

Review

Ecology of the entomopathogenic fungi *Beauveria bassiana* and *Metarhizium anisopliae* in temperate agroecosystems: Potential for conservation biological control

Nicolai V. Meyling*, Jørgen Eilenberg

Department of Ecology, Faculty of Life Sciences, University of Copenhagen, Thorvaldsensvej 40, DK-1871 Frederiksberg C, Denmark

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Abstract

It is increasingly recognized that the biodiversity in agroecosystems deliver significant ecosystem services to agricultural production such as biological control of pests. Entomopathogenic fungi, specifically the anamorphic taxa *Beauveria bassiana* and *Metarhizium anisopliae*, Hypocreales (Ascomycota), are among the natural enemies of pests in agroecosystems and the fungi are candidates for future conservation biological control in temperate regions. Conservation biological control is a biological control strategy in which farming practices and environmental manipulations are adopted to enhance the living conditions for specific natural enemies of pests. However, in order to manipulate the environment for the benefit of populations of the entomopathogens, knowledge of fundamental aspects of the ecology of the fungi considered is necessary. This knowledge is still scarce despite the large bulk of recent research into inoculation and inundation biological control with these fungi. Here, we review the current knowledge of the ecology of indigenous populations of *B. bassiana* and *M. anisopliae* in agroecosystems of temperate regions, primarily Europe and North America. We suggest anamorphic life cycles of *B. bassiana* and *M. anisopliae* in these regions based on the literature of their natural occurrence and distribution in agroecosystems, population dynamics, and interactions with other organisms, environmental factors, and agronomical practices.

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1. Introduction

Studies of biodiversity in agroecosystems and the delivery of ecosystem services to agricultural production have usually ignored the contribution of entomopathogens in the regulation of pest populations (Altieri, 1999; Gurr et al., 2003; Tschardt et al., 2005). However, entomopathogens are among the natural enemies of arthropod pests in agroecosystems. An improved understanding of the ecology of indigenous populations of these beneficial organisms is a prerequisite for the evaluation of their contributions to pest control and

for predicting the impact of agricultural practices on their populations.

The anamorphic entomopathogenic fungi *Beauveria bassiana* (Balsamo) Vuillemin and *Metarhizium anisopliae* (Metschnikoff) Sorokin from the order Hypocreales (Ascomycota) are natural enemies of a wide range of insects and arachnids and both fungi have a cosmopolitan distribution (Roberts and St. Leger, 2004; Rehner, 2005). Much effort has been put into research on the development of *B. bassiana* and *M. anisopliae* as biological control agents (for inundation and inoculation biological control) to be applied in agriculture and forestry in temperate regions. However, this bulk of knowledge is in striking contrast to the lack of research into the fundamental ecology of these fungi in terrestrial ecosystems, including agroecosystems.

* Corresponding author.

E-mail address: nvm@life.ku.dk (N.V. Meyling).

It is a future challenge for sustainable agricultural production to include pest control from entomopathogens in conservation biological control (referred to as CBC below) (Barbosa, 1998; Lacey et al., 2001). CBC is a biological control strategy in which farming management practices are adopted to enhance the living conditions for specific natural enemies of pests with the specific objective to suppress pest populations (Barbosa, 1998; Eilenberg et al., 2001). In recent years, an extensive number of studies have been published with focus on CBC with respect to natural enemies belonging to the arthropods, i.e., predators and parasitoids (e.g., Landis et al., 2000; Gurr et al., 2003; Kean et al., 2003; Chang and Snyder, 2004). So far, limited research effort has been devoted to the effects of environmental manipulations on entomopathogens (Fuxa, 1998; Ekesi et al., 2005). Emphasis has been given to aphid pathogenic fungi from Entomophthorales: *Pandora neoaphidis* (Remaudière and Hennebert) Humber and its potential as a natural enemy in CBC was studied in the UK (Shah and Pell, 2003; Ekesi et al., 2005) and *Neozygites fresenii* (Nowakowski) Batko was studied in the US (Shah and Pell, 2003; Steinkraus, 2006). In both cases the authors concluded that these fungal pathogens showed high potential for CBC of aphids. However, insights into the fundamental ecology of the fungi in agroecosystems are essential to predict the effects of environmental manipulations on the fungal populations and thus to include entomopathogens in CBC (Fuxa, 1998; Lacey et al., 2001; Shah and Pell, 2003; Stuart et al., 2006). Information of pathogen persistence and dispersal in the environment is equally important (Fuxa, 1998). Knowledge of the ecology of indigenous populations of *B. bassiana* and *M. anisopliae* in agroecosystems in temperate regions as well as the effects of environmental conditions and agricultural practices on the fungi is therefore necessary if they are to be manipulated for CBC in the future. Here, we present the current knowledge of these ecological aspects with reference to *B. bassiana* and *M. anisopliae* in temperate agroecosystems.

We have based the review on the published literature on natural occurrence and fundamental ecology of the morphological species *B. bassiana* and *M. anisopliae*. Recent research has shown that the morphological species *B. bassiana* is paraphyletic (Rehner and Buckley, 2005) and consists of two separate clades that should be separated taxonomically. As this redescription has not yet been done, we use *B. bassiana* throughout this review as reference to the morphological species when no information of phylogenetic affiliation is available.

German studies have recently shown that the structure of the agricultural landscape has impact on agroecosystem biodiversity, which also comprises entomopathogenic fungi, and thus the ecosystem services they deliver (Tschardt et al., 2005). We therefore include the aspect of landscape elements in this review. This review aims to create the foundations for future focus on the indigenous

populations of *B. bassiana* and *M. anisopliae* as biological control agents in temperate regions using a CBC strategy.

2. Distribution and diversity of indigenous populations

2.1. Soil

The soil environment is usually the conventional isolation site for hypocrealean entomopathogenic fungi (Keller and Zimmerman, 1989; Hajek, 1997), and several species can be found in both cultivated and more natural habitats (Steenberg, 1995; Vänninen, 1996; Bidochka et al., 1998; Klingen et al., 2002; Keller et al., 2003; Meyling and Eilenberg, 2006b). In studies of natural occurrence of entomopathogenic fungi in the soil, susceptible bait insects such as *Galleria mellonella* L. (Lepidoptera: Pyralidae) or *Tenebrio molitor* L. (Coleoptera: Tenebrionidae) are usually added to soil samples in order to recover fungal isolates; in principle the method can be described as the use of selective media.

Keller et al. (2003) found *M. anisopliae* to be common in both arable fields and adjacent meadows, but the species occurred at higher densities in meadows. In Canada, *M. anisopliae* was most frequent in agricultural fields compared to forest habitats (Bidochka et al., 1998), while *M. anisopliae* in Finland was isolated more often in southern parts of the country and the occurrence was not adversely affected by cultivation of the soil (Vänninen, 1996). In Danish soils *M. anisopliae* was more frequent in sun exposed habitats (i.e., cultivated areas) than in shaded habitats (Steenberg, 1995), which is similar to the Canadian findings. Furthermore, *M. anisopliae* was not among the entomopathogenic fungi isolated in the soil of a Danish forest ecosystem (Nielsen et al., 2004). This implies characteristics of *M. anisopliae* as an 'agricultural' species that is most common in exposed and regularly disturbed soil environments. Local and significant differences in natural distribution on one location can, however, occur. Meyling and Eilenberg (2006b) found *M. anisopliae* to be locally rare in a Danish agricultural field while *B. bassiana* was the dominant fungal species. Bidochka et al. (1998) found *B. bassiana* to be affiliated with shaded and uncultivated habitats (i.e., forests) and *B. bassiana* also occurred frequently in hedgerow soils at a Danish locality (Meyling and Eilenberg, 2006b).

These differences in natural occurrences in soil challenge the CBC strategy. Based on the studies made at a regional scale, indigenous populations of *M. anisopliae* appeared to be the most suitable candidates for environmental manipulations because *M. anisopliae* was most associated with agricultural field soil. However, in the case of the Danish agroecosystem described by Meyling and Eilenberg (2006b), *M. anisopliae* was found to be rare locally and *B. bassiana* would be a more suitable candidate for CBC. Thus the scale of the landscape needs to be considered when evaluating indigenous populations of entomopathogenic fungi in soils.

2.2. Insects

Entomopathogenic fungi occur naturally as infections in insect hosts which can be collected in the field and incubated in the laboratory for documentation of the fungus. *B. bassiana* have been documented to occur naturally in >700 species of hosts (Inglis et al., 2001). Studies on the prevalence of fungi in insects have usually been limited to species that are pests or are important non-target species such as certain predators and parasitoids. However, it is likely that almost any major insect taxon collected intensively will be found to be a natural host for *B. bassiana* in temperate regions. The occurrences of the fungi as infections in hosts are presumably the only part of the fungal life cycle in which the fungi can build up significant population sizes by producing vast numbers of conidia. Thus contributing to the availability of susceptible hosts for fungal population increase is a key component when considering environmental manipulations in CBC strategies.

2.3. Plant associations

Recent evidence suggests that both *B. bassiana* and *M. anisopliae* have the potential to engage in fungus–plant interactions. The large majority of investigated higher vascular plants have been found to host fungal endophytes (Saikkonen et al., 1998; Arnold and Lewis, 2005) including species in Clavicipitaceae contained within Hypocreales (White et al., 2002). *B. bassiana* has also been included in this spectrum of fungi with endophytic activity by infecting corn (*Zea mays*) (Bing and Lewis, 1991, 1992, 1993). Endophytic fungi are often regarded as plant-defending mutualists (Saikkonen et al., 2004) and the presence of *B. bassiana* in internal plant tissue has been discussed as an adaptive protection against herbivorous insects (Elliot et al., 2000; White et al., 2002). Besides natural occurrence in leaf tissue of corn, *B. bassiana* exhibited endophytic activity in cacao (*Theobroma cacao*) (Posada and Vega, 2005), poppy (*Papaver somniferum*) (Quesada-Moraga et al., 2006) and coffee (*Coffea* spp.) and tomato (*Lycopersicon esculentum*) (F.E. Vega, personal communication). In temperate regions, inoculum of *B. bassiana* has furthermore been isolated from phylloplanes of various plants in hedgerows in Denmark (Meyling and Eilenberg, 2006a). This occurrence was hypothesized to be a consequence of deposition from the surroundings but was also suggested to act as a natural infection pathway of endophytic activity (Meyling and Eilenberg, 2006a). These new findings open exciting perspectives for the understanding of the ecology of *B. bassiana*. However, no knowledge is currently available about natural endophytic activity and host plant range of *B. bassiana* in temperate regions or of the significance of *B. bassiana* as an endophyte for fungus or plant fitness.

Plant association was also recently documented for *M. anisopliae*, but this association occurred below ground in the rhizosphere (Hu and St. Leger, 2002). The rhizosphere is the layer of soil immediately surrounding the root and

many interactions between plants and other organisms occur in this interface (Bais et al., 2006). By releasing a recombinant isolate of *M. anisopliae* to the soil of an experimental cabbage field in MD, USA, Hu and St. Leger (2002) were able to demonstrate that the released isolate persisted better in the soil immediately surrounding the cabbage roots as compared to the bulk soil. Factors in the rhizosphere therefore seemed to promote the persistence and biological activity of *M. anisopliae* (Hu and St. Leger, 2002). Wang et al. (2005) further documented that *M. anisopliae* expressed similar genes when growing in exudates from bean roots and on a nutrient rich medium while different genes were expressed by the fungus when growing on insect cuticle and in insect hemolymph. This indicated that *M. anisopliae* has developed different adaptations to function as a pathogen and to grow saprophytically in the rhizosphere (Wang et al., 2005). The implication for biological control with *M. anisopliae* exploring the rhizosphere competence was investigated by Bruck (2005). Inoculated conidia of *M. anisopliae* persisted significantly better (up to one year) in the rhizosphere of *Picea abies* compared to the bulk soil (Bruck, 2005). Survival outside the host may thus be critical for the ability of *M. anisopliae* to control insect pests in the soil (Roberts and St. Leger, 2004; Bruck, 2005). Whether the rhizosphere of plants generally provide a “refuge” (where the fungus can survive outside insect hosts) for *M. anisopliae* in the soil remains to be investigated. Perhaps associations with plants are important in the life cycle of both *B. bassiana* and *M. anisopliae* in temperate regions.

The compartments in temperate terrestrial ecosystems in which *B. bassiana* and *M. anisopliae* occur naturally are summarized in Fig. 1. Compartments are connected with lines to indicate dispersal and infection pathways when these are known; these aspects are presented below. Plant associations are included as potential compartments for the natural occurrence of *B. bassiana* and *M. anisopliae*.

2.4. Genetic diversity in populations of *B. bassiana* and *M. anisopliae*

Biodiversity is usually evaluated by assessment of species diversity. Biodiversity assessment of fungal communities is, however, challenging, because fungal taxa often consist of complexes of cryptic species (Bickford et al., 2007). Cryptic species are found in *B. bassiana* (Rehner and Buckley, 2005; Rehner et al., 2006) and seemingly also in the morphological species *M. anisopliae* (Bidochka et al., 2001, 2005). Evaluating the biodiversity contribution of *B. bassiana* and *M. anisopliae* in agroecosystems must therefore be based on an assessment of the genetic diversity to discover potential cryptic species. Traditional assessment of fungal species diversity is based on morphological features. Unfortunately, few and sometimes ambiguous characters are used for species separation. Furthermore, many entomopathogenic hypocrealean fungi have probably exclusively anamorphic life cycles in temperate regions, at

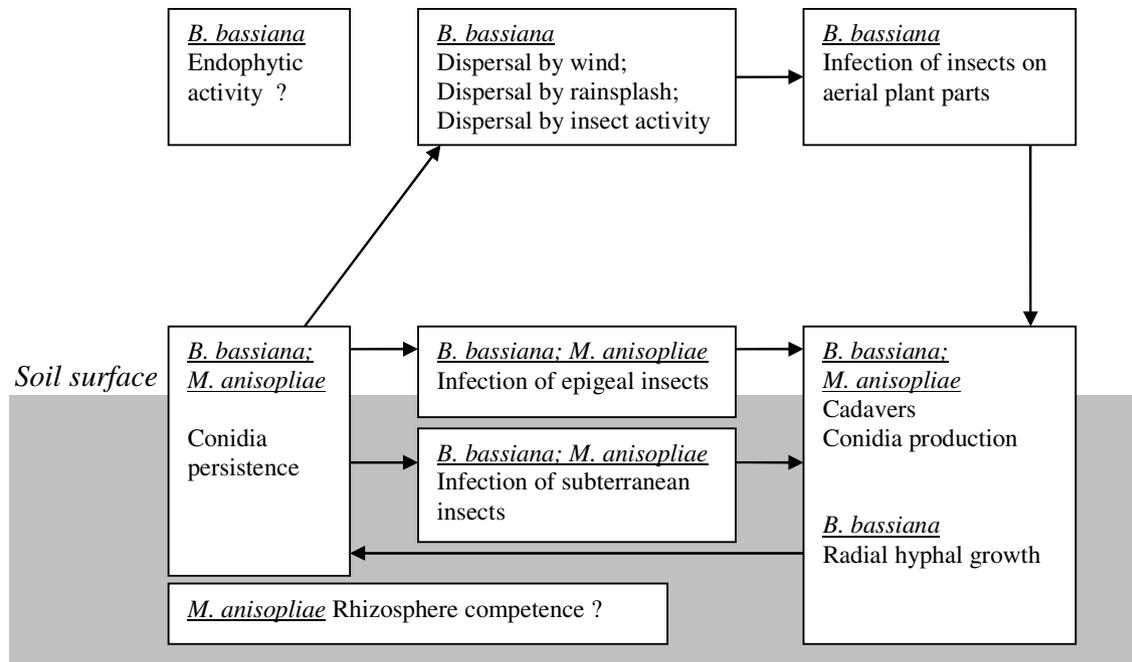


Fig. 1. Suggestions for anamorphic life cycles of *Beauveria bassiana* and *Metarhizium anisopliae* in Northern temperate regions. The grey area represents the soil environment while the white background of the figure is above ground. The life cycles are based on the current knowledge of the ecology of the fungi in temperate regions as presented in the text. Significant dispersal and infection pathways are indicated by arrows. In each ecological compartment, fungus names indicate the significance of the compartment for the life cycles of *B. bassiana* and *M. anisopliae*. Compartments representing plant associations are included with no arrows to indicate the possible significance of these associations, but the unknown relationships with other compartments.

least outside East Asia, which additionally complicates matters about defining biological species and comparing intraspecific and interspecific genetic diversity. Recent advances in molecular techniques have shed new light on our understanding of species boundaries, especially within the genus *Beauveria*. Several studies have revealed much genetic diversity of the morphological species *B. bassiana* (Glare, 2004). However, a recent phylogeny of *Beauveria* spp. showed that the morphological species *B. bassiana* in fact is paraphyletic and consists of two unrelated clades of which one is more related to *Beauveria brongniartii* (Saccardo) Petch than to the second “*B. bassiana*”-group (Rehner and Buckley, 2005). This latter group is tentatively referred to as ‘pseudobassiana’ (Rehner et al., 2006) but it needs a formal description. The existence of two unrelated clades may explain some of the large genetic diversity reported in the morphological species *B. bassiana*. Furthermore, the two groups of *B. bassiana* are themselves assemblages of cryptic species or separate clades (Rehner and Buckley, 2005; Rehner et al., 2006) thus each group also contains much genetic diversity. Both groups infect a wide range of insects and can be isolated from the soil (Meyling, 2005; Rehner and Buckley, 2005) but unfortunately no data currently exists on differences in ecological niches between the groups. As mentioned above, *B. bassiana* is used here to refer to the morphological species when no other information is known.

Most studies of genetic diversity of *B. bassiana* have been based on isolates from culture collections and have

usually been compiled to present isolates from infections in certain pest insects or isolates originating from a (major) geographical region. However, to understand the ecology of the indigenous fungal populations, studies must be carried out on isolates collected at a local scale and in different spatial compartments of the ecosystem. These isolates will represent genotypes that potentially interact with host populations, with each other and the environment under field conditions.

Based on the latter sampling strategy, *B. bassiana* isolates were sampled within the boundaries of a single organic agroecosystem in Denmark with the specific objective to characterize the genetic diversity. Sequence analyses [genomic regions as described in Rehner and Buckley (2005) and Rehner et al. (2006)] showed that several phylogenetic lineages were present in this single agroecosystem (Meyling, 2005; Meyling et al., 2005). Table 1 shows that the Danish locality contained the morphologically similar groups *B. bassiana sensu lato* and ‘pseudobassiana’. Furthermore, isolates from each individual clade of *B. bassiana s.l.* were more related to isolates from other European countries than they were to isolates from other clades at the locality. Only one of these clades was represented among isolates from the arable field soil (Table 1). At the same site, the morphological species *B. bassiana* was the most frequent entomopathogenic fungus in the soil of the agricultural field (Meyling and Eilenberg, 2006b). This study demonstrated that different genetic groups of the morphological species *B. bassiana* coexisted at a local scale

Table 1

Genetic groups of isolates of the morphological species *B. bassiana* collected within a single agroecosystem (an organic field and hedgerow) at Bakkegården, Denmark

Monophyletic group	Habitat of isolates within locality	Country of origin of most related isolate
<i>B. bassiana s.l.</i> ^a		
Eu_1	Arable field; Hedgerow	Hungary, ARSEF 1628
Eu_3	Hedgerow	France, ARSEF 1185
Eu_4	Hedgerow	Belgium, ARSEF 1848
Eu_5	Hedgerow	NA
Eu_6	Hedgerow	France, ARSEF 815
'pseudobassiana' ^b	Hedgerow	

Groups were identified based on DNA sequences of genomic regions as described by Rehner and Buckley (2005) and Rehner et al. (2006). Isolation habitats (i.e., arable field or hedgerow) for isolates belonging to each monophyletic group are presented. Isolates from reference collections that were found to belong to similar monophyletic groups are also presented. Results are summarized from Meyling (2005).

^a Monophyletic clade of the morphological species *B. bassiana* referred to as "Clade A" by Rehner and Buckley (2005) and *B. bassiana s.l.* by Rehner et al. (2006).

^b Monophyletic clade of the morphological species *B. bassiana* referred to as "Clade C" by Rehner and Buckley (2005) and 'pseudobassiana' by Rehner et al. (2006).

in the agricultural landscape. The study further indicated that typical North European agroecosystems bordered by hedgerows may harbor significant sources of genetic diversity of entomopathogenic fungi. However, the agricultural field soil only harbored one of the identified *B. bassiana s.l.* clades, documenting the lack of biodiversity in a monocultural cropping system, even when organic.

Very few studies have been carried out on the genetic diversity of *M. anisopliae* at a local or regional scale. Most knowledge has been generated in Canada on *M. anisopliae* isolates from different habitats, i.e., agricultural and forest sites. Bidochka et al. (2001) demonstrated that *M. anisopliae* isolates from agricultural soils belonged to a specific genetic group distinguished from isolates originating from forest soils. These two groups of *M. anisopliae* could be considered as separate cryptic species (Bidochka et al., 2001, 2005). However, there is currently very limited knowledge about the composition and distribution of *M. anisopliae* populations at a local scale. Hu and St. Leger (2002) described selected indigenous isolates of *M. anisopliae* from a local cabbage field in MD, USA, as belonging to two separate explicit allozyme groups. However, specific genetic studies of local populations of *M. anisopliae* still need to be conducted.

The Canadian studies (Bidochka et al., 2001) on *M. anisopliae* further generated the interesting conclusion that isolates belonging to the genetic group in agricultural habitats exhibited heat-tolerance for *in vitro* growth as well as stronger UV-light resistance as compared to the group from forested habitats (Bidochka et al., 2001). Thus Bidochka et al. (2001) proposed the hypothesis that the abiotic conditions (i.e., UV-radiation, exposure to elevated temperatures) in the habitat selected for the genetic group of

M. anisopliae that could survive in that given habitat. This hypothesis suggested that the time-window experienced outside the host was the most important factor for pathogen survival in the environment. Furthermore, it was indicated that similar characteristics could be found among *B. bassiana* isolates collected in Canada (Bidochka et al., 2002). This corroborates with the distribution of genetic groups of *B. bassiana s.l.* in the Danish agroecosystem summarized in Table 1. Here, only one group could be found in the agricultural soil while several genetic groups were harbored in the soil of the neighboring hedgerow (Meyling, 2005; Meyling et al., 2005). Obviously, more studies are needed to verify if this is a general trend in agricultural landscapes in temperate regions and whether the different genetic groups of *B. bassiana s.l.* exhibit variation in their realized niches under different abiotic conditions. If only specific genetic groups of the fungi can survive in agricultural fields then this will be a challenge for environmental manipulations in a CBC strategy targeting *B. bassiana* and *M. anisopliae*.

3. Population dynamics

3.1. Population increase and infections of hosts

Entomopathogenic fungi rely on arthropod hosts to build up population levels of infective stages (mitospore conidia). During the cropping season outbreaks of diseases can regularly be observed in insect populations in the field, referred to as epizootics. Generally, the development of epizootics rely on host population dynamics, the number of infective stages in the pathogen population and the viability of these, infection efficiency and development (Anderson and May, 1981) and a complex set of environmental factors and timing (Inglis et al., 2001). Considerable information on the biology of the organisms as well as specific environmental parameters (in time and space) is necessary to understand and predict the development of epizootics. Key components of population dynamics of the entomopathogenic fungi are the build up of the population, the infection of hosts, and the survival and dispersal in the environment (Anderson and May, 1981).

Both *B. bassiana* and *M. anisopliae* need resources from a host individual to grow and build up fungal biomass. It is conventional to consider the hypocrealean entomopathogenic fungi as saprophytic because many species grow well on artificial media. However, the status of *Metarhizium* spp. as true saprophytes is not well established (Roberts and St. Leger, 2004). Moreover, *Beauveria* spp. and *Metarhizium* spp. are poor competitors for organic resources compared to opportunistic saprophytic fungi that are ubiquitous in soils (Keller and Zimmerman, 1989; Hajek, 1997). It seems more likely that the fungi lurk as conidia in the soil environment waiting to infect a new host. However, *M. anisopliae* may be activated by root exudates in the rhizosphere as described above. Despite this new evidence, insect hosts should still be considered to constitute the principal

source of organic matter for fungus population build-up. The host is the “home ground” of the entomopathogenic fungi, and opportunistic microorganisms are assumed to be held effectively at bay by antimicrobial substances produced by the fungus (Boucias and Pendland, 1998). However, there is very scant published evidence for the antimicrobial activities of the compounds released by these fungi and accordingly Boucias and Pendland (1998) did not provide any references for their claim. A recent documentation of antimicrobial activity of substances from *B. bassiana* (Oller-López et al., 2005) indicates that the assumption is plausible. Field collected living insects, which are incubated in the laboratory, are regularly found infected by *B. bassiana*, yet limited published quantitative data exists on the prevalence of mycosed cadavers in the field. In Denmark, careful inspection of the litter layer beneath stinging nettles (*Urtica dioica*) in a hedgerow revealed that dead insects sporulating with *B. bassiana* were relatively abundant among leaf litter and soil: densities of 3.5–8.8 cadavers per m² could be recovered in July in separate patches (N.V. Meyling, unpublished data). Although these data were preliminary they indicated that cadavers were common on the soil surface, probably mostly in hedges and under natural vegetation. Furthermore, the results indicated that population levels of *B. bassiana* were boosted during the season by conidia production from mycosed insects in the litter layer beneath their host plants.

Conidia are produced in a single event which is consistent with the definition of semelparous reproduction (Pringle and Taylor, 2002; Hughes et al., 2004). Vast numbers of conidia are produced from a single infected insect cadaver (Gottwald and Tedders, 1982). The production of conidia is a key fitness parameter in asexual semelparous filamentous fungi (Pringle and Taylor, 2002) and has been used as a measure of cost in intraspecific competition in *M. anisopliae* (Hughes et al., 2004). However, the persistence and the effectiveness of infection of conidia are also critical properties for the ecological fitness of entomopathogenic fungi. Most conidia are likely to disintegrate quickly in the environment and only minimal proportions will presumably succeed in infecting new hosts. Infection success is density dependent and the number of conidia must exceed a critical threshold level or minimal viable population size (Hughes et al., 2004). Thus the acquisition of the threshold of infective conidia by a susceptible host is necessary for the continued survival of the fungus.

3.2. Dispersal in the environment

Dispersal of infective stages of a pathogen is an important factor in disease development (Anderson and May, 1981). Infective propagules of entomopathogenic fungi in the Hypocreales are passively dispersed, and this is mainly considered to occur through the action of weather components like wind and rain (Hajek, 1997; Inglis et al., 2001; Shah and Pell, 2003). In air samples, *B. bassiana* was isolated among a large array of airborne fungi (Airaudi and

Marchisio, 1996; Shimazu et al., 2002; Ulevicius et al., 2004) and deposition from the air could be one likely source of the newly documented occurrence of *B. bassiana* on phylloplanes of hedgerow plants (Meyling and Eilenberg, 2006a). However, localized transmission onto plant parts by rain splash has also been shown (Bruck and Lewis, 2002b) but rainfall also removed fungus inoculum that had been applied to foliage (Inglis et al., 1993, 1995, 2000, 2001). In the soil environment the hypocrealean entomopathogenic fungi can persist, but extensive proliferation and dispersal are limited. Population build up relies on the conversion of host cadaver resources into infective conidia that are released from cadavers over time following sporulation (Gottwald and Tedders, 1982). The number of conidia released per host is dependent both on fungus species, host species, and host size. For example, *B. bassiana* released 10–200 times more conidia than *M. anisopliae* from adult pecan weevils (Gottwald and Tedders, 1982). Additionally, *B. bassiana* radiated out from weevil cadavers in the soil by hyphal growth and subsequently infected larvae in neighbouring experimental cells while *M. anisopliae* growth was restricted to the surface of the cadaver (Gottwald and Tedders, 1984).

Entomopathogenic fungi are dispersed by living infected hosts which migrate and die in another place than where they became infected (Hajek, 1997). Several aphid species migrate long distances high in the atmosphere and migrating aphids were found to harbour several entomopathogenic fungi (Entomophthorales and *B. bassiana*) (Feng et al., 2004). This implies that *B. bassiana* is able to travel over long distances as infections in hosts, which can later lead to new infections and establishment far away from the original site of the fungus.

The potential of arthropods to disperse and vector entomopathogenic fungi by their activity has been demonstrated in different terrestrial ecosystems. In the soil, collembolans dispersed conidia of *B. bassiana* and *M. anisopliae* which were not pathogenic to them (Dromph and Vestergaard, 2002), both by carrying conidia on the cuticle and by ingesting conidia which, after passage through the digestive tract, could remain viable (Dromph, 2001). Moreover, collembolans were able to vector inoculum to other soil-dwelling insects and initiate infections in laboratory experiments (Dromph, 2003). Also soil-dwelling mites were shown to be potential vectors of *B. bassiana* (Renker et al., 2005).

Insects inhabiting nettle plants were able to disperse inoculum of *B. bassiana* by their activity (Meyling et al., 2006) and could therefore be the distributors of naturally occurring *B. bassiana* on nettle phylloplanes as an alternative to wind dispersal (Meyling and Eilenberg, 2006a; Meyling et al., 2006). Moreover, predators initiated infections in aphids after vectoring inoculum from sporulating cadavers in the nettle canopy (Meyling et al., 2006). Interspecific vectoring of *B. bassiana* has additionally been shown in corn systems where fungivorous beetles dispersed inoculum to larvae of the European corn borer *Ostrinia nubilalis*

(Lepidoptera: Pyralidae) in the tunnels of the latter (Bruck and Lewis, 2002a). Insect activity may therefore influence the dispersal of conidia of *B. bassiana* as indicated on Fig. 1. Thus CBC strategies that aim to manipulate the dispersal of insects may also affect dispersal of entomopathogenic fungi in the agroecosystem.

4. Effects of agricultural practices and structure of the agroecosystem

4.1. Soil disturbance and environmental factors

Annually cropped agroecosystems are highly disturbed mostly due to tillage regimes and this affects the populations of natural enemies of crop pests. The communities of entomopathogenic fungi in the arable soil environments are different from communities of less disturbed habitats (Steenberg, 1995; Bidochka et al., 1998; Meyling and Eilenberg, 2006b) and less disturbance in the cropping system also affect the populations of the fungi. In corn fields in the US, soil densities of *B. bassiana* (as measured by colony forming units per g of soil) under different tillage regimes were very variable between years, but were seemingly higher in no-tillage systems compared to systems subjected to ploughing and chiselling (Bing and Lewis, 1993). Likewise, conservation tillage regimes, using strip-till and no-till, were more favorable to *B. bassiana* and *M. anisopliae* populations in the soil than conventional tillage regimes employing ploughing and disking (Hummel et al., 2002a). Furthermore, no-till cultivation in soybean and wheat positively affected the population levels of *B. bassiana* and *M. anisopliae* compared to conventional tillage (Sosa-Gomez and Moscardi, 1994). These findings of higher fungal densities in reduced tillage and no-till systems could be observations of indirect effects caused by increased levels of host populations of non-pest insects. High population levels of non-pest insects have been observed in reduced tillage systems (Hummel et al., 2002b). The observations cited above may therefore not necessarily be a direct result of mechanical disturbance on fungal population levels.

Exposed fungal inoculum is usually inactivated by the UV-components of solar radiation (Fargues et al., 1996, 1997b). Other abiotic factors affecting entomopathogenic fungi include temperature (Inglis et al., 2001) with strains exhibiting different temperature optima for growth (Fargues et al., 1997a). Indeed, temperature, moisture and UV-radiation seem to be most important for *B. bassiana* survival (Meikle et al., 2003). Persistence of applied fungus material in soils has been studied for several isolates of different species but the complexity of the soil environment makes it difficult to evaluate single factors determining survival (Inglis et al., 2001). Factors such as soil texture (Grodén and Lockwood, 1991), pH values and moisture contents (Lingg and Donaldson, 1981) have been explored and are thoroughly reviewed by Inglis et al. (2001) and Klingen and Haukeland (2006).

Recent evidence suggests that certain genotypes of *M. anisopliae* and *B. bassiana* are dominating in soils of agroecosystems in Canada (Bidochka et al., 2001, 2002) and this also seems to apply to Danish conditions for *B. bassiana* (Meyling, 2005; Table 1). The reason for this observation could be adaptations of specific genetic groups to be more resistant to UV-radiation and temporal elevated temperatures. UV resistance and growth tolerance at high temperatures were characteristics of the isolates belonging to the genetic groups from agricultural soil in Canada (Bidochka et al., 2001, 2002). Given that these observations apply to populations of *B. bassiana* and *M. anisopliae* in general, other genotypes of these fungi could occur in the cropping system by the provisioning of sheltered and non-tilled habitats close to the crop in a CBC strategy.

4.2. Use of agrochemicals

Chemical insecticides, herbicides and fungicides are usually applied in conventional farming practices. These compounds, especially fungicides applied against plant pathogens, might also negatively affect the populations of entomopathogenic fungi with reduced pest regulation potential as a consequence.

Klingen and Haukeland (2006) provided a detailed review of published studies of effects of chemical pesticides on entomopathogenic fungi and nematodes. Their main conclusions were that insecticides and herbicides were not very harmful to fungal growth while fungicides were sometimes harmful (Klingen and Haukeland, 2006). However, most studies were performed *in vitro* with fungal cultures and extrapolation from studies in laboratory experiments to field conditions may not be straightforward. In the UK, for example, previous field application of the fungicide benomyl correlated with a lower incidence of *B. bassiana* in soil samples (Mietkiewski et al., 1997; Chandler et al., 1998). *In vitro* experiments further showed that the fungicide triadimefon inhibited the growth of *B. bassiana*, but fields previously treated with this product showed a higher frequency of occurrence of the fungus in soil samples than in samples from untreated control soils (Mietkiewski et al., 1997; Chandler et al., 1998). The fungicidal product albicarb even increased activity of *in vitro* cultures of *B. bassiana* (Mietkiewski et al., 1997). This emphasizes that due to the complex interactions and composition of agroecosystems applications of specific fungicides are not necessarily detrimental to the occurrence of entomopathogenic fungi in the soil. Selected compounds could thus possibly be used in integrated pest management (Mietkiewski et al., 1997).

4.3. Crop diversification

Mixtures of plants within the crop can reduce colonization by pest species and the use of trap crops can lure the pest insects away from the crop by a push-pull strategy (Hooks and Johnson, 2003; Cook et al., 2007). Manipula-

tion of insect behavior may also affect the dispersal of entomopathogenic fungi in agroecosystems because fungal inoculum can be distributed by insect activity.

Reducing the area of bare ground between the crop plants by mulching may reduce the population sizes of pests by enhancing conditions for ground dwelling predators (Hellqvist, 1996; Schmidt et al., 2004). Mulching may be unfavorable for hypocrealean entomopathogenic fungi as increased amounts of organic matter in soil have been shown to increase antagonistic activity against the fungi (Fargues and Robert, 1985; Studdert and Kaya, 1990).

Establishment of beetle banks within the fields for CBC targeted at populations of carabid beetles (Landis et al., 2000) could also promote populations of entomopathogenic fungi. Specifically, populations of certain genetic groups of *B. bassiana* or *M. anisopliae*, which have been documented to be absent from the cultivated soils in agroecosystems, could potentially benefit from beetle banks.

4.4. Importance of semi-natural habitats in agricultural landscapes

Semi-natural habitats (e.g., hedgerows) are important refuges for flora and fauna that do not thrive within the cultivated arable fields (Marshall and Moonen, 2002; Maudsley et al., 2002; Pywell et al., 2005). Striking differences in the communities of hypocrealean entomopathogenic fungi in soils between arable fields and hedgerows have been documented (Chandler et al., 1997; Meyling and Eilenberg, 2006b). It is likely that the populations of fungi are depending on the arthropod community in the hedgerows for their survival. Regarding *B. bassiana*, hedgerows constituted a tremendous reservoir of genetic diversity compared to agricultural soil (Table 1; Meyling, 2005). Permanent hedgerow habitats, preferably of some age, are valuable refuges of biodiversity in agricultural landscapes, including *B. bassiana* that could be manipulated for CBC.

Increasing evidence suggests that heterogeneity in the agricultural landscape is crucial for the maintenance of the diversity of species and ecological functional groups of organisms that are relevant for pest management in future sustainable agriculture (Benton et al., 2003; Weibull and Ostman, 2003). Landscape structure is also important when predicting the recruitment potential of organisms for biological control by changes in agricultural practices (Tscharntke et al., 2005). Both empirical evidence as well as simulation studies suggest that diversity in the guild of natural enemies is important for efficient biological pest control in agroecosystems (Wilby and Thomas, 2002; Cardinale et al., 2003). Thus initiatives for enhancing population levels of predators and parasitoids in CBC may simultaneously benefit the communities of entomopathogenic fungi in agroecosystems.

Thorough knowledge of the effect of semi-natural habitats on indigenous populations of entomopathogenic fungi is fundamental for their inclusion in CBC strategies (Shah

and Pell, 2003). In the UK, studies have been carried out to include the entomophthoralean fungus *P. neoaphidis* in CBC of aphids. In this system, field margins constituted an important reservoir of fungus inoculum and predators acted as vectors of conidia among aphid populations (Roy et al., 2001; Ekesi et al., 2005). Nettles were particularly important reservoirs of *P. neoaphidis* because they harbored populations of nettle aphids that were susceptible to the fungus (Roy et al., 2001; Ekesi et al., 2005). In general, nettles in field margins also harbored many predators and parasitoids (Davis, 1973) and both phylloplanes and nettle specific insects harbored *B. bassiana* (Meyling and Eilenberg, 2006a; Meyling, 2005). Thus nettles (*U. dioica*) may be a key plant species for populations of predators, parasitoids and entomopathogenic fungi. Whether management strategies can facilitate the use of indigenous populations of *B. bassiana* in field margins in CBC remains to be elucidated.

5. Conclusion

Recent research has generated more knowledge of the natural occurrence, genetic diversity and dispersal mechanisms of *B. bassiana* and *M. anisopliae* in temperate agroecosystems. This knowledge is crucial to understand the ecology of entomopathogenic fungi and it is essential for the inclusion of the fungi in CBC. Molecular markers to assess genetic diversity are important tools in future studies of indigenous populations of *B. bassiana* and *M. anisopliae*. Initiatives to manipulate populations of predators and parasitoids in agroecosystems for CBC are likely to also benefit the populations of *B. bassiana* and *M. anisopliae*. However, there is a need for further understanding of the ecology of the entomopathogenic fungi in order to predict these effects.

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