Use of Microbes for Control and Eradication of Invasive Arthropods

Progress in Biological Control

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Use of Microbes for Control and Eradication of Invasive Arthropods

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We would like to dedicate this book to the many devoted insect pathologists over many years who have studied and developed entomopathogens for control of invasive arthropods.

Progress in Biological Control

Series Preface

Biological control of pests, weeds, and plant and animal diseases utilising their natural antagonists is a well-established and rapidly evolving field of science. Despite its stunning successes world-wide and a steadily growing number of applications, biological control has remained grossly underexploited. Its untapped potential, however, represents the best hope to providing lasting, environmentally sound, and socially acceptable pest management. Such techniques are urgently needed for the control of an increasing number of problem pests affecting agriculture and forestry, and to suppress invasive organisms which threaten natural habitats and global biodiversity.

Based on the positive features of biological control, such as its target specificity and the lack of negative impacts on humans, it is the prime candidate in the search for reducing dependency on chemical pesticides. Replacement of chemical control by biological control – even partially as in many IPM programs – has important positive but so far neglected socio-economic, humanitarian, environmental and ethical implications. Change from chemical to biological control substantially con- tributes to the conservation of natural resources, and results in a considerable reduc- tion of environmental pollution. It eliminates human exposure to toxic pesticides, improves sustainability of production systems, and enhances biodiversity. Public demand for finding solutions based on biological control is the main driving force in the increasing utilisation of natural enemies for controlling noxious organisms.

This book series is intended to accelerate these developments through exploring the progress made within the various aspects of biological control, and via documenting these advances to the benefit of fellow scientists, students, public officials, policymakers, and the public at large. Each of the books in this series is expected to provide a comprehensive, authoritative synthesis of the topic, likely to stand the test of time.

Heikki M.T. Hokkanen, Series Editor

Preface

One of the main reasons that we organized this edited volume is to increase international awareness of the growing use of invertebrate pathogens for control and eradication of invasive arthropods. As the numbers of invasive species continues to rise, more insect pathologists have been involved with work on their control using entomopathogens. In fact, this is not a new area of focus for insect pathologists; work on microbes against invasive arthropods began more than a century ago with classical biological control introductions of entomopathogenic fungi against invasive species in the 1890s. Chapters in this book cover entomopathogens that have been developed for control of invasive species over many decades (e.g. a nematode against *Sirex noctilio* and *Bacillus thuringiensis* against gypsy moth) while other chapters focus on development of control measures for very recent invasives (e.g. emerald ash borer first found in the US in 2002). Since both the United States and New Zealand are countries with abundant trade, which is a key pathway for invasives, we have been very aware of the growing numbers of invasive pests arriving in our own countries and the need for control strategies. We have been closely involved with their control using microbes, at varying levels (from laboratory bench to field studies to national committees evaluating eradication programs using the entomopathogen *B. thuringiensis*).

Within the past few years, symposia on use of microbes for invasive control have been organized twice at the annual meetings of the Society of Invertebrate Pathology (2005 – Anchorage, Alaska, and 2007 – Quebec City, Quebec, Canada), demonstrating interest in this subject across the international community of invertebrate pathologists. However, no written summaries, covering the different types of pathogens being studied, developed and used for control, have previously addressed this subject. This could be due to the fact that the subject is very diverse, including programs using very different microbes (viruses, bacteria, fungi, protists and nematodes) in a diversity of contexts: from eradication of new populations of invasive species, to control of established populations of invasives as well as basic studies of host/pathogen interactions and epizootiology. Especially for eradication programs, the lack of written summaries may also relate to the practical focus of these programs, which are about applied pest control rather than research. We hope that those working with invasive arthropods will find this book useful as a resource and that it will serve to support further work on this subject as well as, eventually, increased use of entomopathogens for control of invasives.

We would like to thank Cornell University for sabbatical funding for Dr. Hajek while at AgResearch, Lincoln, New Zealand and support from AgResearch, where this book was mostly organized. We would also very much like to thank the many authors who have contributed excellent chapters to this edited book. The final preparation of this book was facilitated by Sue Zydenbos and Lois McKay. We also thank Heikki Hokkanen for organizing this book series and Springer for their support of this subject.

Lincoln, New Zealand

Ann E. Hajek, Travis R. Glare &
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Part I
Introduction

Chapter 1
Invasive Arthropods and Approaches for Their Microbial Control

Ann E. Hajek

Abstract Invasive arthropod species cause ever-increasing economic, environmental and public health problems. Microbes (i.e. viruses, bacteria, fungi, nematodes and protists) have been used very successfully for eradicating and controlling a range of invasive arthropods in diverse ecosystems worldwide. Many eradication and control programs using microbes have used inundative augmentation (widespread application) approaches while some control programs have instead focused on classical biological control (point release and natural spread). This chapter provides a short history of past use of microbes for control of invasive arthropods as well as an introduction to the subjects that will be covered in this book.

1.1 Globalization and Invasive Species

Throughout history, arthropods have always competed with humans for managed and unmanaged resources as well as causing problems to public health. Initially, arthropods that became pestiferous were native species, but as humans began dispersing to new areas, the arthropods associated with humans, their domesticated animals and crop plants accompanied them. A few of the movements of arthropods have been purposeful and beneficial to humans, such as introducing honeybees for pollination and honey production or introducing arthropod biological control agents. However, the vast majority of introductions have been accidental and usually this dispersal is made possible through human means. (Of course, natural dispersal occurs too but this is slow and takes place over evolutionary times, doesn't usually cross biogeographic borders and usually occurs in only one direction (Nentwig 2007b)). While some introduced species have had little impact, failing to establish or not competing strongly for local resources, a low percentage become established and populations have grown, resulting in crop damage, displacement of indigenous species or adversely impacting animal or public health.

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Given the difficulties in detection of small arthropods, many of which exhibit secretive behaviors, along with the constantly increasing movement of items and people around the world, the numbers of arthropods being introduced to new areas are increasing at an alarming rate. It has been estimated that in the United States alone (including Hawaii), 4,500 arthropod species have been introduced (Pimentel *et al*. 2005). We regularly hear of the detection of new invasive species partly due to the ever-increasing rate of new introductions and partly due to improved surveillance methods, reflecting the recognition of the serious risks associated with invasive arthropods. While agriculture began about 10,000 years ago, probably leading to the first major movements of pests, the date that Columbus discovered America is often accepted as an arbitrary timing for the beginning of what we now call 'biological invasions' (Nentwig 2007a). Thus, after Columbus' voyages to America approximately 500 years ago, faster movement of people and goods was possible and, with improvements in transportation methods and availability, the age of globalization began. To aid in globalization, global regulatory organizations work toward facilitating exchanges of goods between all nations, eliminating obstructions to free trade. As global trade increases, so does accidental movements of organisms. Unfortunately, global regulations have not been put in place to prevent the increasing numbers of invasions. For example, in the United States alone, in 1800 only 50 alien arthropods were recorded as established; by 1990, 2000 invasive arthropods had become established (OTA 1993).

Improved transportation speed, access and availability have facilitated dispersal of hitchhiking arthropods from areas where they are native to areas where they are exotic, or alien. Various methods have led to arthropods breaching the biogeographic barriers that defined the original distributions of species. Unintentionally introduced species have been transported as tramps in vehicles, ships and planes; faster means of transportation now allow introductions of species that in past years would not have survived slower voyages over long distances (Nentwig 2007b). For example, cockroach and ant species that are native to more tropical areas would not be able to survive months of transport across colder areas but, when moved quickly by protected means (e.g. within an airplane), they are able to survive and thus some have now been introduced globally as tramps. Some species are transported by waterways and through shipping. The alfalfa snout beetle, *Otiorhynchus ligustici*, was most probably transported in ballast from England to northern New York State (Shields *et al*. 2004). Other species have been introduced with living plants, with harvested plant material including various types of wood or with soil associated with plants (Nentwig 2007b). The global growth in business travel, tourism and immigration from one continent to another adds to possibilities for transporting arthropods that might become introduced to new areas.

In fact, only a small fraction of species that are introduced become established over the long-term (Simberloff & Gibbons 2004) and only a small fraction of those becoming established cause serious problems (Williamson 1996). The alien species that become established and have potential to or actually cause economic or environmental harm, or harm to human health are termed 'invasive species' (National Invasive Species Council 2000). This is a subjective and broad definition.

The necessity to address problems due to invasive species is viewed differently by those mostly interested in preserving native biodiversity versus those purely interested in whether non-native species that have been introduced are having an economic impact.

We have seen that it does not take many new species well-suited to exploiting a new habitat to create catastrophic problems; sometimes only one species can monopolize or take over a previously diverse and balanced ecosystem and change it irreversibly. Ecologists have been very intrigued by the question of what allows a species to become a damaging invasive, especially because in many cases these pests are not pests in their areas of origin. Among the ecological hypotheses that have been proposed, some ecologists think that species that become invasives are pre-adapted to the new environment or are superior in some way when compared with native species (Hufbauer & Torchin 2007). Another hypothesis that has long received support is that when new species enter new environments, they are not accompanied by the natural enemies controlling their populations in their area of origin (= enemy release hypothesis); this hypothesis is supported by the fact that many invasives do not cause problems in their areas of origin and can, in fact, be uncommon endemics. The evidence that introduced species have fewer natural enemies in their new environments compared with their native environments supports this hypothesis (Torchin & Mitchell 2004). It has been hypothesized that the natural enemies attacking invasive species in a new environment would be generalists rather than specialists since generalists would be more likely to shift to new host species (Torchin & Mitchell 2004, van der Putten *et al*. 2005).

Ecosystems that have been altered in some way may be more susceptible to being overcome by an invasive species. For example, when exotic pines were planted as monocultures over large areas in Australia, the system was ripe for an invasive species, the European woodwasp *Sirex noctilio*, to easily spread and kill trees (e.g. Haugen & Underdown 1990). Likewise, agricultural monocultures are highly susceptible to being overcome when invasive species that can utilize the crops being grown are introduced. In most cases, agriculture relies on exotic plant and animal species, which can be susceptible to exotic arthropods, and, in particular, those arthropods from the areas where the agricultural crop or animal originated.

Many books have chronicled the impacts of invasive species, including arthropods (e.g. Van Driesche & Van Driesche 2004). Introduced species that become invasive can have severe impacts on entire ecosystems. For example, over a 20 year period, the European balsam woolly adelgid, *Adelges piceae*, spread and killed over 95% of mature Fraser firs (*Abies fraseri*) in the southern Appalachian Mountains in the eastern US (as cited in Pimentel *et al*. 2002). The extensive tree mortality has been associated with regional loss of two native bird species and invasion by three other bird species due to substantial changes in the forest (Alsop & Laughlin 1991). Although Fraser fir regeneration is now extensive (younger trees are less susceptible to *A. piceae*), stand characteristics such as age and distribution of Fraser fir have been changed. The long-term impacts to the new generation of trees remains to be seen but it seems possible that the overall effect will be that these infested forests will have fewer Fraser firs (Ragenovich & Mitchell

2006). Beginning in the 19th century and through 1979, four species of wasps in the family Vespidae were introduced to New Zealand (Cook *et al.* 2002); New Zealand is now recorded as having the highest density of such wasps in the world. While these wasps cause abundant stings each year, they also have a strong impact on the native beech (*Nothofagus* spp.) forests. In particular, *Vespula vulgaris* and *Vespula germanica* reduce the crop of homopteran-secreted honeydew by >90%, thus impacting food resources of native birds (Beggs & Rees 1999). In addition, the wasps also directly impact native invertebrate biodiversity and compete with native birds for invertebrate prey. The red imported fire ant, *Solenopsis invicta*, has spread throughout the southeastern United States where it has reduced biodiversity and harmed wildlife (Wojcik *et al.* 2001). In these instances, entire communities associated with invasives are affected, often leading to permanent changes in ecosystems.

In general, the impacts of invasive species on native ecosystems and biodiversity are not well documented whereas the economic impacts of invasive species have received more attention. Costs incurred as a result of invasive species take three general forms: direct costs of damage caused by invasives (e.g. productivity losses), costs of control efforts and costs of preventing new introductions. The latter is the concern of quarantine (or biosecurity) agencies and will not be covered in this book. It has been estimated that damage and control costs in the US for the imported fire ant alone equal US$1 billion per year (Pimentel *et al.* 2005). Structural damage caused by the Formosan termite (*Coptotermes formosanus*) in the southern United States has been estimated at US$1 billion per year (Pimentel *et al.* 2005), and this estimate was made before the 2005 hurricanes that resulted in heavy infestations in ravaged areas and increased potential for this destructive termite to be dispersed by humans. It is much more difficult or even impossible to put a cost to environmental changes caused by invasive species. Red imported fire ants kill poultry chicks, lizards, snakes, ground-nesting birds and many native invertebrates and, while some of these can be associated with a monetary loss, it is not so easy to assign a monetary value to loss of native snakes, lizards and many invertebrates. It is likewise difficult to assign a monetary value to loss of native Fraser firs (a species that is not logged) and associated communities in the forests of the Appalachian Mountains of the US.

1.2 Managing Invasive Arthropods

Exotic arthropod pests have been problematic since agriculture began and pest management strategies have been developed for these purposes. So how does controlling the ever-increasing numbers of invasive arthropods differ from controlling native arthropod pests? This book focuses on eradication and control of arthropods that are invasive because this group of pests presents unique challenges.

First, the goal of eradication is never an objective for native pests so this type of control is unique to invasive pests. To confound the difficulty of undertaking an eradication campaign, newly introduced species usually initially exist at low densities and often first invade areas with large human populations (i.e. airports and ports of entry are generally in urban centers), making control efforts more difficult. Detection can be particularly difficult and often invasive species are only discovered by chance. Even where routine surveys are conducted to detect invasives, the chance of successful detection is often dependent on timing of the survey and training of the operators.

Pests of agricultural crops are a mixture of native and introduced arthropods; it has been estimated that 40% of crop pests in the US have been introduced (Pimentel 1993). In New Zealand, it is estimated that 90% of invertebrate pests are aliens (Barlow & Goldson 2002). In cases where the invasive that has become established is an agricultural pest and cannot be targeted for eradication because it is already well-established and has spread, pest management can become more similar to control measures used for native pests. However, many invasives are pests in native ecosystems and, in these cases, standard management practices that have been developed to protect crops in agriculture and forestry are not appropriate, making control efforts more challenging. Invasive arthropods can increase to huge populations that spread like wildfire, leaving behind decimated native ecosystems that will never be the same. For example, the invasive emerald ash borer (*Agrilus planipennis*), first found in the US in 2002 in southeastern Michigan, is currently spreading, already leaving behind > 20 million dead ash (*Fraxinus* spp.) trees (USDA Forest Service, 2007).

Spread of these new pests can be very fast and their population dynamics once they invade new areas can be chaotic; these are unique characteristics of populations of invasive arthropods and, once again, require more creative control strategies. Commonly, there is very rapid population growth of invasive pests once they are established, whereas established populations of these species in their places of origin exist at lower population densities. This ‘outbreak’ phenomenon means there can be large populations at the expanding front of a pest invasion. A newer approach for controlling invasive species that have become established and are spreading (so eradication is no longer possible) is “slow the spread’. This strategy involves aggressively targeting the leading edge of a new invasion to limit the rate of colonization of new areas (see Chapter 5). In addition, this method reduces the outbreak impact at the leading edge.

One type of control that is frequently exploited for combatting invasive arthropods is classical biological control; this strategy is defined as ‘the intentional introduction of an exotic biological control agent for permanent establishment and long-term pest control’ (Eilenberg *et al.* 2001). In fact, historically, practitioners predominantly have focused on invasive pests with classical biological programs (Brewer & Charlet 1999). This strategy is more appropriate for targeting pests occurring in habitats with some degree of permanence (e.g. wetlands, forests, orchards) where effective, environmentally safe natural enemies of invasive pests are not present or effective. It is also a strategy in keeping with the theory that invasive pests succeed due to lack of natural enemies in their new area; this strategy is based on seeking to introduce to the invaded ecosystem the natural enemies of the pest that control its populations in its area of origin.

The other control strategy used against invasive pests is inundative augmentation: 'the use of living organisms to control pests when control is achieved exclusively by the organisms themselves that have been released' (Eilenberg *et al*. 2001). This control method is similar to strategies using synthetic chemical pesticides as it seeks to kill pests by direct mass application. Thus, when living organisms are used in this way, they are often referred to as biopesticides.

Invasions occur in several phases (Liebhold & Tobin 2008) and different methods for mitigation are appropriate for each phase. First, the initial arrival of the pest can be prevented by international quarantines that restrict movement of exotics and by inspections at ports of entry. This first phase is outside of the subject of this book but is covered in a recent review (Follett & Neven 2006). Subsequently, exotics become established, forming initial reproducing populations. Many insects fail to find hosts that can maintain a reproductive population, or they find conditions (i.e. winter) unsuitable for survival. Those that successfully form an initial population can be targeted for eradication if found before significant spread has occurred. Once the population of the invasive has developed and spread, becoming part of new ecosystems, invasives can only be controlled.

1.2.1 Preventing Establishment

Often no one knows when and where invasives were first introduced and only sometimes scientific detective work after the fact can help to trace the source and determine when and how the initial introduction occurred. When invasive pests are initially introduced, the numbers of individuals establishing are frequently very few. If the invasive is a species with a track record elsewhere, then monitoring methods have sometimes already been developed and can be used to aid in detection; in fact, customs and airport authorities are constantly searching for species that are known to be serious pests elsewhere and are also easily transported. However, methods for detection are not always available, either because the new invasive is not a pest elsewhere or simply because the species is not easy to detect, e.g. adults of wood borers that do not rely on sex pheromones can be difficult to detect because a standard detection tool, pheromone traps, is thus not appropriate and, in addition, immature stages of these pests live inside wood and can escape visual inspections. The period while populations of new invasive pests are at very low densities (i.e. just after establishment) is the optimal time when eradication should be undertaken for greatest chance of success; it becomes increasingly difficult or impossible to eradicate when the target is already at moderate densities and/or has already spread very far. Decisions on whether or not to undertake an eradication campaign are often based on costs and benefits of the program as well as the prediction of whether success is possible (Myers *et al*. 2000), although sometimes politics or public attitude can influence whether or not eradication programs are conducted regardless of the economics (see Chapter 18). Of course, availability or development of effective methods for detecting and monitoring low density populations are critically important to success in eradication. Eradication programs require blanketing the areas known to be infested with control agents to drive populations of the invasive pest below levels where they can reproduce; generally highly effective inundative augmentation methods are used. Thus, eradication programs are very expensive, they require large amounts of biopesticide and a very large crew, often needing to be available on short notice, in order to eliminate populations of the invasive pest before the population reaches higher density and spreads so that the species cannot be eradicated. In addition, it is important that authorities do not terminate eradication programs as soon as populations cannot be detected; they must continue surveillance for a time to ensure that the invasive species is truly eradicated (see Chapter 18).

1.2.2 Preventing Increase and Slowing Spread

After an invasive species has become established and is increasing in numbers and spreading, the next step often taken is implementation of a domestic quarantine to prevent movement of the pest (usually via humans) outside of the area of establishment. Alternately, barrier zones are created to prevent spread of the organism on its own. Control is easier for organisms that spread along a continuous population front. However, for organisms with the ability to travel long distances, either on their own or aided by humans, it is more difficult or even impossible to halt spread.

Once a population of an invasive is established in a new area, the focus of the program changes to control. Suppressing the population should aid in decreasing problems locally as well as decreasing the chance of further long distance dispersal into more areas. Suppression of spreading populations is often through inundative augmentation, including the release of large quantities of a pathogen to decrease populations of the invasive. Inundative augmentation is also used for control of established populations of invasives, especially when their populations increase to damaging levels. A more long-term strategy for control of established invasives is introduction of exotic pathogens for permanent long term control (= classical biological control). This strategy has been used extensively through the release of herbivorous arthropods and plant pathogens for control of invasive weeds, and releases of parasitoids and predators for control of invasive arthropods. Although classical biological control of arthropods has not utilized pathogens as frequently, this is not due to lack of success but perhaps more likely due to difficulties in finding and working with microorganisms during foreign exploration (i.e. searching for natural enemies in the area of origin) and possibly due to less knowledge of microbiology among entomologists involved in invasive responses and classical biological control. The numerous classical biological control programs using entomopathogens, including successes, have recently been reviewed (Hajek *et al*. 2007) and some of those pertaining to invasive species are covered in this book.

1.3 Use of Microbes Against Invasive Arthropods

1.3.1 Advantages of Using Microbes

Bacteria, viruses, fungi, nematodes and protists comprise the major groups of arthropod-pathogens used for eradication and control. Along with this diversity in microorganisms comes a diversity in pathogenicity (ability to infect) and virulence (speed of kill). However, in general the pathogens being used only affect arthropods and often have narrow host ranges, so they are more acceptable for use in the urban/suburban areas where invasives are often found first. Due to differing pathogenicity and ecology, different types of arthropod pathogens are appropriate for different pests in different circumstances. For example, strains of the bacterial pathogen *Bacillus thuringiensis* (*Bt*) can kill lepidopteran hosts within a day or two (Glare & O'Callaghan 2000). In addition, *Bt* is relatively easy to mass produce outside of insects and numerous companies sell different strains for pest control. Therefore, *Bt* has been used numerous times in eradication programs in urban areas (see Chapters 4 and 5). However, although *Bt* is a commonly occurring soil bacterium, it has rarely been known to cause epizootics and thus *Bt* is not considered for classical biological control programs. In contrast, the fungal pathogen *Entomophaga maimaiga* presently cannot be mass-produced but persists in the northeastern US, frequently causing epizootics in gypsy moth (*Lymantria dispar*) populations. This species therefore would never be considered for an eradication campaign but is very appropriate for classical biological control as it is capable of maintaining itself in the host population. For both eradication and control programs, entomopathogens offer a natural alternative in comparison with synthetic chemical pesticides. Introductions of invasive pests often occur around ports or airports, areas with large human populations, and extensive use of synthetic chemical pesticides is not possible or is not accepted by the public. Many invasive pests attack plants growing near human habitation or they attack plants in environmentally sensitive natural areas; in either case, the public frequently prefers an environmentally benign pest control option. In many of these environments, non-target impacts on other arthropods may be of concern, so use of host specific entomopathogens is also advantageous.

1.3.2 History of Use of Pathogens for Classical Biological Control of Invasive Arthropods

Classical biological control using pathogens against arthropods was first recorded in 1894–1895 but this strategy was used relatively little until the 1950s (Hajek *et al*. 2005, 2007). For introductions between 1894 and 1950 (about which there is adequate documentation) 81.8% targeted invasive insect hosts instead of native hosts. For all except one of the introductions before 1950, fungal pathogens were introduced and the principal targets were hemipterans and soil-dwelling scarabs.

For the majority (63.6%) of the 131 total release programs for which the area of endemism of the pest(s) and success in establishment could be determined, the targeted arthropod pest was an invasive and not native. The percentage of programs yielding successful establishment did not differ between programs targeting native versus invasive pests (71.4–72.4% establishment). Among the five pathogens released most commonly, the *Oryctes rhinoceros* virus (see Chapter 8), *Entomophaga maimaiga* (the fungal pathogen infecting gypsy moth) (see Chapter 11) and the nematode targeting *Sirex noctilio* (see Chapter 12) all targeted invasive hosts. These pathogens were used frequently because of their success in control of hosts.

Several major successes with classical biological control of invasive conifer-feeding sawflies in North America using viruses occurred in the mid-1900s; there are currently no on-going programs with the viruses so they are not covered elsewhere in this book and are therefore mentioned briefly here. European pine sawfly (*Neodiprion sertifer*) in North America (Hajek *et al.* 2005) was first reported in New Jersey in 1925 and it then spread in eastern North America (Cunningham & Entwistle 1981). A nucleopolyhedrovirus (NPV) was obtained from Sweden in 1949 and was subsequently released in Canada and the USA in the early 1950s and in the UK in the early 1960s. Methods for mass production were developed and this virus was also extensively used for inundative releases by Forest Service personnel, Christmas tree growers and private individuals until 1970 when registration became necessary for further use. Outbreak populations of the invasive European spruce sawfly (*Gilpinia hercyniae*) in eastern Canada and the northeastern US were controlled by an NPV and introduced parasites; the virus was first noted in 1936 but by 1952 it had been transferred or had spread through most infested areas (Cunningham & Entwistle 1981). This NPV had not been purposefully introduced and must have accidentally accompanied sawflies or parasites from Europe. The virus, in combination with parasitoids, appears to have permanently solved problems due to *G. hercyniae* in eastern North America.

1.3.3 History of Use of Pathogens for Inundative Augmentation of Invasive Arthropods

Metchnikoff is generally credited with being the first to conduct experimental work on the application of entomopathogens against economically important pests (Cameron 1973, Zimmermann *et al.* 1995). He worked with *Metarhizium anisopliae* and species of crop pests that were native to eastern Europe and Russia: *Anisoplia austriaca* and *Bothynoderes* (= *Cleonus*) *punctiventris*. Subsequent use of mass-produced entomopathogens for inundative control focused primarily on arthropod pests that were native or which had been moved extensively through agriculture for many years (e.g. scale insects and whitefly on citrus).

However, beginning in the 1920s, research toward use of entomopathogens for control also focused on invasives that were relatively new to North America at that time: the European corn borer, *Ostrinia nubilalis*, and the Japanese beetle, *Popillia japonica*. Although research determined that both *B. thuringiensis* and *M. anisopliae* were effective for control of corn borer, products were not developed and put to use. In the US, research on bacterial pathogens of the invasive Japanese beetle (*Popillia japonica*) yielded a commercially available milky disease product based on *Paenibacillus popilliae*, a localized bacterial species from North America. This bacterium constituted the first insect pathogen that was approved for use by the US government, shortly after WWII (Federici 2005). To hasten spread of the pathogen, 109 tons of *P. popilliae* spore powder was distributed to 90 sites in 13 eastern states from 1939 to 1953 (Falcon 1971). A product based on *P. popilliae* is still available today in the US, since Japanese beetles continue to be a pest problem, however production is limited by *in vivo* methods. A nematode species *Steinernema glaseri* was also isolated from the Japanese beetle and appeared promising but, because of the success of milky disease, this nematode was not developed further. However, this initial work with *S. glaseri* is commonly credited as the beginning of microbial control with nematodes (Lord 2005).

Apparently during WWI, the Colorado potato beetle, *Leptinotarsa decemlineata*, was introduced into western Europe and it subsequently spread to the south and east. Because of much improved potato transportation, Colorado potato beetle was distributed across much of Europe by the 1940s. A *Beauveria bassiana*-based mycoinsecticide for control of the Colorado potato beetle (Boverin) was developed in 1965 in the former USSR (Kendrick 2000) and was used for many years (Ferron 1981) although it is not produced now (Faria & Wraight 2007). In the 1960s, *B. thuringiensis* products were initially commercialized and a few of the major pests targeted in the US (Federici 2005) were invasive species: gypsy moth and diamondback moth (*Plutella xylostella*), both native to Europe. Development of biopesticides has continued since these earlier projects and invasive arthropods continue to be among the principal targets for which microbial biopesticides are developed and used.

1.4 An Overview of Use of Microbes for Control and Eradication of Invasive Arthropods

This book is organized in sections, beginning in Part I with this introductory chapter, followed by two chapters in Part II discussing instances and implications of infection of invasives by endemic pathogens and then modeling dynamics of invasive arthropods with implications for their eradication and control with entomopathogens. The next 12 chapters all present case histories of eradication and control programs using arthropod specific pathogens; covering a diversity of approaches for a diversity of hosts and pathogens in a diversity of ecosystems. Part III includes two chapters describing and discussing eradication programs using *Bacillus thuringiensis*. The next ten chapters (Part IV) are case histories of control programs using entomopathogens. Chapters in Part IV are organized by the hosts, beginning with Hemiptera (1 chapter), Orthoptera (1 chapter), Coleoptera (3 chapters), Lepidoptera (1 chapter), and

Hymenoptera (2 chapters), and finishing with 2 chapters on use of pathogens for control of mites. One of the chapters on beetles (Coleoptera) is not specifically concerned with an invasive beetle but with an invasive nematode that is vectored by a native wood-boring beetle (Chapter 9). Among these chapters, all of the major groups of pathogens are included: viruses, bacteria, fungi, nematodes and protists. Some of the chapters on control cover one host and one pathogen (e.g. Chapter 14 on use of *Neozygites tanajoae* against cassava green mite) while others cover one host and numerous pathogens (e.g. Chapter 11 on gypsy moth includes *Bacillus thuringiensis, Lymantria dispar* nucleopolyhedrovirus, the fungus *Entomophaga maimaiga* and microsporidia). Control strategies that are covered in these chapters range from inundative augmentation to classical biological control.

In some instances, the public has been concerned about use of microbes for control of invasive arthropods, especially when control measures must take place where people live and work. Chapter 16 presents a discussion of the human health effects of *B. thuringiensis*, the entomopathogen that has been used most extensively for inundative applications against invasive arthropods in urban areas. Another concern that is raised is whether use of entomopathogens against invasive arthropods will affect our environment; Chapter 17 addresses non-target impacts of microbial control agents.

There have been some great successes in use of pathogens for control of invasive arthropods. The final chapter synthesizes the material presented in earlier chapters to discuss the constraints experienced in use of entomopathogens against invasive pests and improvements and new approaches for increasing success with entomopathogens against invasive arthropods in the future.

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Part II
Ecological Considerations

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

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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