# Challenges in modelling complexity of fungal entomopathogens in semi-natural populations of insects

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**Abstract** The use of fungal entomopathogens as microbial control agents has driven studies into their ecology in crop ecosystems. Yet, there is still a lack of understanding of the ecology of these insect pathogens in semi-natural habitats and communities. We review the literature on prevalence of fungal entomopathogens in insect populations and highlight the difficulties in making such measurements. We then describe the theoretical host-pathogen models available to examine the role that fungal entomopathogens could play in regulating insect populations in semi-natural habitats, much of the inspiration for which has been drawn from managed systems, particularly forests. We further emphasise the need to consider the complexity, and particularly the heterogeneity, of semi-natural habitats within the context of theoretical models and as a framework for empirical studies. We acknowledge that fundamental gaps in understanding fungal entomopathogens from an ecological perspective coupled with a lack of empirical data to test theoretical predictions is impeding progress. There is an increasing need, especially under current rapid environmental change, to improve our understanding of the role of fungi in insect population dynamics beyond the context of forestry and agriculture.

**Keywords** Pathogen population dynamics · Theoretical modelling · Epizootiology · Fungal entomopathogens · Entomophthorales · Hypocreales · Non-pest insects

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## Introduction

Fungal entomopathogens are diverse and globally ubiquitous natural enemies of arthropods. There has been considerable research focus on their potential as microbial control agents (e.g. Goettel et al. 2005, 2008; Pell 2007; Vega et al. 2009; Hajek and Delalibera 2009; Jaronski 2009; Pell et al. 2009). Indeed, they are considered to have been instrumental in the advent of

modern microbial control (Steinhaus 1949; Burges and Hussey 1971; Krassilstchik 1888; Vega 2008) and our knowledge of fungal ecology in crop ecosystems has largely been driven by applied studies assessing their potential for microbial control. There is no doubt that such studies have provided fundamental information on the host-fungus relationship. However, there are still profound gaps in our understanding of their ecology particularly in semi-natural or minimally managed systems both in terrestrial and aquatic environments (Johnson et al. 2006; Stentiford et al. 2001; Roy and Cottrell 2008; Roy et al. 2009). The role of pathogens as natural enemies of non-pest insects, including those of conservation value, is seldom considered beyond their context as 'non-targets' of microbial control agents (Roy et al. 2009). It is possible that fungal pathogens are playing a hitherto undetected role in documented declines of some insect species (Balmford et al. 2005; Roy and Cottrell 2008). In this review we consider the literature on prevalence of fungal entomopathogens in populations of insects in crop and semi-natural habitats. We then examine the insights provided by ecological models in exploring the role fungi may play in regulating host populations. As much of the inspiration for this work is drawn from forest ecosystems and, due to the paucity of data available from semi-natural ecosystems, we highlight those studies in managed systems that are also particularly relevant to insect populations in semi-natural habitats.

There are over 700 species of fungal entomopathogens and these are broadly found within two main groups: phylum Ascomycota (subkingdom Dikarya) and the order Entomophthorales (Hibbett et al. 2007; Humber 2008; Blackwell 2009). Within the Ascomycota there are two major orders that contain entomopathogens: Hypocreales (class: Sordariomycetes; subclass: Hypocreomycetidae) and Laboulbeniales (class: Laboulbeniomycetes) (Hibbett et al. 2007). The Hypocreales have both sexual (teleomorph) and asexual (anamorph) forms although most research has focused on the anamorphs. Anamorphic hypocrealean fungi are considered to be generalist pathogens with broad host ranges and even switching between pathogenic and saprophytic lifestyles (Blackwell 2009). The Laboulbeniales (Ascomycota: Laboulbeniaceae) are a group of obligate ectoparasitic fungi that are mainly associated with Coleoptera and do not cause death of their hosts (Weir and Hammond 1997; Roy

and Cottrell 2008). The Entomophthorales are all obligate arthropod pathogens historically placed within the phylum Zygomycota but likely to be elevated to a distinct subphylum named Entomophthoramycotina pending resolution of clades from the Zygomycota (Hibbett et al. 2007). Microsporidia are now known to be highly specialised obligate intracellular fungi, closely aligned to the Entomophthorales (Keeling and Fast 2002; Humber 2008) and infecting a diverse array of vertebrate and invertebrate hosts. However, the Laboulbeniomycetes are all associated with insects or other arthropods mostly as biotrophic parasites (Blackwell 2009). There are a number of detailed studies examining the ecological interactions of microsporidia with their hosts particularly in forest Lepidoptera systems (Hoch et al. 2000, 2008; Pilarska et al. 2006; Solter 2006; Solter and Becnel 2007). We will only consider microsporidia superficially in this manuscript; the recent literature on this group is worthy of an entire ecological review. However there are undoubtedly conceptual parallels between this intriguing group of fungi and the others that are described in detail here.

Although the taxonomy of fungal entomopathogens is undergoing significant change, their basic biology and general life history attributes are well understood. All fungal entomopathogens produce infective conidia (spores) that attach to, germinate, and penetrate the cuticle (or digestive tract) of their host. Inside the host they proliferate as single- or multi-celled structures (protoplasts, blastospores, hyphal bodies), usually killing the host and producing either more infective conidia for immediate transmission or resting structures (sexual or asexual resting spores, chlamydospores, mummified hosts) for persistence in the environment (Roy et al. 2006; Pell et al. 2001; Table 1; Fig. 1).

Abiotic and biotic conditions strongly influence key components of fungal activity and fitness including transmission efficiency and persistence within and outside the host (Fuxa and Tanada 1987; Fig. 1). Humidity in excess of 90% in the microenvironment surrounding fungi is required for germination, infection, and sporulation (e.g. Inglis et al. 2001; Wilding 1969) and is considered to be the most critical environmental factor influencing the development of epizootics (Fuxa and Tanada 1987; Hall and Papierok 1982). Ambient temperatures affect speed of germination, growth and kill. There is an inverse relationship

**Table 1** Broad comparison of attributes of the Entomophthorales and Hypocreales (modified from Pell et al. 2001). There is considerable variability between species within these families. Some attributes are host dependent

| Attribute | Entomophthorales | Hypocreales | Comments | References |
|---|---|---|---|---|
| Families | Ancylistaceae, Completoriaceae, Entomophthoraceae, Meristacraceae, Neozygitaceae | Clavicipitaceae, Cordycipitaceae, Ophiocordycipitaceae | | Hibbett et al. (2007), Humber (2008) |
| Spore size | Usually >10 μm | <10 μm | | Balazy (1993), Samson et al. (1988) |
| Reproductive output (spores per cadaver) | Few ($10^4$) | Many ($10^7$–$10^9$) | | Arthurs and Thomas (2001), Eilenberg (1987), Hua and Feng (2003), Posada and Vega (2005) |
| Sporulation rate | Fast (hours) | Slow (days) | | Eilenberg (1987), Arthurs and Thomas (2001), Sierotzki et al. (2000) |
| Germination rate | Fast (hours) | Slow (days) but sometimes fast | | Oduor et al. (1996), Posada and Vega (2005) |
| Life cycle | Fast (few days) | Slow (several days or even weeks) | | Posada and Vega (2005), Roy et al. (2006) |
| Higher order production of spores (primary, secondary, etc.) | Always | Rarely | The hypocrealean genus *Aschersonia* produces higher order conidia | Scholte et al. (2004), Shah and Pell (2003) |
| $LC_{50}$ (spores mm$^{-2}$ or conidia ml$^{-1}$) | Low ($10^0$–$10^4$) | High ($10^2$–$10^9$) | Host dependent: *P. neoaphidis* to *A. pisum* $LC_{50}$ of 19 conidia mm$^{-2}$; *P. neoaphidis* to *U. jaceae* $LC_{50}$ of $10^4$ conidia mm$^{-2}$ (Ekesi et al. 2005). Isolate dependent: Hypocreales to *Aphis fabae* $LC_{50}$ range $1.62 \times 10^2$ - $2.95 \times 10^7$ conidia ml$^{-1}$ (Hesketh et al. 2008) | Eilenberg (1987), Ekesi et al. (2005), Hesketh et al. (2008), Roy et al. (2008), Ugine et al. (2005), Xu and Feng (2000) |
| Active discharge | In most cases | Only in sexual stages | Active discharge is not known for species within the entomophthoralean genus *Massospora*. Active discharge is known for some *Cordyceps* (Hypocreales) | Scholte et al. (2004), Wongsa et al. (2005) |

**Table 1** continued

| Attribute | Entomophthorales | Hypocreales | Comments | References |
|---|---|---|---|---|
| Mucous coated spores? | Often | Rarely | There are exceptions where mucous coated conidia are produced by some Hypocreales for example *Verticillium, Hirsutella, Aschersonia* | Roy et al. (2006), Shah and Pell (2003) |
| Resting spores | Common | Rare | Entomophthorales: resting spores are mostly sexual. *Cordyceps* species also produce sexual spores but not resting spores. Hypocreales: *Sorosporella* spp. produce resting spores and *Beauveria* spp. produce microsclerotia | Roy et al. (2006), Shah and Pell (2003), Scholte et al. (2004) |
| Rhizoids | Present or absent | Absent | | Roy et al. (2006) |
| Host range | Narrow (one host or taxonomically related host species) | Wide (hosts may belong to taxonomically distant groups) | At the species level hypocrealean fungi have broad host ranges but isolates can be more specific. Furthermore, species complexes are known for a number of species in both groups. | Shah and Pell (2003), Scholte et al. (2004) |
| Epizootics | Common | Common | | Scholte et al. (2004) |
| Common transmission mode | Aerial by wind and rain, Host to host | Rain splash, Host to host | | Roy and Pell (2000), Scholte et al. (2004) |
| Pre-death sporulation? | Rare | Rare | Entomophthorales: *Entomophthora thripidium*, *Strongwellsea* species, *Massospora* species. Hypocreales: *Lecanicillium* species | Shah and Pell (2003), Roy et al. (2006) |
| Modification of host behaviour | Common | Rare but occurs in *Cordyceps* species | | Roy and Pell (2000), Roy et al. (2006), Pontoppidan et al. (2009) |
| Primary reservoir | Host | Soil | | Roy et al. (2009) |
| Primary environment | Mostly foliar (resting spores in soil) | Both in soil and foliar | | Shah and Pell (2003) |
| Toxin production | Known for *Conidiobolus* species | Known | | Strasser et al. (2000), Shah and Pell (2003) |
| Saprophytic life strategies | Rare | Common | Species of the entomophthoralean genus *Conidiobolus* can be saprophytic | Shah and Pell (2003) |
| Primary biological control strategies | Conservation, Classical, Inoculation | Augmentation, Inundation, Classical | | Eilenberg et al. (2001), Shah and Pell (2003), Pell (2007) |
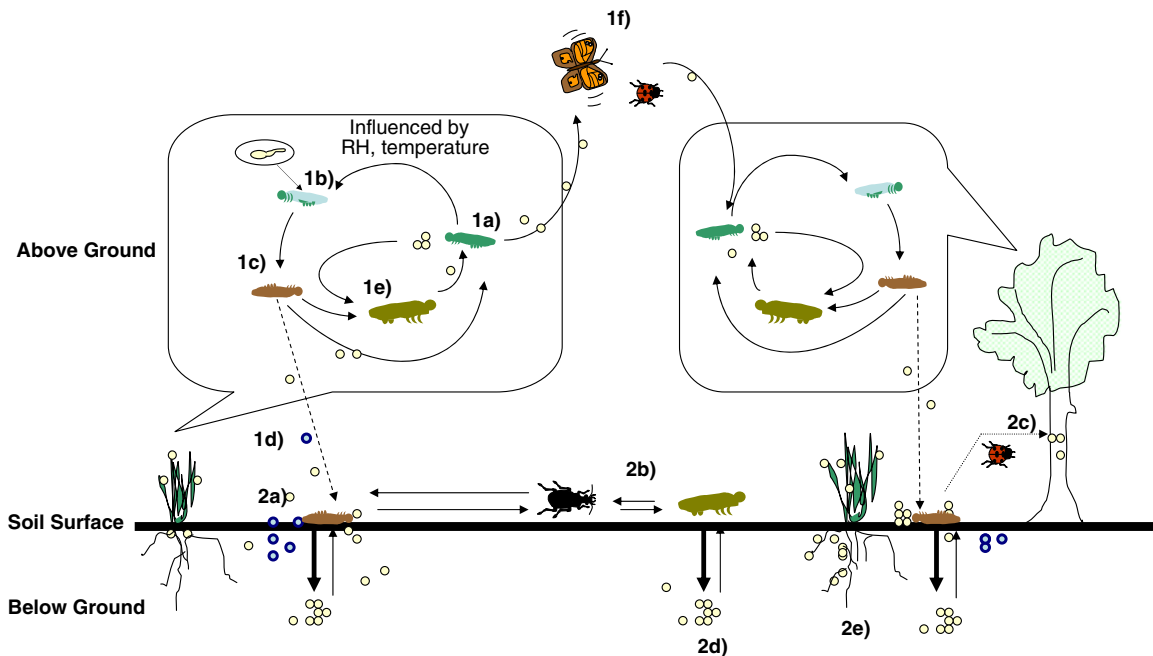
**Fig. 1** Entomopathogenic fungi and their hosts exist in a complex landscape influenced by multi-trophic relationships within the community and modulated by abiotic factors. Environmental change, particularly the arrival of new species (either host or fungus), climate change, habitat fragmentation and/or alteration will have differential effects across this community. Arrow size indicates the direction of interaction that is likely to be greatest in semi-natural habitats. 1a) an insect host contacts infective spores which b) germinate and penetrate the host eventually killing it, c) the sporulating cadaver releases spores for further cycles or d) often (in the case of Entomophthoralean fungi) when the number of susceptible hosts decreases resting spores are produced which survive in the soil and produce infective spores under favourable conditions and e) alternative hosts, often taxonomically related to the primary host, may be infected and produce spores that also infect primary hosts f) Conidia can be transported in wind currents, in infected hosts and on the surfaces of non-host invertebrates to other habitats. 2a) Conidia/resting spore distribution and persistence at the soil surface will be influenced by abiotic factors such as rainfall that influence horizontal transmission by promoting conidium formation on cadavers, mechanically dispersing conidia and potentially increasing vectoring by other invertebrates b) Epigeal predators can also remove inoculum by consuming cadavers but may also vector infective stages to new hosts and habitats at the soil surface and c) into foliar environments. Persistence in the soil profile is affected by d) soil type, soil moisture and pore size and by e) interactions in the rhizosphere with soil microbes, root exudates and secondary plant compounds. Within the soil profile conidia may also be dispersed by species such as *Collembola*

between speed of kill and temperature although overall mortality may not be affected (Ekesi et al. 1999; Thomas and Blanford 2003). Solar radiation is detrimental to persistence, particularly on the phylloplane where fungi can be rapidly deactivated (e.g. Fargues et al. 1996; Furlong and Pell 1997).

The detailed ecology, physiology and life cycles of each species within these groups can be exceedingly varied reflecting adaptations to ensure survival and transmission despite the environmental constraints (Pell et al. 2001; Roy et al. 2006; Table 1). However, it is possible to generalise for taxonomically related species/groups. Entomophthoralean fungi demonstrate a continuum of adaptations for dispersal and transmission. They exhibit dispersive, actively discharged conidia produced externally after host death through to sporulation from living hosts prior to host death which is particularly noted in species which require continued host activity to ensure conidia dispersal (Pell et al. 2001; Roy et al. 2006; Table 1; Fig. 1). Species in the Entomophthorales do not generally produce toxins (secondary metabolites) as part of the infection cycle but are characteristically biotrophic with a narrow host range and are common among foliar arthropods (Pell et al. 2001; Shah et al. 2004; Table 1). Eilenberg and Pell (2007) list a number of host-pathogen systems in which the ecology of Entomophthorales has been discussed.

The anamorphic Hypocreales are generally considered to be opportunistic with broad host ranges and most commonly associated with soil-inhabiting arthropods in temperate regions. They are characteristically hemibiotrophic, switching from a parasitic, biotrophic phase in the haemocoel (sometimes producing toxins) to a saprophytic phase colonizing the host after death. Conidia are produced on the cadaver but, unlike Entomophthorales, are not actively discharged. Both Entomophthorales and Hypocreales produce resting structures for persistence in the absence of new hosts or under adverse environmental conditions. Often assumed to be generalists, they are usually considered to be less well adapted to a parasitic life style than entomophthoralean fungi. However, recent research is demonstrating that the challenges of exploiting a wide range of potential hosts requires adaptations that are just as elegant as those required for a specialist life style (Humber 2008). Furthermore, while Hypocreales tend to be considered as generalists and Entomophthorales as specialists, there is considerable variability amongst species within these orders and this is highlighted in Table 1.

The genus *Cordyceps* (Ascomycota: Hypocreales) is, perhaps, the most studied teleomorph within the Ascomycota and the most common fungus encountered in association with arthropods in tropical forests (Evans 1981). Most *Cordyceps* appear to have a very restricted host range (in contrast to their anamorphic counterparts). This has been clearly demonstrated for ants. Sanjuan et al. (2001) documented the importance of host association in the distribution and incidence of *Cordyceps* in forest systems. Number of ants parasitized by *Cordyceps* was greater in disturbed forests compared to near pristine forests and this was closely correlated to the presence of host species. The taxonomy of these fungi is only just being resolved. Indeed it is only recently that the teleomorph and anamorph states have been linked as one species rather than being assigned to separate divisions. Phylogenetic analysis suggests that the *Cordyceps* are not monophyletic but occur in three families: Clavicipitaceae, Cordycipitaceae and Ophiocordycipitaceae (Sung et al. 2007; Blackwell 2009). There are more than 400 species of *Cordyceps* and a number of studies are emerging on the ecology of a few of these (Chee-Sanford 2008; Sanjuan et al. 2001). It is fascinating to consider that the same fungal species can differ so fundamentally in ecology depending on sexual state and not surprising that many

basic questions remain unanswered such as: why do teleomorphic ascomycetes not occur so widely in temperate habitats? What is driving the host specificity of the sexual stages? Are the telemorphic ascomycetes utilising the functional niches in the tropics that are occupied by the Entomophthorales in temperate zones?

The anamorphic (asexual) states of the Ascomycota have generally been used as inundative biopesticides. In contrast, research on the Entomophthorales has focused on conservation and inoculation biological control. Accordingly, ecological understanding of the Entomophthorales is more advanced than for the Hypocreales. However, recent research efforts are beginning to address this imbalance (Bidochka et al. 2001; Meyling and Eilenberg 2006a, b; Roy et al. 2009). Studies on the anamorphic states of species within the Ascomycota dominate the literature. The teleomorphic (sexual) states are poorly understood but are undoubtedly critical to our ecological understanding of fungal entomopathogens.

## Conceptual framework for understanding the role of fungal entomopathogens in host population regulation

The potential of fungi to regulate insect populations will depend on their abundance in the host population (prevalence) as well as their abundance and persistence in the surrounding environment. Whether or not insect populations are regulated by fungi, our first challenge is to accurately quantify how common fungi are in both hosts and the surrounding environment.

Prevalence in host populations

Accurate measurement of prevalence without biased sampling of either uninfected or diseased insects can be difficult and some challenges are specific to fungal entomopathogens (Fig. 2). A truly accurate assessment of prevalence can only be achieved by sampling all stages of the host in a life table analysis but this is rarely possible. Two methods are usually employed to estimate prevalence (1) sampling living individuals only, followed by laboratory incubation until death when infection can be confirmed by phenotypic characteristics and (2) sampling both living, dead and dying individuals, followed by laboratory incubation and identification (Fig. 2). The choice of sampling
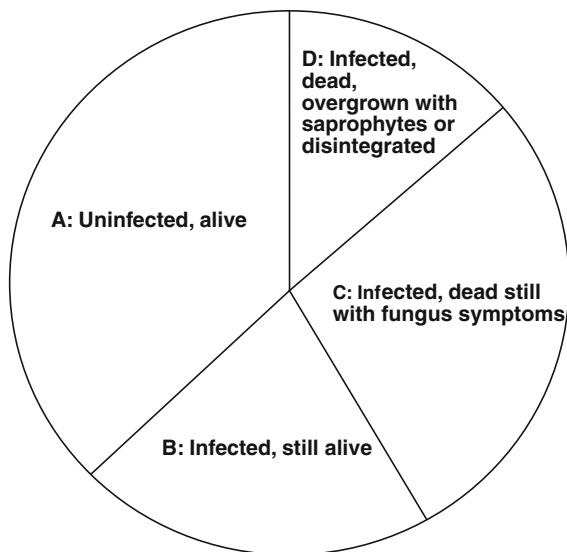
**Fig. 2** (Adapted from Eilenberg and Pell 2007). A diagram of the composition of a natural population of an insect species in relation to infection by a fungus pathogen. A: The population of uninfected individuals; B: The population of living, infected individuals. Fungus prevalence will be documented upon sampling these individuals and incubating them in the laboratory. C: Recently killed fungus-infected individuals located in the field; D: Individuals overgrown with saprophytic fungi for which diagnosis is not possible without molecular probing. Example of prevalence assessment: If living individuals are sampled and incubated alongside scoring of any dead individuals in the field then prevalence is assessed as (B+C)/(A+B+C)

process and the life-stages sampled will be dictated by the practicalities of sampling. The most obvious challenge, however, is ensuring the sample is representative of the entire population (Fuxa and Tanada 1987; Fig. 2). Some insects have behavioural characteristics that cause aggregation at specific locations such as late instar larvae of *Lymantria dispar* L. (Lepidoptera: Lymantriidae) moving off trees onto soil (Hajek 2001) or exhibit behavioural changes due to infection such as increased movement in aphids (Roy et al. 2006; Roditakis et al. 2008). Some life stages cannot be easily located, such as small instars, increasing sampling bias towards the larger late instars. Furthermore, host development time could be altered by infection (Hoch et al. 2000) and this could lead to an inaccurate measure of prevalence. However, it is critical that all juvenile (and in some cases also adult) stages are sampled as insects may demonstrate stage specific resistance to fungal infection (Roy et al. 2008) and in some cases, differential susceptibility based on the life stage exposed (Dromph et al. 2002). Ideally,

sampled insects should be incubated separately to avoid transmission within the sample and under conditions that do not favour infection as this could lead to overestimation of prevalence.

In recent years, molecular techniques have been developed to detect the presence of fungal pathogens in field collected insect samples. Such methods offer opportunities for more rapid assessment in the future and examples include: enzyme-linked immunosorbent assay (ELISA) to detect *Entomophaga maimaiga* Humber, Shimazu and Soper (Entomophthoramycotina: Entomophthorales) in *L. dispar* (Hajek et al. 1991); DNA probes to confirm *L. dispar* deaths due to *Entomophaga aulicae* (Reichardt in Bail) (Zygomycota: Entomophthorales) Humber or *E. maimaiga* (Hajek et al. 1996); PCR detection of *Pandora neoaphidis* (Remaudière & Hennebert) Humber (Entomophthoramycotina: Entomophthorales) in aphids (Fournier et al. 2008; Tymon et al. 2004). Most examples of prevalence assessments using the two methods described above are for pest insects in managed systems but the methods are appropriate in semi-natural systems (see examples in Table 2).

Abundance in the environment

Fungal propagules can persist outside the host on soil and phylloplanes and in the air where they can act as reservoirs of inoculum. Their abundance can be measured directly (conidia capture) and indirectly (baiting) in these habitats (e.g. Bidochka et al. 2001; Bruck 2004; Hemmati et al. 2001; Klingen et al. 2002; Meyling and Eilenberg 2006a; Wilding and Perry 1980). Soil samples are generally incubated with laboratory reared susceptible bait insects such as wax moth *Galleria melonella* L. (Lepidoptera: Pyralidae) and the frequency of insect infection is used as a measure of fungal abundance. Conidia capture in the aerial environment has been measured using selective media (Shimazu et al. 2002) or microscope slides (Steinkraus et al. 1996) exposed to the air above or within plant canopies. More precise measurements are made using volumetric spore traps e.g. Burkhard traps and rotorod samplers that capture conidia on adhesive materials to determine conidia density at specific locations (e.g. Hajek et al. 1999; Hemmati et al. 2001) Occurrence studies, such as these, are useful measurements of fungal reservoirs within a habitat that may have the potential to infect a

**Table 2** Examples of prevalence studies using two methods: collection of live hosts only and collection of both living and dead hosts

| Method | Fungus species | Host species | References |
|---|---|---|---|
| Living hosts only | *Entomophthora schizophorae* | *Chamaepsila rosae* | Eilenberg and Philipsen (1988) |
| | *Entomophaga maimaiga, Isaria farinosus, Lecanicillium sp.* | *Lymantria dispar* | Hajek (1997) |
| | *Strongwellsea castrans* | *Delia radicum* and other diptera | Eilenberg and Michelsen (1999) |
| | *Beauveria bassiana* | *Hypothenemus hampei* | Monzon et al. (2008) |
| | | *Musca domestica* | Siri et al. (2005) |
| | *Lecanicillium* spp., *Beauveria bassiana, Metarhizium anisopliae, Isaria farinosa* | *Taeniothrips inconsequens* | Brownbridge et al. (1999) |
| | *Pandora neoaphidis* | *Sitobion avenae* | Feng et al. (2004) |
| | | | Dean and Wilding (1973) |
| | *Entomophthora planchoniana, Neozygites fresenii* | *Elatobium abietinum* | Nielsen et al. (2001) |
| Living and dead hosts | *Neozygites fresenii* | *Aphis gossypii* | Steinkraus et al. (1995) |
| | *Pandora neoaphidis, Entomophthora planchoniana, Entomophthora thaxteriana* | *Metopolophium dirhodum, Sitobion avenae* | Dean and Wilding (1971) |
| | *Pandora neoaphidis, Entomophthora planchoniana, Neozygites fresenii, Beauveria bassiana, Lecanicillium sp.* | Cereal aphids including *Diuraphis noxia* | Hatting et al. (1999) |
| | *Neozygites floridana* | *Tetranychus urticae* | Klingen et al. (2008) |
| | *Entomophthora planchoniana, Pandora neoaphidis, Neozygites sp.* | *Monella caryella* | Ekbom and Pickering (1990) |
| | *Pandora neoaphidis, Conidiobolus thromboides, Entomophthora chromaphidis, Zoophthora occidentalis, Neozygites fresenii, Lecanicillium sp.* | *Aphids glycines* | Nielsen and Hajek (2005) |

particular insect species, although these studies are again generally focused on insects of economic importance (Bruck 2004; Sookar et al. 2008).

Fungal traits

Research on traits of fungal entomopathogens have largely focused on a single trait: the ability of an isolate or species to cause mortality in the host. In part, this reflects the interest of many pathologists to develop fungi for microbial control and there are, therefore, few studies on non-pest hosts. Examples from non-pest hosts mostly consist of descriptive or observational studies on single or a few species

(Humber 1976; Keller 1987b) or books on diversity and occurrence of fungal entomopathogens (Bałazy 1993; Samson et al. 1988). These researchers use the qualitative term pathogenicity to describe "the quality or state of being pathogenic" whilst they use the quantitative term virulence for "the disease producing power of an organism, i.e. the degree of pathogenicity within a group" (Shapiro-Ilan et al. 2005). Both pathogenicity and virulence are frequently measured in laboratory bioassays (see Navon and Ascher 2000 for examples). Within the field of fungal insect pathology, virulence is expressed as the lethal dose ($LD_{50}$) or lethal concentration ($LC_{50}$) causing mortality of 50% of test insects. In this way,

a fungus may be highly virulent if only a few conidia are required to cause a lethal infection. The definitions of pathogenicity and virulence vary within and between disciplines and depending on the type of pathogen concerned. Cross-disciplinary consensus regarding these definitions is required but this will require wide consultation and is beyond the scope of this paper.

In the general epidemiological literature virulence is defined as a measure of the impact of a pathogen on host fitness, and may be expressed as a reduction in either fecundity or survival of infected hosts compared to uninfected hosts (Solter 2006). It is a biological property of the pathogen that may be altered through abiotic and biotic impacts and thus may vary during the progression of an epizootic. Current studies of fungal entomopathogens often only consider isolates and species that are highly virulent and therefore almost invariably cause host mortality. However, we know that there are fungal isolates that have low virulence and do not generally cause high host mortality (Shah et al. 2004). In these cases, and also for virulent isolates, there are additional effects on the host through other mechanisms such as reduced fecundity (Baverstock et al. 2006; Furlong et al. 1997; Roy et al. 2008; Xu and Feng 2002). Only recently with improved molecular techniques are we becoming aware of the previously underestimated role that covert infections may play in insect populations (Burden et al. 2003). Covert viral infections are increasingly considered as important in infection dynamics (Boots et al. 2003) but as yet, there is no evidence to suggest fungi harbour similar covert infections although these may be more likely in the microsporidia.

## To what extent do fungal entomopathogens play a role in regulating populations of insects in semi-natural ecosystems?

This question would be best answered by classic life table studies of host populations, yet few such studies exist as previously mentioned. Examples in the ecological literature tend to focus on insect hosts and their parasitoids (Hawkins et al. 1997; Paniaqua et al. 2009), reflecting perhaps the technical difficulties in detecting pathogens in the field as we highlighted earlier. The best examples emanate from the USA, where populations of Lepidoptera are monitored in forests for economic reasons. Although these studies are from forests that are managed monocultures allowing the host species in question to reach high population densities (Dwyer et al. 2004), they still provide the best empirical and theoretical examples of populations to date in which pathogen prevalence has been monitored over time, and illustrate how theoretical models may be used to unravel the relative contributions of different entomopathogens in the control and regulation of their hosts. In the case of invasive non-native insects, a special situation may occur if the invasive species has escaped from its specialized natural enemies and for that reason, significantly increased in population size. This hypothesis, termed 'natural enemy release', (Torchin et al. 2003; Roy et al. 2008) needs confirmation for host specific entomopathogenic fungal species or isolates.

## Potential of specialist fungal entomopathogens to regulate host populations

The earliest host pathogen models established the principle that pathogens with persistent stages external to their hosts have the ability to regulate their hosts if sufficiently persistent in the environment (Anderson and May 1981). These models also assume that insect hosts do not acquire immunity to their pathogens and therefore do not include a resistant class of hosts immune to further infection (Grenfell and Dobson 1995). Indeed, it was illustrated that such specialist pathogens (or parasitoids) could be responsible for population cycles in which the period extends over many host generations. These principles were established using models in which, quite deliberately, the host was not influenced by any other form of population regulation, including intraspecific density dependence. The features of the host-pathogen interaction that resulted in population cycles included the density dependent nature of horizontal transmission which is well recorded for fungal entomopathogens (Johnson et al. 2006; Thomas et al. 1995), and the persistent nature of the external infectious stages (Baverstock et al. 2008; Weseloh and Andreadis 1997; Table 1). The density dependence of horizontal transmission ensures that the prevalence of the fungus in susceptible hosts rises as host population density rises, so checking the exponential growth of the host population.

The best studies that demonstrate insect population regulation by fungal entomopathogens are those involving pest insects in agroecosystems (e.g. Klubertanz et al. 1991; Nielsen and Hajek 2005; Smitley et al. 1986) but there are also examples from aquatic systems (Burns 1979; Johnson et al. 2006). External infectious stages ensure that the fungi persist during periods of low host population density, when horizontal transmission is insufficient to maintain the prevalence in the host population (Filotas and Hajek 2004; Hajek et al. 2004). Thus early theoretical work established that pathogens with these life history characters could potentially both regulate, and cause cycles in host populations. This caused considerable interest at the time, because forest insect pests displayed such cycles with no convincing explanation for them and this has been an area of much research and debate ever since (e.g. Abbott et al. 2008; Abbott and Dwyer 2007; Buntgen et al. 2009; Liu et al. 2007; Myers 1988). As fungal entomopathogens possess these life history attributes (Table 1) it is likely that they also have the potential to regulate host populations.

Two important concepts arose from these early models, one of these being the basic reproductive rate of the pathogen ($R_0$). This is defined as the number of new infections that arise from one primary infection in a wholly susceptible population. This must be greater than one for the pathogen to persist and spread, and so defines the conditions under which the pathogen could invade the host population. Due to the density dependent nature of transmission, host populations with higher densities of susceptible hosts will have higher contact rates with infective conidia, and so will give rise to higher values of $R_0$. The second concept, the host density threshold ($H_T$) is related to $R_0$, and is the density at which $R_0 = 1$. Thus $H_T$ is a critical threshold below which prevalence will decline and above which it will rise. Comparing how assumptions alter the expressions for $R_0$ and $H_T$ provides a convenient way of comparing different models.

## Potential of generalist fungal entomopathogens to regulate host populations

Theoretical models exploring the potential for natural enemies to regulate populations usually consider specialist natural enemies, the densities of which are tightly coupled to the host populations. However, any density dependent relationship may regulate or stabilize a population through heterogeneity in attack rates, and even density independent patterns may do this if there is sufficient heterogeneity in risk from patch to patch (Hassell and May 1988). Consequently, generalist natural enemies may also hold the potential to be prime regulating factors, even though their dynamics may be uncoupled to some degree from the host species.

Both manipulative empirical and theoretical studies have illustrated that attack rates from generalist natural enemies are usually high enough at low host population densities to prevent population outbreaks. For example, the white footed mouse, *Peromyscus leucopus* Rafinesque (Rodentia: Neotominae), is a generalist predator of the gypsy moth *L. dispar*. Empirical data is consistent with this predator regulating the moth at low densities and a nucleopolyhedrovirus regulating the moth at high densities (Elkinton et al. 1996). In another study of the forest tent caterpillar *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), generalist avian predation was found to be the dominant mortality factor, in strong contrast to five specialist parasitoid species (Parry et al. 1997). A review of two herbivore species (the autumnal moth, *Epirrita autumnata* Borkhausen (Lepidoptera: Geometridae) and voles of the genus *Microtus* and *Clethrionomys*) concluded that the population cycles observed in northern Fennoscandia were likely to be caused by specialist natural enemies and the more stable dynamics on the south to be caused by an increase in the density and diversity of generalist natural enemies (Klemola et al. 2002).

Although this evidence is drawn largely from generalist predators, generalist fungal entomopathogens possess the life history characteristics to fill this role very effectively; host-fungus interactions exhibit heterogeneity in attack rate, and they can increase in abundance rapidly in response to the presence of hosts (Kamata 2000). However, the degree to which they cause mortality in populations, outside of the context of crop systems, is virtually unknown.

## Combined effects of specialist and generalist natural enemies on host populations

It has long been established by theory and observation that host populations exhibit many different equilibrium states, and consequently it is unlikely that any one natural enemy is responsible for regulating a

host species (Henson et al. 2009). Indeed food webs consist of both specialist and generalist natural enemies, with fungal entomopathogens playing both of these roles (Roy and Pell 2000; van Veen et al. 2008), and it is important to consider the combined effect of the suite of natural enemies present; no one pathogen acts in isolation. Furthermore, models in which only one natural enemy is responsible for regulating a host population frequently fail to capture the observed dynamics, with the time between host outbreaks being far more irregular than traditional models would predict. More recently, in a few cases, models are now being developed to include more than one natural enemy, with the stochastic influence of abiotic factors causing the host population to move between a low, stable, equilibrium which may be maintained by generalist natural enemies, and more cyclic dynamic behaviour which is the classic hallmark of a specialist natural enemy (Dwyer et al. 2004). These more complex models can produce behaviour which is more consistent with field observations, namely irregular outbreaks separated by long intervals during which the host is present at low densities, and represent a significant step forward in our understanding of the potential role of complexes of natural enemies in the regulation of herbivores and is applicable to fungal entomopathogens.

## Making the models more realistic

### Pathogen reservoirs

Clearly host populations are likely to be influenced by constraints on resources, or other factors that will act in a density dependent manner on population growth. Host density dependence has been incorporated into early models in more than one way, and one case concluded that cyclical behaviour occurs over great regions of parameter space (Dwyer 1994), and in another case that cycles were less likely, with the cycle period depending upon parameter values (Bowers et al. 1993). The range of parameter values considered and the form of the density dependence is likely to be influential in determining which outcome is most probable. Perhaps a more significant extension of theory was to include the concept of a 'pathogen reservoir', in which pathogens cannot infect hosts but where their degradation rate is low (Hochberg 1989).

Pathogens may also move out of the reservoir to re-enter the infection cycle, or hosts may 'visit' the reservoir and acquire infection (Fig. 1). The ability of fungal conidia or resting spores in reservoirs to re-enter the infection cycle has been demonstrated (Bitton et al. 1979; Hajek 1999). The presence of such a reservoir has a storage effect, which dampens cycles and increases the likelihood of a stable equilibrium. Environmental reservoirs of fungal entomopathogens have been found in a number of circumstances of which a few examples are: *E. maimaiga* in forest soil (Hajek 1999); *Beauveria bassiana* (Balsamo) Vuillemin (Ascomycota: Hypocreales) on logs (Reay et al. 2007) and within agricultural soils (Meyling and Eilenberg 2006b); *P. neoaphidis* within agricultural soil (Baverstock et al. 2008; Nielsen et al. 2003); *Entomophthora planchoniana* Cornu (Entomophthoramycotina: Entomophthorales) as hyphal bodies on tree trunks or resting spores in soil (Keller 1987a, b); *Neozygites fresenii* (Nowakowski) Batko (Entomophthoramycotina: Entomophthorales) as resting spores on trees (Bitton et al. 1979).

### Transmission and disease resistance

In contrast to the experimental literature on viral entomopathogens (Elderd et al. 2008), there are no studies directly examining heterogeneity in transmission rates for fungal entomopathogens. Heterogeneity in transmission is expected, however, due to individual differences in host susceptibility observed in the laboratory (Ferrari et al. 2001; Keller et al. 1999; Roy et al. 2008) and the heterogeneous distribution of infective conidia in the field (Meyling and Eilenberg 2006b; Tscharntke et al. 2008). Such heterogeneity in natural-enemy attack rates is strongly stabilizing (Hassell et al. 1991) and produces stable cycles for a range of parameter values in host-pathogen models (Dwyer et al. 2000).

An element of heterogeneity in host susceptibility has a genetic basis. It has been illustrated that host populations can develop a degree of resistance or at least reduced susceptibility, to some fungal entomopathogens within and between generations (Ferrari et al. 2001; Milner 1982, 1985; Stacey et al. 2003). This phenomenon has also been illustrated in response to other entomopathogens (Boots and Begon 1993; Cooper et al. 2002). Indeed, Stow et al. (2007) suggest that selection by microbial pathogens, and more

specifically production of antimicrobial defences, was critical to the evolution of sociality. However, few studies show that host investment in resistance to fungal entomopathogens may change depending upon host density and these are limited to species exhibiting density-dependent phase polyphenism (Wilson et al. 2001, 2002). The hypothesis is that at high host densities, insects are more likely to encounter inoculum due to the density dependent nature of horizontal transmission, and that some species can exhibit a plastic response to this and allocate more of their limited resources to disease defence than at low densities. This has also been illustrated for some species in response to nucleopolyhedroviruses (Reeson et al. 1998, 2000), but for others the reverse pattern is suggested, with susceptibility increasing at high densities, and this has been postulated to be due to stress (Reilly and Hajek 2008). The form of the relationship between disease resistance and density dependence will influence the impact on population dynamics, with the inverse relationship between population density and disease resistance having a stabilizing influence (Reilly and Hajek 2008).

Given that there is a heritable element to resistance in some cases, it is possible that susceptibility to entomopathogens may change during the course of an epizootic, particularly if there is a cost to resistance. Again there is supporting empirical evidence for this in the case of viruses (Cory and Myers 2009) but evidence for fungal entomopathogens is limited (Miller et al. 2009). If natural selection drives rates of transmission through altered host susceptibility, theoretical models suggest that cycles are more likely to be observed even at high rates of heterogeneity in transmission (Elderd et al. 2008). This illustrates the importance of including natural selection in host-pathogen models when attempting to discover the role of entomopathogens in host population dynamics.

Summarising, theory illustrates that host specific fungal entomopathogens could potentially regulate their host populations, but the question remains open as to whether such pathogens really are the prime regulating factor in many cases. There are many details of the host-pathogen interaction that would benefit from further empirical data. It is notable that vertical transmission of fungi has only been demonstrated in very few cases (e.g. Tarrant and Soper 1986). High rates of vertical transmission would make the

conditions for regulation less stringent (Anderson and May 1982).

Dispersal: keeping up with your host

Greif and Currah (2007) demonstrated the importance of arthropods in dispersing fungi but highlighted the need for more data comparing patterns among substrates, fungal species and their arthropod carriers. Most ecological studies are conducted at a small spatial scale. More recently, and particularly in the context of arthropod species shifting their ranges as a consequence of climate change, there has been greater focus on the mechanisms and rate at which pathogens spread through host populations. One fundamental constraint on the part of a specialist pathogen is that, when considering the regional scale, it is unlikely to arrive in a new habitat ahead of the host. This has led to the hypothesis that the increased abundance observed at the leading edge of species shifting their ranges is due to the host escaping, albeit temporarily, the regulating influence of some natural enemies (Gaston 2009; Menendez et al. 2008). In some cases, pathogens may hitch a ride with their hosts in the form of covert infections vertically transmitted to offspring (Burden et al. 2003). Covert infections are uncommon in fungal entomopathogens (Tarrant and Soper 1986), however, modern molecular tools may reveal hitherto hidden fungal infections at non lethal levels.

The simplest theoretical models describing pathogen dispersal within a host population are based on the process of diffusion and provide a moderately good description of dispersal at small spatial scales (Dwyer et al. 1998). These relatively simple models assume that conidia obey the laws of diffusion, although the precise shape of the dispersal kernel is unlikely to be Gaussian, and more likely to be 'fat-tailed'. The moderately good fit between models and data suggest that the majority of fungal infection at small spatial scales represented by experimental plots is due to a process akin to diffusion. However, a study of the regional spread of E. maimaiga through gypsy moth populations in North America found that rates of spread at the regional scale could not be predicted from diffusion models fitted to data obtained at local scales (Dwyer et al. 1998). Similarly, more detailed simulation models incorporating local abiotic factors such as temperature, rainfall and humidity could only accurately represent patterns of spread over a 3 km

area if airborne conidia are allowed to freely disperse over the whole area (Weseloh 2003, 2004). This suggests that dispersal mechanisms, such as wind currents above the forest canopy, which operate at long distances, are crucial in explaining observed patterns of dispersal of conidia independent of their hosts. There are parallels here with studies on the dispersal of seeds, in which models have been developed combining local and long distance dispersal processes (Wichmann et al. 2009), and there is a strong argument that similar theoretical developments, combining local and regional processes in an analytical framework, would be appropriate for fungal entomopathogens (Dwyer et al. 2004).

Spatially heterogeneous environments

Habitat loss through environmental change leads to an increasingly fragmented landscape, with only patches of habitat that are suitable for hosts to persist. How will this influence host-pathogen dynamics, particularly in light of the broad host range of some fungi, and the dispersal ability of conidia discussed above? Hess (1996) developed a host-pathogen model from the classical Levins (1969) metapopulation model to explore the conditions under which hosts and pathogens may persist in a fragmented landscape. This original model was based on direct transmission between infected and susceptible hosts although subsequently, we have explored similar models based on pathogens such as baculoviruses and many fungal entomopathogens which infect by means of free-living infective stages, and the conclusions are not qualitatively different (White and Hails personal communication). Hess (1996) concluded that host dispersal between patches enhanced the spread of disease and thus could lead to host extinction. Fungus-infected hosts have the ability to disperse and to spread disease into new colonies as documented for aphid species (Feng and Chen 2002; Feng et al. 2004). Some specialist fungi such as *Strongwellsea* spp. sporulate from one or two holes on living hosts and conidia are dispersed in this way. Whether hosts themselves are the principle means by which fungal pathogens disperse between patches in a fragmented landscape has yet to be determined.

McCallum and Dobson (2002) further developed this framework to consider a 'generalist' pathogen, the abundance of which is maintained in a second host species which acts as a reservoir. In contrast to Hess (1996), they concluded that greater landscape connectance enhanced the stability of the host-pathogen interaction. Habitat corridors allow host species to disperse and 'escape' pathogens, effectively creating a form of refuge. However, complete connectance is equivalent to a homogenous habitat; and a degree of habitat partitioning actually promotes co-existence of host species by, for example, relaxing apparent competition mediated by a shared natural enemy (Holt 1984). A general principle that emerges from these and other studies is that the spatial complexity of population structure is a source of heterogeneity that can promote the co-existence of hosts and pathogens. However, the precise dynamics will depend upon the spatial distribution of hosts, the productivity of patches (in terms of host growth rates), the life history characteristics of the pathogens and the mobility patterns of hosts and pathogens (Namba et al. 1999; Rodriguez and Torres-Sorando 2001). Consequently, the response of fungal entomopathogens to habitat fragmentation would be best explored in specific host populations using models of intermediate complexity that have been adapted to incorporate species specific information.

## Conclusions

Fungal entomopathogens are ubiquitous in semi-natural habitats and play a role in insect population dynamics. There is, however, a scarcity of empirical data available to evaluate their relative importance in controlling and regulating insect populations in semi-natural ecosystems. Even within well studied crop systems such as forest insects, we have a limited understanding of the role of fungal entomopathogens and insect population dynamics. Anticipated changes in disease prevalence due to key anthropogenic drivers (Millennium Ecosystem Assessment 2005) such as climate change and habitat fragmentation as well as the arrival of invasive species are likely to affect the prevalence of all entomopathogens in semi-natural ecosystems (Roy et al. 2009). The effects of such changes in disease prevalence will be relevant to the management of both pest insects and insects of conservation interest (Roy et al. 2009). The practicalities of studying fungal entomopathogens in any system can be challenging; there are limitations

imposed by the research tools available and many of the complex multitrophic interactions are yet to be revealed (Cory and Ericsson 2009). However, it is imperative that we drive research effort forward by coupling rigorous research in the field with theoretical modelling in order to unravel the complexity of interactions between fungal entomopathogens and their hosts in semi-natural habitats.

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