Chapter 2
Naturally Occurring Pathogens and Invasive Arthropods

Ted E. Cottrell and David I. Shapiro-Ilan

Abstract Establishment of introduced pest arthropods has been attributed, in part, to the pest arthropods' separation from natural control agents in their native ranges. Here we focus on the role of endemic pathogens in establishment and population regulation of exotic pest and beneficial arthropods and explore factors affecting their regulation by endemic pathogens. We do not attempt an exhaustive list of examples but illustrate some instances showing diverse aspects of the host-pathogen relationships involved. As a case study, we discuss establishment of the multicolored Asian lady beetle and its rapid spread across North America as related to its resistance to an endemic fungal pathogen to which some native lady beetle species are susceptible. It is clear that advances in our knowledge about the epizootiology of endemic pathogens with exotic arthropods will enhance our understanding of invasion biology and assist in regulation of invasive pests.

2.1 Introduction

The successful establishment of introduced pest arthropods has been attributed, in part, to the pest arthropods' separation from natural control agents in their native ranges (Williamson 1996, Ehler 1998). This concept, i.e. the 'enemy release hypothesis', is commonly referenced in the literature as a mechanism that fosters invasive species (Keane & Crawley 2002, Torchin *et al*. 2003, Clay 2003, Prenter *et al*. 2004). For example, in a study of invasive plant species, Mitchell and Power (2003) found that each invasive species was infected by 77% fewer fungal and viral pathogen species in naturalized versus native ranges. Similarly, Torchin *et al*. (2003) reported that invasive species possess about half the number of parasites as compared with native species. Based on examples such as these, one might extend the argument to pathogen load in invasive arthropods, i.e. one would predict a low prevalence

---

T.E. Cottrell
USDA, Agricultural Research Service, SE Fruit and Tree Nut Research Lab, 21 Dunbar Rd., Byron, Georgia 31008 USA
e-mail: ted.cottrell@ars.usda.gov

A.E. Hajek et al. (eds.), *Use of Microbes for Control and Eradication of Invasive Arthropods*,

of disease in invasive arthropods. And indeed this is the case in certain invasive arthropods as we illustrate later in the chapter. However, we would be remiss not to acknowledge that isolates of some endemic pathogens can be quite virulent to exotic insects (Lacey *et al*. 2001, Koppenhöfer & Fuzy 2003, Duncan *et al*. 2003). In this chapter we focus on the role of endemic pathogens in establishment and population regulation of exotic arthropods.

For this discussion the term endemic refers to an organism that naturally occurs in the area and has not been introduced. Estimating the impact of endemic pathogens on introduced arthropods is difficult. One difficulty is that it is not always clear whether a pathogen is endemic or whether it may have been introduced along with its host. Certainly some introduced pathogens have become established in particular regions and may have significant impact on their host populations (Hajek *et al*. 2007), e.g. the case of the fungus *Entomophaga maimaiga* Humber, Shimazu, and Soper and its effect on the gypsy moth, *Lymantria dispar* (L.) (Weseloh & Andreadis 1992, Hajek 1997). Yet for our purposes these established introductions are not considered endemic. In cases where the host-pathogen relationship is highly specific (e.g. many baculoviruses and microsporidia) it is likely the pathogen was introduced along with its host. Yet even in cases where the pathogen has a broad host range (e.g. many entomopathogenic fungi and nematodes), it may not be clear if the particular strain or species of pathogen was present prior to the arthropod's introduction. In this chapter, the pathogens we discuss are, to the best of our knowledge, endemic. Here we first address, in a general sense, factors that contribute to endemic pathogen impact on invasive arthropods. We then offer a case study, i.e. the establishment and spread of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) across North America, to serve as a basis for discussion of natural enemy release and the role of entomopathogens in invasion biology.

2.2 Factors Affecting Endemic Entomopathogen Regulation of Introduced Arthropod Populations

This section explores factors that may affect the regulation of exotic arthropods by endemic pathogens. The intent is not to provide an exhaustive list, but rather to use several examples to illustrate some of the diverse aspects of the host-pathogen relationships involved. Various abiotic and biotic factors are known to affect the ability of entomopathogens to cause disease in host populations (Fuxa 1987, Fuxa & Tanada 1987, Lacey & Shapiro-Ilan 2008). Generally, many factors affecting regulation of introduced arthropods by endemic entomopathogens can be expected to be similar to other pathogen-host relationships that include endemic hosts or introduced pathogens. Yet some nuances may be anticipated given that, in the case of interest here, it is the host species that has the challenge of adapting to the new environment whereas the endemic pathogen is already established and has managed to exist and evolve in the native ecosystem. Indeed, it is arguable that environmental barriers influencing population regulation may not be as pronounced in endemic pathogens as compared with introduced pathogens (due to the former's inherent establishment in the environment). Examples of endemic pathogens exhibiting superior persistence and efficacy in controlling introduced arthropod pests include entomopathogenic nematode control of the Japanese beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae) (Lacey *et al.* 2001, Koppenhöfer & Fuzy 2003), and control of a root weevil, *Diaprepes abbreviatus* (L.) (Coleoptera: Curculionidae), by *Steinernema diaprepesi* Nguyen & Duncan (Duncan *et al.* 2003).

The impact of endemic pathogens on introduced arthropods can vary. Some examples of endemic pathogens that have caused substantial mortality in introduced insect pests include: 84% of soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), infected with entomopathogenic fungi (Nielsen & Hajek 2005), up to approximately 53% mortality in *D. abbreviatus* infected by entomopathogenic nematodes (Duncan *et al.* 2003), and a 79% reduction in a whitefringed beetle population, *Graphognathus leucoloma* (Boheman) (Coleoptera: Curculionidae) associated with the presence of *Heterorhabditis* sp. (Sexton & Williams 1981). Additionally, the introduced millipede *Ommatoiulus moreletii* (Lucas) has declined in Australia as a result of natural biological control by the native nematode *Rhabditis necromena* Sudhaus and Schulte (McKillup *et al.* 1988, Schulte 1989, Sudhaus & Schulte 1989). In contrast, contributions by endemic entomopathogens can also be minimal; for example, in southern Michigan, entomopathogenic nematode infections in *P. japonica* were <1% (Cappaert & Smitley 2002), yet substantially higher impact by entomopathogenic nematodes has been observed in the eastern US (Campbell *et al.* 1998). The reasons for varying impacts of endemic pathogens are unclear. Some factors that have been documented to affect population regulation by endemic pathogens include the environment, host density and host range.

Although endemic pathogens are adapted to their native ecosystem, environmental factors still contribute to epizootics and population regulation. For example, Wraight *et al.* (1993) observed that prevalence of fungal infection in the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae), was substantially higher in irrigated fields relative to non-irrigated fields. Additionally, soil type was found to impact the prevalence and relative distribution of endemic entomopathogenic nematodes in citrus (Duncan *et al.* 2003).

Host density may also be a factor affecting population regulation in some systems. Generally, increases in host density are expected to increase the chances of an epizootic (Fuxa 1987). Nielsen and Hajek (2005) observed that mycosis induced by endemic fungi was proportional to the population density of the soybean aphid, *A. glycines*. Contrarily, mycosis was not correlated to host density of *D. noxia* (Feng *et al.* 1991).

Perhaps most importantly, the potential for population regulation is likely to be limited by the innate host range of the endemic pathogen in question. However, establishment of pathogenicity in the laboratory does not necessarily predict an endemic pathogen-exotic host relationship as physiological host range is not equivalent to ecological host range (Federici & Maddox 1996, Solter & Maddox 1998). In order for an endemic pathogen to impact an introduced host's population, the two must be biologically and environmentally compatible in terms of the niche they occupy in the ecosystem.

Based on known host ranges and the biology/ecology of endemic pathogens, we can predict or make some generalizations regarding which groups of endemic pathogens have potential to impact particular arthropods. For example, disease prevalence may be predicted in part by a pathogen's adaptation to infection in soil versus above ground. Aphid species tend to be susceptible to certain fungi that are capable of effectively causing infection aboveground, e.g. fungi in the order Entomophthorales. Indeed, a number of endemic Entomophthorales, such as *Pandora* (=*Erynia*) *neoaphidis* (Remaudiere & Hennebert) and *Conidiobolus* spp., can cause substantial mortality in established populations of exotic *D. noxia* (Wraight *et al.* 1993, Feng *et al.* 1991, Hatting *et al.* 1999, 2000) and *A. glycines* (Nielsen & Hajek 2005). In contrast, ground-dwelling larvae of Coleoptera tend to be susceptible to entomopathogenic nematodes and hypocrealean fungi (Ascomycota: Clavicipitaceae) (e.g. *Beauveria bassiana* (Balsamo) Vuillemin and *Metarhizium anisopliae* (Metchnikoff) Sorokin). Examples of introduced Coleoptera that support this generalization include larvae of *D. abbreviatus* (Beavers *et al.* 1983, McCoy *et al.* 2000, Duncan *et al.* 2003) and *P. japonica* (Campbell *et al.* 1998, Lacey *et al.* 2001, Koppenhöfer & Fuzy 2003). One interesting example where an endemic pathogen affects an introduced insect both in the soil and above ground is *B. bassiana* infection of the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae). In corn fields, *B. bassiana* can infect a substantial proportion of overwintering larvae in the soil (up to 84%), but also infects *O. nubilalis* larvae within the corn plant, a process that is facilitated by the ability of the endemic fungus to function as an endophyte and colonize corn (Bing & Lewis 1991, 1993).

The ability of endemic pathogens to regulate introduced pests can be complex. Not only can the pathogens be differentially affected by environmental factors and other endemic soil organisms (Fuxa 1987, Koppenhöfer & Grewal 2005) but endemic pathogens may interact (indirectly) with introduced pathogen populations as well. In some cases introduced pathogens can out-compete endemic pathogen populations, potentially reducing the overall level of arthropod suppression (Duncan *et al.* 2003). Yet in other cases introduced pathogens may not cause displacement of endemic pathogens since they occupy different niches in the soil (Millar & Barbercheck 2001). Our knowledge and understanding of the complexities affecting population regulation of introduced arthropods by endemic pathogens is severely limited by the paucity of studies addressing the issue. Clearly additional research in this area is required.

2.3 A Case Study: Endemic Pathogens and the Multicolored Asian Lady Beetle

Here we will examine the case of an introduced species of lady beetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) (Fig. 2.1), and the emerging evidence that this species exhibits resistance to some endemic entomopathogens in North America. It is likely that freedom from endemic predators, parasites and possibly pathogens benefited those early populations of *H. axyridis* that became established.

Fig. 2.1 An adult of the highly invasive *Harmonia axyridis*

Pest management through classical biological control has led to the introduction of numerous exotic insect predators and parasites into the U.S. Some of these introduced natural enemy species became established but many did not, even when apparently suited to the target pest species and the new habitat. In order for an introduced species to be considered established, Andow *et al*. (1997) proposed that more than one generation of that species must have been recovered far from introduction sites. When introduced natural enemy species fail to establish, specific reasons for failure generally are not known. Sometimes the assumption is made that numbers of released individuals were too low or attempts to establish natural enemies were hampered by weather, insecticide usage, competition with native natural enemies, diseases decreasing the population of the target pest, and the disruptive effects of crop harvest (van den Bosch *et al*. 1959, Simmonds 1966, DeBach & Rosen 1991). Other ambiguous reasons stated for failure of an introduced species to establish relate to inadequate biological information about the introduced natural enemy, indifference by researchers, lack of persistence by the introduced natural enemy, technical problems and climatic factors (van den Bosch 1968). The possible role of pathogens, specifically endemic pathogens, is rarely broached in the research literature regarding success or failure of an introduced natural enemy. Thus, examples of endemic pathogens impacting exotic natural enemies by hampering their establishment are lacking.

If we consider the process of intentionally introducing natural enemies through classical biological control, these natural enemies should be free from most of their own natural enemies. Before the release of natural enemies into a new environment, Simmonds (1966) states that the removal of parasites from predators and hyperparasites from parasites is necessary. Additionally, the culturing of insects before release can free them from pathogens that are associated with their native habitats (Simmonds 1966), especially pathogens transmitted horizontally. Accidentally released arthropods that establish may also be free from a percentage of their natural complement of pathogens due to the expected small size of the establishing population and due to complex life cycles of pathogens that may not be compatible with the transport and establishment process.

When data are presented concerning the effect of naturally-occurring pathogens upon beneficial arthropods, i.e. parasitoids and predators, it concerns rates of infection by nematodes or gregarine protozoa (see Ceryngier & Hodek 1996), mortality of overwintering populations when beetles aggregate (Iperti 1966a, b, Ceryngier 2000) or male-killing bacteria (Hurst & Jiggins 2000). But by far, most information regarding the impact of pathogens on beneficial arthropods concerns the non-target impacts of commercially-available, biorational products (e.g. fungi) applied in an insecticidal fashion (Magalhaes *et al.* 1988, Giroux *et al.* 1994, James & Lighthart 1994, Todorova *et al.* 1994, James *et al.* 1995, Pingel & Lewis 1996, Poprawski *et al.* 1998, James *et al.* 1998, Cagáň & Uhlík 1999, Todorova *et al.* 2000, Smith & Krischik 2000, Pell & Vandenberg 2002, Laird *et al.* 1990, Ludwig & Oetting 2001). Relatively little information exists with regard to how endemic pathogens affect populations of beneficial arthropods (native and exotic), especially with regard to the arthropod's viability in biological control programs (Vinson 1990). Kuznetsov (1997) reviewed research on pathogens of coccinellids in eastern Russia and found that *Coccinella septempunctata* L., *H. axyridis, Calvia quatuordecimguttata* (L.) and *Hippodamia tredecimpunctata* (L.) were infected by *B. bassiana* and *Beauveria brongniartii* (Saccardo) Petch (=*B. tenelle*). He considered their impact minimal on those predaceous coccinellids. Yinon (1969) found adult *Chilocorus bipustulatus* (L.) (Coleoptera: Coccinellidae) infected by the laboulbenialean fungus *Hesperomyces virescens* and larvae infected by 'white mycelium' on trunks in citrus groves but no supporting data were provided to indicate the prevalence of these diseases in field populations or the impact of these pathogens on predation by *C. bipustulatus*.

The introduction of lady beetles into North America for pest control was common following successful control of the exotic cottony-cushion scale, *Icerya purchasi* (Homoptera: Coccidae), on citrus by *Rodolia cardinalis* (Coleoptera: Coccinellidae) in California during the late 1880s (Hagen 1974, Gordon 1985, DeBach & Rosen 1991). During this pre-insecticide era, 179 foreign species of Coccinellidae were purposely released into the U.S. As an end result of these intentional introductions, 16 exotic species of Coccinellidae were established in the U.S. (Gordon 1985). *Harmonia axyridis* was first recorded being intentionally introduced into North America as early as 1916 and more releases were made by various federal and state researchers into the 1980s (Gordon 1985). Establishment of *H. axyridis* via accidental introductions at seaports remains a possibility (Krafsur *et al.* 1997). Nonetheless, established *H. axyridis* populations in North America were not detected until 1988 in Louisiana and thereafter *H. axyridis* quickly spread across much of the United States and southern Canada (Tedders & Schaefer 1994, Coderre *et al.* 1995, Lamana & Miller 1996, Brown & Miller 1998, Colunga-Garcia & Gage 1998). Although the intent of establishing *H. axyridis* was for control of plant pests, several negative impacts have developed. The overwhelming successful establishment of this insect negatively affects competing native lady beetles (Cottrell & Yeargan 1998), it can overwinter in buildings including homes where it can be a great nuisance (Nalepa *et al.* 2000) and it has been implicated as a pest of midwestern wine grapes when adults feed on damaged grapes and are harvested along with the crop, resulting in the wine flavor being tainted (Koch 2003).

It is likely that the initial population of *H. axyridis* that became established in North America faced many hurdles commonly encountered when attempting to establish any beneficial arthropod in a new habitat, and for those reasons, many of the numerous, early introductions failed to establish. But once a population did establish, inherent traits gave this species a competitive edge over native guild species. Traits that suggest why *H. axyridis* has apparently out-competed native coccinellid species in some habitats include its polyphagous diet, high fecundity (Michaud 2002), aggressive behavior (Cottrell & Yeargan 1999, Michaud 2002), high mobility (With *et al*. 2002) and large body size (Cottrell & Yeargan 1999, Michaud 2002). Another factor influencing population dynamics of native and exotic species may involve attack by parasites. Obrycki (1989) reported on differential susceptibility of certain native and exotic coccinellid species to the cosmopolitan parasitoid *Dinocampus coccinellae* Schrank (Hymenoptera: Braconidae). Following this trend, Hoogendorn and Heimpel (2002) showed that successful parasitism of *H. axyridis* by *D. coccinellae* was lower than parasitism of the native *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae) even though the proportion of each species attacked was similar. However, it is questionable whether a dearth of endemic pathogens adapted to attack this exotic species could have contributed, in part, to its successful establishment and rapid dispersal across much of North America. Recently, we suggested that reduced susceptibility to endemic pathogens facilitated the establishment and quick dispersal of *H. axyridis* (Cottrell & Shapiro-Ilan 2003, Shapiro-Ilan & Cottrell 2005).

Initial support for our hypothesis was based on differential susceptibility of *H. axyridis* and the native coccinellid *Olla v-nigrum* (Mulsant) to *B. bassiana*. The suspected differences were first based on preliminary field observations of these two species' susceptibility to *B. bassiana*. It was discovered that some adults of the native *O. v-nigrum* overwintering under pecan bark (*Carya illinoinensis*) were infected with *B. bassiana* (Cottrell & Shapiro-Ilan 2003). These infected, dead adults had visible mycosis typical of *B. bassiana* (Fig. 2.2). Some *O. v-nigrum* adults collected

Fig. 2.2 An adult *Olla v-nigrum* infected by *Beauveria bassiana*

alive from under pecan bark and held in the laboratory with aphids and water died and also exhibited mycosis. However, mycosis of *H. axyridis* had never been observed whether insects came from overwintering aggregations in buildings or from field collections in various habitats including pecan orchards. These observations prompted Cottrell and Shapiro-Ilan (2003) to test the pathogenicity of *B. bassiana* collected from infected *O. v-nigrum* against the exotic *H. axyridis* and against the native *O. v-nigrum*. We discovered that *B. bassiana* isolated from *O. v-nigrum* was substantially more virulent to *O. v-nigrum* than *H. axyridis*. A concentration of 2.5×10^5 conidia/ml was found to be the LC_{50} for *O. v-nigrum* but this concentration did not cause any mortality in *H. axyridis*. In fact, even a concentration of 3.9×10^8 conidia/ml was not pathogenic to *H. axyridis*. The commercially-available GHA strain of *B. bassiana* was not virulent against either the native *O. v-nigrum* or the exotic *H. axyridis* when assayed at the LC_{50} for *O. v-nigrum*. This is interesting given the incredibly broad host range of *B. bassiana* (Goettel *et al.* 1990). Nonetheless, the results when using *B. bassiana* isolated from the native *O. v-nigrum* indicate lower susceptibility of the exotic *H. axyridis* to an endemic pathogen and support our hypothesis. James & Lighthart (1994) comment that information from the field is needed to determine how direct effects seen in the laboratory play out in habitats where multiple species interact. Again, field data from Cottrell & Shapiro-Ilan (2003), although geographically limited, was suggestive that isolates of *B. bassiana* exist that are pathogenic to native coccinellids but not to *H. axyridis*.

Harmonia axyridis occupies many habitats and overlaps both temporally and spatially with many native species of North American Coccinellidae. If our hypothesis regarding *H. axyridis* is correct, we should expect that some of these other native competitors will be negatively affected by endemic pathogens. To partially address this issue, Cottrell and Shapiro-Ilan (2008) used an isolate of *B. bassiana* collected from a naturally-infected *O. v-nigrum* adult (as used by Cottrell & Shapiro-Ilan 2003) and tested it against four species of Coccinellidae native to North America, i.e. *O. v-nigrum, Cycloneda munda* (Say), *Hippodamia convergens* (Guérin-Méneville) and *C. maculata*. The hypothesis was supported in that *C. munda, O. v-nigrum* and *H. convergens* were susceptible but *H. axyridis* was not susceptible. Further support comes from the fact that another exotic lady beetle established in North America, *C. septempunctata*, was not susceptible to this same isolate of *B. bassiana. Coleomegilla maculata*, however, was the only native species tested that was not susceptible. Additionally, only the native species *C. munda, O. v-nigrum* and *H. convergens* exhibited visible signs of mycosis when treated with *B. bassiana* isolated from *O. v-nigrum*. Results such as these show that specific isolates could play a key role in the population regulation of native natural enemies while allowing resistant, newly-established natural enemies to gain a competitive edge over native species.

In addition to the observed differential susceptibility to an isolate of *B. bassiana*, more evidence of *H. axyridis* being less susceptible to disease than native species is provided by Shapiro-Ilan and Cottrell (2005). In this study, two species of native coccinellids (i.e. *C. maculata* and *O. v-nigrum*) and two species of exotic coccinellids (i.e. *H. axyridis* and *C. septempunctata*) were assessed for their relative susceptibility to entomopathogenic nematodes. The nematode strains used, i.e. *Steinernema carpocapsae* (Cxrd) and *Heterorhabditis bacteriophora* (VS), were both originally isolated in North America. Given the widespread geographic distribution of both the nematode species and the native coccinellids *C. maculata* and *O. v-nigrum*, it is likely that natural interaction between these organisms would occur. Although most coccinellid species would be expected to spend more time on plants, coccinellid-nematode interaction is most likely to occur with larval stages that can be found on the soil. Interactions between the nematodes and adults would be limited but possible, especially for *C. maculata* adults that spend time on low-growing plants. Larval coccinellids often fall to the soil from host plants while searching for prey and will even disperse from plants via the soil (Cottrell & Yeargan 1999). Thus, the native species would be expected to have had more contact with these endemic pathogens compared with the exotic coccinellids. Indeed, Shapiro-Ilan and Cottrell (2005) showed that mortality of native coccinellids was generally higher than mortality of exotic coccinellids when treated with *S. carpocapsae* (Cxrd), whereas *H. bacteriophora* (VS) had less effect overall on coccinellids with the only difference being higher mortality of the native *O. v-nigrum* versus *H. axyridis*. Again, our hypothesis that the establishment of some exotic species may be fostered by their resistance to endemic pathogens is supported.

2.4 Conclusions

The effect of endemic pathogens upon native versus exotic species can play out in different ways. For example, the endemic pathogens could exhibit high virulence to the exotic arthropod, regardless of virulence toward native arthropods, and thus negatively affect establishment of the exotic arthropod, or, the endemic pathogens could exhibit low virulence to the exotic arthropod and high virulence to native competitors thus facilitating establishment of the exotic arthropod. The former could provide a partial explanation why only 16 of the 179 species of coccinellids intentionally introduced into North America have become established (Gordon 1985). Although there is no direct evidence to support this supposition regarding all of those introduced coccinellids, the impact of endemic pathogens on introduced arthropods can be highly significant as demonstrated with entomopathogenic fungi against *A. glycines* (Nielsen & Hajek 2005) and entomopathogenic nematodes infecting *D. abbreviatus* (Duncan *et al.* 2003) and *G. leucoloma* (Sexton & Williams 1981). The latter, i.e. low virulence to the exotic arthropod and high virulence to native competitors, provides an explanation for the success of *H. axyridis* in North America and favors the enemy release hypothesis. This hypothesis has been used to explain the success of some invading plants and animals but has not (previous to our work) been suggested specifically as a mechanism fostering establishment of exotic natural enemies such as *H. axyridis* where lower susceptibility to specific strains or isolates of endemic pathogens has been demonstrated compared with some native competitors. It is likely that the successful establishment and widespread distribution of another exotic coccinellid, *C. septempunctata*, across North America was also fostered by its reduced susceptibility to endemic pathogens. Thus the role of endemic pathogens upon establishment of exotic arthropod species should be examined further. This can be done by examining the natural prevalence of pathogens in native and exotic species where both exist at different geographic locations and comparing their relative competitiveness as correlated with disease prevalence. It should also be determined if differential susceptibility between native and exotic species occurs with more isolates of endemic pathogens. Additionally, the virulence of pathogens from the native range of the exotic species could be tested to further determine the relevance of the enemy release hypothesis in this situation.

An understanding of the physiological and ecological host range of endemic pathogens can have positive impacts on the success of biological control. With respect to potential biological control agents that are being considered for introduction, it would be useful to know their physiological susceptibility to a suite of endemic pathogens known to attack similar native species at the proposed introduction site. Although the physiological susceptibility will likely exceed the ecological susceptibility, knowing which pathogens will not infect the host under optimum conditions is useful and would allow for further refining of ecological susceptibility assays and could aid in decision-making regarding releases. Additionally, little information is available on the prevalence of endemic pathogens naturally infecting beneficial arthropods in the field and what impact they may have upon beneficial arthropod populations.

Advances in our knowledge about the epizootiology of endemic pathogens with exotic arthropods will enhance our understanding of invasion biology, and assist in regulation of invasive pests. The threat of exotic arthropod species becoming established may be related to the pathogenicity and virulence of endemic pathogens to those exotic species. Thus, we may be able to predict the outcome of endemic pathogens on potential exotic arthropod threats in order to categorize risk levels relating to the potential for those exotic arthropods to establish and have a positive (e.g. predators and parasitoids) or negative (e.g. pests) ecological, economical or social impact. For example, if we know that certain endemic pathogens tend to control certain orders, families or genera of pests (and specific virulence can be tested under quarantine) then conceivably the risk level for exotic arthropod species, within that order, family or genera, would be deemed low. With continued globalization, there has been a parallel increase in the number of invasive pests (Perrings *et al.* 2005); therefore the importance of elucidating the role of endemic pathogens in preventing establishment or controlling exotic pests post-establishment carries an increasingly greater weight.

References

Andow DA, Ragsdale DW, Nyvall RF (1997) Biological control in cool temperate regions. In: Andow DA, Ragsdale DW, Nyvall RF (eds) Ecological interactions and biological control. Westview Press, Boulder, CO. pp 1–28

Beavers JB, McCoy CW, Kaplan DT (1983) Natural enemies of subterranean *Diaprepes abbreviatus* (Coleoptera: Curculionidae) larvae in Florida. Environ Entomol 12:840–843

Bing LA, Lewis LC (1991) Suppression of *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae) by endophytic *Beauveria bassiana* (Balsamo) Vuillemin. Environ Entomol 20:1207–1211

Bing LA, Lewis LC (1993) Occurrence of the entomopathogen *Beauveria bassiana* (Balsamo) Vuillemin in different tillage regimes and in *Zea mays* L. and virulence towards *Ostrinia nubilalis* (Hübner). Agric Ecosys Environ 45:147–156

Brown MW, Miller SS (1998) Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. Entomol News 109:136–142

Cagáň L, Uhlík V (1999) Pathogenicity of *Beauveria bassiana* strains isolated from *Ostrinia nubilalis* Hbn. (Lepidoptera: Pyralidae) to original host larvae and to ladybirds (Coleoptera: Coccinellidae). Plant Prot Sci 35:108–112

Campbell JF, Orza G, Yoder F, Lewis E, Gaugler R (1998) Spatial and temporal distribution of endemic and released entomopathogenic nematode populations in turfgrass. Entomol Exp Appl 86:1–11

Cappaert DL, Smitley DR (2002) Parasitoids and pathogens of Japanese beetle (Coleoptera: Scarabaeidae) in southern Michigan. Environ Entomol 31:573–580

Ceryngier P, Hodek I (1996) Enemies of Coccinellidae. In: Hodek I, Honěk A (eds) Ecology of Coccinellidae. Kluwer Academic Publishers, Boston. pp 319–350

Ceryngier P (2000) Overwintering of *Coccinella septempunctata* (Coleoptera: Coccinellidae) at different altitudes in the Karkonosze Mts, SW Poland. Eur J Entomol 97:323–328

Clay K (2003) Parasites lost. Nature 421:585–586

Coderre D, Lucas E, Gagne I (1995) The occurrence of *Harmonia axyridis* (Coleoptera: Coccinellidae) in Canada. Can Entomol 127:609–611

Colunga-Garcia M, Gage SH (1998) Arrival, establishment, and habitat use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. Environ Entomol 27:1574–1580

Cottrell TE, Yeargan KV (1998) Intraguild predation between an introduced lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). J Kans Entomol Soc 71:159–163

Cottrell TE, Yeargan KV (1999) Factors influencing the dispersal of larval *Coleomegilla maculata* from the weed *Acalypha ostryaefolia* to sweet corn. Entomol Exp Appl 90:313–322

Cottrell TE, Shapiro-Ilan DI (2003) Susceptibility of a native and an exotic lady beetle (Coleoptera: Coccinellidae) to *Beauveria bassiana*. J Invertebr Pathol 84:137–144

Cottrell TE, Shapiro-Ilan DI (2008) Susceptibility of endemic and exotic North American ladybirds to endemic fungal entomopathogens. Eur J Entomol 105:455–460

DeBach P, Rosen D (1991) Biological control by natural enemies, 2nd edition. Cambridge University Press, New York

Duncan LW, Graham JH, Dunn DC, Zellers J, McCoy CW, Nguyen K (2003) Incidence of endemic entomopathogenic nematodes following application of *Steinernema riobrave* for control of *Diaprepes abbreviatus*. J Nematol 35:178–186

Ehler LE (1998) Invasion biology and biological control. Biol Control 13:127–133

Federici BA, Maddox J (1996) Host specificity in microbe-insect interactions: Insect control by bacterial, fungal, and viral pathogens. Bioscience 46:410–421

Feng M-G, Johnson JB, Halbert SE (1991) Natural control of cereal aphids (Homoptera: Aphididae) by entomopathogenic fungi (Zygomycetes: Entomophthorales) and parasitoids (Hymenoptera: Braconidae and Encyrtidae) on irrigated spring wheat in southwestern Idaho. Environ Entomol 20:1699–1710

Fuxa JR (1987) Ecological considerations for the use of entomopathogens in IPM. Annu Rev Entomol 32:225–251

Fuxa JR, Tanada Y (1987) Epizootiology of insect diseases. John Wiley & Sons, New York

Giroux SJ, Côté C, Vincent C, Martel P, Coderre D (1994) Bacteriological insecticide M-One effects on predation efficiency and mortality of adult *Coleomegilla maculata lengi* (Coleoptera: Coccinellidae). J Econ Entomol 87:39–43

Goettel MS, Poprawski TJ, Vandenberg JD, Li Z, Roberts DW (1990) Safety to nontarget invertebrates of fungal biocontrol agents. In: Laird M, Lacey LA, Davidson EW (eds), Safety of microbial insecticides. CRC Press, Boca Raton, FL. pp. 209–231

Gordon RD (1985) The Coccinellidae (Coleoptera) of America north of Mexico. J New York Entomol Soc 93:1–912

Hagen KS (1974) The significance of predaceous Coccinellidae in biological and integrated control of insects. Entomophaga Mem H S 7:25–44

Hajek AE (1997) Fungal and viral epizootics in gypsy moth (Lepidoptera: Lymantriidae) populations in central New York. Biol Control 10:58–68

Hajek AE, McManus ML, Delalibera I Jr (2007) A review of introductions of pathogens and nematodes for classical biological control of insects and mites. Biol Control 41:1–13

Hatting JL, Humber RA, Poprawski TJ, Miller RM (1999) A survey of fungal pathogens of aphids from South Africa with special reference to cereal aphids. Biol Control 16:1–12

Hatting JL, Poprawski TJ, Miller RM (2000) Prevalences of fungal pathogens and other natural enemies of cereal aphids (Homoptera: Aphididae) in wheat under dryland and irrigated conditions in South Africa. BioControl 45:179–199

Hoogendorn M, Heimpel GE (2002) Indirect interactions between an introduced and a native ladybird beetle species mediated by a shared parasitoid. Biol Control 25:224–230

Hurst GDD, Jiggins FM (2000) Male-killing bacteria in insects: Mechanisms, incidence, and implications. Emerg Infect Dis 6:329–336

Iperti G (1966a) Natural enemies of aphidophagous coccinellids. In: Hodek I (ed) Ecology of aphidophagous insects. Academia, Prague and Dr. W. Junk, The Hague. pp 185–187

Iperti G (1966b) Protection of coccinellids against mycosis. In: Hodek I (ed) Ecology of Aphidophagous Insects. Academia, Prague and Dr. W. Junk, The Hague. pp 189–190

James RR, Lighthart B (1994) Susceptibility of the convergent lady beetle (Coleoptera: Coccinellidae) to four entomogenous fungi. Environ Entomol 23:190–192

James RR, Shaffer BT, Croft B, Lighthart B (1995) Field evaluation of *Beauveria bassiana*: Its persistence and effects on the pea aphid and a non-target coccinellid in alfalfa. Biocontrol Sci Tech 5:425–437

James RR, Croft BA, Shaffer BT, Lighthart B (1998) Impact of temperature and humidity on host-pathogen interactions between *Beauveria bassiana* and a coccinellid. Environ Entomol 27:1506–1513

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–169

Koch RL (2003) The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. J Insect Sci 3:1–16

Koppenhöfer AM, Fuzy EM (2003) *Steinernema scarabaei* for the control of white grubs. Biol Control 28:47–59

Koppenhöfer AM, Grewal PS (2005) Compatibility and interactions with agrochemicals and other biocontrol agents. In: Grewal P, Ehlers RU, Shapiro-Ilan D (eds) Nematodes as biological control agents. CABI, New York. pp 363–381

Krafsur ES, Kring TJ, Miller JC, Nariboli P, Obrycki JJ, Ruberson JR, Schaefer PW (1997) Gene flow in the exotic colonizing ladybeetle *Harmonia axyridis* in North America. Biol Control 8:207–214

Kuznetsov VN (1997) Lady beetles of the Russian Far East, memoir no. 1, Center for Systematic Entomology. The Sandhill Crane Press, Inc, Gainesville, FL. 248p

Lacey LA, Rosa JS, Simoes NO, Amaral JJ, Kaya HK (2001) Comparative dispersal and larvicidal activity of exotic and Azorean isolates of entomopathogenic nematodes against *Popillia japonica* (Coleoptera: Scarabaeidae). Eur J Entomol 98:439–444

Lacey LA, Shapiro-Ilan DI (2008) Microbial control of insect pests in temperate orchard systems: Potential for incorporation into IPM. Annu Rev Entomol 53:7.1–7.24

Laird M, Lacey LA, Davidson EW (1990) Safety of microbial insecticides. CRC Press Inc., Boca Raton, FL, USA

Lamana ML, Miller JC (1996) Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. Biol Control 6:232–237

Ludwig SW, Oetting RE (2001) Susceptibility of natural enemies to infection by *Beauveria bassiana* and impact of insecticides on *Iphesuius degenerans* (Acari: Phytoseiidae). J Agric Urban Entomol 18:169–178

Magalhaes BP, Lord JC, Wraight SP, Daoust RA, Roberts DW (1988) Pathogenicity of *Beauveria bassiana* and *Zoophthora radicans* to the coccinellid predators *Coleomegilla maculata* and *Eriopis connexa*. J Invertebr Pathol 52:471–473

McCoy CW, Shapiro DI, Duncan LW, Nguyen K (2000) Entomopathogenic nematodes and other natural enemies as mortality factors for larvae of *Diaprepes abbreviatus* (Coleoptera: Curculionidae). Biol Control 19:182–190

McKillup SC, Allen PG, Skewes MA (1988) The natural decline of an introduced species following its initial increase in abundance; an explanation for *Ommatoiulus moreletii* in Australia. Oecologia 77:339–342

Michaud JP (2002) Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cycloneda sanguinea*. Environ Entomol 35:827–835

Millar LC, Barbercheck ME (2001) Interaction between endemic and introduced entomopathogenic nematodes in conventional-till and no-till corn. Biol Control 22: 235–245

Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. Nature 421:625–627

Nalepa CA, Kidd KA, Hopkins DI (2000) The multicolored Asian lady beetle (Coleoptera: Coccinellidae): Orientation to aggregation sites. J Entomol Sci 35:150–157

Nielsen C, Hajek AE (2005) Control of invasive soybean aphid, *Aphis glycines* (Hemiptera: Aphididae), populations by existing natural enemies in New York State, with emphasis on Entomophthorales fungi. Environ Entomol 34:1036–1047

Obrycki JJ (1989) Parasitization of native and exotic coccinellids by *Dinocampus coccinellae* (Schrank) (Hymenoptera: Braconidae). J Kans Entomol Soc 62:211–218

Pell JK, Vandenberg JD (2002) Interactions among the aphid *Diuraphis noxia*, the entomopathogenic fungus *Paecilomyces fumosoroseus* and the coccinellid *Hippodamia convergens*. Biocontr Sci Technol 12:217–224

Perrings C, Dehnen-Schmutz K, Touza J, Williamson M (2005) How to manage biological invasions under globalization. Trend Ecol Evol 20:212–215

Pingel RL, Lewis LC (1996) The fungus *Beauveria bassiana* (Balsamo) Vuillemin in a corn ecosystem: Its effect on the insect predator *Coleomegilla maculata* DeGeer. Biol Control 6:137–141

Poprawski TJ, Legaspi JC, Parker PE (1998) Influence of entomopathogenic fungi on *Serangium parcesetosum* (Coleoptera: Coccinellidae), an important predator of whiteflies (Homoptera: Aleyrodidae). Environ Entomol 27:785–795

Prenter J, MacNeil C, Dick JTA, Dunn AM (2004) Roles of parasites in animal invasions. Trends Ecol Evol 19:385–390

Sexton SB, Williams P (1981) A natural occurrence of parasitism of *Graphognathus leucoloma* (Boheman) by the nematode *Heterorhabditis* sp. J Aust Entomol Soc 20:253–255

Schulte F (1989) The association between *Rhabditis necromena* Sudhaus & Schulte, 1989 (Nematoda: Rhabditidae) and native and introduced millipedes in South Australia. Nematologica 35:82–89

Shapiro-Ilan DI, Cottrell TE (2005) Susceptibility of lady beetles (Coleoptera: Coccinellidae) to entomopathogenic nematodes. J Invertebr Pathol 89:150–156

Simmonds FJ (1966) Insect parasites and predators. In: Smith CN (ed) Insect colonization and mass production. Academic Press, New York, NY, USA. pp 489–499

Smith SF, Krischik VA (2000) Effects of biorational pesticides on four coccinellid species (Coleoptera: Coccinellidae) having potential as biological control agents in interiorscapes. J Econ Entomol 93:732–736

Solter LF, Maddox JV (1998) Physiological host specificity of Microsporidia as an indicator of ecological host specificity. J Invertebr Pathol 71:207–216

Sudhaus W, Schulte F (1989) *Rhabditis* (*Rhabditis*) *necromena* sp. n. (Nematoda: Rhabditidae) from South Australian Diplopoda with notes on its siblings *R. myriophila* Poinar, 1986 and *R. caulleryi* Maupas, 1919. Nematologica 35:15–24

Tedders WL, Schaefer PW (1994) Release and establishment of *Harmonia axyridis* (Coleoptera: Coccinellidae) in the southeastern United States. Entomol News 105:228–243

Todorova SI, Côté JC, Martel P, Coderre D (1994) Heterogeneity of two *Beauveria* strains revealed by biochemical tests, protein profiles and bio-assays on *Leptinotarsa decemlineata* (Col.: Chrysomelidae) and *Coleomegilla maculata lengi* (Col.: Coccinellidae) larvae. Entomophaga 39:159–169

Todorova SI, Coderre D, Côté J (2000) Pathogenicity of *Beauveria bassiana* isolates toward *Leptinotarsa decemlineata* [Coleoptera: Chrysomelidae], *Myzus persicae* [Homoptera: Aphididae] and their predator *Coleomegilla maculata lengi* [Coleoptera: Coccinellidae]. Phytoprotection 81:15–22

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. Nature 421:628–630

van den Bosch R, Schlinger EI, Dietrick EJ, Hagen KS, Halloway JK (1959) The colonization and establishment of imported parasites of the spotted alfalfa aphid in California. J Econ Entomol 52:136–141

van den Bosch R (1968) Comments on population dynamics of exotic insects. Bull Entomol Soc Amer 14:112–115

Vinson SB (1990) Potential impact of microbial insecticides on beneficial arthropods in the terrestrial environment. In: Laird M, Lacey LA, Davidson EW (eds) Safety of microbial insecticides. CRC Press Inc., Boca Raton, FL, USA. pp 43–64

Weseloh RM, Andreadis TG (1992) Epizootiology of the fungus *Entomophaga maimaiga*, and its impact on gypsy moth populations. J Invertebr Pathol 59:133–141

Williamson M (1996) Biological invasions. Chapman and Hall, Cornwall, UK

With KA, Pavuk DM, Worchuck JL, Oates RK, Fisher JL (2002) Threshold effects of landscape structure on biological control in agroecosystems. Ecol Appl 12:52–65

Wraight SP, Poprawski TJ, Meyer WL, Peairs FB (1993) Natural enemies of Russian wheat aphid (Homoptera: Aphididae) and associated cereal aphid species in spring-planted wheat and barley in Colorado. Environ Entomol 22:1383–1391

Yinon U (1969) The natural enemies of the armored scale lady-beetle *Chilocorus bipustulatus* (Col. Coccinellidae). Entomophaga 14:321–328