BioControl (2024) 69:199–214
https://doi.org/10.1007/s10526-024-10253-6

REVIEW

Ecology and management of the coffee berry borer (*Hypothenemus hampei*): the potential of biological control

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Received: 2 June 2023 / Accepted: 5 March 2024 / Published online: 15 April 2024

Abstract Coffee is an important commodity in Latin America that is grown by smallholder farmers and large-scale coffee producers. The coffee berry borer, *Hypothenemus hampei* Ferrari (Coleoptera: Curculionidae: Scolytinae) is a major pest of coffee that originates from West Africa and has invaded all coffee-producing regions. With climate change, the problems that this beetle poses to coffee production are expected to increase. Controlling this pest is a true challenge and chemical insecticides still are one of the main tools used, despite the environmental and human-health issues associated with this approach. To find sustainable alternatives for chemical control of the coffee berry borer, classical biological control, augmentative biological control, and integrated pest management have received extensive attention. Parasitoids, predators, entomopathogenic fungi, and nematodes have been identified and studied for their potential to manage the infestations of this major coffee pest. Conservation biological control has recently gained more attention, but its development is still in its infancy. In this review, we examine strategies for the control of the coffee berry borer in Latin America. We identify knowledge gaps for developing sustainable biological control programs, including conservation biological control within the context of farming systems, land use in the surrounding landscape, as well as the vision of coffee growers.

Keywords Biological control · Scolytinae · Conservation biological control · Habitat management · Natural enemies · Latin America

Handling Editor: Dirk Babendreier.

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Introduction

The coffee berry borer (CBB), *Hypothenemus hampei* (Ferrari 1867), is the most damaging insect pest of coffee worldwide, affecting the yield and quality of coffee in almost all coffee-producing regions (Johnson et al. 2020; Fotso Fotso et al. 2023). CBB has spread from Africa to nearly all coffee-producing countries in the world (Benavides et al. 2005; Johnson et al. 2020) causing losses worldwide of over 500 million US$ annually (Vega et al. 2015) and pest management costs amount up to 10% of the total production costs (Aristizábal et al. 2016). The CBB affects coffee beans when the adult females drill the berries to lay their eggs and the offspring feed on the bean tissue. This damage is particularly severe in arabica and robusta coffee crops growing at altitudes between 1000 and 1400 m.a.s.l. (Damon 2000; Jaramillo et al. 2009).

Different approaches have been developed to manage CBB infestations in coffee farms, including pest monitoring, the use of chemical insecticides, sanitation, biological control, and integrated pest management (IPM) (Johnson et al. 2020). However, the adoption and effectiveness of these practices may depend, for example, on climatic conditions, landscape heterogeneity, crop characteristics, labour availability, financial resources and farmers' perceptions and knowledge. Under the current dynamic context of coffee production imposed by changing climate patterns, fluctuations in coffee prices and increasing consumer demand for sustainably produced coffee, it is challenging for farmers to make informed decisions about CBB pest management.

Here, we review the literature, including gray literature and technical reports, to assess how CBB infestations and their control in Latin American coffee systems are influenced by environmental and socio-economic conditions. First, we introduce the pest, providing information on its origin, distribution, and control practices. Next, we appraise the current status of CBB control, including the environmental and socio-economic drivers, and discuss recent, novel advances in studies on conservation biological control of CBB. Finally, we identify knowledge gaps and promising research directions for pesticide-free control of CBB. For a global perspective on CBB and its natural enemies we refer to reviews of Johnson et al. (2020) and Escobar-Ramírez et al. (2019), respectively.

The origin and spread of the coffee berry borer

The precise origin of the coffee berry borer is uncertain, but it may have originated in low-altitude *Coffea robusta* crops in West and Central Africa (Damon 2000; Jaramillo et al. 2009) from where it subsequently spread to arabica coffee in Ethiopia and Saudi Arabia (Murphy and Moore 1990). The coffee berry borer was first described as *Cryphalus hampei* by Ferrari in 1867 from specimens obtained in traded green coffee beans imported to France from an unknown location (Waterhouse and Norris 1989) and was later reported in Liberia in 1897 (Hopkins 1915), the Republic of Congo in 1901 (Le Pelley 1968), and Zaire in 1903 (Murphy and Moore 1990). Currently, CBB can be found in arabica and robusta coffee crops at altitudes from 1100 to 1600 m.a.s.l. in all coffee-producing countries, except for Nepal and Australia (Jaramillo et al. 2009). The CBB is still expanding its geographical range as it has been recently reported in China (Sun et al. 2020).

Molecular analysis suggests that CBB was introduced to Latin America from Western Africa (Benavides et al. 2005). The initial introduction happened through the import of green coffee beans to Brazil, followed by multiple introductions in Colombia and Peru (Benavides et al. 2005). Currently, CBB can be found in all coffee-producing countries in Latin America causing major losses in coffee production in Brazil, Colombia, Costa Rica, Ecuador, and Mexico (Johnson et al. 2020).

The life cycle of the coffee berry borer

Hypothenemus hampei belongs to the Scolytinae subfamily ("bark beetles"). The genus *Hypothenemus* is one of the largest genera of this subfamily with 130 species of small (< 2 mm long) wood-boring beetles (ITIS 2023). CBB differs from other *Hypothenemus* species (and other coffee-related insect pests) in its ability to feed and complete its life cycle inside the coffee seed. CBB has this unique ability because it can detoxify caffeine and use it as a source of carbon and nitrogen due to an association with a gut microbiome, which is rich in *Pseudomonas* bacteria (Ceja-Navarro et al. 2015).

The CBB life cycle starts between 90 and 120 days after the flowering of coffee plants when the female beetle colonizes a developing green coffee berry (Friederichs 1922; Jaramillo et al. 2009). It takes between two to eight hours for the female to enter the berry and create the galleries inside the bean (Vega et al. 2015). Once these galleries are created, she lays approximately 30–100 eggs, with an average of 2–3 eggs per day. At optimal temperatures between 25 and 27 °C, CBB egg development takes 3–4 days. Larval development takes approximately 19 and 15 days for females and males, respectively, while the prepupal stage takes 8–14 days for both female and male CBB

(Fig. 1) (Damon 2000; Jaramillo et al. 2009). Due to the difference in the juvenile developmental period, male adults emerge earlier than females. Three days after emergence from the pupae, females are ready to mate. Mating takes place between siblings inside the berry (Vega et al. 2015). In Colombia, the completion of the CBB cycle is estimated to take 45 days at 22 °C, and 60 days at temperatures below 19 °C (Bustillo 2006).

The average body length of adult male and female coffee berry borers is around 1.5 and 1.8 mm, respectively (Vega et al. 2015). The wing muscles of males do not develop completely, impairing their flight capacity, and therefore males stay in the coffee berry. Fertilized females leave the berry to search for new coffee berries for egg laying (Baker et al. 1992; Johnson et al. 2020). Usually, one berry is colonized by a single female. However, during heavy infestations more than one female can be found per berry. Sex determination in CBB is influenced by the endosymbiotic bacterium *Wolbachia pipientis* and the offspring sex ratio is female-biased: 5:1 (Vega et al. 2002; Benavides 2005).

The development and phenology of CBB is influenced by environmental factors, such as temperature, food availability, and RH (Baker et al. 1992). Higher temperatures and limited food generally result in faster development and shorter life spans. At optimal conditions between 15 and 25 °C (Azrag et al. 2020), females live around 68, 20 days longer than males, whose life span is around 48 days (Baker 1999). CBB females start egg laying when temperatures range between 20 and 30 °C and RH is around 70–90% (Baker et al. 1992; Damon 2000). The number of generations is highly variable and can range from two to 13 per season, increasing with higher temperatures (Baker 1999; Johnson et al. 2020).

Long, dry seasons can elicit reproductive diapause in CBB females. During this period, the CBB slows down its activity and aggregates in groups inside dark-red coffee berries to survive unsuitable inter-harvesting seasons (Aristizábal et al. 2016; Vega et al. 2019). Once the rainy season starts and the RH increases, large numbers of CBB females emerge from these overripe berries and colonize the green berries of the new production cycle (Cárdenas 2015).

Host plants of the coffee berry borer

Although coffee (*Coffea* sp.) is the most attractive host plant for the coffee berry borer, CBB can feed and reproduce on more than 40 plant species, mainly from the Rubiaceae and Fabaceae families (Damon 2000; Vega et al. 2019). These alternative host plants can be important to sustain CBB populations in areas with seasonal coffee crops, especially between coffee harvesting seasons.

Due to the resemblance of CBB to other co-existing beetles of the subfamily Scolytinae, there is some

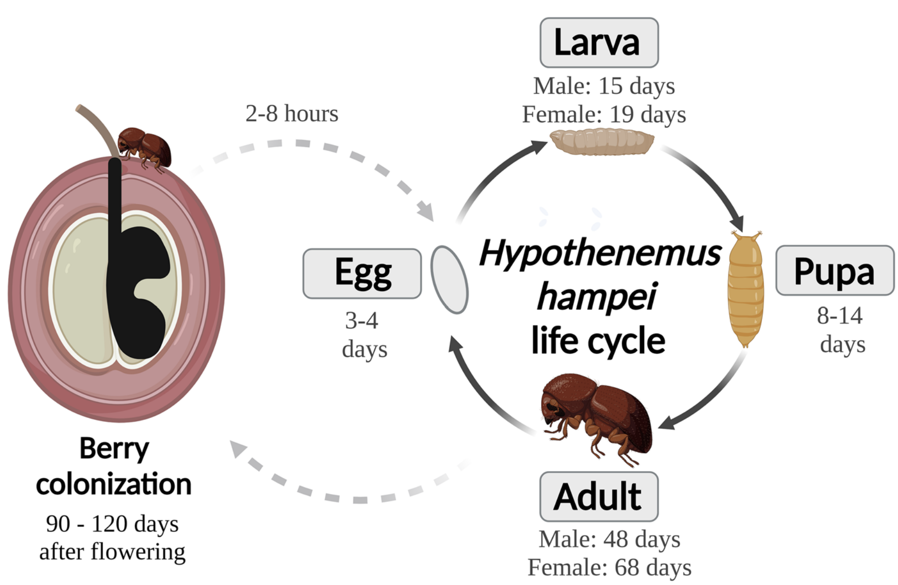

Fig. 1 Life cycle of *Hypothenemus hampei*, the coffee berry borer (CBB). The CBB life cycle starts 90–120 days after flowering of coffee plants. It takes between two to eight hours for the CBB females to enter the berry, create the galleries, and start laying eggs. Females live longer on average, with a life span of 68 days compared to males, with an average lifespan of 48 days. (Color figure online) Source: Damon (2000) and Vega et al. (2015)

uncertainty as to whether CBB uses these plant species. Using molecular analysis, Vega et al. (2019) identified CBB beetles on fruits of *Inga vera* Willd. (Fabaceae), *Guarea guidonia* L. (Meliaceae), and *Cajanus cajan* L. (Fabaceae), which are often used as shade trees in coffee crops in Puerto Rico. However, in choice experiments in the laboratory CBB preferred coffee beans to feed and reproduce over *Inga* sp., *Guarea* sp., and *Cajanus* sp. fruits.

Arabica and robusta coffee are considered the most attractive host plants for CBB, but the beetle can also infest other species in the *Coffea* genus, such as *Coffea liberica* L. and *Coffea canephora* Pierre, as well as some wild coffee relatives (Jaramillo et al. 2009). So far, none of the currently used coffee varieties have shown resistance against CBB. However, recent studies on transgenic varieties of *C. arabica* have shown the potential to induce CBB mortality and low seed damage through the expression of the *Bacillus thuringiensis* Berliner toxin Cry10Aa (Valencia-Lozano et al. 2021; Molina et al. 2022).

Strategies to control the coffee berry borer

Monitoring and decision making

Since CBB individuals are small and spend most of their lives inside coffee berries, they are difficult to detect until their population has increased and crop injury has been caused. Monitoring CBB infestations can inform farmers whether there is a risk that the economic damage threshold will be exceeded (Pereira et al. 2012; Aristizábal et al. 2015). Coffee plants are most susceptible to CBB infestations at approximately 90–120 days after the flowering season when coffee berries reach 20% of their total dry weight (Friederichs 1922; Jaramillo et al. 2009). Using attractant-baited traps or visual assessments of infested berries are the most common ways to monitor CBB infestations (Johnson et al. 2020). For instance, alcohol-baited traps are used to monitor the flight activity of the adult females in many coffee-growing countries, including Colombia, Costa Rica and Nicaragua (Pereira et al. 2012; Aristizábal et al. 2015). The alcohol-based baits mimic the kairomones produced by developing coffee berries and the baits can be active for up to eight weeks (Mendesil et al. 2009; Aristizábal et al. 2015). Coffee berry borer infestations can also be visually assessed using the 30-tree sampling method developed by Cenicafé (Aristizábal et al. 2016). This methodology entails the assessment of the fraction of CBB-infested berries on one representative branch of 30 randomly selected coffee trees per hectare (Aristizábal et al. 2016).

Monitoring the presence of CBB adult females, the number of infested berries and the position of the female inside the berries can inform farmers whether pest management actions are needed, and, if so, what is the appropriate timing (Aristizábal et al. 2016). Insecticide applications are most effective before CBB females enter the coffee berry. Once inside, CBB is protected and is less susceptible to control measures (Pereira et al. 2012; Aristizábal et al. 2015). Despite the merits of monitoring for making informed pest-management decision making, it is not a standard practice because it is labor intensive and requires training or technical assistance (Johnson et al. 2020). In Colombia, coffee growers also base their CBB control measures on the "performance factor" of their coffee of the previous season. This factor is a quality score based on the level of CBB infestation of coffee beans by coffee buyers, which influences the price that growers receive for their produce (Pabón and Osorio 2019).

Crop sanitation

Crop sanitation has become a key practice for the control of the coffee berry borer (Bustillo 2006; Aristizábal et al. 2016), which, when conducted properly, can reduce CBB infestations from 70% to less than 6% (Aristizábal et al. 2002, 2004a). Infested coffee berries that remain on the coffee trees or that have fallen on the ground can be reservoirs of CBB (Bustillo 2006). To reduce these reservoirs and avoid the carry-over effects of CBB to the next season, farmers can manually collect as many CBB-infested coffee berries as feasible throughout the growing season. In Spanish, this practice is referred to as "Re–Re" [combination of "recolección" (collection) and "repase" (appraisal)] (Waterhouse and Norris 1989). Sanitation should not be limited to the coffee crop, but should also be conducted in other locations that may act as potential reservoirs of CBB, such as sites where the coffee is processed (Moreno et al. 2001; Aristizábal 2018). Once berries are collected, farmers must keep them isolated with plastics under direct sunlight (solarization) or bury them at least 10 cm in the ground to kill the CBB and prevent their spread (Aristizábal 2018). In regions where coffee berries are developing throughout the year, it is recommended to sanitize the crop every 2–3 weeks to avoid reinfestations of CBB and overuse of insecticides (Sponagel 1994).

Sanitation practices are labor intensive (Bustillo et al. 1998; Aristizábal et al. 2017) and the feasibility and efficacy of sanitation depend on the characteristics of the site and coffee crop, financial resources, and the availability of berry collectors and their skills (Aristizábal 2018). For instance, steep slopes of the coffee plantation, large coffee trees, and many fallen berries can make the manual work more challenging and less effective (Baker 1999; Damon 2000).

Biological control

Biological control of CBB has been studied and implemented extensively since the early 1900s as an alternative to the use of synthetic insecticides (Vega et al. 2015; Johnson et al. 2020). Birds, lizards, insects, entomopathogenic nematodes and fungi have been found feeding on and infecting CBB (Escobar-Ramírez et al. 2019). Biological control of CBB may comprise classical biological control (i.e., the use of natural enemies in inoculative releases; usually, both the pest and the natural enemy are of exotic origin), augmentative biological control (i.e., the use of natural enemies in inundative and seasonal inoculative releases) and conservation biological control (i.e., the management of the environment to improve the effectiveness of already established natural enemies). Current biological control practices for CBB include the augmentative release of natural enemies, including parasitoids and entomopathogenic fungi (Vega et al. 2015; Escobar-Ramírez et al. 2019). These will be discussed below.

Parasitic wasps

Parasitic wasps native to Africa, such as *Cephalonomia stephanoderis* Betrem, *Prorops nasuta* Waterston, and *Physmaticus coffea* LaSalle, have been used worldwide in CBB biological control programs because they can parasitize immature stages of CBB and feed on the adult females (Bustillo 2006). In Central and South America, classical biological control programs using *C. stephanoderis* and *P. nasuta* were implemented by Cenicafé for the first time during the 1980s and 1990s to suppress CBB populations in coffee berries on trees and on the soil (Bustillo 2006). However, parasitization levels of CBB in Central and South America were significantly lower than previously reported in African countries (Escobar-Ramírez et al. 2019). For instance, CBB infestation levels decreased by less than 10% even when a large number of wasps were introduced into the field (Baker et al. 2002; Jaramillo et al. 2006). After release, the parasitoids were hardly detected anymore after 12 months (Vega et al. 2015).

Phymasticus coffea was introduced to South America from West Africa in 1996. In contrast to *C. stephanoderis* and *P. nasuta*, *P. coffea* attacks CBB females before they enter coffee berries and cause damage. Parasitization of CBB females impairs oviposition and CBB females are killed after approximately 12 days (Infante et al. 1994). *Phymasticus coffea* is highly specific to beetles from the genus *Hypothenemus* (Jaramillo et al. 2006) and very effective in parasitizing CBB adults (Escobar-Ramírez et al. 2019). For instance, over a two-year period, *P. coffea* reduced CBB infestations by up to 50%, resulting in significant improvements in coffee yields in Mexico (Infante et al. 2013).

Phymasticus coffea has established in several coffee farms in Colombia (Baker 1999; Aristizábal et al. 2004b; Bustillo 2006) and in other coffee-growing regions, such as Hawaii (Yousuf et al. 2021) and Mexico (Castillo et al. 2006). In 2005 the first field release of mass-reared *P. coffea* was made in Colombia and over a period of two years *P. coffea* reduced CBB infestation levels from 80% to levels ranging from 5 to 30% (Aristizábal et al. 2012). However, parasitism rates of *P. coffea* strongly depend on the time of release because it can only parasitize CBB females before they drill into coffee berries and not after that (Jaramillo et al. 2005). While *P. coffea* parasitism rates of up to 85% have been reported when CBB infestation levels were below 5% (Vergara et al. 2001), *P. coffea* is less effective in suppressing CBB when crop infestations are severe (Jaramillo et al. 2005).

The augmentative biological control of CBB using parasitic wasps is relatively costly and labor-intensive (Vega et al. 2015). For instance, the commercial rearing of *C. stephanoderis* and *P. nasuta* has so far not been cost-effective because of the relatively long development time of the immature stages and the associated high number of immature CBB beetles required for their rearing (Baker 1999). *P. coffea* requires a large number of CBB females for their mass rearing and adults only live for two or three days (Bustillo et al. 2006; Escobar-Ramírez, et al. 2019). Yet, to achieve high parasitization levels, at least ten *P. coffea* wasps have to be released per adult CBB in the field (Rodríguez et al. 2017). Innovations, such as the development of an artificial diet for mass rearing of CBB and parasitic wasps, hold promise to further upscale production and reduce costs for mass rearing of CBB biological control agents (Baker et al. 2002).

Although augmentative biological control has achieved some successes in CBB control (Escobar-Ramírez et al. 2019; Johnson et al. 2020) this practice has not been broadly adopted by coffee farmers as it is not compatible with the use of insecticides and crop sanitation (i.e., without CBB-infested berries in the crop, parasitic wasp populations cannot survive). Moreover, the access, cost, and labor requirement for releasing high numbers of biological control agents can restrain farmers from adopting this practice (Damon 2000; Vega et al. 2015).

Entomopathogenic fungi

The entomopathogenic fungus *Beauveria bassiana* Bals-Criv is the most used biological control agent worldwide for augmentative biological control of CBB (Aristizábal et al. 2016). *Beauveria bassiana* infects CBB females before they enter the berry and may lead to mortality levels of up to 70% under optimal environmental conditions (Damon 2000; Vega et al. 2015). However, when CBB infestation levels are high at the beginning of the coffee growing season, *B. bassiana* applications are unlikely to substantially reduce crop damage (Hollingsworth et al. 2020).

Beauveria bassiana is most effective at temperatures ranging between 20 and 30 °C, RH levels of 70–90%, and low exposure to solar radiation (Jaramillo et al. 2006). These conditions are best met in humid and cloudy weather conditions, and more often at high-elevation than low-elevation conditions (Johnson et al. 2020). However, high precipitation can wash away *B. bassiana* spores, thus reducing the proportion of spores reaching CBB (Hollingsworth et al. 2020).

Since the environmental conditions are a key determinant for effective *B. bassiana* conditions and these can change quickly, the timing of *B. bassiana* applications is key to the effective control of CBB (Mascarin and Jaronski 2016). Coffee growers typically apply *B. bassiana* and/or the entomopathogenic fungus *Metarhizium anisopliae* Sorokin between three and eight times per year, but timing, dosage, and interactions with other management practices are often barely taken into account (Johnson et al. 2020). Mejía and López (2002) reported that 51% of visited farms in the Antioquia department of Colombia have tried entomopathogenic fungi for CBB control, but that 71% of these farmers did not continue using the fungi because of a limited efficacy.

Entomopathogenic nematodes

Entomopathogenic nematodes (EPNs) are natural enemies of CBB that can be found in the soil with the potential to be used for augmentative control, especially to control CBB reinfestations from fallen berries (Lara et al. 2004; Benavides et al. 2010). The nematodes *Steinernema carpocapsae* Weiser (Manton et al. 2012), *Steinernema feltiae* Filipjev (Molina and López 2002; Lara et al. 2004), *Metaparasitylenchus hypothenemi* Poinar (Poinar et al. 2004) and *Heterorhabditis* sp. (Molina and López 2002; Lara et al. 2004) can infect larval and adult CBB stages, and can inflict mortalities of 5% in adults and 17% in immature stages under laboratory conditions (Benavides et al. 2010; Manton et al. 2012). Currently, the use of EPNs for CBB biological control is still in development, and not yet used in practice.

Insecticide use

The use of synthetic insecticides is a pest management practice often implemented when coffee berry damage is significant in conventionally managed coffee systems. The first report of the use of synthetic insecticides to control CBB infestations was the application of benzene hexachloride (BHC) powder in selected experimental coffee plantations in Brazil in the early 1940s (Sauer 1947 in Mansingh 1991). By the 1960s, the use of chemical insecticides was adopted across all coffee-producing countries and in particular the use of the organochlorine endosulfan became prevalent (Johnson et al. 2020).

Chemical insecticides can be effective in reducing CBB infestations by up to 88% in one single application when applied before CBB females drill their entry tunnels (Vijayalakshmi et al. 2014). Applying insecticides when CBB already tunnelled into coffee berries is likely to be much less effective (Vega et al. 2015). Currently, the main marketed insecticides against CBB in Latin America include neonicotinoids (e.g., clothianidin, imidacloprid, sulfoxaflor, and thiametoxam), organophosphates (e.g., dimethoate, phentoate), pyrethroids (e.g., cypermethrin, phallethrin), and hormonal inhibitors (e.g., lufenuron, novaluron, spiromesifen) (ICA 2024). However, the use of insecticides can lead to unintended, undesirable side effects (Brun et al. 1994; Lubick 2010; Infante 2018). First, the broad-spectrum insecticides commonly used against CBB, such as endosulfan, chlorpyrifos, fenitrothion, fenthion, and pirimiphos-methyl, accumulate in the environment (Olisah et al. 2019) and may pose a health risk to consumers (Rotterdam Convention 1998; UNEP-POP 2011; Vasseghian et al. 2021). As a consequence, Colombia recently banned the use of endosulfan and chlorpyrifos (Swissinfo 2022). Second, the use of broad-spectrum insecticides against CBB can give rise to non-target effects in other organisms, including natural enemies and pollinators. Lethal and sublethal effects of endosulfan and chlorpyriphos have been reported in coffee agroecosystems in multiple species of beneficial insects across countries (Reis et al. 2015). The European Union banned the outdoor use of clothianidin, imidacloprid and thiamethoxam due to the sublethal and lethal non-target effects on pollinators such as bees in 2018 (Stokstad 2018). Third, the indiscriminate and inadequate use of insecticides can trigger resistance development in CBB (Monzón et al. 2008). Brun et al. (1994) were the first to report CBB resistance to endosulfan after ten years of biannual applications in five localities in New Caledonia. Resistance to endosulfan has been reported in Colombia, where CBB populations have developed a mutation in the *Rdl* gene that triggers resistance to endosulfan and other insecticides (Navarro et al. 2010). Since Brun et al. (1994) first studies, research related to insecticide resistance has been carried out in other coffee-producing countries, such as Nicaragua (Pérez et al. 2000), the Philippines, Guatemala, Brazil, and Cameroon (Kern and Geib 1998). To counteract CBB resistance to insecticides, products with alternative modes of action, such as chlorantraniliprole, have been developed (Plata-Rueda et al. 2019). Nevertheless, there is a potential risk that these new products may initiate the next cycle of the pesticide treadmill (Bakker et al. 2020).

While botanical insecticides, i.e., naturally occurring chemicals extracted or derived from plants or minerals, may have potential for the control of CBB, we did not find reports of coffee growers using these. Experimental field trials with azadirachtin and castor oil applications resulted in 41 and 54% CBB mortality, respectively, even though castor oil had a low persistence in the environment (Celestino et al. 2016). The application of mixed neem and D-limonene oils caused a 63% reduction in CBB on coffee trees (Brito et al. 2021). Research on botanical insecticides is still limited, and further studies on effective application methods, doses and formulations are needed before these products are ready for commercial use.

Integrated pest management

Integrated pest management (IPM) programs for CBB have been developed to reduce the reliance on synthetic insecticides and enhance CBB suppression through the combination of monitoring, sanitation, biological control, and as a last resort, selective chemical control practices (Fig. 2). CBB monitoring can inform whether action is needed. Once the berries are infested, sanitation reduces the spread of CBB through the crop and to the next harvest season. The implementation of pest suppression practices, such as biological control, may limit further coffee bean injury, and practices such as sanitation will help to reduce the overall infestation of the crop. The use of chemical insecticides is only recommended as a last option when damage by CBB has exceeded the economic damage threshold (Johnson et al. 2020).

Economic damage thresholds are based on the cost of the control measure *versus* the cost associated with the crop injury when the pest is not managed (Duque et al. 2003). Economic damage thresholds for CBB vary across regions due to differences in coffee cultivation practices and economic conditions (Wegbe et al. 2003). In Colombia, this threshold is 2% infested berries (Posada et al. 2003), which aligns well with reported thresholds of 2.3% in Togo (Wegbe et al. 2003) and 2.7% in Guatemala (Duque

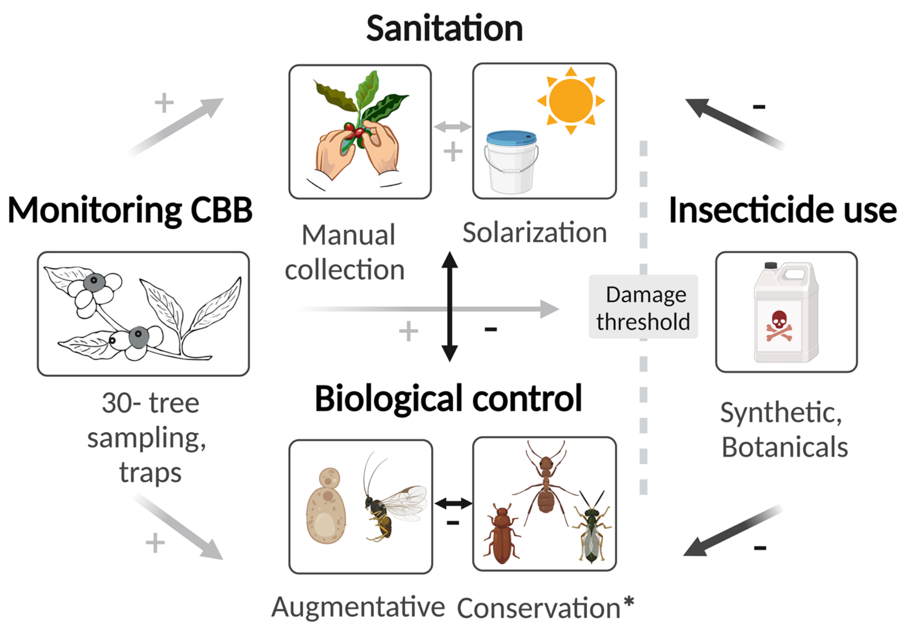

Fig. 2 Positive and negative interactions between current and potential* practices of IPM programs to control coffee berry borer (CBB) in coffee crops. Light-gray and dark-gray lines represent positive (+) and negative (−) interactions between practices, respectively. The gray dashed line represents the economic damage threshold. Insecticide use only should be considered once this threshold has been reached. *Conservation biological control is not included as part of IPM recommended practices yet. (Color figure online) Source: Johnson et al. (2020)

and Baker 2003). In contrast, the economic damage threshold in Mexico is 30%, which is associated with relatively high labor costs (Duque and Baker 2003).

An appropriate and accurate implementation of IPM recommendations is crucial for its success (Benavides et al. 2002; Aristizábal et al. 2006). If a CBB control action is needed in the crop, using biological control agents rather than synthetic insecticides is highly encouraged in IPM programs to avoid the use of toxic chemicals in the crop. Different IPM practices targeted at CBB are likely to interact with each other (Fig. 2). For instance, the use of broad-spectrum insecticides often reduces the diversity and abundance of non-target insects in the crop, including natural enemies of CBB (Mejía et al. 2000). Moreover, biological control agents, such as *B. bassiana* and *M. anisopliae,* may also affect predators and parasitoids, potentially compromising the predation and parasitization of CBB (Bustillo et al. 1998). Crop sanitation reduces CBB abundance in coffee plantations, but at the same time reduces the availability of CBB as prey and/or host for predators and parasitic wasps. While some natural enemies, such as fire ants, can contribute to CBB predation, they can also interfere with sanitation as these ants can be annoying for the berry collectors (Johnson et al. 2020).

IPM practices can serve as integral components of coffee certification schemes, such as Fair Trade, UTZ Certified, Organic Certification, 4C Association, and C.A.F.E., providing coffee growers the opportunity of receiving higher prices and other commercial advantages compared to non-certified coffee Willer et al. (2022). In 2021, 23% of the global coffee production (> 1.2 GT coffee) was certified by Rainforest Alliance, of which 65% was produced in Latin America. Brazil is the main producer of certified coffee (29% of the global production), followed by Vietnam (16%), and Colombia (12%) (Rainforest Alliance 2021).

Conservation biological control

Conservation biological control entails the conservation and enhancement of natural enemy communities that are already present in the agroecosystem via habitat management to improve the provision of food and shelter and minimize activities that are harmful to natural enemies (e.g., minimizing the use of broad-spectrum insecticides) (Begg et al. 2017). Currently, research and development for CBB are broadening from the traditional focus on classical biological control to include conservation biological control approaches. Habitat management practices for conservation biological control of CBB have been studied at the crop level (e.g., intercropping, shade-coffee management, and weed management), the farm level (e.g., crop diversification, organic management), and the landscape level (e.g., conservation of forest and semi-natural areas) (Escobar-Ramírez et al. 2019).

A broad range of natural enemy groups in coffee crops have been studied to find potential CBB biological control agents (Morris et al. 2018; Escobar-Ramírez et al. 2019). For instance, adults and larvae of the wasp *Heterospilus coffeicola* Schmiedeknecht have been reported feeding on CBB eggs and larvae causing up to 16% mortality of CBB in coffee fields in Uganda (Morris et al. 2018). *H. coffeicola* females lay their eggs inside CBB-infested berries, and once the eggs hatch, the larvae feed on CBB eggs and larvae. In addition to *H. coffeicola*, the adult flat bark beetles, *Leptophloeus* sp. and *Cathartis quadricollis* Guérin-Méneville, have been reported feeding on immature stages of CBB mainly inside ripe berries (Follet et al. 2016). Probably the best-documented group of natural enemies of CBB are ants (Morris et al. 2018), which will be discussed below.

Ants

Ants are generalist predators that, depending on the species, can attack both immature and adult stages of CBB, inside and outside of coffee berries. Ants are common in most coffee systems and can reach CBB by climbing the coffee trees or by attacking CBB inside or outside fallen coffee berries (Vélez et al. 2006; Morris et al. 2018). Ants can exert a high predation pressure on CBB for extended periods because borers are not directly consumed but are stored in their nests. Indeed, ants have been reported to control seasonal CBB infestations and outbreaks of CBB during the dry season (Morris et al. 2018).

Ants represent a wide diversity of species, with specific foraging and nesting behaviors, and can suppress CBB infestations through several mechanisms. There are two broad guilds of CBB-predating ants: arboreal and ground-dwelling ants (Perfecto and Vandermeer 2013). Arboreal ants, such as twig-nesting, carton-nesting, and weaver ants, often nest and forage in the coffee or shade trees (Gillete et al. 2015). Ground-dwelling ants, such as soil-nesting, carpenter, and fire ants, can attack and remove CBB in fallen berries (Morris et al. 2018). However, ground-dwelling ants can also be found in coffee trees where they may predate on CBB or throw CBB females off the trees that search for coffee berries (Philpott and Armbrecht 2006; Morris et al. 2018).

Research on the role of ants in the conservation biological control of CBB has been especially extensive in Mexican coffee agroecosystems (Morris et al. 2018). The keystone and native ant species *Azteca sericeasur* Longino has been associated with lower CBB abundance and coffee infestation levels (Perfecto and Vandermeer 2006). In Costa Rica, Vélez et al. (2006) identified *Solenopsis geminata* Fabricius, *Mycocepurus smithii* Forel, *Dorymyrmex* sp., and *Pheidole* sp. ants as important natural predators of CBB in coffee crops. In Colombia, at least six ant genera have been observed feeding on the beetle, including *Solenopsis* sp., *Pheidole* sp., *Wasmannia* sp., *Paratrechina* sp., *Crematogaster* sp., and *Brachymyrmex* sp., with *Solenopsis picea* Emery reported as a highly effective CBB predator (Bustillo et al. 2002; Armbrecht et al. 2005). Most of these ant species are relatively small and can penetrate CBB-infested coffee berries through the galleries created by the female CBB and take out the CBB larvae and eggs to transport them to their nests (Bustillo et al. 2002). This removal behavior has also been observed in *Wasmania auropunctata* Roger and *S. picea* under laboratory conditions (Morris et al. 2015).

Ants can suppress CBB infestations in coffee systems. It is well documented that ants suppress the damage of CBB in both the laboratory (Pardee and Philpott 2011; Philpott et al. 2012) and the field (Gonthier et al. 2013; Jiménez-Soto et al. 2013). Coffee fields with at least one ant species that feeds on CBB had at least 10% lower CBB infestation levels and shorter CBB gallery lengths in infested berries compared to fields without ants (Jiménez-Soto et al. 2013). Ant exclusion experiments revealed that *A. sericeasur* and *Pheidole synanthropica* Longino reduced CBB infestation levels in coffee fields by 12.3 and 15.4%, respectively. *A. sericeasur* often drops CBB off trees, while *P. synanthropica* takes CBB beetles back to their nest (Jiménez-Soto et al. 2013). Overall, a reduction in CBB infestation levels was reported in the presence of ants (Jiménez-Soto et al. 2013). When *A. sericeasur*, *Pseudomyrmex simplex* Smith, and *Procryptocerus hylaeus* Kempft ants were present, this resulted in an approximately 50% reduction of the CBB population in laboratory experiments (Philpott et al. 2012).

Although ants have the potential to suppress CBB populations, this potential is mediated by other factors, such as the ecological networks in which these ant communities are embedded, the intensity of the coffee farm management, and the composition of the agricultural landscape (Morris et al. 2018). Dominant ant species may compete with and exclude small ground-dwelling ants, thereby interfering with CBB predation within the berries fallen on the ground (Trible and Carrol 2014). Moreover, a higher diversity of arboreal and ground ants has been associated with coffee crops with a higher density and diversity of shade trees (Larsen and Philpott 2010) and more heterogeneous agricultural landscapes (Escobar-Ramirez 2019, 2020; Ibarra-Isassi et al. 2021). Promoting ant community diversity on farms might enhance CBB control. However, the specific management practices to support these ant communities are not well understood at present. Further quantification of the contribution of ants to CBB control is still needed (Morris et al. 2018).

Coffee management for natural enemy conservation

Coffee management practices are a key factor for the conservation of natural enemies of CBB (Harelimana et al. 2022). Farm practices, such as limited use of chemical insecticides and the addition and/or conservation of shading trees, can influence the community of natural enemies and their trophic interactions in the coffee crops (Perfecto et al. 2014; Bongers et al. 2015). For instance, reducing insecticide use in coffee agroecosystems had a positive effect on natural enemies of CBB, such as predatory ants (Perfecto et al. 2014). Shade-grown coffee systems, in which coffee is grown under a canopy of trees, provide relatively favorable conditions to support abundant and diverse communities of native natural enemies, and the associated potential for CBB suppression (Vandermeer et al. 2010; Perfecto et al. 2014) (Fig. 2). Predatory ants, spiders, and birds have been shown to be effective in reducing CBB populations (Philpott et al. 2008; Perfecto et al. 2013), and parasitic wasps provide better CBB control in shade-grown coffee than in sun coffee systems (Johnson et al. 2010; Martínez-Salinas et al. 2022). Shade-grown coffee farms create a more favorable microclimate for natural enemies of CBB as canopy trees can help to regulate temperature and humidity (Jaramillo et al. 2009) by reducing incoming solar radiation (López-Bravo et al. 2012), and mitigating climate change effects and variability (Méndez-Rojas et al. 2022). However, shade-grown coffee systems do not consistently benefit from enhanced CBB suppression and crops within different farm types and agroecological contexts may display contrasting responses. For instance, Mendez-Rojas et al. (2022) found that the frequency of predation events in sun coffee systems was higher than in shade-grown coffee. This warrants studies on the underlying mechanisms of the effects of shade on the biological control of CBB by native predators.

Besides the conservation of shade trees, little is known about the influence of other farm features (e.g., farm size, crop diversity) and habitat management practices (e.g., establishing flowering plant resources, tailored weed management) on endemic CBB natural enemies. For instance, larger farms often experience different pest and management pressures compared to smaller farms (Bongers et al. 2015; Perfecto et al. 2019). Furthermore, since ants are known to feed on extra-floral nectar sources (Lange et al. 2017), establishing plant species that provide nectar or extrafloral nectar in coffee agroecosystems may enhance ant predation activity (sensu Schifani et al. 2020; Fernandez de Bobadilla et al. 2024). A better understanding of the habitat needs of naturally occurring natural enemies and key characteristics of agroecosystems to support these natural enemies can help to further improve conservation biological control of CBB.

The landscape context of conservation biological control

The surrounding landscape of coffee farms may influence CBB populations and their natural enemy communities (Escobar-Ramírez et al. 2020). CBB females and their natural enemies are mobile and need to find resources such as food and shelter scattered across space and time. For instance, coffee crops and other habitats containing CBB host plants can act as potential source habitats for CBB, from which CBB can colonize other nearby areas, including nearby coffee crops. However, coffee crops infested with CBB may also be source habitats for natural enemies, if natural enemies are able to build up their populations (Bianchi 2022).

Forest and other semi-natural habitats are often associated with abundant and diverse natural enemy communities because these habitats may provide alternative food resources, breeding sites, and shelter for natural enemies (Bianchi et al. 2006), even though there are notable exceptions (Tscharntke et al. 2016; Karp et al. 2018). For instance, the diversity of rove beetles (Coleoptera: Staphylinidae) in coffee crops, which are potential predators of CBB, was positively associated with the number of forest patches in the surrounding area (Méndez-Rojas et al. 2022). Moreover, there was a high degree of species turnover of rove beetles within and between coffee plantations, which point to a high mobility and/or strong population dynamics of rove beetles (Méndez-Rojas et al. 2022). The strong population dynamics may be in part explained by management practices of the local or surrounding farms, such as the use of insecticides that kill natural enemies in the local or surrounding coffee crops, reducing the recolonization of natural enemies from the wider environment (Bianchi et al. 2013). Furthermore, fragmentation of natural habitats can reduce the population of natural enemies of CBB by limiting their movement (spillover) and access to food sources and breeding sites (Rand et al. 2006; Méndez-Rojas et al. 2022).

Relatively little is known about how farm and landscape characteristics influence populations of CBB and their natural enemies in coffee crops, hampering making recommendations for landscape-scale conservation biological control. Since only small (i.e., < 1.5 mm) natural enemies can enter CBB-infested berries, and the capacity for directed movement (but not passive movement) of small arthropods is often limited (Schellhorn et al. 2014), the appropriate spatial scales for habitat management to support natural enemies of CBB still need to be assessed.

Conclusions

The coffee berry borer CBB is an important pest of coffee, and crop losses are expected to increase and expand geographically in the near future as a result of increasing temperatures and erratic rainfall patterns. The current IPM practices that combine cultural, biological, and chemical control methods can be effective in managing CBB populations, but the efficiency of these practices is context-dependent, and may be insufficient to control CBB infestations under conditions of changing climate patterns, low availability of labor, or insufficient financial resources to hire workers or purchase biological control agents. While there have been noteworthy successes with classical biological control, the adoption of this practice has been limited because of the associated costs and efforts, the perceived limited efficacy and the low availability of skilled labor. Conservation biological control of CBB has received relatively limited attention, and there is often only incomplete understanding of which naturally occurring natural enemies contribute to CBB suppression in coffee fields and what their ecological requirements are. While CBB and their natural enemies are expected to be influenced by land use in the surrounding landscape and farm management, the exploration of these relationships is still in its infancy. Current knowledge gaps for developing conservation biological control programs include what habitat management practices can support these naturally occurring natural enemies in coffee systems, what are the appropriate spatial scales for implementing habitat management, and what are the considerations of coffee growers for the uptake of habitat management practices. Therefore, the development of CBB management strategies should also include the perception and knowledge of coffee growers to ensure that the management meets their visions and needs.

Acknowledgements We thank the Graduate School for Production Ecology & Resource Conservation (PE&RC) of Wageningen University and Research for funding this work through the Graduate program 2021, Dr. Ana Pineda for her insightful feedback on the manuscript, and Dr. Pablo Benavides for providing some literature.

Funding Funding was provided by the Graduate School for Production Ecology & Resource Conservation (PE & RC).

Declarations

Conflicts of interest The authors declare that there are no conflicts of interest.

Informed consent The review did not involve human participants and/or animals and so informed consent is not applicable.

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