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Conservation biological control using fungal entomopathogens

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Abstract Conservation biological control relies on modification of the environment or management practices to protect and encourage natural enemies that are already present within the system, thereby enhancing and improving their ability to control pest populations in a reliable way. Such strategies are only possible when based on a strong understanding of the ecology of the species concerned at the individual, community and landscape scale. Conservation biological control with entomopathogenic fungi includes the manipulation of both the crop environment and also habitats outside the crop. Further investment in conservation biological control with entomopathogenic fungi could make a substantial contribution to sustainable crop production either as stand alone strategies or, more importantly, in support of other biological and integrated pest management strategies.

Keywords Ecology · Epizootiology · Entomophthorales · Hypocreales · Pest control · Conservation

Introduction

Unlike other biological control strategies, conservation biological control does not require the introduction or augmentation of natural enemies. Instead, it relies on modification of the environment or management practices to protect and encourage natural enemies that are already present within the system. This improves their ability to control pest populations in a reliable way and is only possible if the biology, behaviour and ecology of both the pests and their natural enemies are understood (Eilenberg et al. 2001; Hajek 2004; Pell 2007; Pimentel 2008). Unfortunately, for most entomopathogenic fungi, our understanding of their ecology and epizootiology is incomplete. The majority of examples of conservation biological control to date have been for arthropod natural enemies (e.g. Barbosa 1998; Gurr et al. 2004; Fiedler et al. 2008; Griffiths et al. 2008; Jonsson et al. 2008; Wade et al. 2008). However, similar approaches are relevant to entomopathogenic fungi where fungi are principal enemies of the target pest and where their ecology and epizootiology are understood (Fuxa 1998; Pell et al. 2001; Pell 2007; Tscharntke et al. 2008).

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The entomopathogenic fungi are a diverse assemblage of fungi with one thing in common: they infect and cause disease in insects and other arthropods. Most are found within two main groups: the order Hypocreales within the phylum Ascomycota (subkingdom Dikarya) and the order Entomophthorales (Hibbett et al. 2007; Blackwell 2009).

Natural control by entomopathogenic fungi

Entomopathogenic fungi play major roles in the natural regulation of many insect and mite species. It is well known that they can develop dramatic epizootics that lead to rapid declines in host populations. In these systems the regularity and intensity of epizootics could be enhanced through conservation biological control and should be a primary target. However, in systems where fungi currently appear to have little regulatory impact on pest populations, there remains the possibility that this is as a result of management practices and could still be improved through conservation biological control.

Without doubt, the monetary value of un-manipulated, natural control of pests exerted by fungi worldwide is already substantial. Examples from the Entomophthorales include *Entomophaga grylli* that is capable of reducing destructive grasshopper outbreaks to negligible proportions in some years (MacLeod 1963). Gypsy moth (*Lymantria dispar*) populations in North America are regularly controlled by outbreaks of *Entomophaga maimaiga* (Hajek 1999), cotton aphid (*Aphis gossypii*) populations by *Neozygites fresenii* (Steinkraus 2007; Abney et al. 2008), various aphid populations by *Pandora neoaphidis* (Pell et al. 2001) and spider mite (*Tetranychus* spp.) populations on soybean by *Neozygites floridana* (Klubertanz et al. 1991). Examples from the Hypocreales are more commonly associated with hosts that spend some or all of their time in the soil, where hypocrealean fungi are ubiquitous. Epizootics of *Beauveria bassiana* in the scarab beetle *Costelytra zealandica* can reduce the host population by 99% (Townsend et al. 1995). *Nomuraea rileyi* has been shown to greatly reduce populations of *Pseudoplusia gemmatalis* overwintering in soil (Carruthers and Soper 1987) and *Tolypocladium cylindrosporum* severely reduces populations of *Agrotis segetum* dormant in soil (Steenberg and Ogaard 2000).

Although our understanding of the ecology and epizootiology of entomopathogenic fungi is often incomplete (Vega et al. 2009), a conservation biological control approach could have significant potential if we identified and filled the gaps in our ecological knowledge. By understanding the factors that promote or inhibit epizootic development, strategies can be identified that ensure favourable conditions for entomopathogenic fungi, and consequently reliable epizootics (Pell et al. 2001; Pell 2007). This is a significant challenge requiring an understanding of the persistence, transmission, dispersal and host range of fungi in cropped and semi-natural areas within managed ecosystems. Furthermore, these factors will vary considerably depending on the species of fungus and its life history strategy. As described by Hesketh et al. (2009) entomophthoralean and the anamorphic stages of hypocrealean fungi have contrasting life history attributes (with few exceptions). Entomophthoralean fungi are generally associated with foliar insect hosts, they are biotrophic and have limited host ranges. The soil is purely a reservoir environment in which their conidia and resting spores must persist, often when hosts are absent in the foliar environment above. In contrast, many hypocrealean fungi are hemibiotrophic, have broad host ranges and are associated with hosts that spend at least some of their life cycle in or on the soil. The soil is not just a reservoir environment in which they persist but also the habitat in which much of their lifecycle occurs, including multiplication within hosts and also, potentially, saprophytic growth. These differences have important implications for the conservation biological control approaches used.

Conservation biological control strategies applied within the crop; factors for consideration

Abiotic environment

Without doubt, high relative humidity is the most essential criterion for fungal activity. Ambient humidities in excess of 90% are usually required for germination, sporulation and infection (Tanada and Kaya 1993). Increasing the relative humidity through crop irrigation can, therefore, significantly enhance the activity of many entomopathogenic fungi. Clear examples of this come from species in the Entomophthorales, but the principle also applies to species in the Hypocreales where increasing humidity has been used widely to improve their efficacy in inundative control. Irrigation increased the prevalence of *P. neoaphidis* in aphid populations in alfalfa, field beans, pecan and spinach (Hall and Dunn 1957; Wilding et al. 1986; Pickering et al. 1989; McLeod and Steinkraus 1997). Prevalence of *Erynia ithacensis* in mushroom gnats was greatly increased by spraying water in the mushroom houses (Huang et al. 1992). Increasing relative humidity by water mists, irrigation and sprinkler systems is a relatively simple method that could be applicable for a wide range of crops, but can prove too costly if the value of the crop is low.

There are also methods to increase humidity without application of water. In crops that are harvested more than once, such as alfalfa, appropriate timing of the first cut allows manipulation of humidity and associated enhanced pest control by fungi. An early first cut concentrated weevil pests in the humid windrows where they were more likely to become infected by the fungal pathogen *Zoophthora phytonomi*. Although the profit from the first cut was reduced using this method, because the harvest was early, the resulting weevil control improved the yield from the second cut significantly (Nordin 1984; Brown and Nordin 1986).

All entomopathogenic fungi spend some part of their life cycle outside of their hosts, as conidia or resting structures (resting spores, chlamydospores, hyphal bodies), on leaf surfaces, bark and soil. In the phylloplane, conidia of all fungi are particularly susceptible to UV degradation (e.g. Furlong and Pell 1997; Fargues et al. 1996). Reducing the row spacing of crops, thereby increasing canopy cover, is one relatively simple method for improving protection from UV while simultaneously elevating ambient relative humidity. In the soybean system, Sprenkel et al. (1979) found higher prevalence rates of *N. rileyi* in lepidopteran larvae from plots that had been planted early, in narrow rows and at a high seed density compared to conventionally planted plots. If higher density plantings are compatible with other agronomic/economic aspects of soybean production, this represents a simple way to increase control by entomopathogenic fungi in soybean and may be applicable in other crops. Intercropping with plant species that increase canopy cover may also prove useful by raising ambient humidity.

Soil composition and disturbance

Soil structure, temperature, pH and water availability will all influence the species diversity and abundance of entomopathogenic fungi in soil and indeed which species may predominate in a given field or region (Klingen and Haukeland 2006; Meyling and Eilenberg 2007). Although it is important to recognize these influences, they are not open to easy manipulation for conservation biological control. However, physical and chemical perturbations due to tillage practices are open to manipulation within conservation biological control (Pell et al. 2001; Meyling and Eilenberg 2007; Pell 2007).

Any fungal propagule could be affected by tillage practices. This could have negative effects if fungal structures are buried deep within the soil where they would no longer be able to contact potential hosts or positive if they are moved closer to hosts at the surface, or if dispersal to new host populations is facilitated. Such factors can only be understood by detailed evaluation of each system and examples of this are scarce. However, Bing and Lewis (1993) found that *B. bassiana* infected more *Ostrinia nubilalis* in no-till corn crops than in corn from conventionally ploughed fields. In a different study, *B. bassiana*, *Metarhizium anisopliae*, and *Isaria* spp. were all more abundant in pest populations in no-till compared to tilled plots (Sosa-Gomez and Moscardi 1994). Furthermore, in a study in vegetable crops, the number of *G. mellonella* that became infected by *B. bassiana* and *M. anisopliae*, when used as bait on the soil, was significantly greater when they were exposed to soil from no-till rotations compared to soil that had been tilled (Hummel et al. 2002). In soybean crops in Brazil, selective media were used to compare the abundance of entomopathogenic fungi from tilled and no-till soils. This study found significantly more colony forming units (a measure of fungal abundance) in soil that had not been tilled compared to tilled soil. However, the number of colony forming units of the same pathogens in the canopy was not significantly different in the two systems. The reduced quantity of inoculum in the soil did not, therefore, translate into reduced exposure of insects inhabiting plants in the same field (Sosa-Gomez et al. 2001). Conservation tillage practices are now widely available and could enhance the level of control provided by entomopathogenic fungi above and below ground in a number of cropping systems, although this requires further evaluation. Within-crop strategies already employed to encourage arthropod natural enemies, such as mulching and beetle banks, may also have the potential to enhance the efficacy of entomopathogenic fungi, although this is as yet unproven (Meyling and Eilenberg 2007).

Pesticide applications

Applications of insecticides, fungicides and herbicides are a common component of crop management and these could impact entomopathogenic fungi in both the soil and foliar environment directly (by killing or inhibiting fungal propagules) and indirectly (by removing hosts) (Wekesa et al. 2008; Klingen and Haukeland 2006; Mochi et al. 2005; Morjan et al. 2002; Chandler et al. 1998; Lagnaoui and Radcliffe 1998; McLeod and Steinkraus 1997; Mietkiewski et al. 1997). Some of the effects are not easy to interpret, particularly when many studies have been done *in vitro* (Meyling and Eilenberg 2007). However, overall, Klingen and Haukeland (2006) suggested that insecticides and herbicides were less harmful than fungicides, although this was dependent on particular circumstances; insecticides may not be damaging directly but can remove hosts for subsequent transmission. Interestingly, the importance of entomopathogenic fungi for the control of pests is sometimes revealed in studies with fungicides. In a study on the green peach aphid (*Myzus persicae*), on potato, Ruano-Rossil et al. (2002) found that when fungicides were applied, extremely high aphid populations developed. They found that the fungicides were disrupting the natural control provided by *P. neoaphidis*, *Entomophthora planchoniana*, and *Conidiobolus obscurus*.

Reducing or targeting pesticide applications is the simplest way to mitigate any potential negative impacts and can be achieved by identifying and monitoring the activity of beneficial fungi in the crop, predicting their efficacy and thereby recommending when insecticides need not be applied (Pell et al. 2001; Pell 2007). The best example of this is for the entomophthoralean fungus *Neozygites fresenii* and cotton aphid control in the southern states of the USA. Studies in the USA showed that *N. fresenii* epizootics in *Aphis gossypii* occurred annually between June and August over wide areas of cotton production and that their occurrence could be predicted by diagnosis of aphid samples (Hollingsworth et al. 1995; Steinkraus et al. 1995). When fungus prevalence reached 15% in the aphid samples tested, declines caused by epizootics were certain within the week (within days if prevalence reached 50%) and recommendations could be made to farmers not to spray insecticides. Because this approach not only conserved fungal and insect natural enemies but also saved farmers money it has been widely adopted. An extension-based service to determine fungal prevalence and provide advice was established in 1993 in Arkansas and eventually covered Alabama, Florida, Georgia, Louisiana, Mississippi, Missouri, North Carolina, South Carolina and Tennessee (Steinkraus et al. 1998; Steinkraus and Zawislak 2005). Aphid samples submitted by farmers, extension agents, crop consultants and others were diagnosed and reports on prevalence provided to the senders. The diagnosis service provided detailed information via a website (http://www.uark.edu/misc/aphid) so that farmers could follow the spread of the fungus in their area and rationalise their pesticide use in response (Steinkraus et al. 1996, 1998; Steinkraus and Boys 1997).

Burning of crop residues

Very little research exists on the effects of fire on entomopathogenic fungi. However, it is likely that they could be important in areas where burning crop residues is still used as a management tool. Unfortunately, with such a limited body of literature on the topic, we can only make speculative hypotheses. Fire is known to reduce the activity of many plant pathogenic fungi (Hardison 1976). Some Entomophthorales, like *N. fresenii*, produce resting structures that persist on plant material, including crop stubble (Byford and Ward 1968). Presumably, in areas where fire is used to clear stubble, these resting structures would be destroyed. In Australia, aphid populations increased following controlled burns, suggesting either a direct positive effect of fire on aphid population growth or negative effects on their natural enemies, such as entomopathogenic fungi (Briese 1996). Fire could also have impacts on the soil environment, thereby indirectly affecting entomopathogenic fungi. After fire, soil can become hydrophobic (MacDonald and Huffman 2004), its pH rises (Hennig-Sever et al. 2001), and the soil nutrient composition changes (Kaufmann et al. 1994). There is some evidence that *M. anisopliae* may become more abundant in the soil from forests which have been burned (Bastias et al. 2008).

Extending conservation biological control strategies beyond the crop; the importance of reservoirs and complexity

Biological control must be effective in the crop environment and so conservation strategies that can be applied within the crop are an obvious first target. However, while some aspects of crop management can be modified to improve the efficacy of entomopathogenic fungi, many are not easy to modify. The soil structure and profile on a farm are controlled principally by the geology of the site, some level of tillage is essential and pesticides will need to be applied, even when integrated pest management strategies are practiced. Entomopathogenic fungi also need populations of hosts for their multiplication and, when these hosts are pests, a delicate balance between host and pathogen populations on the crop must be achieved. For these reasons, conservation biological control strategies that manage areas outside of the crop to encourage natural enemies have advantages. These semi-natural habitats can provide alternative hosts for multiplication of enemies and will not receive pesticide applications. Ensuring appropriate humidity and UV protection through canopy management could be easier and furthermore, they are semi-permanent and not tilled. However, the entomopathogenic fungi utilizing these resources must have the capacity to disperse from the reservoirs into adjacent crops. The value of dispersal potential has been identified for *F. virescens* infecting *Pseudaletia unipuncta* on undisturbed fescue. The same insect in surrounding wheat crops never became infected suggesting that the fungus may have been unable to disperse between habitats (Steinkraus et al. 1993). Although research in this area has been led by studies on arthropod natural enemies, as described previously, they are also extremely relevant for entomopathogenic fungi.

Alternative hosts as inoculum sources

Using a modelling approach to understand the parameters influencing epizootic development of *Entomophthora muscae* in the onion fly, *Delia antiqua*, the presence of a secondary host (the seed corn maggot, *D. platura*) in field border plants significantly increased the prevalence of *E. muscae* in *D. antiqua* on onions (Carruthers et al. 1985; Carruthers and Soper 1987). Elegant observational studies have also shown that hedgerows are important for the persistence and spread of *E. muscae* and *E. schizophorae* in other dipteran populations, e.g. carrot root fly, *Chamaepsila rosae* (Eilenberg 1985, 1988). The prevalence of fungus was always greater in carrot flies from hedges than from carrot fields. Hedges were the preferred sites for flies to rest and where infected flies died. This made the hedges important sites for transfer of conidia from one host to the next (Eilenberg 1987). Similar observations have been made in aphid populations in Switzerland (Keller and Suter 1980). Large populations of economically unimportant aphid species developing in meadows (lucerne and alfalfa) in the spring, were correlated with *P. neoaphidis* and *C. obscurus* rapidly achieving levels sufficient to regulate aphid populations in adjacent fields of annual crops. When aphids were scarce in the spring this did not happen suggesting that the presence of alternative aphid hosts in nearby meadows was critical. Grass and legume rich field margins and woodlands are also thought to have great potential as reservoirs for the aphid pathogen *P. neoaphidis* in South Africa (Hatting et al. 1999a, b). Other aphid pathogenic species, such as *Zoophthora aphidis, Z. phalloides* and *E. planchoniana*, are also known to overwinter in hosts in hedges and forest borders (Keller 1987a, b; Nielsen et al. 2001).

All the studies described above demonstrate the potential that managed habitats outside crops could have for pest control within the crop. However, the underpinning ecological data that would allow optimization in these systems is often incomplete and, where it is available, demonstrates the levels of ecological complexity that must be considered. An interesting case study on the potential utility of managed field margins to encourage *P. neoaphidis* is currently receiving significant attention and practical and ecological data sets in support of this are being collected and integrated. In Europe farmers receive subsidies for planting a diversity of field margins to encourage biodiversity. Some of these schemes have demonstrable benefits for particular arthropod natural enemy abundance, and in some cases relationships between arthropod natural enemy abundance in margins and pest suppression in adjacent crops has also been demonstrated (Collins et al. 2002; Powell et al. 2003; Holland 2007; Pell 2007). These margins could also be useful reservoirs of *P. neoaphidis* (and potentially other entomopathogens) if they contain plants that support alternative, susceptible aphid hosts throughout the season and if virulent isolates of the fungus could disperse from the margin into adjacent crops and initiate infection.

Pandora neoaphidis is an aphid specialist and has been recorded from numerous aphid species on crops, weeds and wildflowers (Pell et al. 2001). Laboratory bioassays against a range of pest aphid species identified considerable variability in susceptibility (e.g. Shah et al. 2004a). In these studies the pea aphid, *Acyrthosiphon pisum*, was the most susceptible pest aphid evaluated. Many non-crop legume plants are common in existing non-crop habitat mixes and also support *A. pisum* suggesting that the pea aphid could be a useful source of fungal inoculum when feeding in non-crop habitats and also a relatively easy target when on the crop. As a large species it would also produce more inoculum when dead than smaller species (Baverstock et al. 2005). In contrast *Rhopalosiphum padi*, an aphid pest on cereals, was far less susceptible than *A. pisum* and may therefore be less useful as a reservoir for *P. neoaphidis* in non-crop habitats and a harder target in the crop. It should be noted that these results were for a limited number of isolates and single biotypes of each aphid species. Biotypes of *A. pisum* can vary significantly in their susceptibility to *P. neoaphidis* (Ferrari et al. 2001), and infected *R. padi* have been recorded in the field (Pell et al. 2001) highlighting the complexity of the interactions (Pell 2007).

To avoid encouraging pest aphid species at field boundaries, non-pest aphids as sources of *P. neoaphidis* infection would be valuable. Ekesi et al. (2005) demonstrated that some non-pest aphids were also susceptible to infection: *Microlophium carnosum* a specialist on the perennial stinging nettle (*Urtica dioica*) was very susceptible. Furthermore, isolates of *P. neoaphidis* from field collected *M. carnosum* were virulent against a number of pest aphid species, indicating the potential for transmission from non-pest aphid reservoirs to pest aphids on crops (Shah et al. 2004a). This was confirmed by molecular studies that found no relationship between the aphid host from which an isolate originated and its host range (Tymon et al. 2004; Tymon and Pell 2005). *Microlophium carnosum* populations peak very early in the season (Perrin 1975) providing a source of *P. neoaphidis* for infection of adjacent crop aphids before their populations reach damaging levels. In food web studies of aphids and their fungal enemies in a natural meadow, aphids on nettles were identified as an important source of *P. neoaphidis* for infection of other aphid species (van Veen et al. 2008). Other hedgerow plants that support non-pest aphids throughout the season include hogweed (*Heraclium sphondylium*), teasel (*Dipsacus fullonum*) and bramble (*Rubus fruticosus*) and, therefore, also have potential as reservoirs for *P. neoaphidis* (Shah et al. 2004b). Such habitats could also be important for overwintering of *P. neoaphidis* as they are undisturbed and protected. *Pandora neoaphidis* is likely to persist in overwintering anholocyclic aphids via continuous cycles of infection and as conidia on the soil (Nielsen et al. 2007). *Pandora neoaphidis* remains able to infect aphids under simulated winter conditions and preliminary studies suggest that managed non-crop habitats with dense canopies also improve inoculum survival (Baverstock et al. 2008a).

Dispersal into crops from reservoirs

The studies above have identified plants that could be useful in supporting alternative hosts for *P. neoaphidis* and circumstantial evidence for the ability of *P. neoaphidis* to transmit between aphids in semi-natural habitats and crops. However, concrete evidence is required to confirm that this actually happens—a challenge in any conservation biological control approach. As with other entomophthoralean fungi, *P. neoaphidis* produces conidia that are actively discharged, leaving the boundary layer and entering the airstream (Hemmati et al. 2001a, b). Field studies have shown that they travel at least 20 m in the air, and probably considerably further, giving them the potential to move between distant habitats (Hemmati 1999). Sentinel aphids placed downwind from sources in the field and in polytunnel experiments became infected, demonstrating that conidia remained viable in the airstream, at least over short distances (Shah et al. 2004b; Ekesi et al. 2005). However, this mechanism of dispersal is entirely passive, diminishing chances of landing on a suitable host. More directed and long distance dispersal can occur through the movement of infected winged (alate) aphids between plants in response to overcrowding or during dispersal between primary and secondary host plants (e.g. Feng and Chen 2002; Feng et al. 2004). Of course, the movement of pest aphids from margins into crops, even if they are infected, is a significant trade off and would require careful consideration. Furthermore, there are other mechanisms of targeted dispersal that do not rely on the movement of aphids. In both laboratory and field studies, predators such as the ladybird *C. septempunctata*, become contaminated with conidia of *P. neoaphidis* while foraging on aphids on both crop and non-crop plants and are able to carry sufficient conidia to healthy aphid populations to initiate infection (Pell et al. 1997; Roy et al. 2001; Ekesi et al. 2005). As ladybirds also use non-crop habitats as reservoirs, particularly nettles, early in the year before moving into the crop, this represents a very important targeted mechanism of dispersal for *P. neoaphidis* both within and between non-crop and crop habitats as they will be carried with the predator that is actively seeking out aphid prey.

Considering the wider natural enemy community

Entomopathogenic fungi do not occur in isolation but within diverse guilds of natural enemies. The importance of considering the entire guild when developing conservation biological control is important but has not always been considered. For example, the predatory ladybird *C. septempunctata* will consume *P. neoaphidis*—infected aphids, inhibiting transmission (Pell et al. 1997; Roy et al. 1998, 2003). However, they can simultaneously significantly increase local transmission from sporulating cadavers which greatly outweighs the detrimental effect of feeding (Roy et al. 1998; Ekesi et al. 2005). This enhanced transmission in conjunction with passive vectoring of inoculum, as described previously, is likely to benefit *P. neoaphidis* significantly (Roy et al. 2001). Parasitoid wasps also enhance local transmission of *P. neoaphidis* although they do not contribute significantly to passive vectoring of inoculum (Fuentes-Contreras et al. 1998; Baverstock et al. 2008b, 2009a). However, in contrast to the fungus/ predator interaction, *P. neoaphidis* and parasitoids compete within individual aphid hosts: parasitoids take longer to develop than the fungus and so are often outcompeted in aphids that are already infected by fungi (Powell et al. 1986; Fuentes-Contreras et al. 1998; Furlong and Pell 2005). Parasitoids are also detrimentally affected by intraguild predation by predators such as ladybirds although some parasitoid species can recognise chemical trails produced by the predator and so avoid oviposition in aphid populations in which predators are foraging (Nakashima et al. 2004).

These outcomes are context specific, continually co-evolving and can be variable both for the enemies themselves and for overall aphid population control (Sunderland et al. 1998; Brodeur and Boivin 2006). From the point of view of aphid management, field studies demonstrate that different natural enemy groups are responsible for aphid control in different years (Sunderland et al. 1998) and, in the laboratory, that a combination of predators, parasitoids and *P. neoaphidis* has the greatest impact on aphid population suppression, although it can also lead to exclusion of some natural enemy species in the short term (Baverstock et al. 2009a). Furthermore, we know that susceptibility to *P. neoaphidis* varies amongst aphid species and biotypes (Shah et al. 2004a; Ferrari et al. 2001) but that the pathogen—resistant forms are attacked by predators and parasitoids. For these reasons it is a widely accepted belief that, for long term and resilient pest management, a diversity of natural enemies with contrasting requirements is required to deliver pest management in a constantly changing environment (Tscharntke et al. 2005, 2008; Pell 2007).

Conclusions and considerations for the future

Development of entomopathogenic fungi within conservation biological control strategies has received far less attention than their development for augmentation (Pell 2007). In the cases where conservation approaches have been considered, the focus has often been with the Entomophthorales because their epizootiology is generally better understood than the Hypocreales. Understanding the ecology of hypocrealean fungi in their favoured habitats and their relationships with above and below ground hosts would be a major step forward in untapping their potential (Bruck 2009; Cory and Ericsson 2009).

For example, *B. bassiana* is ubiquitous in soil but has recently been shown also to be common in the plant canopy, active against plant pathogens and even systemically active within plants, providing further opportunities for exploitation (Meyling and Eilenberg 2007; Pell 2007; Vega et al. 2009; Ownley et al. 2009). These aspects of their ecology would certainly improve the opportunities for exploitation in conservation biological control but should also underpin their use in other strategies (Roy et al. 2009; Jackson et al. 2009; Jaronski 2009; Hajek and Delalibera 2009; Baverstock et al. 2009b). It is certainly likely that if conservation approaches were used in conjunction with augmentation that the effectiveness of the augmentation strategy would be improved. There remain significant gaps in ecological understanding and examples of ‘proof of concept’ for conservation biological control with entomopathogenic fungi are rare. It is clear that for us to advance, greater investment in long-term, in depth studies, aimed at understanding the most important factors governing survival and spread of entomopathogenic fungi are essential. These studies should be coupled with replicated experimentation at the field and landscape scale to evaluate the strategies robustly.

A key factor for further study is the dispersal capability of entomopathogenic fungi between host populations and has particular relevance for conservation strategies in which the fungus multiplies outside of the crop and moves into the crop to be effective. Such studies would benefit from insights from theory, particularly metapopulation theory that considers populations linked by dispersal (Meyling and Hajek 2009) and modeling studies that seek to understand the role of reservoirs in pathogen population dynamics (Hesketh et al. 2009).

The implications of interactions between fungal and arthropod enemies and the requirement for diverse enemy guilds for resilient pest control should also receive more attention. When enemy interactions are complex and can have both positive and negative impacts, it is a challenge for conservation biological control but one that could be achieved by manipulating habitat diversity at a landscape scale. The particular requirements of each enemy group must be considered alongside the aspect and location of managed non-crop habitats and farm practices. The quantity and distribution of the various alternative habitats could have a significant effect on natural enemy diversity and pest management function and all these aspects require further study to link function at the individual level through to populations and communities at the field, farm and landscape scale. Such studies will become increasingly important as crop ecosystems respond to changes in climate and as new crops are introduced for other purposes (e.g. bioenergy).

The value of biodiversity in delivering a particular ecosystem function applies more generally than described above. There are undoubtedly many isolates and/or species of fungi that play as yet unknown roles in the regulation of pest populations. This may be because the systems in which they are active are understudied or because they are considered unimportant based on our existing knowledge of their ecology—but this could change as our climate and cropping landscapes change.

Conservation biological control with entomopathogenic fungi could make a substantial contribution to sustainable crop production, either as a stand alone strategy or, more importantly, in support of other biological and integrated management strategies. Its development and implementation must be underpinned by fundamental ecological understanding of the fungi concerned and their complex interactions with their hosts and the wider community at the individual to landscape scale. Although, like any control strategy, uptake will rely on economics and incentives (Gelernter 2005; Pell 2007; Cullen et al. 2008; Griffiths et al. 2008) the potential is there and warrants further investment.

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