ) of (A 2) gives the inflow of uninfected and infected seeds per patch at equilibrium.

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