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Review

The Current State and Future Potential of Microbial Control of Scarab Pests

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Abstract: Injury and control costs for the invasive scarab Japanese beetle (Family Scarabeidae, *Popillla japonica*) alone is estimated at $450 million per year in the U.S. Chemical controls are commonly used to control scarab pests, but concerns about human safety and negative impacts on beneficial and non-target organisms, such as pollinators, are increasingly driving the market towards less toxic and more environmentally friendly management options. Microbial entomopathogens are excellent candidates for biopesticides and biocontrol agents. Although microbial pesticides currently make up only 1–2% of the insecticide market, the discovery and development of new microbes are increasing. Microbial products are non-toxic to humans and most are species-specific, reducing non-target effects. While some are slow-acting, others provide rapid control and some can be as efficacious as chemical insecticides, particularly when used in combination. Another major advantage of microbial controls is that many can persist in the environment, and become biocontrol agents, providing long-term control and reducing costs. This article provides a summary of the microbial entomopathogens that are known to infect scarab beetle species including bacterial, fungal, viral, microsporidian, and protozoan taxa, as well as the existing formulations and their efficacy. Lesser-known microbial species are also discussed as potential future controls. We also discuss the development of new techniques for improving efficacy, such as genetic engineering, synergistic interactions, auto-dissemination strategies, and improved formulations.

Keywords: white grub; scarabaeidae; *Beauveria*; *Ovavesicula*; entomopathogenic; fungi; bacteria; protozoa

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1. Introduction

In 2019, the U.S. horticulture sector reported a total of $13.8 billion in sales of plants and products [1]. The U.S. turfgrass industry maintains an estimated worth of $40–60 billion per year [2] and accounts for 50 million acres, making it the fourth largest crop and the largest irrigated crop in the U.S. [3]. Horticultural plants and turfgrass are hosts to several different insect pests, including caterpillars, mole crickets, mites, and various fly and beetle species. Of these, scarab beetles (Coleoptera: Scarabaeidae) are arguably the most damaging [4,5]. The majority of damage occurs from white grub (larval) feeding on the roots of plant hosts but adult defoliation can also cause economic damage and aesthetic damage on the foliage of over 300 species of plants. The most damaging endemic turf-feeding species in U.S. include: *Aphodius* beetles (*Aphodius granarius*), black turfgrass *Ataenius* (*Ataenius spretulus*), June beetle (*Phyllophaga* species), masked chafer (*Cyclocephala* species), false Japanese beetle (*Strigoderma arboricola*), and green June beetle (*Cotinis nitida*). Turf damage can also be caused by exotic species, such as Japanese beetle (*Popillia japonica),* oriental beetle (*Anomala orientalis*), European chafer (*Amphimallon majalis*), and the Asiatic garden beetle (*Maladera castanea*) and tend to cause more damage than endemic species [4]. Of these species, masked chafers, *Ataenius, Aphodius* species, European chafer, and oriental beetle are larval pests, while June beetle, false Japanese beetle, Japanese beetle, green June beetle, and the Asiatic garden beetle are pests at both larval and adult stages [6].

2. Non-Target Effects of Entomopathogens

Scarab pests incur significant economic losses across horticultural sectors, with injury and control costs for the Japanese beetle alone estimated at $450 million per year [7]. Despite the availability of effective chemical controls, which include carbamates, organophosphates, pyrethroids, diamides, and neonicotinoids, concerns about human safety and negative impacts on bees, butterflies and other beneficial non-target organisms, are increasingly driving the market towards less toxic, more environmentally friendly insecticides. Central in this pursuit, is the use of microbial entomopathogens that can provide targeted control through classical or augmentative biocontrol strategies. Microbial pesticides currently make up only 1–2% of the market but their portion is increasing due to health and environmental safety concerns surrounding the use of synthetic insecticides and regulatory changes, particularly in European markets (Lacey et al., 2015). Due to this, new opportunities exist for novel microbial products and/or control programs to be developed and implemented.

This review summarizes the microbial entomopathogens that have been discovered in scarab species, the formulations developed from them, and their efficacy. Lesser-known microbial species are also discussed as potential up-and-coming novel controls. In addition, we address the relative utility of different microbes to serve as biocontrol agents versus biopesticides as determined by their capability to produce natural epizootics. Finally, we explore the development of new techniques for improving efficacy, such as genetic engineering, synergistic interactions, auto-dissemination strategies, and improved formulations.

3. Short Term Biopesticides versus Long Term Biocontrol

Biopesticides are derived from naturally occurring biocontrol organisms. The biocontrol agent is modified and packaged with inert ingredients to increase its efficacy. Before we provide an overview of the microbial options available for controlling scarab pests, it is necessary to discuss some of the terminology associated with microbial pest control. Entomopathogenic microbes and their byproducts are often described as biopesticides or biocontrol agents. In both cases, these terms indicate that these products provide a safer alternative to synthetic chemicals, and, in some cases, genetically engineered options [8]. For instance, although the term biocontrol consistently specifies the use of living organisms to control insect pests that are self-replicating in the environment [9], some of the broadest definitions of biopesticides also include the use of live organisms that are repeatedly applied as a pesticide [10,11]. Stricter definitions only pertain to the products produced by living things [12], but some, such as that of [13], combine definitions to include both the direct and indirect activity of living organisms. Additionally, some definitions of biopesticides encompass only natural plant- or microbe-derived substances, while others allow for synthetic compounds based on these chemistries [12]. The U.S. EPA outlines three different classes of biopesticides: (1) microbial pesticides, which include live bacteria, fungi, viruses, or protozoa as the active ingredient, (2) plant-incorporated-protectants, which are substances produced by genes engineered into plants, and (3) biochemical pesticides that are naturally occurring and operate using non-toxic mechanisms, such as mating-disrupting pheromones or chemical deterrents [14].

In this review, we define biocontrol as the use of living organisms to control insect pests that are self-replicating in the environment. Biopesticides or biorational pesticides are defined as commercial formulations used to manage pests that usually must be reapplied on a consistent basis, and hence the economic incentive for a producer to make them, as they are active for the short term and reapplication and repurchasing is necessary. Biocontrol organisms persist longer and are self-replicating in the environment. *Beauveria bassaina* strain GHA when registered as a biopesticide at EPA by Micotech Corp. was found not to persistent in the environment, although naturally occurring Beauveria acts like a biocontrol agent and persists in the environment. Clearly, different strains may be chosen as biopesticides so they do not create epizootics that reduce the need for future purchases and sprays.

We would like to discuss an important distinction between biopesticide and biocontrol definitions that relates to the practical role of persistence. The use of live organisms in biocontrol can operate in an acute or chronic manner depending on the system. In many instances of classical biocontrol, agents have become established in areas where they were released [15–17]. In this way, biocontrol agents can persist in the environmental for longer periods than biopesticides, improving their utility for pest control.

As will be shown in the following sections, many microbial agents can be difficult to culture and slow-acting. Additionally, few microbial options, on their own, fail to match the quick knockdown and efficacy of chemical insecticides. However, many of these entomopathogenic biocontrol agents have the potential to become locally established and provide long-term population suppression. This capability, along with their reduced risk to human health and non-targets, makes microbial agents an increasingly attractive option for minimizing the negative impacts of routine chemical insecticide use, particularly when it comes to protecting pollinators and other beneficial insects. Ultimately, much more research is needed for the development of microbial agents, especially for scarab pests, but there is a wealth of naturally occurring entomopathogens to choose from and even more opportunities for customizable control when combinations of microbes are considered.

4. Bacteria

Although many bacterial species live symbiotically with insects across all developmental stages, at least 100 species of bacteria act as insect pathogens. The majority of these species are found in the Bacillaceae, Pseudomonadaceae, Enterobacteriaceae, Streptococcaceae, and Micrococcaceae families [18]. Relationships between insects and bacteria, whether beneficial or harmful, can be obligate or facultative, leading to complex ecological interactions. Entomopathogenic bacteria have been used to develop a range of insect control products that utilize spore and/or bacteria-derived toxin formulations. These formulations must be ingested, after which the bacterial spores proliferate in the hemocoel, causing death by starvation and/or septicemia. Bacterial toxins, on the other hand, create perforations in the gut epithelium and typically cause death through secondary infections [19]. Currently, only three bacterial species are available for biocontrol of scarabs in the U.S.; *Paenibacillus popilliae* and *P. lentimorbus*, which make up milky spore disease, and the *Bacillus thuringiensis* subspecies galleriae (Table 1). In other parts of the world, however, other bacterial species have been isolated from scarabs, such as *Serratia entomphilia*, which is commercially available for biocontrol in New Zealand to control grass grub (*Costelytra zealandica*) and *Yersinia entomphaga*, which shows additional activity against some other scarab species.

While natural epizootics in field and laboratory populations have been documented for several bacterial strains in lepidopteran populations [20–22], fewer example are found for scarabs. Milky spore disease (*P. popilliae*) and *B. thuringiensis*, however, have been found to persist in the soil for years or decades after application [23], suggesting that they may be capable of producing epizootics under the right conditions. In general, the evolutionary history of these bacteria and their scarab hosts are poorly understood but the identification of new scarab-specific bacterial toxins show strong potential for future development.

Table 1. A list of microbial products commercially available in the U.S. for scarab pests and their estimated cost per acre, given recommended concentrations.

Product	Species/Strain	Estimated Cost/Acre
Bacteria		
Milky Spore Powder (St. Gabriel Organics)	*P. popilliae*	$320
grubGONE! G (Phyllom BioProducts)	*Bt* galleriae	$533–800
beetleGONE! (Phyllom BioProducts)	*Bt* galleriae	$179–787
grubHALT! (Phyllom BioProducts)	*Bt* galleriae	$1346–2019

Table 1. *Cont.*

Product	Species/Strain	Estimated Cost/Acre
Fungi		
BotaniGard 22WP (GHA; BioWorks)	*B. bassiana*	$245–900
BotaniGard ES (GHA; BioWorks)	*B. bassiana*	$23–92
Mycotrol WPO (GHA; BioWorks)	*B. bassiana*	$74–295
Mycotrol ESO (GHA; BioWorks)	*B. bassiana*	$30–117
XPULSE OD (GHA; LAM International)	*B. bassiana*	n/a
BioCeres WP (ANT-03; BioSafe Systems)	*B. bassiana*	$1130–4520
Velifer (PPRI 5339; BASF)	*B. bassiana*	$14–61
balance Darking Beetle Bait (JABB; HF)	*B. bassiana*	$128
Natuarlis L (ATCC 74040; Lallemand)	*B. bassiana*	$35
Met52 EC (F52; Novozymes Biologicals Inc.)	*M. anisopliae*	$50–200
PFR-97 20% WDG (Apopka 97; Certis USA)	*I. fumosorosea*	$36–72
NoFly WP (FE9901; Blacksmith Bioscience)	*I. fumosorosea*	$56–225
Nematodes		
NemaSeek (Arbico Organics)	*H. bacteriophora, S. kraussei, H. indica*	$72
NemAttack (Arbico Organics)	*H. bacteriophora, S. feltiae, S. riobrave, S. carpocapsae*	$72
Larvanem (Koppert Biologial Systems)	*H. bacteriophora*	$652
Millenium (BASF)	*S. carpocapsae*	$64–1920
Nemgard (Purely Organic Products, LLC)	*S. scarabaei*	$320
Nemashield (BioWorks)	*S. feltiae*	
Entonem (Koppert Biologial Systems)	*S. feltiae*	$604
Nema Globe Grub Busters (The Environmental Factor Inc.)	*S. carpocapsae* and *S. feltiae*	$441
Field Guardian Nematode Mix (Hydro-Gardens)	*Heterohabditidae*/*Steinernematidae*	$1389
H. bacteriophora (Rincon-Vitova Insectaries)	*H. bacteriophora*	$380
Nemasys (G) (BASF)	*H. bacteriophora*	$300–600
Grub Away (Gardens Alive!)	*H. bacteriophora*	$400
Nema-green (Biolgicher Pflanzenchutz)	*H. bacteriophora*	$656
Terranem (Koppert Biologial Systems)	*H. bacteriophora*	$644
Heteromask (BioLogic)	*H. bacteriophora*	$1000
Scanmask (BioLogic)	*S. feltiae*	$1000
Ecomask (BioLogic)	*S. carpocapsae*	$1000
Capsanem (Koppert Biologial Systems)	*S. carpocapsae*	$800
Nemastar (Bioforce Limited)	*S. carpocapsae*	$900

4.1. Bacillus thuringiensis

Bacillus thuringiensis (*Bt*) is a Gram-positive bacteria commonly found in soil habitats throughout the world. Tens of thousands of *Bt* strains exist, and they produce over 300 different types of toxins, many of which possess insecticidal properties [24], making *Bt* arguably the most useful microbe for insect control. *Bt* endotoxins facilitate the germination of bacterial spores by binding to receptors on the gut epithelium and forming pores in the gut wall. This allows the spores to enter the hemocoel and germinate, resulting in the death of the larvae through septicemia and/or starvation [19,25]. As a soil-dwelling bacteria, *B. thuringiensis* live in a close association with white grubs. Although *Bt* toxins are predominantly used to control lepidopteran, and to a lesser extent, coleopteran pests, several *Bt* subspecies also produce endotoxins that negatively affect scarabs. Of the 25 different *Bt* toxins that have demonstrated toxicity on white grubs, only one bacterial strain, *Bt* galleriae, is commercially available as a spore formulation to control white grubs in the U.S. (Table 1).

Table 2 shows all of the *Bt* endotoxins that have exhibited some degree of toxicity to scarab species. The *Bt* subspecies shown to control larval scarabs are *Bt* tolworthi (expressing Cry3Ba endotoxin) [26], *Bt* kumamotoensis (expressing Cry7Ab, Cry8Aa, and Cry8Ba) [27], *Bt* galleriae (expressing Cry8Da) [28–30], and *Bt* japonensis (expressing Cry8Ca) [30–33]. Several scarab species are also susceptible to a range of endotoxins from other *Bt* strains, shown in Table 2 [33].

Table 2. *Bt* toxins (n = 25) with demonstrated toxicity and negative effects on scarab species and the subspecies or strains they are derived from.

Bt Toxin	Subspecies/Strain	Insect Targets
Cry3Aa	*Bt* tenebrionis	*A. corpulenta, A. solstitiale, M. melolontha*
Cry3Ba	*Bt* tolworthi	*Cyclocephala* spp., *P. japonica*
Cry7Ab	*Bt* kumanotoensis	A. corpulenta
Cry8Aa	*Bt* kumanotoensis	*Cotinis* spp., *H. oblita, H. parallela*
Cry8Ba	*Bt* kumanotoensis	*Cotinis* spp., *C. borealis, C. pasadanae, P. japonica*
Cry8Ca	*Bt* japonensis	*A. corpulenta, A. cuprea, A. exolete, Cotinis* spp., *Cyclocephala* spp., *H. parallela*
Cry8Da	*Bt* galleriae	*A. cuprea, A. orientalis, P. japonica*
Cry8Db	*Bt* BBT2-5	*P. japonica*
Cry8Ea	*Bt* BT185	*A. corpulenta, H. parallela, P. japonica*
Cry8Fa	*Bt* BT185	*A. corpulenta, H. oblita, P. japonica*
Cry8Ga	*Bt* HBF-18	*H. oblita, H. parallela*
Cry8Na	*Bt* Q52-7	*A. corpulenta, H. oblita, H. parallela*
Cry8Sa	*Bt* 62	*H. serrata*
Cry9Da	*Bt* japonensis	*A. cuprea*
Cry18Aa1	*Bt* laterosporus	*M. melolontha*
Cry23Aa/37Aa	*Bt* (unknown)	*P. japonica*
Cry43Ba	*P. lentimorbus*	*A. cuprea*
Cry43Aa	*P. lentimorbus*	*A. cuprea*
Cyt2Ca	*Bt* SK-1007	*P. japonica*
Vip1Ac	*Bt* kurtaki	*H. oblita*
Vip1Ad	*Bt* HBF-18	*H. parallela*
Vip2Ae	*Bt* BREF24, *B. cereus* HL12	*H. oblita*
Vip2Ag	*Bt* HBF-18	*A. corpulenta, H. oblita, H. parallela*
Vip1Ac+Vip2Ae	*B. cereus* HL12	*H. oblita*
Vip1Ad+Vip2Ag	*Bt* HBF-18	*A. corpulenta, H. oblita, H. parallela*

Redmond et al. [34] showed that a commercial formulation (wettable powder) of *Bt* galleriae sprayed on foliage reduced adult Japanese beetle feeding for up to 14 days after the initial spray. However, a granular formulation applied to the soil was less effective for controlling early and late-instar grubs. Importantly, foliar applications of *Bt* galleriae also showed nontarget effects on butterflies and caused 97–100% mortality of early instar monarch larvae. Bixby et al. [32] showed that a liquid spore/toxin formulation of *Bt* japonensis, that is not commercially available, effectively controlled oriental beetle and Japanese beetle grubs, as well as Asiatic garden beetle and to a lesser extent, European chafer grubs in turf grass sites in Rhode Island. Given the large number of available toxins and the success of other *Bt* strains for managing non-scarab pests, the future development of scarab-specific *Bt* products is highly likely.

The potential for these *Bt* strains to produce epizootics under natural conditions is not well-documented. While epizootics have been recorded for several lepidopteran populations [20,21], none have been observed in scarab populations. The scarab-specific effects found for some *Bt* toxins have largely been discovered through laboratory surveys, rather than observable epizootics.

4.2. Paenibacillus popilliae/Paenibacillus lentimorbus (Milky Spore Disease)

Bacterial control of white grubs has a long history, as the first microbial pesticide registered in North America in 1948 was *P. popilliae*, otherwise known as milky spore disease, used to combat Japanese beetle [35,36]. This bacterium was first detected in New Jersey in 1933, and it became available commercially for use on turfgrass in 1948. Milky spore disease was used in a large-scale insect control program against Japanese beetle in the 1940s [7,37]. Isolates found in infected grubs from the field showed that milky spore disease resulted from a combination of two *Paenibacillus* species, *P. popilliae* and *P. lentimoribus* [19,37,38]. These species are known to infect several scarab species, including

Japanese beetle, masked chafer, and oriental beetle in the U.S. [39]. Spores exist in the soil and when ingested act very similarly to *Bt*, germinating in the midgut and eventually penetrating the gut epithelium. As the bacteria multiply in the hemocoel they give the abdomen a milky white appearance and disrupt larval development. Grubs eventually die from either starvation or septicemia but mortality may not occur for several months under field conditions [19,40].

A large-scale campaign to inoculate new areas with milky spore disease ran from 1939–1953 and was declared successful in suppressing of Japanese beetle populations [40–42]; however, subsequent issues with the large-scale production of milky spore disease have limited its effectiveness as a commercial product. The initial inoculum for the Japanese beetle control campaign were generated in vivo by grinding up infected beetles. Commercial outfits eventually claimed to develop a more cost-effective in vitro method, but issues with contamination quickly became apparent. Stahly and Klein [43] found that the commercial product Grub Attack was comprised, not containing P. popilliae, but rather *Bacillus polymyxa* and *B. amylolyticus*, which do not produce milky spore disease. Subsequent attempts to correct this issue relied on additions of in vivo-produced *P. popillae* but formulations were still largely contaminated with other bacterial species [40]. There is a general lack of data available on the relative effectiveness of in vivo and in vitro formulations of milky spore [40], but of the studies that have tested commercial formulations, both show low infectivity and efficacy across field trials [40,43]. Despite this, commercial formulations of milk spore disease are still available (Table 1).

Although milky spore is routinely found infecting Japanese beetle grub populations and is able to control grub densities in areas where it has been introduced or naturally spread [44] no accounts of natural epizootics have been recorded. Despite this, data show that milky spore can persist in the soil for decades [45,46] and attempts to inoculate new locations have led to successful establishment. Efforts to create epizootics in the field with artificial introductions, however, have been variable [38,45,47].

4.3. Serratia Species

Several *Serratia* species, a genus of non-spore-forming bacteria in the family Enterobacteriaceae, have been documented to infect several scarab species [48]. In 1981, two *Serratia* species were isolated from a declining population of New Zealand grass grubs (*C. zealandica*). *S. entomophila* and *S. proteamaculans* were implicated in producing amber disease in this population [49], which causes larvae to stop eating or producing digestive enzymes, giving the grubs a translucent coloration and eventually weakening them so that the bacteria can enter the hemocoel [19]. Grubs die from septicemia within months of infection [48,50]. Pathenogenic and non-pathenogenic strains of *S. entomophila* and *S. proteamaculans* are found in the field and is dependent on the presence of a specific plasmid that carries the sep and afp genes required for virulence [51]. While these two species appear to be exclusively toxic to *C. zealandica* and *Pyronota* species [52,53], other Serratia species are known to infect other scarabs. *S. marcescens* was isolated from May beetles in New Zealand (*M. melolontha*) [54], and several strains were isolated from May beetles in Mexico, showing differing degrees of toxicity [55]. A strain of *S. entomophila* was also cultured from a date palm scale (*Parlatoria blanchardi*) in Mexico and was found to cause significant mortality in intracoelomic inoculations and feeding trails with various *Phyllophaga* and *Anomala* species [56]. In the U.S., *Serratia* species have only been found in Japanese beetle and masked chafer grubs in Kentucky, albeit at low levels [57,58].

Serratia entomophila was developed as a commercial product in New Zealand in the 1980s. Despite high efficacy, the first incarnation, called Invade and produced by Monsanto, had a short shelf-life and required specialized application. Invade was eventually taken off the market [59], but in the early 2000s, a much more stable granular formulation, called Bioshield, was developed and is still currently available in New Zealand as a liquid formulation [59,60]. While there are no data available on the efficacy of Bioshield, lab studies

testing *S. marcescens* and *S. entomophila* strains from Mexico documented high mortality in May beetles (*P. blanchardi*) and leaf chafers (*A. donovani*) after oral inoculation [55,56].

The distribution of *Serratia* species in the U.S. is largely unknown, as is their ability to produce natural epizootics. However, studies from New Zealand show that field applications of commercially available *S. entomophila* readily create established populations [59,61]. In fact, Bioshield's documentation claims that *Serratia* populations may last 3 to 5 years after application. More work is needed to understand the ecology of *Serratia* species and their role as insect pathogens in the U.S., but given their ability to recycle in the soil, they may become a viable option for novel scarab biocontrol in the future. One potential drawback, is that some strains of *S. marcenscens* infect honey bees [62], which cautions that the selection of a scarab-specific *Serratia* species must be an important aspect of future product development to reduce non-target effects.

4.4. Rickettsiella Species

Rickettsiella is a Gram-negative bacterial genus, of which many different species infect coleopteran, dipteran, orthopteran and lepidopteran insects [19]. *Rickettsiella* is an intracellular pathogen that primarily targets the fat body. It proliferates within cytoplasmic vacuoles, eventually lysing the cell and moving into the hemolymph, which often gives the abdomen of infected larvae a bluish coloration. The bacteria weakens the larvae over time, making them sluggish, but death typically takes over a month to occur [19]. *Rickettsiella popilliae* is the most entomopathogenic species to scarabs and was isolated from June chafer (*A. solstitialis*) in Germany [63], the New Zealand grass grub (*C. zealandica*) [64], in New Zealand, *Odontria* species [64], and African black beetle (*Heteronychus arator*) [65] populations in New Zealand. Various *Rickettsiella* species also infect grasshoppers, aphids, wireworms, and ticks.

Despite its well-documented occurrence in natural systems, little research has been conducted on *Rickettsiella* as a biocontrol option for insect control. As a result, little is known about its infectivity or virulence. Natural epizootics involving *Rickettsiella*, however, have been documented in a New Zealand population of manuka beetles (*Pyronota setosa* and *P. festiva*) [66,67] and a German population of cockchafers (*Melolontha* species) [68]. *Rickettsiella* infections have also been documented in Japanese beetle and May beetle (*Phyllophage anxia*, and *P. ephilida*) larvae in Pennsylvania [69], Japanese beetle, European chafer, and Asiatic garden beetle in Connecticut [70], and masked chafer in California [71]. Although these instances show potential for *Rickettsiella* as a biocontrol agent for scarab pests, more work is needed to determine its efficacy.

4.5. Yersinia Species

Similar to *Serratia*, *Yersina* represents another genus from the Enterobacteriaceae family that has potential for scarab control. Additionally, isolated from the New Zealand grass grub, *Y. entomophaga* has been shown to infect the Tasmanian grass grub (*Acrossidius tasmaniae*), redheaded cockchafer (*Adoryphorus couloni*), African black beetle (*H. arator*), and chafer beetles (*Odontria* species) with high mortality [72,73]. *Y. entomophaga* utilizes a toxin complex encoded by five genes; two chitinases that likely degrade the peritrophic membrane and three protein subunits that bind to the gut epithelium [74]. This toxin complex is homologous to the *sep* genes found in *Serratia* and also those found in *Photorabdus* and *Xenorhabdus*, which are bacterial symbionts of entomopathogenic nematodes [75]. Although *Y. entomophaga* has not been tested against any scarab pests found in the U.S. and has not been developed for commercial use, this bacteria and its toxin complex appears to have a broader toxicity across scarab taxa than *Serratia* species [76], making it a viable option as a future microbial products. Despite this, no natural epizootics of *Yersinia* have been documented in scarab species.

5. Fungi

Entomopathogenic fungi are the most widely used microbes for insect control. Entomopathogenic fungi can be found in almost all fungal lineages, with the exception of Glomeromycota [77]. Entomopathogenic fungi can be found in the orders Hypocreales (*Beauveria*, *Metharizum*, *Isaria, Lecanicillium*), Entomophthorales, Onygenales (*Ascosphaera* species), and Neozygitales (*Entomophthoromycota*) [77]. Entomopathogenic fungi infect insects through spore attachment to the cuticle, where enzymatic and mechanical processes eventually allow germination inside the insect. The fungi then use the nutrients in insect tissues to grow and proliferate, killing their host. The ability of entomopathogenic fungi to infect a broad range of arthropod pests and to easily be mass-produced have led to the development of many commercial products (Table 1). Some genera contain species/strains that are species-specific, while others have broad insecticidal activity. Various species, including those from the genera *Beauveria*, *Metarhizium*, *Entomopthora*, *Lecanicillium* (formerly *Verticillium*), and *Isaria* (formerly *Paecilomyces*), have been isolated from different scarab species and documented in epizootics [42,78–84]. However, of these, *Beauveria bassiana* and *Metharizium anispoliae* dominate in soil systems, and as a result, are the most widely used for insect biocontrol (Table 1).

5.1. Beauveria Species

Strains of fungi in the *Beauveria* genus represent some of the most widely used microbial agents for insect control [85]. *Beauveria bassiana* is the most commonly used strain, and, in fact, was the first disease to be discovered in insects. It causes white muscardine disease, which almost destroyed the European silk industry in the 18th and 19th centuries when infection spread through captive silkworm (*Bombyx mori*) populations. *B. bassiana* is widely distributed globally and alone can infect more than 700 different insect species [86,87], including a variety of different scarab species all over the world. *B. brongniartii* is another common species but one with a much narrower host range that is largely restricted to scarabs [88,89]. Recently, six additional species of *Beauveria*, including: *B. majiangensis*, *B. malawiensis*, *B. scarabaeidicola*, *B. songmingensis*, *B. subscarabaeidicola*, *B. yunnanensis*, were discovered in scarabs collected throughout China and Thailand and were placed in a *B. scarabaeidicola* complex [90].

B. bassiana comprises about 34% of the commercially available mycoinsecticidal products worldwide [91]. There are currently four strains of *B. bassiana* registered with the U.S. Environmental Protection Agency (EPA), HF23, GHA, ANT-03, and PPRI 5339, corresponding to over 45 different registered products. Several other formulations are available globally [36,84]. Although *B. bassiana* is generally very effective, with most studies showing about 70% mortality at high spore concentrations within 2–3 weeks after application [92–95], its efficacy on scarab species is variable across strains and larval instars [95–100]. *B. brongniartii* appears to provide more consistent control of scarab pests than *B. bassiana* [101–106], but it is only commercially available in European markets [5,84]. Most of the species in the *B. scarabaeidicola* complex and have not yet been tested extensively; however, Wang et al. [90] did test these four of these species (*B. scarabaeidicola*, *B. subcarabaeidicola*, *B. songmingensis*, and *B. yunnanensis*) against the white-spotted flower chafer (*Protaetia brevitarsis*), and two non-scarabs, *B. mori* and *Tenebrio molitor.* Species from the *B. scarabaeidicola* complex did not infect *B. mori* or *T. molitor* larvae but did produce ~45% mortality in *P. brevitarsis* adults. Despite this, the mortality rates of species from the *B. bassiana* complex were much higher for *P. brevitarsis*.

Epizootics of *Beauveria* strains have been widely reported for different insect pests [107–110], including several scarab species [42,63,81,82,111]. Townsend et al. [111] documented two epizootics in the New Zealand grass grub, involving both *B. bassiana* and *B. brongiartii*, which resulted in 30% and 99% mortality. Experimental plots of *B. tenella* were also found to continually infect local larval populations of cockchafer across a four-year study in France [63]. Even in the absence of epizootics, there is considerable evidence that *Beauveria* can persists in the soil long-term, depending on formulation type, application

strategy, soil type, and field management [112–115] and may become infectious under the right abiotic conditions [116].

5.2. Metarhizium Species

Metarhizium anisopliae was first discovered in the cereal chafer (*Anisoplia austriaca*) by E. Metschnikoff in 1879 and was also the first putative fungi to be used as a biocontrol for insects in the 1880s [117]. It produces green muscardine disease and is documented to infect more than 200 insect species in agricultural and forest environments [118]. Many different species and/or strains of *Metarhizium* exist and exhibit insecticidal activity. *M. flavoviride* and *M. album* are two other species known to be broadly entomopathogenic [119–122]. For scarabs, *M. brunneum* was recently shown to infect Japanese beetle [123] and *M. anisopliae* var. *majus* is a strain associated with the rhinoceros beetle in the South Pacific [101].

Like *B. bassiana*, *Metarhizium* is easily cultured and is a popular microbial option for pest control, comprising a comparable share of the global mycoinsecticidal market, at about 34% [91]. In fact, *Metarhizium* is the most commonly introduced entomopathogen used for insect biocontrol [124]. There are currently two strains registered with the U.S. EPA, ESF1 and F52, which are available across seven registered products but many others are available globally [36,84]. For scarab species, studies show that *M. anisopliae* is broadly effective on several species [95–98,101,125–128]. Poprawski and Yule [95] reported 82–97% mortality of second and third instar June beetles after a soil application of *M. anisopliae*. Fernando et al. [129] reported 100% mortality of *O. rhinoceros* and Nong et al. [98] 100% of first-instar *A. corpulenta* larvae after treatment with *M. anisopliae*. Rodríguez-del-Bosque et al. [126] reported 96% mortality of *P. crinita* and *A. flavipennis* 10 days after exposure, and Morales-Rodriguez et al. [127] reported mortalities of greater than 70% for *A. majale*, *M. catanea*, and *A. orientalis*. *M. anisopliae* and *M. brunneum* is also highly effective on Japanese beetle grubs and adults [92,123,130].

Only a couple epizootics of *Metarhizium* have been documented, one for the large brown cicada (*Graptopsaltria nigrofuscata*) in Japan and one in the Chinese burrower bug (*Schiodtella formosana*) in China [131,132]. No *Metarhizium* epizootics have been reported in any scarab populations. Despite this, *Metarhizium* has been shown to persist in the soil, particularly in the rhizosphere, for years after application [133–137], bolstering its potential as an effective biocontrol agent.

5.3. Other Fungi

Lecanicillium lecanii (formerly *Verticillium lecanii*) infects several beetle species, however, only a few studies are published on its infectivity in scarabs. Saleem and Ibrahim [138] found that *L. lecanii* produced between 17.4–29.2% mortality in rhinoceros beetle larvae (*Oryctes agamemnon*) in Saudi Arabia, and a *L. lecanii* soil application was reported to cause 48–53% grub mortality for the sugarcane beetle (*Holotrichea consanguinea*) in India [139]. To our knowledge, *L. lecanii* has not been tested on any scarab species found in the U.S.

Isaria fumosoroseus (formerly *Paecilomyces fumosorosea*) has been isolated from the New Zealand grass grub [140] and cockchafer (*M. melolontha*) [78] and has been shown to cause larval mortality. However, while it is used for the control of some other beetle species, it has not been used for the biocontrol of any scarab species. Other fungi that have been isolated from scarabs but little-studied are *Entomophthora brahminae*, *Aspergillus flavus*, *Fusarium solani*, and *Rhizopus oryzae* [84,141,142]. Much more research is needed to determine their potential for scarab biocontrol.

5.4. Microsporidia

Microsporida are spore-forming unicellular parasites that were once classified as Protozoa but are now placed in the Fungi kingdom. Despite this, their biology and morphology are largely unlike most fungi. Microsporida persist in the environment as resistant spores, and once ingested by a host, the spore contents are inserted into gut epithelial cells through a polar filament. Vegetative growth occurs within the host cells and eventually infective

spores develop. Often times, spores will move to other parts of their host, as certain species are often associated with specific tissues [143,144]. Microsporida, as a phylum, infect a wide range of organisms, from protists to vertebrates, but are often species-specific [144,145]. Infection gradually wears down the host and death takes a long time to occur.

Several entomopathogenic microsporidia are known to infect coleopteran, dipteran, hymenopteran, lepidopteran, and orthopteran species around the world [146]; however, only one species, *Paranosema locustae*, is currently registered as a microbial pesticide for grasshoppers (Henry ad Oma, 1981). Only six microsporidian species have been documented to infect scarabs: *Nosema costelytrae* [147], *N. takapauensis* [147], and *Vavraia oncoperae* [148–151], found in the New Zealand grass grubs (*C. zealandica*), *Pleistophora tanzaniae* in coconut beetle (*Oryctes monoceros*) [152], *N. melolonthae* in the cockchafer (*Melolontha melolontha*), [153,154], and *Ovavesicula popilliae* in Japanese beetle [57,155–159]. The two *Nosema* species found in *C. zealandica* infect the fat body, causing developmental delays and larval mortality [147]. *V. onocoperae* infects muscle tissue but is also found in several other tissues, including the Malpighian tubules, gut caecae, nerves, and gonads; however, the pathology is not well-understood [147,160]. *P. tanzaniae* was infects midgut epithelial cells in the coconut beetle, but again, information about its transmission and pathology are lacking [152,160]. *O. popilliae* is the only microsporidian known to infect Japanese beetle and has been detected in populations throughout the U.S. but is most common in the Northeast and Midwest [159,161]. *O. popilliae* is multi-sporous species that infects the Malpighian tubules. When *O. popilliae* spores are ingested by larvae they infect midgut cells and eventually move to the hindgut, where they produces sporophorous vesicles that disrupt mineral reabsorption, waste-removal, and fluid balance. Spores are largely spread through frass. Larval infection increases overwintering mortality by as much as 100% [162] and reduces egg production by as much as 50% [157]. Research on *O. popilliae* has increased over the last decade, improving our understanding of its distribution and potential use as a biocontrol agent for Japanese beetle, which is the most damaging scarab pest in the U.S. The fact that microsporidia must be produced in vivo, limits its potential for commercial formulations. They also slow-acting. Due to these factors, microsporidia are most appropriate for long-term biocontrol in areas where species can become established in the soil.

Nosema species have also been implicated in natural epizootics in grass grub and locut populations [150,163]. For scarabs, natural epizootics of *O. popilliae* have been reported to diminish local populations [164]. Although spores of some *Nosema* species can persist for ~300 days under optimal temperature conditions [165], spores generally do not do well outside of hosts. As a result, horizontal and vertical transmission are key to the persistence of microsporidia. The inoculative release of *Nosema portugal* to control spongy moth (*Lymantria dispar*), formerly gypsy moth, was reported to persist in the population for ~1 year due to vertical and horizontal transmission [166]. *N. locustae* and *Perezia dichroplusae* have also been consistently documented in the same Argentinian grasshopper populations for nine years in some cases [163]. For scarab control, artificial inoculations of *O. popilliae* have led to successful establishment in new areas that provide continuous control of Japanese beetle [156,157,162]. These examples show that microsporidia have the potential to persist locally and can create epizootics under the right conditions, making them great candidates for long-term biocontrol programs.

6. Protozoa

Protozoans are single-celled eukaryotes from a subkingdom of Protista. Over 50,000 species of protozoa are described, and while most are free-living, many are parasitic [167]. Several types of protozoa are known to infect insects; however, this group of microbes is by far the least studied and developed as biocontrol agents. Most protozoa are species-specific but rather slow-acting, conferring either larval mortality in early instar infections or reduced reproductive output through chronic infections [160,168]. Although little is known about their ecology, persistent establishment in host populations

is likely possible, as they are transmitted through the ingestion of oocysts or spores. A major drawback to their development as biocontrol agents is our lack of information about their biology/ecology and thus, how to culture them, but in vivo methods would likely be required. Nonetheless, their ubiquity in natural scarab populations makes them an interesting potential option for long-term localized biocontrol programs.

6.1. Eucoccidiorida

Eucoccidiorida is a protozoan order in the phylum Apicomplexa, which contains several important human parasites, such as *Toxoplasma gondii*. *Adelina* is the most common entomopathogenic genera in Eucoccidiorida, which infects coleopteran, dipteran, collembolan, embiopteran, lepidopteran, and orthopteran hosts, including several scarab species. *Adelina melolonthae* has been found in cockchafer beetle (*M. melolontha*) in France [154,169–173] and Turkey [174], *A. sericesthis* found in pruinose scarab (*Sericesthis pruinose*), *M. hippocastani* and *Aphodius howitti* [175,176], *A. tenebrionis* in African black beetle (*H. arator*) and the large sand scarab beetle (*Pericoptus truncates*) [65,177–179], and an unidentified *Adelina* species found in European rose chafer (*Cetonia aurata*), Asiatic garden beetle, European chafer, Northern masked chafer (*C. borealis*), and Japanese beetle [70,158,180]. *Klossia* is another genus known to contain entomopathogenic species. *Klossia aphodii* has been found in *Aphodius fimetarius* and *A. contaminates* in Sweden [181]. In all cases, the coccidia infected the fat body and were found to increase larval mortality or reduce adult fecundity in late-instar infections [160].

Epizootics of *Adelina* species have been reported in the confused flour beetle (*Tribolium confusum*) and the wax moth (*Galleria mellonella*) [182–184] but no incidences have been documented in scarab populations. Our limited knowledge about the biology and pathogenicity of these species are an obstacle their development as biocontrol agents. Most work has been focused on stored grain pests, such as *Tribolium* species [185,186] but much more work will be needed to determine their potential role as biocontrol agents for scarabs.

6.2. Gregarinasina

Gregarines, sub-class Gregarinasina, are Apicomplexan protozoa that live as gut parasites of invertebrates, particularly arthropods and annelids. It is not uncommon for an insect to be infected by multiple gregarine species. Approximately 500,000 gregarine species are estimated to infect coleopteran hosts alone [187]. Gregarines exist in the environment as oocysts and are typically ingested by their hosts. The parasites grow in host intestinal epithelial cells and are released back into the environment as gametocysts, typically in the feces of the host, where they undergo gametogenesis and fusion to create zygotes that eventually develop into new oocysts. The two orders that are most relevant as scarab parasites are the Eugregarines and the Neogregarines.

Eugregarines are the largest and most diverse order of gregarines, encompassing 27 families and at least 240 genera [188]. They routinely infect insects hosts and are the most common protozoa found in scarab species, where infection is typically associated with a reduction in fat reserves and failure of larvae to pupate [160]. *Euspora* species have been documented to infect New Zealand grass grub (*E. zealandica*) and cockchafer (*E. fallax*) [189,190]. *Stictospora* species infect a wide range of grubs, including Japanese beetle, New Zealand grass grub (*S. costelytrae*), *Oryctes* species (*S. kurdistana*), *Rhizotrogus* and *Melolontha* species (*S. provincialis*) [156–158,169,189] and typically at high rates [57,156,191]. Cappaert and Smitley [156] found *Strictospora* in 36.1% of all Japanese beetle grubs collected in a Michigan study, making it the most common parasite found. Hanula and Andreadis [70] also reported that 50–100% of Japanese beetle grubs collected in a Connecticut sample contained, what was believed to be, *Strictospora* [70]. An *Actinocephalus* species and an unidentified gregarine have also been documented in Japanese beetle [192], while other undescribed gregarines have been found in Asiatic garden beetle, oriental beetle, rose chafer (*Macrodactylus subspinosa*), and Northern masked chafer [70]. *Didymophes* species are found in *Geotrupe stercorarius*, *G. pyrenaeus* (*D. paradoxa*), dung beetle (*Sisyphus schaefferi*) and European rose chafer (*Cetonia* species) (*D. sisyphi*) [193], while *Monocystis* and

Pseudomonocystis hopliae are found in both cockchafer (*M. melolontha*) and monkey beetle (*Hoplia* species) [177,194,195].

Neogregarinida is another gregarine order known to infect insect hosts. They have been studied most extensively in the boll weevil (*Anthonomus grandis*) and the khapra beetle [196–198]. Of the 13 genera, only three are documented to infect scarabs [160]. The first is *Ophryocystis oryctesi*, which was been found in rhinoceros beetle (*O. monoceros*) in Tanzania, where it infects the Malpighian tubules, causing hypertrophy and damage [199]. The other are species of the genus *Mattesia*, known to infect the New Zealand grass grub (*C. zealandica*). These protozoa infect the fat body and can cause weight loss and larval mortality [200,201]. *Aranciocystis mukarensis* was also found infecting cereal chafer (*Anisoplia segetum*) in Turky [202]. Both species are transmitted by the ingestion of oocytes [160]. The potential use of neogregarines as biocontrol agents has been studied a little more extensively than the eugregarines, but this work is still in the early stages and not currently focused on any scarab species [203].

Although gregarines are commonly found infecting insect hosts, they're impacts on host survival and/or performance is usually limited and/or very slow-acting [204]. Due to this, epizootics are rarely observed, despite gregarines being persistent in insect populations. This low efficacy, along with a serious lack of information about host range and pathology, has limited the development of gregarines for insect biocontrol. However, given their ubiquity, future development is probative, and they may be particularly useful when combined with other microbial agents.

7. Nematodes

Entomopathogenic nematodes (EPN) are roundworms that live in the soil and are obligate parasites of insect hosts. Despite the existence of over 14,000 known species of nematodes, only two genera, *Steinernema* and *Heterorhabditis*, comprising ~120 species, are used for insect biocontrol. Many species of *Steinernema* and *Heterorhabdits* naturally occur globally. Both genera associate with bacterial symbionts, *Steinernema* with *Xenorhabdus* and *Heterorhabditis* with *Photorhabdus*, that assist the nematodes in sequestering their host by producing toxins that kill the insect and inhibit other bacteria from utilizing the cadaver [205].

EPNs are an excellent option for insect biocontrol, as they are non-toxic to humans, and therefore not regulated by the U.S. Environmental Protection Agency (EPA). Most can be mass-produced and applied with common pesticide equipment. They can also be used therapeutically, as they can kill their hosts within days of infection [205,206]. In natural systems, the most widespread EPN species infecting white grubs are *S. carpocapase*, *S. feltiae*, *S. glaseri*, *H. bacteriophora*, and *H. megidis*; however, studies reporting EPN distribution are limited and often not randomly sampled [207,208]. *S. carpocapsae*, *S. feltiae*, and *H. bacteriophora* are generalist species but only *H. bacteriophora* has been documented to infect white grubs to any extent under natural conditions [207]. *S. glaseri* and *H. megidis* appear to have close natural associations with scarabs, and it is hypothesized that the less well-known *S. anomoli* and *S. kushidai* species may also be scarab-specialists [207,209]. Despite these natural associations, other EPNs have been tested on different white grub species under field and lab conditions [210,211]. Table 3 shows summaries of these studies, indicating which EPN species have been tested on scarab species and whether the results showed high or low efficacy. Across field studies, *H. bacteriophora*, *S. scarabaei*, and *S. carpocapsae* show the broadest efficacy for scarab species. In the lab, results were more mixed for *H. bacteriophora*, while *S. scarabaei* maintained high efficacy (Table 3). Differences between field and lab results are likely due to many environmental factors but also to differences in methodology and the nematode concentrations tested.

Table 3. Effectiveness of nematodes species tested on different scarab hosts found in the U.S. in field and greenhouse (pot) studies. (x) indicates that greater than 50% larval mortality was found across studies, (-) indicates that less 50% mortality was documented across studies, and (x-) indicate that results were mixed. Scarabs tested include: *Phyllophaga* species (PH), *Cyclocephala* species (CL), *Ataenius spretulus* (AT), *Aphodius* species (AP), *Cotinis nitida* (CT), *Popillia japonica* (PJ), *Anomala orientalis* (AO), *Amphimallon majalis* (AM), and *Maladera castanea* (MC).

Nematode Species	Field Effectiveness									Pot Effectiveness								
	PH	CL	AT	AP	CT	PJ	AO	AM	MC	PH	CL	AT	AP	CT	PJ	AO	AM	MC
Heterorhabditidae																		
H. bacteriophora	x	x		x		x	x	-	-	x	x	x		x-	x	x-	-	-
H. zealandica		x				x				-	x				x			
H. megidis	-			-						x	x				-	-		
H. marelatus											-				-			
H. heliothidis																		
H. indica						-				x	-				-			
Steinernematidae																		
S. glaseri		-	-			x	x	-		x	x	x		x-	x	x	-	-
S. scarabaei	x	x				x	x	x	x	x	x	x		-	x	x	x	x
S. carpocapsae	x		x			x	x			-	-			x				
S. arenarium						-												
S. kushidai		x				x					x				-	x		-
S. feltiae	x					-				x	-			-		-		
S. longicaudum							x											
S. krausei		x				-												
S. riobrave						-					-							

Across the range of existing EPN species, *H. bacteriophora*, *S. carpocapsae*, *S. feltiae* are the most widely available commercial EPNs, followed by *S. kraussei*, and *S. glaseri* (Table 1). Surprisingly, *S. scarabaei*, which shows the most consistent infectivity on white grub species across studies, is only currently available in one product, Nemgard (Table 1). Although some white grub species have developed barriers to EPN infection [212], Japanese beetle, which is the most problematic species in the U.S., appears to be highly susceptible to EPNs [212,213]. Overall, studies have shown that under the right conditions, EPN can control white grub populations as effectively as conventional insecticides [214–216]. However, results vary considerably across environments. Soil temperature, texture, and oxygen levels impact EPN activity and viability, while pH and salinity appear to be less important [217–219]. Selecting the appropriate EPN species for white grub control is also important, as different species employ foraging strategies that are optimized for pest occurring above-ground, at the surface, and below-ground. The timing of application is key, as grub instar also strongly impacts pathogenicity, with EPN effectiveness being better on early versus late instars [220,221]. Despite being a fast-acting, biorational option, EPNs continually constitute a small share of the biopesticide market [222]. Their short shelf life, cost, and requirement for technical knowledge in selecting and applying different strains are likely impediments to market expansion. Combining EPNs with other control tactics has been shown to be effective (see Synergistic Interactions section) which may increase their popularity in the future.

As mentioned, epizootics have been reported but data on natural infections are very limited. Peters [207] reviewed reports of natural EPN infections that ranged from persistently stable with moderate infection rates to epizootics that resulted in negative density-dependent impacts on the host population. Of the documented reports, only two involved scarabs; the garden chafer (*Phyllopertha horticola*) (Smits, 1994) in the Netherlands and a *Lepidiota* complex [223] in Germany. Both occurred on sugarcane and involved *Heterorhabditis* species that caused 70–80% infection rates.

Nematodes can persistent for years after application but usually do so at low levels unless hosts are continually present [224]. Many abiotic factors, such as temperature, moisture, and soil type, as well as biotic factors, can limit persistence [221,225,226]. Due to this, the use of entomopathogenic nematodes as biocontrol agents would likely require multiple applications.

8. Viruses

Insect viruses are obligate intracellular parasites. They are quite ubiquitous, with over 1100 documented viruses known to infect insects from over 20 different families [227]. These viruses encompass several different families of RNA and DNA viruses. Entomopathogenic RNA viruses include cypovirus, dictstrovirus, nodavirus, and tetravirus, while DNA viruses include densovirus, entomopoxvirus, ascovirus, iridovirus, nudivirus, hytroavirus, iflaviruses, and baculovirus. Of these, baculoviruses are the most widely used for insect biocontrol. Epizootics of insect viruses are quite common. Many, but not all, insect viruses are surrounded by a crystalline protein matrix, called an occlusion body that protects the virons outside of the host. This allows these viruses to persist in the environment and be taken up by new insect hosts [228]. Viruses typically enter insect hosts through the gut, where occlusion bodies dissolve, releasing the virons into the midgut. The virons then infect gut epithelial cells, proliferate, and spread to other cells and tissues as secondary infections [229]. Most insect viruses are very species-specific and, as a result, safe for humans and other non-target species. They are also fast-acting, exhibit high infectivity, and are high lethality, making them great biocontrol options for insect pests.

The use of entomopathogenic viruses for biocontrol has been studied since the 1940s. The susceptibility of various insect species to baculoviruses, specifically nucleopolyhedroviruses and granuloviruses, has resulted in the registration of several commercial products. Although several viruses have been registered as biopesticides, the vast majority target lepidopteran, hymenopteran, and orthopteran taxa, and no commercial products are currently available for scarab pests [35,36,168]. Despite this, some scarab-specific viruses have been discovered that show great potential for future development.

8.1. Oryctes Nudivirus

The *Oryctes* virus (*Rhadionvirus oryctes*; OrNV) is a rod-shaped non-occluded virus in the family of Nudiviruses, which are closely related to baculoviruses [229]. In one of the most successful examples of viral biocontrol, OrNV was used against the rhinoceros beetle (*O. monocerus*), a scarab species that infests coconuts and other palms throughout the South Pacific [35]. In the Palau Islands, rhinoceros beetle infestations were reported to have destroyed as many as 50% of coconut palms in 10 years after introduction [230,231]. The discovery and use of the OrNV has provided the only effective control option for growers in these areas. The virus was initially found in infected grubs from oil palms in Malaysia [232] and adult inoculation programs were carried out in 10 India-Pacific Island nations throughout the 1970s. Early inoculation trials with grubs quickly determined that adults were highly susceptible, averaging a 40% infection rate, and able to spread the virus quickly and effectively to new areas [35,231].

OrNV has been found to infect several other scarab species, including *H. arator*, *C. zealandica*, *Adoryphorus coulina*, and *Pericoptus* species, but no non-scarab insects [233]. After ingestion, the virus initially infects midgut epithelial cells but largely proliferates in the fat body. Days after infection, grubs stop eating, their abdomen becomes turbid and distended, and they display severe diarrhea. The virus is spread effectively through contact with infected feces. Mortality occurs between 6 to 30 days post-infection [231,232].

The OrNV is effective in producing epizootics and reducing local populations. In fact, the success of the biocontrol programs in the South Pacific is largely due to OrNVs ability persist and recycle locally, which has reduced the need for additional financial inputs into the program. In 2012, an OrNV strain was implicated in an epizootic in Japanese rhinoceros beetle (*Allomyrina dichotoma*) populations throughout Korea. It was presumably introduced

to the area, though its source has not been identified [234]. Although local inoculations are still performed in the South Pacific, OrNV is not commercially available for insect control.

8.2. Iridescent Virus

Named for the characteristic blue hue seen in host cells, iridescent virus (IV) is a non-occluded isoahedral virus that has been documented to infect a range of arthropod taxa, including insects of the orders Diptera, Coleoptera, and Lepidoptera [235,236]. IV has a broad host range, and even the same type of IV is capable of infecting different species [237]. IV is also capable of infecting insects during all life stages. Various types of IV have been documented in scarab pests, including pruinose scarab (*Sericesthis pruinose*) in Australia [238], the New Zealand grass grub (*C. zealandica*) [64], African black beetle (*H. arator*) in South Africa [65,239], and May beetle (*Phyllophaga anxia*) in Canada [95] and Puerto Rico (*Phyllophaga vandinei*) [240], as well as an introduced population of Japanese beetle in the Azores [92]. IV has not been documented in any scarab species in the U.S. The virus can be fast-acting under laboratory condition, with mortality occurring within a week of infection, but it appears to exhibit very low infectivity rates in the field [95,241]. Jenkins et al. [240] reported mortality rates of only 30% in artificially infected May beetle larvae but did observe effective transmission from infected to uninfected individuals. Though not a scarab species, McLaughlin et al. [197] reported greater than 60% mortality of adult boll weevils fed a *Chilo*-derived IV. They also reported persistence of infectivity across 5 days when the virus was mixed with a bait formulation and sprayed onto cotton leaves. Although IV is not available in any commercial formulation, largely due to its instability outside of a host, it may have future potential in biocontrol programs, particularly those utilizing pathogen vectors such as parasitoids or nematodes. Certain IV types have been shown to infect insect cell lines, including that of the scarab *Anomala costata* [242], which will be useful for future research in the development of these viruses for biocontrol. Epizootics of IV have been reported in several non-scarab hosts, including corn earworm (*Helicoverpa zea*), blackfly (*Simulium*), velvetbean caterpillar (*Anticarsia gemmatalis*), and the mole cricket (*Scapteriscus borellii*) [237,243]. Despite being found in many scarab species, no incidences of epizootics in scarab populations have been reported.

8.3. Entomopoxvirus

Entomopoxviruses (EPV) are a subfamily of Poxviridae, which includes several important vertebrate viruses, such as smallpox. EPVs are occluded DNA viruses that replicate in the cytoplasm and consist of three genera, containing 31 different species. EPVs have been found to infect several coleopteran, lepidopteran, orthopteran, and dipteran species, including several scarabs [235,244]. In fact, *Vagioavirus*, a type of EPV, was first discovered in cockchafer beetles (*M. melolontha*) in France by Vago [245], and subsequently by Weiser [246]. A similar virus was later discovered in *Othnonius batesi* in Australia [247,248] and in two other Australian scarab populations, cane beetle (*Dermolepida albohirtum*) and *Aphodius tasmaniae* [249]. This EPV has most recently been found in rose beetle (*Adoretus versutus*) in Fiji [250] and in a cockchafer (*M. melolonthae*) population in Turkey [251]. Thus far, EPVs have not been found in any scarab species in the U.S.

While the potential of EPVs as viable biocontrol options is still in development, they have many characteristics that make them good candidates. EPVs have been found to be infectious at all insect life stages [236], and while the infection period of EPVs can be quite long, at upwards of 40 weeks [236], a strain found in Turkey was particularly virulent, causing mortality as quickly at 15 days after infection [251]. Some evidence suggests that long-term inoculation is achievable, as Hurpin and Robert [194] found that *Vagoiarvirus* could become established in field plots by introducing artificially infected larvae. However, much more work is needed to identify EPVs present in U.S. scarab populations and to develop techniques for efficient inoculation, which may involve the use of vectors such as parasitoids or nematodes. Some EPVs are able to replicate in insect cell lines [252], making future research on these viruses more feasible.

Although EPVs have been isolated from a range of different insect species, epizootics of EPV are rare and have only been reported in winter websworm (*Ocnogyna baetica*) in Spain [253], a midge population (*Chironomus decorus*) in California [254], and rose beetles (*Adoretus versutus*) in Fiji [250]. As EPV is not commercially available there is limited information on its ability to persist in field populations. However, Hurpin and Robert [154] found consistent EPV infection rates and control of cockchafer grubs in plots over a four-year period, suggesting that EPV infections may persist for long periods.

9. Synergistic Interactions

Given that most microbial controls are slower-acting than curative chemical options, many studies have explored the possibility of combining different microbes to improve infectivity, mortality, and/or mortality rate. Combining the use of nematodes, which are more mobile, with bacterial and fungal options can increase microbial contact with hosts and infectivity, while other combinations might simply weaken the host faster, leading to faster mortality rates. Few studies have looked at interactions between bacteria and fungi. However, in a lab experiment, Glare [255] found that dual exposure of New Zealand grass grub larvae (*C. zealandica*) to *M. anisopliae* and *S. entomophila* resulted in synergistic negative effects on larval mortality. Importantly, the dual treatment was not impacted by larval instar, while the single exposure treatments were. Given that larval instar strongly impacts the efficacy of most microbial pathogens, this result highlights how dual treatments may overcome some of the common obstacles found for microbial insecticides.

Far more research has been performed on nematode-bacteria and nematode-fungi combinations and their impacts on scarab pests. Thurston et al. [256] found that dual infection with *B. popilliae* bacteria and the nematode *H. bacteriophora* increased the nematodes' ability to penetrate the midgut in of masked chafer larval hosts, greatly increasing the subsequent number infective juveniles emerging from *B. popilliae*-infected cadavers. However, in a subsequent pot trail, Thurston et al. [257] showed that *B. popilliae*-nematode combinations only resulted in increased grub mortality when *S. glaseri* was used, not *H. bacteriophora*. This suggests that dual treatments of *B. popilliae* and *S. glaseri* may increase grub mortality in the field but also that pre-treatment with bacterial pathogens may improve the ability of other nematode species to become established by improving host utilization.

Another pot study with *C. hirta* and *C. pasadenae* showed that dual exposure to *B. thuringiensis japonensis* (Buibui strain) and either *H. bacteriophora* or *S. glaseri* resulted in additive and synergistic effects on grub mortality [258]. No interactions were found for *S. kushidai* and larvae had to be exposed to *B. thuringiensis japonensis* for at least 7 days before nematode inoculation. Another study on the oriental beetle (*A. orientalis*) also showed synergistic effects of *B. thuringiensis japonensis*-*S. glaseri* dual treatment [259]. While *H. bacteriophora* and *S. glaseri* are easy to find, unfortunately *B. thuringiensis japonensis* is not currently commercially available in the U.S.

Wu et al. [260] tested interactions between the entomopathogenic fungi, *B. beauveria* and *M. anisopliae*, with two nematode species, *H. megidis* and *H. bacteriophora*, on the southern masked chafer (*C. lurida*) under lab and greenhouse conditions. In the lab, neither fungus had an impact on grub mortality alone, but when applied in combination with nematodes, they found additive or synergistic effects in all *M. anisopliae*-nematode combinations and mostly additive effects in all *B. beauveria*-nematode combinations. In the greenhouse, additive/synergistic effects were found for *M. anisopliae*-nematode combinations but only some *B. beauveria*-nematode formulations. In fact, the control seen in some combinations was comparable to that of imidacloprid application. Nematode infection rate and/or infective juvenile production, however, was not impacted, suggesting that, unlike bacteria, fungi do not facilitate nematode infection.

M. anisopliae was also found to increase monkey beetle (*H. philanthus*) grub mortality in lab and greenhouse experiments when combined with either *H. megidis* or *S. glaseri* [261]. Effects were additive or synergistic, and longer incubation periods with *M. anisopliae* enhanced effects. Again, combinations appeared to have no effect on nematode reproduction,

suggesting that increases in mortality were due to a weakening of the host rather than increased infectivity. A subsequent field trial with a *M. anisopliae* and *H. bacteriophora* combinations in turf also showed additive/synergistic effects, producing 95% grub mortality at a 4-week nematode application interval, which was comparable to a tested chlorpyrifos treatment [262]. It has also recently been shown that nematodes can help to disseminate bacterial for fungal entomopathogens in the soil. Nermut et al. [263] showed that *S. feltiae* and *H. bacteriophora* were capable of the moving the fungus *I. fumosorosea* across different substrates.

Some studies have also shown synergistic interactions between nematodes and chemical insecticides, such as chlorpyrifos, imidacloprid, and diazinon [264–266]. While this may be a good option in agricultural applications, incorporating chemical controls into biocontrol programs, even at low concentrations, puts non-target organisms at risk, and counteracts a primary objective of biocontrol.

The use of entomopathogens can also be combined with other non-microbial control tactics to increase effectiveness. For instance, several studies have found that combining diatomaceous earth with *M. anisopliae* and *B. beauveria* treatments increase mortality for stored grain pests [267–269]. While no studies have been carried out on scrab pests, these combinations would likely be effective on white grubs, as diatomaceous earth can be easily incorporated to soil. Insect growth regulators have also been used to slow insect development, reducing cuticle shed and increasing the infectivity of entomopathogenic fungi [270,271]. Again, more work is needed to determine whether this combination would work for scarab pests, but the growth regulator halofenozide is effective on Japanese beetle, European chafer, and oriental beetle [272,273].

Indirect interactions between entomopathogens and natural enemies can also augment control [274]. The presence of predators or parasitoids can affect host movement patterns in ways that increase the dispersal of pathogens, and this has been demonstrated in several systems [274–276]. Natural enemies other organisms, such as earthworms, can also move viruses [277–282], bacteria, fungi [283–286], and nematodes [287–289] throughout their environment on their cuticle or as vectors. Unfortunately, little research has been conducted on the potential impacts of non-host vectors in creating epizootics in scarab populations or in underground soil systems.

10. Future Advancements

The management of insect pests through biocontrol is an incredibly complicated endeavor. It not only requires a thorough understanding of the pest and its potential pathogens, but also how other ecosystem factors affect the host, the pathogen, and host-pathogen interactions; a level of understanding is often lacking for microbial entomopathogens, as their life cycles and pathologies are complex and often difficult to study. This is reflected in the many limitations that microbial pesticides possess, particularly when compared to chemical controls. Many are slow-acting, environmentally unstable, and exhibit variable efficacy. However, new technologies may be able to overcome some of these obstacles by improving their spread, infectivity, reliability, and persistence in the environment. While many of these technologies are still in the developmental phase, they show great promise for future formulations.

10.1. Paenibacillus

Genetic engineering of pathogens provides an opportunity to increase lethality, by creating strains that are hyper-pathogenic [290]. This can be accomplished by inserting genes for toxins, hormones, or enzymes, often sourced from other taxa, that increase pathogen kill time. Genes encoding toxins found in mites, scorpions, spiders, and sea anemones have all been engineered into baculoviruses and tested on a range of insect pests [291,292]. Toxins from scorpions, spiders, and sea slugs have also been introduced into recombinant fungi, yielding up to a 22-fold decrease in lethal dose [293–295]. The homologous toxin complex found in *Serratia* and *Photorhabdus*, which consists of a plasmid

carrying the *sep*ABC genes responsible for the symptoms of amber disease, have also been engineered into other bacteria and shown to increase insect mortality [76].

Cell signaling molecules and hormone genes, including diuretic, prothoracicotropic, and eclosion hormones [296–298], have been inserted into baculoviruses to increase insect killing speed. Many of these genes have also been engineered into fungi, such as *B. bassiana,* to improve insecticidal activity [299–301]. RNA interference was used to increase the pathogenicity of a strain of *I. fumosorosea* by inserting the sequence for a dsRNA that successful knocked down an immunity gene in infected whitefly nymphs [302]. Genes encoding enzymes, such as juvenile hormone esterases, chitinases, and proteases, have also been engineered into entomopathogens. Chitinase gene insertions into *Trichoderma konigii* from *M. anisopliae* increased the mortality of Asian corn borer and silkworm [303]. The insertion of chitinase and protease genes from the silkworm (*Bombyx mori*) into *B. bassiana* has been reported to improve cuticle penetration [304–306].

Additionally, genes providing tolerance to environmental factors have also been introduced into fungi [307] and to a lesser extent, entomopathogenic nematodes, to increase their stability in the environment. Photolyase and thioredoxin genes from bacteria have been engineered into *B. bassiana* and *M. robertsi* to improve UV tolerance and reduce the damage caused by UV radiation, making the recombinant fungi more stable in sunny environments [308,309]. Similarly, a recombinant strain of *S. feltiae* was engineered to be more osmo- and desiccation-tolerant by introducing a heat shock gene from *Caenorhabditis elegans* [310].

The expression of existing and introduced genes can also be modulated through the insertion of different promoters to increase or decrease gene expression [291,292]. This has been carried out to increase chitinase, trehalase, and protease expression in *B. bassiana* and *Metarhizium* species [311–314]. Expression of superoxide dismutase has also been overexpressed in *B. bassiana* to improve UV tolerance [315]. Alternatively, genes involved in delaying host mortality in viruses can also be deleted. O'Reilly and Miller [316] successfully deleted the *egt* gene in a recombinant baculovirus (AcMNPV), which reduced feeding behavior in the infected host and decreased the time to mortality.

10.2. Microbial Formulations

Several advancements are being made to improve the shelf life and stability of entomopathogens in field. While fungi and bacteria are available as sprayable powders with long shelf-lives, once they are in aqueous solution and distributed in the field, their bioactivity can be reduced by environmental degradation. Although it is perhaps less relevant for soil-dwelling microbes, UV radiation is probably the most damaging environmental factor to entomopathogens. Suspending conidia in various substances, including different oils [317,318] and sunscreens [319–323] are effective for UV protection [324]. In fact, oil dispersions are the most common-used formulations for fungal biocontrol products [91]. Coating conidia with lignin and cross-linking the molecules with $CaCl_2$ to increase solubility has also been effective in reducing spore loss in the field [325]. For viruses, several plant extracts [326], optical brighteners [327], and encapsulation with particles from gas-saturated solutions (PGSS) [328] have been shown to protect baculoviruses from UV degradation.

10.3. Delivery Systems

A major issue with using entomopathogens for biocontrol in soil systems is the ability of the pathogens to effectively disperse throughout the soil and make contact with target hosts. Entomopathogenic fungi must penetrate the insect cuticle at high concentrations to cause mortality and this requires a homogenous distribution and high concentration of conidia in the soil. For this reason, granular formulations, which consist of conidia-packed granules that can easily be mixed into soil, are preferable. Most fungal products consist of conidia and spores, but certain fungi, including *Metarhizium* species, are also able to produce microsclerotia, which is a more resistant fungal stage that is less susceptible to environmental stressors and the presence of fungicides [329–331]. This increases their

storage capacity, stability in the environment, and use in systems that require fungicide applications. It also increases their ability to be produced as granular formulations or seedcoats, which increase their infectivity in the field [332–334]. Recently, a method for producing microsclerotia of *B. bassiana* has also been developed [335].

One of the most efficient ways to disperse entomopathogens is to let the insects do it themselves. This is particularly helpful when populations are patchy, their habitats are not well-known or are difficult to treat, such as soil systems. The simple, yet effective, method of autodissemination has been useful for distributing insecticides [336,337], growth regulators [338–340], and microbes [341–345] for a range of insect pest species. For entomopathogens, autodissemination can increase individual mortality by improving pathogen contact with hosts, but it can also increase population-level infection rates through the transmission of pathogens between individuals, creating the potential for localized epizootics to occur. Autodissemination systems typically use some kind of attractant to lure adult insects into a trap where they are exposed to a microbial formulation. Adults then disperse, distributing the pathogen to feeding and mating sites, either as infected vectors or by carrying the microbes on their cuticle. Autodissemination systems have been tested on Japanese beetle, using commercial formulations of *M. anisopliae* and *M. brunneum* [346,347]. In the Benvenuti et al. [347] study, the traps increased the mortality of individual beetles that were directly exposed but also beetles that mated with infected individuals. These traps have also been found effective for infecting *Oryctes* species with *M. anisopliae*, with one study showing 66.7% mortality of trapped beetles, but more importantly, 91% larval mortality in areas where the beetles transferred to spores to breeding sites [348,349]. *Metarhizium* autodissemination traps have also been effective on sorghum chafer (*Pachnoda interrupta*) popluations in Ethiopia [350,351]. Although baculoviruses have been successfully used in autodissemination traps for lepidopterans [60,341,352,353], they have not been attempted with scarab-specific viruses. The autodissemination of entomopathogenic nematodes has also been proposed for Japanese beetle [354] but has yet to be tested. To our knowledge, no microsporidan species have been tested in autodissemination traps.

Nanoparticles also offer tremendous potential for increasing the distribution and infectivity of entomopathogens. Nanoparticles made from *B. thuringiensis* culture have been shown to be more virulent [355,356], and while the association of fungal spores/conidia with nanoparticles is less developed, nanoparticles containing *B. bassiana* and *M. anispoliae* have been created [357]. Nanoparticles of *Nomuraea rileyi* have been shown to increase virulence against the potato tuber moth under lab and field conditions [358]. Double-stranded DNA and dsRNA have also been used in conjunction with nanoparticles to create non-viral gene delivery systems in insects [359–361]. These are particularly useful for insects lacking SID-1 proteins, which limit systemic RNA interference. Nanotechnology has perhaps been most successful in creating nanoparticles made of fungi-produced insecticidal compounds, such as silver [362–364], various metal sulfides [365], titanium dioxide [366], and chitosan [367].

Lastly, advances in the use of non-host vectors to increase the transmission of bacterial and viral entomopathogens is also a promising option; however, it is one of the least developed delivery methods. Muttis et al. [368] documented the transmission of IV to mosquito larvae via the nematode *Strelkovimermis spiculatus*, with the viral particles not infecting the nematode but rather sticking to its cuticle. The use of endophytic or entomopathogenic fungi as vectors of insect viruses is another potential mechanism. Liu et al. [369] demonstrated that a fungal DNA virus could be transferred to a mycophagous insect and transmitted transovarially; however, to our knowledge, this is the only study that has been conducted on using entomopathogenic fungi to transmit insect viruses. As mentioned earlier, the ability of parasitoids to vector insect viruses is well-established and represents another option for increasing pathogen dispersal but has not been explored for scarab pests. There is also potential for using autodissemination traps to attract and inoculate non-vector hosts that associate with pest species as a way to increase the spread of a pathogen and/or its contract with target hosts.

11. Conclusions

Under the shadow of chemical controls, microbial pesticides have largely been viewed as less-effective alternatives. They are often slower-acting, less efficacious, and less predictable than chemical insecticides. However, as the negative impacts of synthetic chemicals continue to outweigh their conveniences, interest in microbial options is increasing. Due to this, advances in the development of microbes for insect biocontrol are occurring at an unprecedented rate. New formulations are making microbial options more effective and easier to use, while also capitalizing the inherent advantages they have over chemical controls. Table 4 summarizes some key characteristics of the microbial options discussed in this review and shows that most entomopathogens are very species-specific, and once established, can persist in the environment, providing long-term control and reducing costs. Additionally, commercial microbial products are non-toxic to humans and other vertebrates, in addition to being non-threatening to beneficial insects, such as pollinators. Microbial options are particularly useful for scarabs, as soil systems can be difficult to treat with conventional insecticides and scarab pests are often associated with urban systems, such as golf courses, parks, nurseries, and gardens, making health and safety a top priority. Table 4 also highlights the many opportunities that still exist for developing new biocontrol products, such as those utilizing microsporidian, viral, and protozoan agents. As issues with insecticide resistance and non-target toxicity continue to trouble agricultural and horticultural pest management, microbes will undoubtedly be at the forefront of new, safer, more sustainable strategies.

Table 4. Generalized characteristics associated with different types of microbial biocontrol for scarab pests.

Microbe	Species-Specific	Kill Time	Relative Cost	Ease of Use	Shelf Life	Potential Persistence	Commercial Products
Bacteria	yes	weeks	$$	easy	3 years	decades	yes
Fungi	no	days	$	easy	1.5 years	years	yes
Microsporidian	yes	≥month	-	-	-	years	no
Nematodes	somewhat	days	$$$	moderate	3 weeks–1 year	years	yes
Viruses	yes	weeks	-	-	-	variable	no
Protozoa	yes	≥month	-	-	-	unknown	no

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