Received: 30 October 2020 | Revised: 26 December 2020 | Accepted: 19 January 2021

DOI: 10.1111/jen.12868

JOURNAL OF APPLIED ENTOMOLOGY WILEY

REVIEW ARTICLE

The challenge of biological control of *Cosmopolites sordidus* Germar (Col. Curculionidae): A review

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Funding information
European Community (ERDF); French National Research Agency under the Investments for the Future Program, Grant/Award Number: ANR-16-CONV-0004

Abstract

The banana weevil (also known as banana root borer) *Cosmopolites sordidus* Germar (Coleoptera Curculionidae) is the major pest of banana and plantain. Because banana ranks 2nd in fruit production worldwide, this pest has substantial social and economic importance. The biological control of the *C. sordidus* remains challenging because of its behaviour and resistance to parasitism and predation. The last review concerning the biological control of *C. sordidus* was published two decades ago, and relevant knowledge and methods have developed in the interim. The present paper provides an update of that knowledge and summarizes past and current challenges as well as providing perspectives on achieving sustainable control of *C. sordidus*. We first discuss studies on the classical biological control of *C. sordidus*, underlining the limits of classical biological control methods such as the importation of predators, parasitoids or pathogens. Next, we consider conservation biological control of *C. sordidus*, with a focus on ants. We also highlight an 'arthropod bias' that has led to a lack of information on the role of vertebrates in the regulation of *C. sordidus*.

KEYWORDS

ants, banana weevil, conservation biological control, Musa, predation, vertebrates

1 | INTRODUCTION

With growing human populations in Africa, Asia and South America, securing food production in tropical areas is increasingly important. Banana ranks 2nd in fruit production worldwide (FAO, 2018) and along with plantains is an essential component of the nutrition of a large population.

The most important pest of banana and plantain is the banana root borer *Cosmopolites sordidus* (Gold et al., 2001; Okolle et al., 2009). Females of this weevil lay eggs in the lower pseudostem and corm, and larvae develop in the corm. This weakens the plant and can lead to dramatic losses, both directly because of toppling and indirectly because of lower yields and increased infections by plant pathogens (Gold et al., 2001). Damage caused by *C. sordidus* is difficult to assess, however, because the immature stages of the weevil are hidden in the pseudostem and corm and their detection requires destructive sampling (Vilardebo, 1973). Furthermore, because the damage is not immediately visible and because *C. sordidus* effects are partly indirect, the full extent of *C. sordidus* damage is often underestimated until toppling occurs.

The banana weevil can be described as a K-selected species (Pianka, 1970), with a long holometabolan development (almost two months; Vinatier et al., 2009), a low fecundity (two eggs per week; Vinatier et al., 2009) and an extended lifespan (up to 4 years (Gold et al., 2001)). With these features, *C. sordidus* differs from pests like aphids, flies or moths that are typically r-selected species that generate damage because of their ability to rapidly produce large numbers of offspring (Williamson, 1996). However, K-selected species may also be important pests (Duyck et al., 2007).

Its K-selected characteristics should have consequences for the biological control of *C. sordidus*. Because of its slow rate of reproduction, for example, the elimination of a few individuals could have a greater suppressive effect than the same level of suppression in the case of an r-selected pest. The cryptic behaviour of *C. sordidus* also alters the possible interactions with other species. The adults are active at night and are otherwise hidden in the soil (Carval et al., 2015) and larval stages take place inside the banana corm (Gold et al., 2001). These behavioural traits would have strong implications on the possibilities of biological control.

In most zones that produce banana for export, *C. sordidus* is controlled with insecticides (e.g. Armendariz et al., 2014; Okolle et al. 2020; Shinde et al., 2015). In the French West Indies (FWI), the use of chlordecone between 1972 and 1993 caused major and persistent public health problems (Devault et al., 2018; Joachim et al., 2019). For the past three decades, control of *C. sordidus* in FWI has relied on integrated pest management (IPM) strategies based on the use of pitfall traps emitting an aggregation pheromone, on fallow periods that break the reproductive cycle of the pest and on in vitro-produced banana plants (Beauhaire et al., 1995; Duyck et al., 2012; Okolle et al. 2020). However, these cultural practices have not yet been applied in many regions that produce export banana and are often unaffordable for small growers that produce banana and plantains for local markets. In the current context of biodiversity decline and the need for sustainable food production, biological control in general and conservation biological control (CBC) in particular is needed for the banana weevil. Classical biological control can be achieved through the introduction of known enemies of a pest (DeBach & Rosen, 1991) while CBC is based on the natural enemies hypothesis (see Elton, 1958; Root, 1973), that is, CBC relies on the conservation and augmentation of natural enemies already present in the geographic area of concern (Ehler, 1998). CBC is usually considered more sustainable than classical biological control, because imported species may attack non-target species (Stiling & Cornelissen, 2005). Furthermore, the introduction of a single predator or parasite is not always followed by a decrease in pest numbers or damage (Letourneau et al., 2011).

Several studies have been conducted to identify enemies of *C. sordidus*. In 1951, Cuillé (1951) published a broad review of what was then known about *C. sordidus* and its control. A very complete review on IPM strategies was subsequently published by Gold et al. (2001). However, knowledge about the biological control of *C. sordidus* has increased since then and study methods are rapidly evolving. The aim of this article is to provide a synthesis of the recent knowledge and to highlight most promising perspectives on the biological control of *C. sordidus*, with a special emphasis on agroecological practices. First, we describe classical biological control via the importation of parasites, parasitoids or predators. We then review research on CBC, with emphasis on recent approaches including the use of environmental DNA metabarcoding and analysis of in-field images. Finally, we discuss how the constraints and biases that limit the biological control of *C. sordidus* can be overcome.

2 | BIOLOGICAL CONTROL OF *Cosmopolites sordidus* WITH INTRODUCED ORGANISMS

2.1 | Limits of entomopathogenic fungi and nematodes

Biological control of *C. sordidus* includes microbiological control with the entomopathogenic fungus *Beauvaria bassiana*, which has been shown to substantially reduce weevil populations in laboratory experiments (up to 100% larval mortality, Kaaya et al., 1993; Lopes et al., 2011), in greenhouse trials (up to 88.9% larval mortality, Akello et al., 2007) and with artificially inoculated weevils (42% adult mortality, Godonou et al., 2000; 72% mortality Nankinga & Moore, 2000). Although results have been promising under these controlled settings, the efficiency of *B. bassiana* in the field is unclear (González et al., 2018; Lopes et al., 2014; Tinzaara et al., 2007). Tinzaara et al. (2007) explore the possibility of enhancing the dissemination of *B. bassiana* with the use of aggregation pheromones (sordidin, see Beauhaire et al., 1995). González et al. (2018) also assessed the suitability of the fungus *Metarhizium anisopliae* for microbiological control of *C. sordidus* and obtained results that were similar as *B. bassiana* (up to 76.9% of adult mortality under laboratory conditions and 48.5% in field trials). Consequently, fungus-based strategies remain scarcely used to control *C. sordidus*. Furthermore, *B. bassiana* has a broad host range (Devi et al., 2008; McKinnon et al., 2017) and may therefore be harmful to non-target species. The entomopathogenic nematodes *Steinernema carpocapsae* and *Heterorhabditis bacteriophora* have also been shown to control *C. sordidus* (up to 68% infected larvae, Sepúlveda-Cano et al., 2008; Treverrow et al., 1991). To our knowledge, however, their effectiveness has only been documented under controlled conditions, and these nematodes can also parasitize a broad range of non-target species (de Doucet et al., 1999). Their potential effects on non-target organism have been discussed (e.g. Hodson et al., 2012).

2.2 | Introduction of predators

When looking for potential enemies of *C. sordidus*, researchers first searched the native region of *C. sordidus*. Since the beginning of the 20st century, researchers have looked for the pest's natural enemies in Java and Indonesia (Froggatt, 1924, 1928; Jepson, 1914). More recently, studies have identified *Plaesius javanus* (Coleoptera, Histeridae) and various ant species as potential predators of *C. sordidus* (Abera-Kalibata et al., 2006; Froggatt, 1928; Jepson, 1914).

For experimental purposes, some researchers introduced Indonesian predators of *C. sordidus* into new regions of banana production. In 1988, Neuenschwander et al. considered the feasibility of introducing several predators into Africa such as the beetles *P. javanus*, *Hololepta quadridentata* (Coleoptera, Histeridae), *Plaesius laevigatus* (Coleoptera, Histeridae) and *Dactylosternum hydrophiloides* (Coleoptera, Hydrophilidae), as well as the ant *Tetramorium* *guineense* (Hymenoptera, Myrmicinae) without further conclusions. *Plaesius javanus* has been successfully introduced and established to the Fiji and Jamaica, *Hyposolenus laevigatus* to Cook Island and Dominica, *D. hydrophiloides* to Australia and Jamaica and *H. quadrientata* (Coleoptera, Histeridae) to Saint Vincent. Following its introduction (Cruz & Segarra, 1992), *P. javanus* has also been detected in Puerto Rico (Pantoja et al., 2007) but at low densities and with limited effects in terms of the biological control of *C. sordidus*; the authors found only three specimens of *P. javanus* in the harvest of 50 non-pesticide-treated plantain corms and the corms were heavily infested by *C. sordidus*. To our knowledge, there has not been further research on the introduction of predators to control *C. sordidus* since then.

2.3 | Parasitism and parasitoids

Parasitoids are used as control agents for various pests because they are often specific and effective (Brodeur & Boivin, 2006). For these reasons, several parasitoids have been assessed for control of *C. sordidus*. In Benin, Traoré (1995) was unable to obtain control of *C. sordidus* with the parasitoid *Anaphes victus* (Hymenoptera: Mymaridae). In Uganda, researchers reported that no parasitoids emerged from *C. sordidus* eggs and larvae that were collected in the field and then incubated in the laboratory (Gold et al., 2001). The lack of effective parasitoids may be explained by the fact that the developmental stages of *C. sordidus* are mostly hidden and are therefore difficult for common species of parasitoid wasps or flies to access (Vinson, 1976).

Mites that were presumed to be parasitic were observed on *C. sordidus* adults (ElJaouhari, 2019). However, the mites have not been identified, and the thick cuticle of *C. sordidus* could prevent effective parasitism.

3 | CONSERVATION BIOLOGICAL CONTROL OF *Cosmopolites sordidus*

Given the lack of on-field success with classical biological control methods, researchers studying the biological control of *C. sordidus* in banana systems are now focusing on the control provided by generalist predators that naturally occur in banana fields. Agroecological banana systems currently designed are relying on introduction and the management of plant diversity, especially cover crop; more recently, there is a growing interest or on agroforestry (Poeydebat et al., 2017). In contrast to classical biological control, the aim of CBC is to favour local species and to maximize the regulation they provide. CBC has the advantage of being sustainable over time, but its efficacy can be limited by the behaviour of *C. sordidus*. This is because adult banana weevils are relatively large, and therefore, predators must be either large or numerous to attack an adult or must be small enough to target the larval stages in the galleries in the corm.

3.1 | Generalist arthropod predators

Natural predators of *C. sordidus* were first studied in Javanese and Indonesian banana fields (Froggatt, 1924, 1928; Jepson, 1914) but have since been reported in every major banana production zone. In 1992 and 1993, Koppenhöfer and colleagues reported that the predators of various stages of *C. sordidus* were dominated by coleopterans and dermapterans including *Eutochia pulla* (Coleoptera, Tenebrionidae), *Euborellia annulipes* (Dermaptera, Anisolabididae) and *Dactylosternum abdominale* (Coleoptera, Hydrophilidae) (Koppenhöfer, 1993; Koppenhöfer et al., 1992). In the FWI, identified predators of *C. sordidus* include the ants *Solenopsis geminata* (Hymenoptera, Myrmicinae) and *Camponotus sexguttatus* (Hymenoptera, Formicinae), as well as earwig *Euroborellia caraibea* (Dermaptera, Anisolabididae) (Carval et al., 2016; Duyck et al., 2011; Mollot et al., 2012, 2014; Tixier et al., 2013). Poeydebat et al. (2017) found a negative correlation between generalist predator abundance and *C. sordidus* abundance. In Costa Rica, cockroaches have been observed to feed on exposed *C. sordidus* larvae (Tresson, Tixier, Puech, Bagny Beilhe, et al., 2019). Vinatier et al. (2009) also emphasized the effect of predators on the developmental stages of *C. sordidus*; the authors indicated that generalist predators and particularly egg predators help reduce banana weevil numbers.

3.2 | Special case of ants

As early as the 1940s, Hargreaves (1940) suggested that ants are potential predators of the banana weevil. The subsequent advent of insecticides limited research on ants as predators of the pest. The predation of *C. sordidus* by ants has been proven, however, in various locations in Africa, South America and the Caribbeans (e.g. Abera-Kalibata et al., 2007; Armendariz et al., 2014 and Mollot et al., 2012, respectively). Ants may be more able than other predators to access the eggs and larvae of *C. sordidus*, which are located in the corm. As pointed out by Abera-Kalibata et al. (2007), ants have substantial foraging abilities and may therefore be useful predators of *C. sordidus* eggs and larvae. Ants are known to control other borer pests (Way et al., 1992; Way & Khoo, 1992) and to be efficient generalist predators (Offenberg, 2015; Philpott & Armbrecht, 2006). Although ants have been observed foraging in the tunnels of *C. sordidus* larvae (Abera-Kalibata et al., 2007), the tunnels were in a very damaged or within dead corms, and it is unclear whether ants could forage in galleries of more intact corms because such galleries are usually filled with latex (Gold et al., 2001). In a field study, Poeydebat et al. (2017) found that *C. sordidus* damage was negatively correlated with the abundance of omnivorous ants, but the abundance of *C. sordidus* adults was not correlated with the abundance of omnivorous ants; the authors therefore suggested that ants might preferentially attack eggs or immature stages of *C. sordidus*. The latter study and also Mollot et al. (2012) demonstrated the difficulty in quantifying the effects of ant-based CBC on *C. sordidus* numbers.

Since 1975 ability of ants to control *C. sordidus* has been studied extensively in Cuba, where *Pheidole megacephala* (Hymenoptera, Myrmicinae) and *T. guineense* have been identified as potential predators of *C. sordidus* (Bendicho, 1987; Castiñeiras & Ponce, 1991; Neuenschwander et al., 1988; Roche, 1975; Roche & Abreu, 1983). These species have therefore been deployed in Cuban banana plantations where they have been reported to control *C. sordidus* (Perfecto, 1994; Perfecto & Castiñeiras, 1998).

The potential of predatory ants to regulate *C. sordidus* numbers has been investigated in Uganda by Abera-Kalibata et al. (2007), Abera-Kalibata et al. (2008); ants (*Pheidole* sp. and *Odontomachus troglodytes* (Hymenoptera, Ponerinae)) reduced numbers of *C. sordidus* eggs, larvae and pupae inside crop residues in controlled conditions (up to 65% egg removal for *Pheidole* sp.). In a field trial, ant-enhanced plots showed 2.8 times less eggs per sucker than ant-excluded plots (1.8 ± 0.2 versus 0.64 ± 0.1, respectively). However, at the end of a full growth cycle (30 months), damages were not significantly different. In Kenya and Cameroon as well, several ant species have been reported to be predators of *C. sordidus* (Dassou et al., 2015; Fansi & Okolle, 2008; Uronu, 1992). In Cameroon, *C. sordidus* abundance was negatively correlated with the abundance of some ant species (*Axinidris* sp., *Monomorium* sp., *Pheidole* spp. and *Tetramorium* sp.). In the same study, the abundance of other species (*Paratrechina longicornis* (Hymenoptera, Formicinae), *Camponotus* spp. and *O. troglodytes*) was in contrast positively correlated with *C. sordidus* abundance, perhaps because the habitat was favourable for both the ants and the weevil or because of intra-guild predation and competition among on ant communities (Dassou et al., 2015). There is a promising field of research in unravelling what mosaics of habitats, composed of plants from different stata, plant residues, bare soil, favour most *C. sordidus* predatory ants.

Ants have also been hypothesized to be predators of *C. sordidus* in Venezuela (Goitia & Cerda, 1998) and mentioned as predators of *C. sordidus* in Colombia and Ecuador (Armendariz et al., 2014). During several experiments in FWI, DNA metabarcoding and stable isotope analysis of gut contents demonstrated the role of ants (particularly *S. geminata* and *C. sexguttatus*) in the predation of *C. sordidus* (Duyck et al., 2011; Mollot et al., 2014; Tixier et al., 2013).

The value of ants as biological control agents may be ambiguous because they also can be regarded as pests in other crops or as harmful for the farmers (e.g. fire ants, see Eubanks, 2001). Moreover, for many ants that have been reported as potential predators of *C. sordidus*, identification was not always performed to the species level. Ant species of the same genus may behave very differently and may differ in size and diet, and this lack of species identification complicates the ability to assess the role of ants in *C. sordidus* control.

Photographs taken in the field allowed detailed analysis of the behaviours of different ant species in Costa Rica (Tresson, Tixier, Puech, Bagny Beilhe, et al., 2019). *Camponotus atriceps* (Hymenoptera, Formicinae) were observed to feed on dead adults but not on any living stages of *C. sordidus*; *S. geminata* consumed *C. sordidus* eggs and larvae but were unable to kill a live adult; *Pheidole radoszkowskii* (Hymenoptera, Myrmicinae), *O. bauri* and *Nylanderia* sp. consumed larvae and also were scavengers. Furthermore, a single individual of *O. bauri* was able to seize a larva, while at least five *P. radoszkowskii* were needed to capture a larva (Tresson, Tixier, Puech, Bagny Beilhe, et al., 2019). Ants show a great variety of behaviour, size and activities that are relevant to their role as biological control agents.

3.3 | Vertebrates as predators

Reports of predation of *C. sordidus* by vertebrates have generally been considered to be anecdotal (Gold et al., 2001). The giant toad *Rhinella marina* (Dawl, 1985) and the large arboreal lizard *Anolis cristaelus* (Wolcott, 1923) have been reported as predators of the *C. sordidus*. In New South Wales, Australia, Hely et al. (1982) suggested that rats, bandicoots frogs and birds may as well be predators of *C. sordidus*. Radiotelemetry approaches (Vinatier et al., 2010) may provide new information on predation by the toad *Rhinella marina* (F. Vinatier, 2019, pers. com.). Overall, biological control studies often focus on the predation of arthropods by other arthropods and often ignore predation by other taxa. This arthropod bias could result in an underestimation of the predation of *C. sordidus* by other taxa (see Section 4.2).

3.4 | Diversification of plant species may favour CBC

Diversification of plant species in the field is now often suggested as a way to increase regulation of *C. sordidus* by natural enemies (Mollot et al., 2012; Poeydebat et al., 2017; Tixier et al., 2013). The abundance of predators was generally higher in more diversified systems (Dassou et al., 2016); in this study, associated plants to plantain included in particular cocoa trees (*Theobroma cacao*), palm trees (*Elaeis guineensis*), papaya and a wide range of root and tuber vegetables. The addition of a new plant species (in particular grasses from the family of Poaceae as *Brachiara decumbes* and *Cynodon dactylon*) in a banana field can reduce the intra-guild predation and thereby favour predation of *C. sordidus* (Duyck et al., 2011; Tixier et al., 2013). Predation of *C. sordidus* eggs was higher in plots with cover crops (*B. decumbes*) than with bare soil (Mollot et al., 2012). Very simple diversification strategies, however, can result in less predation of *C. sordidus* than occurs with bare soil. Mollot et al. (2014), for instance, showed that predators consumed fewer *C. sordidus* in a monospecific cover crop of *B. decumbens* than on bare soil. Similarly, Carval et al. (2016) found that a monospecific cover of *Paspalum notatum* reduced *C. sordidus* abundance but not *C. sordidus* damage to banana plants. These latter two studies suggest that more complex plant diversification may be needed to enhance the natural control provided by predators. The integration of shrubs and trees appears to be useful for enhancing predation in general and predation by ants in particular (Dassou et al., 2017). Diversification may also have a dilution effect on pests, diminishing their abundance (Root, 1973). Finally,

TABLE 1 Reported predators of *Cosmopolites sordidus*. The species in bold have been confirmed to consume of *C. Sordidus* in reproducible experiments; the other species have been assumed to be predators of *C. sordidus* or have been considered to be predators based on personal observations or correlations

Order	Family	Observed enemies	Enemy stade	Target stade	Estimated regulation	Place	Reference
Araneae	Lycosidae	spider				Martinique	Tixier et al. (2013); Duyck et al. (2011)
Blattodea		**cockroach**	Adult	Larva		Costa Rica	Tresson, Tixier, Puech, Bagny Beilhe, et al. (2019)
Coleoptera	Carabidae	***Abacetus optimus***	Adult	Egg, larva		Kenya	Koppenhöfer et al. (1992)
		Galerita tristis				Martinique	Tixier et al. (2013); Duyck et al. (2011)
	Cucujidae	*Canthartus* sp.				Java	Froggatt (1924, 1928); Jepson (1914)
		Alegoria dilatata				Colombia	Armendariz et al. (2014)
	Histeridae	***Hister niloticus***	Adult	Larva		Kenya	Koppenhöfer et al. (1992)
		Hololepta quadridentata				Cuba	Neuenschwander et al. (1988)
		Hololepta striaditera	Adult	Egg, larva		Kenya	Koppenhöfer et al. (1992)
		Plaesius javanus	Larva, adult	Immatures	88%–53% 70% Larva–pupa (lab) in tunnels (Abera 2006)	Java, Indonesia, Ecuador	Jepson (1914); Froggatt (1928); Abera-Kalibata et al. (2006); Armendariz et al. (2014)
		Plaesius laevigatus				Cuba	Neuenschwander et al. (1988)
	Hydrophilidae	***Dactylosternum abdominale***	Larva, adult	Egg, larva	50–39%–90% Suckers-stumps-pseudostem residues	Kenya	Koppenhöfer et al. (1992); Koppenhöfer (1993)
		Dactylosternum hydrophiloides				Cuba	Neuenschwander et al. (1988)
	Labiidae	***Labia borellii***		Egg, larva		Kenya	Koppenhöfer et al. (1992)
		Labia curvicauda		Egg, larva		Kenya	Koppenhöfer et al. (1992)
	Staphylinidae	*Belonuchus ferrugatus*				Java	Froggatt (1924, 1928); Jepson (1914)
		***Charichirus* sp.**	Larva	Egg, larva		Kenya	Koppenhöfer et al. (1992)
		Hesperius sparsior	Larva	Egg, larva		Kenya	Koppenhöfer et al. (1992)
		Leptochirus unicolor				Java	Froggatt (1924, 1928); Jepson (1914)
		Thyreocephalus interocularis	Larva, adult	Egg, larva, pupa		Kenya	Koppenhöfer et al. (1992)
	Tenebrionidae	***Eutochia pulla***	Adult	Egg	20,50%	Kenya	Koppenhöfer et al. (1992); Koppenhöfer (1993)
	Trogossitidae	Tenebroinids				Kenya	Uronu (1992)
	Anisolabididae	***Euborellia annulipes***	Adult	Egg, larva	28,00%	Kenya	Koppenhöfer et al. (1992); Koppenhöfer (1993)
		Euborellia caraibea		Egg, larva		Martinique	Duyck et al. (2011); Carval et al. (2016); Mollot et al. (2014); Tixier et al. (2013)
	Forficulidae	*Forficula* sp.				Kenya, Ecuador, Colombia	Uronu (1992); Armendariz et al. (2014)

(Continues)

TABLE 1 (Continued)

Order	Family	Observed enemies	Enemy stade	Target stade	Estimated regulation	Place	Reference
Diptera	Rhagionidae	*Chrysophilus ferruginosus*	Larva			Java	Froggatt (1928)
Hymenoptera	Formicidae	*Axinidris* sp.	Adult			Cameroon	Dassou et al. (2015)
		Camponotus sexguttatus	Adult			Martinique	Mollot et al. (2014)
		Camponotus atriceps	Adult	Adult (scavenging)		Costa Rica	Tresson, Tixier, Puech, Bagny Beilhe, et al. (2019)
		Camponotus sp.	Adult			Kenya, Colombia, Ecuador	Uronu (1992); Armendariz et al. (2014)
		Dorylus sp.	Adult			Kenya	Uronu (1992)
		Ectatomma ruidum	Adult			Venezuela	Goitia and Cerda (1998)
		Lepisiota sp.	Adult	Egg		Uganda	Abera-Kalibata et al. (2007)
		Monomorium sp.	Adult			Cameroon	Dassou et al. (2015)
		Myopopone castanea	Adult	Egg, larva		Indonesia	Abera-Kalibata et al. (2006)
		***Nylanderia* sp.**	Adult	Larva		Costa Rica	Tresson, Tixier, Puech, Bagny Beilhe, et al. (2019)
		Odontomachus bauri	Adult	Egg, larva, adult		Martinique, Costa Rica	Duyck et al. (2011); Tresson, Tixier, Puech, Bagny Beilhe, et al. (2019)
		Odontomachus troglodytes	Adult	Egg	33%–68% eggs removed	Uganda	Abera-Kalibata et al. (2007), Abera-Kalibata et al. (2008)
		Paratrechina sp.	Adult	Egg		Uganda	Abera-Kalibata et al. (2007)
		Pheidole megacephala	Adult	Egg, larva		Cuba	Perfecto and Castiñeiras (1998); Castiñeiras & Ponce (1991)
		Pheidole radozkowskii	Adult	Egg, larva		Costa Rica	Tresson, Tixier, Puech, Bagny Beilhe, et al. (2019)
		***Pheidole* sp.**	Adult	Egg	38%–65% eggs removed (Abera et al. 2008)	Uganda, Kenya, Cameroon	Abera-Kalibata et al. (2007), Abera-Kalibata et al. (2008); Uronu (1992); Dassou et al. (2015)
		Solenopsis geminata	Adult			Martinique, Costa Rica	Mollot et al. (2014); Tresson, Tixier, Puech, Bagny Beilhe, et al. (2019)
		Tetramorium guineense	Adult	Egg, larva	65,00% trap catches (Roche & Abreu)	Cuba	Neuenschwander et al. (1988); Roche (1975); Roche and Abreu (1983); Perfecto and Castiñeiras (1998); Bendicho (1987)
		Tetramorium sp.	Adult			Cameroon	Dassou et al. (2015)
		Wasmannia auropunctata				Venezuela	Goitia and Cerda (1998)
Scolopendromorpha	Cryptopidae	centipedes				Martinique	Duyck et al. (2011)

(Continues)

TABLE 1 (Continued)

Order	Family	Observed enemies	Enemy stade	Target stade	Estimated regulation	Place	Reference
vertebrate		*Anolis cristatelus*				Puerto Rico	Wolcott (1923)
		bandicoots				New South Wales	Hely et al. (1982)
		birds				New South Wales	Hely et al. (1982)
		Rhinella marina				Philippines	Dawl (1985)
		unidentified frogs and toads				New South Wales, Martinique	Hely et al. (1982); Vinatier et al. (2010)
		rats				New South Wales.	Hely et al. (1982)

Collard et al. (2018), who used a modelling approach, recommended that CBC could be enhanced by increasing the edge length or interface between the crop and non-crop habitat of the predators.

3.5 | Limits of CBC

CBC is by nature very context-dependent. This can be a major drawback when studying or applying CBC (Rusch et al., 2017). Ecological communities and their predation services may be specific to certain regions or landscapes. It can therefore be a heavy constraint for a farmer to conduct a diverse agrosystem without guaranty of success if a desired predator species does provide regulation services.

4 | DISCUSSION

4.1 | Accurate assessment of *C. sordidus* abundance, damage to the crop and regulation by predators

Accurate assessment of *C. sordidus* populations is still difficult, because pitfall traps catch only adults, and enumerating eggs and larvae is destructive. Furthermore, damage is not always well correlated with numbers of adults (Gold et al., 2001; Poeydebat et al., 2017). Quantifying with certitude the effect of a given species of predator on *C. sordidus* abundance and damage is also difficult. Although these assessments are possible under controlled conditions, the assessments obtained may not be transferable to the field. For instance, the efficient regulation of *C. sordidus* by ants under controlled conditions in the greenhouse (Abera-Kalibata et al., 2008) has not been reported in field trials. Accurate damage assessment is also difficult because it is destructive and can therefore be estimated only after harvest. *C. sordidus* damage is usually measured by using the coefficient of infestation proposed by Vilardebo (1973) or by using methods based on the coefficient of infestation (e.g. Ogenga-Latigo & Bakyalire, 1993). This coefficient relies on a subjective scoring by the researcher while observing a corm cross section (0 being a sane corm and 100 a fully infested corm). The difficulties in assessing *C. sordidus* numbers and damage have limited the ability of researchers to produce quantitative and accurate results (Ogenga-Latigo & Bakyalire, 1993). New approaches are therefore needed to achieve a non-destructive and accurate measurement of *C. sordidus* populations and damages. An interesting perspective would be to improve the damage indicator used on banana and to standardize the measurement of the predation intensity, for instance using sentinel cards.

As noted above, assessment of predation is also difficult and can be considered imprecise for most of the studies presented in this review. In Table 1, species that have been identified with certainty as predators of *C. sordidus* are highlighted. When available, assessments or estimates of *C. sordidus* population regulation are also provided. Most of the studies conducted before 2000 identified organisms as predators of *C. sordidus* based only on limited observation or on common knowledge; that is, the status of the organism as a predator was not firmly established.

Densities and a closed space, for example, could alter the feeding behaviour of a predator. The cryptic and nocturnal behaviour of *C. sordidus* tends to suggest that potential predators should be either nocturnal or with abilities to search in the soil and in plant residues. Within controlled conditions, some predators may have consumed weevils but since they have diurnal feeding behaviour in natural settings, they are unlikely to be effective predators in field conditions.

More recent studies have mostly relied on correlation to infer the regulation of *C. sordidus* by predators. Although these assessments are usually conducted in the field and therefore reflect the reality of the field, correlative approaches cannot prove cause-and-effect, that is, cannot demonstrate with certainty the predation of *C. sordidus* by a given species of predator.

Most recently, the DNA contained in gut content appears to have a great potential to prove the trophic link between a predator and its preys in field conditions (Sow et al., 2020), but to date such approaches still need to be applied in broader conditions to provide a wider insight on *C. sordidus* predation. This method has been applied to the identification of species as predators of *C. sordidus* were done (Mollot et al., 2014). As mentioned by the latter authors, however, there are also biases with the use of metabarcoding, in particular with ant predation. Because of the social behaviour of ants, the stomach content of a worker may not reflect the collective regime of a colony. For instance, even though Mollot et al. (2014) observed *S. geminata* workers capturing *C. sordidus* eggs, the authors failed to find residues of *C. sordidus* DNA in the stomachs of workers. Mollot et al. (2014) proposed that the eggs might have been fed to and consumed by the larvae rather than by the foraging workers. Metabarcoding also does not enable researchers to discriminate between predation, scavenging and secondary predation (Hagler, 2019).

More recently, methods have been developed that rely on the combined use of sentinel prey and automated image analysis (Tresson, Tixier, Puech, Bagny Beilhe, et al., 2019; Tresson, Tixier, Puech, & Carval, 2019). Images as a source of information have the advantage of showing predation with certainty and with fewer behavioural biases than occur in laboratory experiments. Automated image analysis enables the recording of real predation events under relatively unbiased field conditions (see Grieshop et al., 2012; Zou et al., 2017). Furthermore, the combined use of sentinel prey cards and automated image analysis enables researchers to differentiate between trophic and non-trophic interactions in the arthropod community.

4.2 | Arthropod bias

As noted earlier in this review, most studies of predation of *C. sordidus* have focused on predation by arthropods (mainly insects). Among the 49 studies reviewed in this paper, only three mentioned vertebrates as predators (Dawl, 1985; Hely et al., 1982; Wolcott, 1923). This may be due to the methods used to assess biodiversity (e.g. pitfall traps), which readily sample small animals (and therefore arthropods) rather than vertebrates. For instance, Zou et al. (2017) used video monitoring to determine that predation of brown planthopper by frogs in rice fields was substantially underestimated. Given that the banana weevil is a relatively large insect, it is reasonable to suspect that predation by larger animals (toads, lizards, rats etc.) may be significant. Therefore, further studies should be conducted to assess the potential of regulation of *C. sordidus* by vertebrates. This could be achieved by experiments combining the use of sentinel prey and automated image analysis in experimental or production plots. It would also be valuable to better quantify the importance of predation of *C. sordidus* by vertebrates (toads, lizards, birds, etc.) using exclusion experiments in field conditions.

5 | CONCLUSION

The biological control of *C. sordidus* is an old but persistent challenge in all banana production zones. After a century of research across the globe, we are able to draw several conclusions about the biological control of *C. sordidus*. Classical biological control of this pest seems to be ineffective. Recent studies therefore tend to favour CBC and generalist predators. Among generalist predators, ants seem capable of attacking eggs and larvae of *C. sordidus*. However, our understanding of the trophic network around *C. sordidus* and of predator reduction of the damage caused by *C. sordidus* requires improvement. Most of the knowledge about the predation of *C. sordidus* comes either from laboratory experiments or from observations and correlations, that is, with so much control of organisms and conditions such that we do not gain much understanding of actual behaviour in the field or with so little control of organisms and conditions that causal relationships remain uncertain. As a consequence, our understanding of the regulation of *C. sordidus* by predators remains quite limited. However, novel approaches such as the use of images, immunomarking techniques or metabarcoding may help better understand the behaviour of *C. sordidus* and its enemies on the field.

ACKNOWLEDGEMENTS

This review was carried out as part of the CIRAD DPP COSAQ agronomical research programme (activities 20152021) funded by a grant from the European Community (ERDF) and the Conseil Régional de La Réunion. This review was also supported by the French National Research Agency under the Investments for the Future Program, ANR-16-CONV-0004. The Ph.D. thesis of P. Tresson was funded by CIRAD and #DigitAg grants. The authors thank Bruce Jaffee for revision of the English composition of the manuscript.

CONFLICTS OF INTEREST

All the co-authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTION

P.T., D.C. and Ph.T conceived research. P.T. reviewed the literature. P.T., D.C. and Ph.T. wrote the manuscript. All authors read and approved the manuscript.

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How to cite this article: Tresson P, Tixier P, Puech W, Carval D. The challenge of biological control of *Cosmopolites sordidus* Germar (Col. Curculionidae): A review. *J Appl Entomol*. 2021;145:171–181. https://doi.org/10.1111/jen.12868