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Review

Can Biological Control Overcome the Threat From Newly Invasive Coconut Rhinoceros Beetle Populations (Coleoptera: Scarabaeidae)? A Review

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Abstract

The coconut rhinoceros beetle (CRB: *Oryctes rhinoceros* Linnaeus) is one of the most damaging pests to coconut and oil palms in Asia and the Pacific Islands. Adults bore into the crown and damage developing fronds, which affects tree development and yield. The insect is native to South and Southeast Asia and was inadvertently introduced into the Pacific in 1909. It has since spread to several Pacific island nations and territories, causing significant economic impact on these important coconut and palm-growing regions. In the 1950s and 1960s, an international biological control effort was initiated to search for and release natural enemy species. Release of the *Oryctes rhinoceros* nudiviruses Huger (OrNV) and the species complex of *Metarhizium* Sorokin (Hypocreales: Clavicipitaceae) was successful in controlling CRB in its invaded range. Recently a new biotype of the beetle, known as CRB-G, has spread into the Pacific Islands causing unprecedented levels of damage due to the failure of previously successful biological control agents (BCAs) to suppress this biotype. The re-emergence of CRB as a serious pest warrants a rigorous re-evaluation of potential BCAs and a new search for effective natural enemies if necessary. In this article, we review literature on CRB to 1) analyze past introductions of BCAs and their effectiveness; 2) identify potentially important natural enemies and their geographical origins; and 3) assess possible approaches for utilization of BCAs against the new wave of CRB invasion. Research gaps and directions deserving future attention are highlighted and a strategy for renovation of biological controls for CRB suggested.

Key words: coconut rhinoceros beetle, CRB-G, *Oryctes rhinoceros* nudiviruses, *Metarhizium*, integrated pest management, biological control

The coconut rhinoceros beetle (CRB), *Oryctes rhinoceros* Linnaeus (Coleoptera: Scarabaeidae) is one of the most destructive insect pests of coconut and oil palms (Bedford 2013a). It is native to South and Southeast Asia, where economic losses are estimated to be at around 10% in both India (coconut: ~ 159.4 million US\$) and Indonesia (coconut: ~ 299.3 million US\$), and 25% in Malaysia (oil palm: ~ 2,853.7 million US\$) (Catley 1969, Manjeri et al. 2014, Fauzana et al. 2018, FAOSTAT 2020). The pest was inadvertently introduced into the Pacific in 1909 (Bedford 1980). CRB then spread rapidly throughout Pacific island nations and territories (Fig. 1) and became a major economic threat. In its invaded range, damage from CRB attack can be severe with tree mortality reaching 50–100% (Gressitt 1953, Manjeri et al. 2014). The economic damage from CRB in South Pacific territories in 1968 was estimated to be over one million USD (Catley 1969). Coconut

and oil palms are widely cultivated commodities in these areas, with significant contributions toward livelihoods for small holder farmers (Young 1986, Bennett 2020).

The scattered nature of CRB outbreaks and its comparatively low density, in combination with the often-low commercial value of coconuts, have made self-replicating and self-dispersing biological control agents (BCAs) the most feasible option for control of the beetle (Young 1986). Natural enemies of CRB were either introduced from the pest's native range into the invaded range (classical biological control) or the performance of those natural enemies already present in an affected area were improved by augmentation, manipulation, or other means. The first attempts at biological control, with introduction of exotic *Metarhizium* Sorokin (Hypocreales: Clavicipitaceae) spores, were carried out by Friederichs (1913) and followed intermittently with introductions of

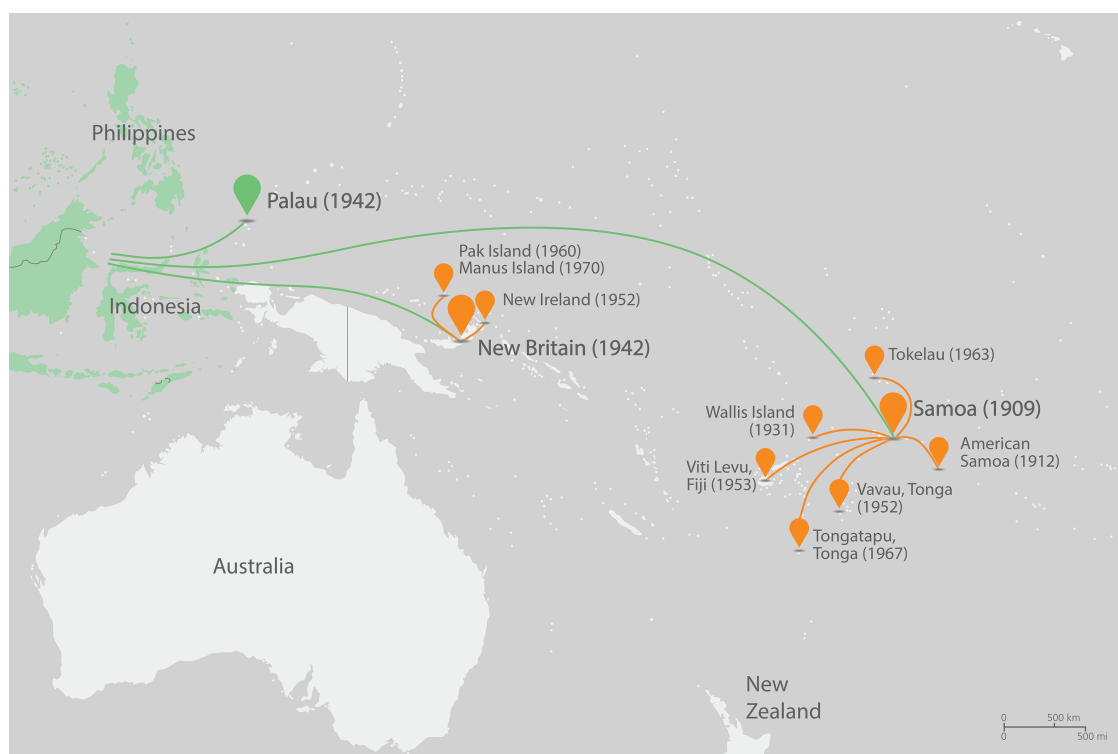


Fig. 1. Invasion history and distribution of CRB (*Oryctes rhinoceros*) in the Pacific. Green indicates the native range whereas invaded range is indicated by orange (redrawn from Catley 1969).

BCAs collected from many parts of the world (Surany 1960, Swan 1974, Waterhouse and Norris 1987); mostly organized through the South Pacific Commission (SPC). A major program for control of CRB, with introduction and testing of BCAs, was initiated by United Nations Development Program (UNDP)/SPC in 1965 (Young 1986). The discovery and introduction of a viral pathogen, *Oryctes rhinoceros* nudivirus Huger (OrNV; formerly *Rhabdovirus oryctes* and *Baculovirus oryctes*) not only reduced CRB populations and associated damage effectively but also prevented further spread for more than 30 yr (Huger 2005, Bedford 2014, Marshall et al. 2017).

A new wave of CRB invasion into previously CRB free countries and territories was first noted from Guam in 2007, followed by mainland Papua New Guinea (PNG) in 2009, Hawaii in 2013, Solomon Islands in 2015, and New Caledonia in 2019. This has rejuvenated interest in the pest (Mankin and Moore 2010, Ero et al. 2016, Adams 2019, Benedict 2019). The CRB populations in these outbreaks can be distinguished genetically from CRB of the earlier waves of invasion (herein referred to as CRB-S) by a variation in the CO1 gene and were categorized as a new CRB biotype, CRB-G, based on apparent tolerance to commonly used isolates of OrNV (Marshall et al. 2017, Reil et al. 2018). Biotype is used to define a subgroup that is distinct in terms of functional traits such as pathogen resistance or host preference within a wider group of similar genetic composition and morphology (Diehl and Bush 1984). Tolerance of the CRB-G biotype to commonly used isolates of OrNV circulating within the Pacific region is presumed to be one of the phenotypic factors facilitating the rapid expansion and recent invasion wave into the Pacific Island countries and territories (Marshall et al. 2017, Reil et al. 2018).

During the last decade, CRB has spread at a rate of approximately one new island state every 2 yr, threatening food security and livelihoods for millions of small holder farmers in the region (Ero et al. 2016, Marshall et al. 2017, Benedict 2019). In 2014, a live CRB

adult was also intercepted in Mexico with a palm furniture shipment from Indonesia, demonstrating that the pest could pose a threat to Central and South America (Jiménez Quiroz et al. 2017). The new CRB biotype, CRB-G, has already caused catastrophic damage to coconut palms in the invaded areas (Marshall et al. 2017). Two years post-invasion (2015–2017), 70% of the palms in Honiara, Solomon Islands were severely damaged or dead, posing a significant threat to the country's 17 million USD coconut industry (~12% of GDP) and food security of more than 40,000 rural households (Vaqalo et al. 2017, Tsatsia et al. 2018). In addition to the production and economic losses, the aesthetic value of tourism locations like Guam and Hawaii are lost due to damage to ornamental palms (Smith and Moore 2008).

CRB adult females lay eggs in standing palms, empty fruit bunches or decomposed stumps where the larvae develop (Bedford 1976, 1980). Adults bore holes into palm crowns and damage developing fronds, resulting in truncated or distorted leaves, often displaying a distinctive 'notched' appearance (Fig. 2). CRB damage can predispose palms to subsequent attack by different insects (e.g., palm weevils) and diseases (e.g., bud rot, leaf rot). Excessive feeding damage may also eventually result in tree mortality. The preferred hosts of CRB are coconut palms (*Cocos nucifera* Linnaeus) and oil palms (*Elaeis guineensis* Jacquin), but they are recorded to attack more than 30 different genera of plants, including sugarcane, pineapple, pandanus, banana, taro, cycads, and agaves (Gressitt 1953, Bedford 1980, Izaitul Aida et al. 2020, Marler et al. 2020). CRB populations in their native range are controlled by various biotic factors including predators, parasitoids and diseases (e.g., viral, fungal), but it becomes a major threat when introduced to new areas due to a lack of natural enemies to limit population growth (Gressitt 1953). The biology and ecology of CRB are covered in detail in several previous reports (Young 1975, Bedford 1980, Pallipparambil 2014).



Fig. 2. Characteristic damage to coconut palm fronds caused by adult CRB (*Oryctes rhinoceros*). Inset (lower left) shows the adult.

In this review, we provide a global overview of the status, use and effectiveness of exotic and indigenous natural enemies (predators, parasitoids, and pathogens) against CRB in both native and invaded areas and identify some of the major successes and failures from the past. A critical assessment of the past claims on BCAs against a current view of potential effectiveness and appropriateness is provided. The emerging threat of CRB-G in the Pacific region is also discussed with future potential of BCAs to limit the spread and associated palm damage from this pest. While there are several complementary integrated pest management (IPM) strategies (e.g., sanitation, pheromone trapping, and insecticides) that are effective against CRB, this review is solely focused on biological control. IPM strategies for CRB in coconut and oil palm have been reviewed elsewhere (Bedford 1980, 2014; Manjeri et al. 2014; Pallipparambil 2014).

Natural Enemies of CRB in Its Native Range

The intransigence of the CRB problem in the Pacific islands and the dominance of the biological control paradigm led to numerous searches, collections, and tests for biological control agents for CRB, which are summarized by Gressitt (1953), Surany (1960), Hoyt and Catley (1967), Manjunath et al. 1969, Swan (1974), and Waterhouse and Norris (1987). Eighty species are reported as putative natural enemies of CRB (predators: 48, parasitoids: 12, pathogens: 18, ectoparasites: 2) from various areas within South and Southeast Asia, Africa, Oceania, North and South America and Europe (Supp Table S1 [online only]). The majority of these natural enemies ($\approx 75\%$) were reported from the native range of South and Southeast Asia. A brief overview of major natural enemies from the native range is given below.

Predators

Coleopteran predators, notably elaterids (*Lanelater fuscipes* Fabricius, Coleoptera: Elateridae), carabids (*Catascopus facialis* Jedlicka and *C. hithilli* Hope; Coleoptera: Carabidae) and histerids (*Pachylister chinensis* Quensel, Coleoptera: Histeridae) were found associated with the immature CRB life stages (Manjunath et al. 1969). Elaterids were considered good biological control candidates compared to other predators, as they penetrate logs to attack CRB larvae inside their breeding sites and once established they provided consistent predation pressure on the pest population (Swan 1974).

Among other predators, the reduviid bugs (*Estrichodia* spp. and *Sirthena* spp.; Hemiptera: Reduviidae), were occasionally found in CRB breeding sites (Hoyt 1957, Manjunath et al. 1969, Karim et al.

2019). The ant species, *Myopopone castanea* Smith (Hymenoptera: Formicidae) produced 100% CRB larval mortality under laboratory conditions and 45–50% larvae died in the field, 5 d post-release in Indonesia (Widiastuty et al. 2018, Widiastuty et al. 2020). Both *M. castanea* and CRB larvae occupy a similar niche (e.g., decayed oil trunks, organic materials), which provides an opportunity to use it in biological control programs. Large centipedes, *Scolopendra* spp. (Chilopoda: Scolopendridae) were reported from CRB breeding sites in Southeast Asia and are also very common in Palau Islands and Samoa (Hinckley 1967, Swan 1974). Mite species (Acari: Acaridae), *Hypoaspis rhinocerotis* Oudemans and *Coleopterophagus procerus* Ferrière were reported from Southeast Asia to feed on eggs, larvae, and adults (Manjunath et al. 1969, Swan 1974, Gima 2017).

Entomopathogens

The soilborne fungi, *Metarhizium* species complex have been known as pathogens of CRB in its native range since the early 1900s, when reports were first published from Sri Lanka (formerly Ceylon) and Philippines (Friederichs 1913, Bryce 1915, Surany 1960). While the natural infection rate is relatively low, *Metarhizium* species complex are considered effective BCAs against CRB (Catley 1969, Fernando et al. 1995, Bischoff et al. 2009). These fungi infect all life stages of CRB, with the greatest effect on third-instar larvae (Ramle et al. 2006). Although several *Metarhizium* species have been assessed against CRB under laboratory and field conditions, *M. majus* (J.R. Johnston) J.F. Bischoff, Rehner & Humber (formerly *M. anisopliae* var *majus*) has been the most effective (Velavan et al. 2017). Several other fungal species including *Metarhizium guizhouense* Q.T. Chen & H.L. Guo, *Beauveria brongniartii* (Saccardo) Petch (Hypocreales: Cordycipitaceae) and *Trichoderma* sp. (Hypocreales: Hypocreaceae) have been isolated from the native range and tested against CRB, but very few have been studied in detail (Swan 1974, Ferron et al. 1975, Nasution et al. 2018).

In India, more than 90% of CRB adults collected from manure heaps and coconut palms were infested with the nematodes, *Rhabditis* species complex Dujardin (Secernentea: Rhabditidae) but pathogenicity against the host was not studied (Manjunath et al. 1969). Other entomopathogenic nematodes reported from the native range of CRB are *Steinernema carpocapsae* Weiser (Chromadorea: Steinernematidae), *Heterorhabditis indica* Poinar, Karunakar & David (Secernentea: Heterorhabditidae), and *Heterorhabditis* spp. (Secernentea: Heterorhabditidae) (Manjunath et al. 1969; Swan 1974; Patil et al. 2014; Indriyanti et al. 2017b, 2018; Manandhar et al. 2020). Several bacterial species were also identified from CRB in India during the 1960s and 1970s, but pathogenicity was not tested (Supp Table S1 [online only]) (Surany 1960, Manjunath et al. 1969). In other reports, *Acinetobacter calcoaceticus* Beijerinck (Pseudomonadales: Moraxellaceae) and *Pseudomonas alcaligenes* Monias (Pseudomonadales: Pseudomonadaceae) produced infectivity of more than 50% in India (Kannan et al. 1980, Sathiamma et al. 2001, Gopal and Gupta 2002, Gopal et al. 2002).

Alois Huger first discovered the OrNV in 1963 from Malaysia within the native range of CRB (Huger 1966, 2005). Using peroral injections, 100% CRB mortality was observed within 1–4 wk of OrNV exposure (Huger 2005). The virus is specific to CRB and results in persistent suppression of populations. In larvae, swelling of the body, a translucent or waxy appearance, and visible fat bodies through the integument are some of the major symptoms of OrNV infection, whereas symptoms are not so definitive with adults (Huger 2005, Bedford 2013a). Adult beetles efficiently disseminate OrNV to breeding sites through defecation at mating, feeding and breeding

sites, spreading the infection and leading to a significant reduction in damage and pest populations (Zelazny 1976).

Classical Biological Control of CRB: Successes and Failures

Classical biological control is the introduction of co-evolved natural enemies (parasitoids, predators, and pathogens) from the pest's native range to manage invasive pests of exotic origin (Lockwood 1993). Classical biological control has been most successful when the pest and its natural enemy have a close ecological relationship, such that the natural enemy is a specialist on the target pest (Hoddle 2002). There were widespread efforts during the 1950s and 1960s to introduce BCAs from Southeast Asia, Africa, Europe, New Zealand, and the United States of America into the South Pacific Islands against CRB (Supp Table S1 [online only]). Some of the major introduced biocontrol agents, including predators, parasitoids, and entomopathogens, are described below and the reasons for their success or failure to control CRB are considered.

Predators

Two predatory elaterids (Coleoptera: Elateridae), *Pyrophorus pellucens* Eschscholtz and *L. fuscipes* were introduced against CRB in the Pacific islands during 1953–1954 (Swan 1974, Waterhouse and Norris 1987). The former failed to establish in Fiji and Papua New Guinea but both species established successfully in Western Samoa and were recorded to have spread further onto other islands (Manjunath et al. 1969, Swan 1974). *Lanelater fuscipes* was also reported from Guam recently and is usually effective against CRB once established (Catley 1969, Moore et al. 2015). Several *Alaus* species Eschscholtz (Coleoptera: Elateridae) were also tested but with limited success (Hinckley 1967, Manjunath et al. 1969). Among many, *A. speciosus* Linnaeus was the only species later recovered following its initial introduction into Western Samoa from India and Sri Lanka (Catley 1969).

Several carabids were also introduced but they either failed to establish or could not control the pest, even when established. For example, *Pheropsophus* sp. (Coleoptera: Carabidae) introduced into Mauritius from India established successfully but failed to exert predatory pressure on the target pest (Rao and Manjunath 1964, Monty 1974, Bedford 1980). Similarly, *Scarites madagascariensis* Dejean (Coleoptera: Carabidae), considered as an efficient biological control agent of dynastid larvae in Madagascar, was introduced into Fiji and Wallis Island but failed to establish; giant (cane) toads probably preyed on the beetles in Fiji (Swan 1974). A large flightless beetle, *Mecodema spinifer* Smith (Coleoptera: Carabidae), that is endemic to New Zealand was introduced into Fiji in 1954 but failed to adapt to the tropical Pacific climate (Hoyt 1957, Manjunath et al. 1969, Swan 1974).

A complex of species belonging to two histerid genera (*Pachylister* and *Hololepta*, Coleoptera: Histeridae) were introduced widely into the Pacific Islands against CRB. *Pachylister chinensis* was introduced originally into Palau Islands in 1952 to manage *Musca domestica* Linnaeus (Diptera: Muscidae) but was found to feed on CRB larvae. *Pachylister chinensis* beetles were then sent to Papua New Guinea (New Britain) from Fiji in 1953 to manage CRB, where it established successfully (Gressitt 1953, Surany 1960, Hinckley 1967, Swan 1974). *Hololepta quadridentata* Oliver and *H. columbiana* Oliver (Coleoptera: Histeridae) were introduced into Fiji, Palau Islands, and Wallis Island from Trinidad during 1952–1954 but failed to establish (Hoyt 1957, Manjunath et al. 1969, Swan 1974). Among

hemipterans, *Platymeris laevicollis* Distant (Hemiptera: Reduviidae) was introduced from Tanzania and released into the South Pacific Islands (Papua New Guinea, Western Samoa, and Tonga) during the 1960s (Vanderpalnk 1958, Manjunath et al. 1969, Sathiamma et al. 2001, Karim et al. 2019); however, it failed to establish due to predation of eggs and nymphs from the ant, *Pheidole megacephala* Fabricius (Hymenoptera: Formicidae) (Manjunath et al. 1969, Swan 1974).

Parasitoids

Scoliid wasps were the most tested parasitoids against CRB, targeting larvae. *Elis romandi* de Saussure, *Scolia cyanipennis* Fabricius, *Scolia oryctophaga* Coquerel, *Scolia procer* Illiger, *Scolia quadripustulata* Fabricius, and *Scolia ruficornis* Fabricius, (Hymenoptera: Scoliidae) were introduced into the Pacific Islands from African and Asian countries during 1940s to 1960s, but most of them never established (Hoyt 1957, Manjunath et al. 1969, Swan 1974, Clausen 1978, Sathiamma et al. 2001, Manjeri et al. 2014). Failure to adapt to the tropical Pacific environment is considered to be one of the major factors contributing to lack of establishment (Swan 1974). Among the introduced scoliids, only *S. ruficornis* established successfully in the Pacific: Palau Islands, Samoa, Papua New Guinea, and Wallis Island (Simmonds 1949, Swan 1974, Bedford 1980, Waterhouse and Norris 1987, Gerlach 2003). The initial parasitism rate in Samoa was 30% (Hoyt and Catley 1967), and Wilson (1960) considered that CRB suppression in New Britain, PNG was sufficient to permit replantation of palms. The impact of these wasps on CRB was somewhat limited because they were unable to penetrate fresh logs, which are important breeding sites. Their activities were restricted to breeding sites containing friable materials, such as sawdust heaps, compost and decayed logs (Catley 1969).

The egg parasitoid, *Pediobius (Pleurotropis) parvulus* Ferrière (Hymenoptera: Eulophidae) was introduced from Fiji into Papua New Guinea (New Britain) in 1938 and established successfully; but the extent that this parasitoid suppressed CRB populations is not known (Hoyt 1957). Attempts to introduce the tachinid fly, *Microphthalma europaea* Egger (Diptera: Tachinidae) into Western Samoa during the 1960s were unsuccessful; the parasitoid failed to adapt fully to the target host because parasitoid larvae were unable to break out of the host integument when ready to pupate (Hoyt and Catley 1967, Cochereau 1970, Swan 1974).

Entomopathogens

Entomopathogenic nematodes and bacteria have been introduced and tested against CRB (Bedford 2013a). *Rhabditis* sp. was introduced into Fiji, Samoa, and Wallis Island from Sri Lanka; nematodes were recovered from Fiji but further exploration of its establishment and control efficiency was never made (Swan 1974). The bacterial pathogen, *Paenibacillus popilliae* Dutky (formerly *Bacillus popilliae*) (Bacillales: Paenibacillaceae) was introduced into Palau Islands from the United States of America in 1951, but whether it established or not is unknown (Hoyt 1957). Similarly, *Bacillus lentimorbus* var. *australis* Beard and *Bacillus euloomarabae* Beard (Bacillales: Bacillaceae), isolated from the larvae of *Sericesthis pruinosa* Boisduval (Coleoptera: Scarabaeidae) were introduced into Western Samoa from Australia in 1954 but failed to proliferate in sufficient numbers (Cumber 1957, Manjunath et al. 1969).

OrNV has been the most effective classical BCA and continues to be widely used within CRB management programs (Jackson

2009). It was so successful that the virus is considered one of the landmark classical biological control programs (Caltagirone 1981, Young 1986, Zelazny et al. 1992, Huger 2005, Hajek et al. 2006). First released in Western Samoa in 1967, the virus reduced CRB populations and successfully maintained low numbers in invaded countries and territories for more than 30 yr. For example, 62–85% of CRB beetles were infected with the virus 3 yr post-release in two Indian Islands, Lakshdweep, and Andamans, reducing damage by 82–96% during the 1980s (Gopal et al. 2001). In Oman, more than 40% of the local CRB population were infected 2 mo after release of 900 OrNV-infected beetles in 1989; 3 yr after virus introduction (1992), CRB damage was reduced by 50% compared to the year before (Kinawy et al. 2008). In Fiji, damage from CRB was maintained at low levels even 35 yr after introduction (Bedford 2013b). The effectiveness of the virus was so apparent that research on biocontrol releases against CRB declined to low levels after the initial OrNV releases (Young 1986). Further spread of CRB to new areas was not reported until 2007, when a new wave of invasion into previously CRB-free Pacific Islands countries and territories began (Bedford 2013a, Marshall et al. 2017).

Early attempts at classical biological control for insect pests were often opportunistic, used generalist rather than specialist natural enemies, and were unable to draw on previous examples or analysis of factors involved in success and failure (Barratt et al. 2000, Hoddle 2002). Clearly, very few natural enemies introduced for control of CRB were successful, either failing to establish at all, or with little evidence of impact on CRB after establishment. First, many putative natural enemies were introduced without considering the degree of similarity of ecological and environmental conditions between the country of origin of the biological agent(s) and the intended area of introduction. Introduction of *M. spinifer*, from New Zealand and *Microphthalma europaea* Egger, from Europe, were probably doomed as these regions are vastly different from the tropical Pacific environment (Swan 1974). Second, several predators and parasitoids were introduced from outside the native range of CRB based on their efficiency against other *Oryctes* species (e.g., scoliids from Africa, and histerids from Tanzania and Trinidad) (Swan 1974, Bedford 1980, Waterhouse and Norris 1987). There was no evidence supporting the effectiveness of these species against CRB prior to their introduction. Third, possible predators and parasitoids of the candidate BCAs in the introduced area were rarely considered, which led to several failures. For example, *P. laevicollis*, which was introduced from East Africa, failed to establish because of predation from the native ant, *P. megacephala* (Manjunath et al. 1969). Similarly, *S. madagascariensis*, introduced from Madagascar, were eaten by cane toads contributing to their failure (Swan 1974). Lastly, most of the introduced BCAs were generalists with a broad host range. While some of these generalist BCAs included CRB or another *Oryctes* species in their host range, others had no co-evolutionary history with CRB and were effectively new associations, an approach sometimes termed as the neoclassical biological control (Hokkanen and Pimentel 1989, Lockwood 1993, Ehler 2000). Potential nontarget impacts from these BCAs on biological communities and environments of the introduced area were also never considered (Howarth 1991, Sands and Van Driesche 1999), reflecting what was common practice for biological control at that time. While there were limitations in terms of capacity, knowledge, and resources in the past, future introductions against CRB should fulfill the current expectation of BCAs to ensure that the classical

biological control programs are effective and minimize the risk of nontarget impacts (Hoddle 2002).

Augmentative Biological Control For CRB

Augmentative biological control aims to increase populations of existing natural enemies through deliberate releases to successfully manage insect pests (Collier and Van Steenwyk 2004). Augmentative releases of entomopathogens have been tested widely and used to manage CRB in its native range. In Southeast Asia, incorporation of the *Metarhizium* fungus into breeding sites (e.g., compost heaps) is a popular method (Ramle and Norman 2014, Chandrika et al. 2016, Indriyanti et al. 2017a). The process is relatively cost effective and provides adequate control in some instances. In Malaysia, *M. majus* conidia produced 37% CRB larval mortality within 3 mo when sporulated maize substrates were applied to breeding sites (Ramle et al. 1999). Conidia suspensions obtained after washing the sporulated substrate were also drenched in oil palm replanting areas; a single application of 5×10^8 conidia/m² resulted in 51% CRB larval mortality and was found comparatively more effective and economical than broadcasting sporulated substrates (Ramle et al. 1999). Treatment of vermicompost sites in India with *M. majus* spores produced in coconut water (10^8 spores/mL) successfully reduced CRB larval populations by 72% compared to the control (Gopal et al. 2006). In Thailand, treatment of empty oil palm fruit bunches with *M. guizhouense* resulted in mortality of first-, second-, and third-instar CRB by 93%, 96%, and 76%, respectively after 35 d under field conditions (Pansuwan et al. 2019).

Conidia formulations have been developed and evaluated under laboratory and field conditions against CRB larvae and adults with mortality rates reported between 40 and 100% (Ramle et al. 2006, Ramle et al. 2007, Ramle et al. 2013, Chandrika et al. 2016, Mohd et al. 2016, Indriyanti et al. 2017b). Formulations have been developed as wettable powders (WP), with the most common composition being a mixture of dried conidia and kaolin (20:80) (Hamid et al. 2005, Ramle et al. 2006, Ramle et al. 2007, Indriyanti et al. 2017b). In India, fresh conidial suspensions (TCS) and powder-based formulations (PBF) of *M. majus* resulted in 85–90% mortality of third-instar CRB larvae within 2 wk (Velavan et al. 2017). Similarly, the treatment of rotting oil palm debris with *M. majus* based formulations (WP) that were reconstituted in water reduced larval populations by 80% in Malaysia (Ramle et al. 2006).

Direct treatment of breeding sites (decomposing trunks or manure/compost heaps) with the *Metarhizium* fungus is considered an efficient strategy against CRB in the field (Ramle et al. 2006, Mohan et al. 2010). Notably, the fungal spores in the breeding sites are reported to survive up to 24 mo postapplication under ideal conditions (Latch and Falloon 1976). Artificial breeding sites (ABS: a trough with logs of trunk and decomposing chipped mature palms) treated with *Metarhizium* are also used to infect and disseminate the fungus and control CRB by attracting the beetles with pheromone traps toward decomposed materials that act as breeding habitat (Ramle et al. 2013). The CRB adults are strong fliers, therefore, the concept is that infected beetles can quickly disperse and distribute conidia to other breeding and feeding sites. In Malaysia, 43% of the CRB populations were infected with the fungus in plots with ABS compared to 32% infection from random field spraying (Ramle et al. 2013). In Thailand, pellet formulations of *M. anisopliae* Sorokin resulted in 87% CRB larval infection when applied to ABS (Popoonsak et al. 2018).

Despite its potential, widespread use of *Metarhizium* fungus against CRB has had some challenges (Surany 1960, Bedford 1980). The fungus requires a specific temperature range of between 28°C and 32°C and humidity above 80% to be effective (Mohan et al. 2010). Spore formulation and mycelial growth of a local Sri Lankan isolate of *M. anisopliae* was negatively affected at a higher temperature of 32.5°C (Subhathma et al. 2013). In Kerala, India, natural infection rates from the fungus are much higher during the rainy season due to high humidity (Gopal et al. 2002). Therefore, the use of the fungus in countries or seasons with relatively less rainfall and higher temperatures is not optimal (Indriyanti et al. 2017b). It is also important to note that heavy rainfall reduces dissemination of the fungus and consequently lowers CRB mortality rates (Indriyanti et al. 2017b). Due to these factors, *Metarhizium* fungus requires repeated applications leading to increased costs of labor and materials (Vargo 1995, Gopal et al. 2002). The shelf life of fungus sporulated substrates and fresh conidia suspensions is limited, and requires refrigerated storage, which increases the storage cost (Ramle et al. 2013). However, conidia viability can be extended by using proper formulations (e.g., kaolin-based) under suitable temperatures (Hamid et al. 2005).

Entomopathogenic bacteria, nematodes, and viruses have also been tested for augmentative release against CRB. Two bacterial pathogens, *B. thuringiensis* Berliner (Bacillales: Bacillaceae) and *P. popilliae* produced 100% mortality in CRB larvae within 3–4 wk in India (Babu et al. 1971). In Malaysia, bacterial pathogens (*B. thuringiensis* and *P. popilliae*) in combination with OrNV and *Metarhizium* sp. produced 88% mortality of third instar CRB larvae (Kamarudin et al. 2007). Two indigenous strains of nematodes from India, *S. carpocapsae* and *H. indica*, significantly increased larval mortality in neonates and third-instar larvae in compost heaps (Patil et al. 2014). *Heterorhabditis* sp. (commercial pesticide, Coleonema) produced 100% mortality 8 wk postapplication in Indonesia, while it only took 5 wk when the nematodes were used in combination with the fungus, *M. anisopliae*, suggesting a synergistic interaction between BCAs (Indriyanti et al. 2018). A list of commercially available biopesticides from Asia for CRB management is provided in Table 1. Most of them are based on *Metarhizium*, while a few have *B. bassiana* and *Heterorhabditis* sp. as the active ingredients. Novel isolates should be rigorously tested to ensure efficacy before application in widespread control programs.

Inundative releases of OrNV were successful in several Southeast Asian countries, resulting in significant reduction of CRB populations. In India, the release of OrNV-infected beetles reduced spear damage in oil palms from 71 to 21% (Dhileepan 1994), and frond damage in coconut palms from 34 to 7% (Babjan et al. 1995). Release of OrNV in the Philippines reduced the CRB population by 10–20% compared to preinoculation levels (Zelazny and Alfiler 1987, Zelazny and Alfiler 1991). Similarly, the proportion of infected beetles increased by 35–90% 3 mo postrelease of OrNV in Malaysia (Ramle et al. 2005).

Managing the New Wave of CRB Invasion Using BCAs: Future Perspectives

In the last decade, the new wave of CRB invasion has emerged as one of the major challenges of palm trees in Pacific island countries and territories (Marshall et al. 2017, Tsatsia et al. 2018). Central to the resurgence is the new biotype, CRB-G, which is tolerant to the OrNV isolates commonly used for biological control. Geographical variations in OrNV virulence and genetic diversity, however, are not new. Infection periods and mortality rates of CRB larvae differed after infection with OrNV isolates from the Philippines and Western Samoa (Zelazny 1977). Similarly, genetic variability of OrNV isolates sampled from different locations within Malaysia and Indonesia are also reported (Ramle et al. 2005, Rahayuwati et al. 2020). Therefore, improved understanding of interactions between CRB and entomopathogens (e.g., OrNV, *Metarhizium*) in different regions are especially important for development and implementation of targeted region-specific biological control programs.

Entomopathogens have proven effective against scarabs in general (Jackson and Klein 2006). Since OrNV and *Metarhizium* were the most successful BCAs in the past, variants of these entomopathogens are the most likely candidates to manage the new wave of CRB invasion in the Pacific region and beyond. Viewed through a modern lens, OrNV stands out as a suitable agent for classical biological control of CRB. It is comparatively host-specific and has a well-documented impact on the target pest (Huger 2005, Bedford 2013b). Despite tolerance to the standard OrNV biocontrol strains (Marshall et al. 2017), some isolates of OrNV from the Philippines (imported through AgResearch, New Zealand) have produced promising results against CRB-G in Solomon Islands (Tsatsia

Table 1. Details of commercially available biopesticides for CRB management in Asia

Product name	Active ingredient	Formulation	Manufacturer	Country
ORY-X	<i>Metarhizium anisopliae</i> var. <i>majus</i>	Wettable powder (WP)	FGV Agriservices SDN VHD	Malaysia
Multiplex Metarhizium	<i>Metarhizium anisopliae</i>	Suspension (S) Wettable powder (WP)	Multiplex Fertilizers Private Ltd.	India
Metarhizep	<i>Metarhizium anisopliae</i> and <i>Beauveria bassiana</i>	Wettable powder (WP)	Prima Agro Tech	Indonesia
Metarhizium anisopliae	<i>Metarhizium anisopliae</i>	Wettable powder (WP)	Agrikencana Perkasa	Indonesia
Super Meta (Mosa Meta)	<i>Metarhizium anisopliae</i>	Wettable powder (WP)	Mosa Mandiri Corporation	Indonesia
Metaribb	<i>Metarhizium anisopliae</i>	Wettable powder (WP)	Riset Perkebunan Nusantara (Pusat Penelitian Bioteknologi dan Bioindustri)	Indonesia
Metatech	<i>Metarhizium anisopliae</i>	Wettable powder (WP) Granules (G) Sporulated rice	SVGroup	Thailand
Uyir Beauveria brogniartii	<i>Beauveria brogniartii</i>	Suspension (S)	Uyir Organic Farmers Market	India
Coleonema	<i>Heterorhabditis</i> sp.	Liquid in sponge	Agencia Hayati Pembunuh hama	Indonesia

et al. 2018). In Guam, various OrNV isolates (OrNV-X2B from Philippines, OrNV-I from India, OrNV-TAS and -TAP from Samoa, and OrNV-Ma1B from Malaysia) produced CRB adult mortality following hemocoelic injection, but statistically significant mortality was not observed through oral delivery (Marshall et al. 2017).

Most of the many other BCAs (predators, parasitoids, and pathogens) considered previously for classical biological control (Supp Table S1 [online only]) were imported without consideration of the factors that have become standards of modern biological control: host specificity, climate matching, or significant impact on population suppression of the target pest (Hoddle 2002). Despite this, some did establish successfully (Supp Table S1 [online only]). For example, predatory beetles, *A. speciosus* and *L. fuscipes*, that were imported into Western Samoa from the native CRB range, did establish successfully and preyed on CRB (Catley 1969). Similarly, establishment of *P. laevicollis*, and *P. parvulus* was also confirmed but their impacts are not known (Catley 1969, Swan 1974). The parasitic wasp, *S. ruficornis*, is reported to have established in several Pacific Island countries (Catley 1969, Swan 1974). These BCAs may be potential candidates for conservation or augmentative biological control. There are, however, no published studies since the mid-1970s that report the activity or impact of these agents on CRB and they are not commonly found in field sampling. Thorough assessments of these agents' geographic and habitat range, predation or parasitism rates, and their current contribution to CRB control are needed. Similarly, further investigation is needed to determine whether local predators and parasitoids, that were historically reported as enemies of CRB, are still contributing to population control. Without recent data, it is impossible to determine what impact these introduced agents and local natural enemies, both individually and in combination, now have on CRB populations. The rapid expansion of newly invasive populations in the Pacific does suggest that there is very little natural control. There may be potential to increase the impact of these BCAs through habitat manipulation or deliberate mass rearing and release. Their impacts could enhance the biological control provided by OrNV, or by new classical BCAs that may be introduced against CRB in future.

Failure of the majority of BCAs to either establish or reduce CRB populations does not mean that there are no other potential agents available within the native range of CRB. It is often noted that CRB damage is much worse in the invasive zones than within its native range, indicating suppression of the native populations by biotic factors (Gressitt 1953). The successful agent, OrNV, was isolated from diseased CRB larvae in Malaysia (Huger 2005), which is considered the center of origin for this pest. Scarab BCAs are often highly host specific (Jackson and Klein 2006), so care should be taken to search for new agents in the center of origin, not just of the species as a whole, but also of specific CRB biotypes. Scarabs are frequently resistant to commonly known generalist entomopathogens, but effective BCAs for the Scarabaeidae often show a high level of host specificity. This, coupled with a wide range of microbial agents from different classes for different species, suggests a high level of co-evolution between these pathogens and their scarab hosts (Jackson 1999). With modern developments in genetic screening and identification of potential pathogens, it is possible that new pathogens may be isolated and identified from CRB. Recently, a novel Picorna-like virus (OrPV1) was reported in CRB larvae collected from Taiwan. This novel virus shared some genetic identity with viruses infecting honeybees and Asian lady beetle (Etebari et al. 2020), but pathogenicity toward CRB has yet to be demonstrated for this novel virus. The picorna-like viruses are also reported from *Helicoverpa armigera* Hübner (HaNV), infecting gut tissues of both adults and larvae (Yang et al. 2019). Sequencing results from Hawaiian CRB

specimens identified three contigs displaying similarity matches to genes from other insect associated DNA viruses (classified under the Baculoviridae, Entomopoxvirinae, and Genomoviridae families), which are known to be capable of infecting beetles and other insect species (Mitsuhashi et al. 2014, Adams 2019). Further details are needed to determine the potential suitability of these viruses, or others yet to be discovered, as possible classical BCAs: 1) to test their efficacy against CRB; 2) investigate their climatic range; and 3) to conduct host specificity tests with potential nontarget species. All these steps are best conducted initially in the native range of the potential agent. Only if the agent passes this initial screening, should it be considered for further testing under quarantine conditions in the proposed country or region of introduction. If quarantine facilities are not available in the region of introduction, collaboration with international partners may be needed to complete the risk assessment and provide sufficient information to determine the agent's suitability. Finally, the potential for competition between the new agent and other pre-existing control agents, particularly OrNV and *Metarhizium*, should be investigated before a new agent is released (Gopal and Gupta 2002, Kamarudin et al. 2007).

Based on current knowledge, biopesticides containing *M. majus* are the strongest candidate for augmentative biological control against the emerging CRB threat (Moore 2018). Three weeks postrelease of *M. majus* (imported from the Philippines), 10–38% of field collected CRB were infected with the fungus in Guam (Moore 2018). The fungus established successfully in the area but did not have sufficient impact to manage the CRB outbreak on its own. The potential effectiveness of *M. majus* (commercial product: Ory-X imported from Malaysia) against CRB was also reported from Solomon Islands (Fig. 3) (Tsatsia et al. 2018).

Investigation of local entomopathogens is warranted through collection of potentially infected CRB because there may be opportunities to enhance the activity of local species against CRB. In an experiment conducted in a research laboratory in Hawaii, more than 60% CRB mortality was recorded from five *Metarhizium* isolates collected from O'ahu, Hawaii (KO-001, KO-002, LA-016, LA-025, and LA-026) (Russo 2019). Similarly, a few local *Heterorhabditis* spp. from O'ahu, Hawaii also caused first-instar larval mortality after 2–7 d of exposure (Manandhar et al. 2020). While *B. thuringiensis* and *P. popilliae* have demonstrated some potential to infect CRB (Babu et al. 1971, Kamarudin et al. 2007), there are no suitable products available commercially (Table 1). Therefore, identifying local entomopathogenic



Fig. 3. *Metarhizium majus* sporulated CRB (*Oryctes rhinoceros*) larvae in a fungus propagation chamber in Solomon Islands.

species may provide opportunities to develop local industries that produce biopesticides. Several biopesticide products based on entomopathogenic fungi and nematodes are produced commercially in South and Southeast Asian countries (e.g., India, Indonesia, and Thailand) for CRB control (Table 1). It is vital that robust formulations, produced under strict quality control, are used to maintain the activity of the agent for distribution in tropical conditions.

In summary, ongoing research efforts are needed to design an effective biological control program against the emerging threat of newly invading CRB populations, such as CRB-G. A crucial part of this effort is to enhance existing biological control and to identify and evaluate potential new BCAs for CRB. Investigation of the native range of the invasive species, including specific biotypes, is a high priority in the search for candidate entomopathogens, or other natural enemies. The impact of local natural enemies and past biological control introductions also needs re-evaluation to determine what contribution, if any, these make to CRB control. It is important that BCAs are incorporated into IPM programs for CRB that include other complementary strategies that enhance CRB control, such as sanitation. It is preferable if these complementary strategies are feasible and cost-effective for resource-poor smallholder farmers, as well as commercial plantation operations. Collaboration among government, non-governmental organizations, local industries and farmers through awareness campaigns, field sanitation and biosecurity measures will be extremely important to limit further spread by CRB to new regions. Despite the recent expansion of its range in the Pacific, biological control remains central to effective management of CRB.

Supplementary Data

Supplementary data are available at *Annals of the Entomological Society of America* online.

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