Responses of Parasitoids (Hymenoptera) of Diaspis boisduvalii (Hemiptera: Diaspididae) to Insecticides and Herbicides in Costa Rican banana plantations.

Minor Solano-Gutiérrez
`minor.solanogutierrez@ucr.ac.cr`

Universidad de Costa Rica https://orcid.org/0000-0002-5661-0890
Paul Hanson
Universidad de Costa Rica
César Guillén-Sánchez
Universidad de Costa Rica

Research Article

Keywords: banana cultivation, biological control, weed management, Aphytis, Coccobius, Plagiomerus

Posted Date: January 11th, 2024

DOI: https://doi.org/10.21203/rs.3.rs-3838716/v1

Abstract

Armored scale insects (Hemiptera: Diaspididae) have been identified as pests worldwide. In Costa Rica, various armored scale insects are economically important in the production of agricultural and horticultural products for exportation. *Diaspis boisduvalii* Signoret is a primary insect pest in banana plantations, causing substantial economic losses and high control costs. In order to determine the effect of insecticide and herbicide use on percent parasitism of *D. boisduvalii* on banana (*Musa* AAA “Cavendish”) in Costa Rica, six commercial plantations with varying insecticide and herbicide use were sampled over a five-month period. Pseudopetioles from the oldest pseudoleaf of banana plants infested with scale insects were collected monthly at each site. Each pseudopetiole fragment (55 cm^2) was stored in a well-ventilated glass tube and monitored daily for parasitoid emergence, percent parasitism, and sex ratio. Four parasitoid species from two families were identified. A gregarious ectoparasitoid *Aphytis* sp., a solitary endoparasitoid *Coccobius* sp. and a very rare hyperparasitoid *Ablerus* sp. (Aphelinidae), and a solitary endoparasitoid *Plagiomerus peruviensis* (Girault) (Encyrtidae). The study revealed a significant negative impact of insecticides ($p < .001$), but species-specific responses to herbicides. Rather suprisingly, *P. peruviensis* showed a higher percent parasitism in plantations with herbicides than without herbicides, unlike the other parasitoids. Results from sex ratios suggest that *P. peruviensis* reproduces via thelytokous parthenogenesis.

Introduction

Armored scale insects (Hemiptera: Diaspididae) have been identified as pests of perennial plant species worldwide (Miller and Davidson 2005; Mauchline et al. 2011). It is the largest family within the superfamily Coccoidea and has about 2600 described species in 395 genera (Normark et al. 2019). Outbreaks are most common in disturbed environments such as agricultural landscapes, especially if control by natural enemies is removed or reduced (Howard 2001; Ouvrard et al. 2013). In Costa Rica various armored scale insects have economic significance in the exportation of agricultural and horticultural products such as bananas, pineapples, ornamental plants and citrus (Malumphy 2015; Evans and Dooley 2013). Among these, the Boisduval scale (*Diaspis boisduvalii* Signoret) stands out as a primary insect pest in banana plantations, causing substantial economic losses and incurring high control costs (Guillén and Laprade 2016).

Boisduval scales can be found on the pseudostem, pseudopetioles, leaves and fruits of banana (Guillén et al. 2010; Guillén and Laprade 2016) and they are quarantined in most export destinations of Costa Rican bananas (Malumphy 2015; Guillén and Laprade 2016). For the management of this insect, polyethylene bags impregnated with insecticides and targeted applications of horticultural oils, potassium salts of fatty acids and insecticides are used (Guillén et al. 2010; Guillén and Laprade 2016). Little is known about biological control agents of this pest (Solano-Gutiérrez et al. 2019) despite the fact that most successes in the use of biological control have been obtained against scale insects, which are not easily controlled by insecticides (Dhaliwal and Arora 2001; Koul and Dhaliwal 2003).

Parasitic wasps (Hymenoptera: Chalcidoidea) are among the main natural enemies of armored scale insects and are often successful in regulating their populations (Hunter and Wolley 2001; Schmidt and Polaszek 2007; Xiao et al. 2016; Amouroux et al. 2019; Ramos et al. 2018). Effective pest control by parasitoids often correlates positively with diversification of cover crops and reduction in insecticide use, thereby offering techniques for enhancing conservation biological control (Hawkins 1994; Begg et al. 2017; Zaviezo and Muñoz 2023). In contrast, the suppressive effect of residual insecticides on natural enemies is pronounced and negatively affects the community of parasitic wasps of armored scale insects (Raupp et al. 2001). Therefore, the objective of this work was to determine the effect of insecticide and herbicide use on percent parasitism of *Diaspis boisduvalii* in Costa Rican banana plantations.

Materials and methods

Study sites

In order to determine the impact of insecticide use and weed management on parasitism of *Diaspis boisduvalii* in banana (*Musa* AAA "Cavendish"), six plantations were sampled from April to August of 2018. The six sampling sites were commercial banana plantations, each with an area over 100 hectares, dedicated to export production, located on the Caribbean side of the country, and with varying use of insecticides and herbicides (Fig. 1).

Insecticide use and weed management

Weed management was classified as herbicide use or no herbicides use, according to the type of management at each sample site. Intensity of insecticide use was based on ground level insecticide and nematicide applications, where low insecticide use refers to sites that did not use these pesticides to control insects and nematodes at the time of sampling; sites with at least two applications, one each of the aforementioned pesticides, were considered as high intensity of insecticide use (Table 1). Aerial applications of fungicides were not considered since they are used to protect banana plants from diseases such as black sigatoka (Barraza et al. 2011; Bravo Durán et al. 2013; Brühl et al. 2023); all sites received weekly applications because current conditions do not easily allow a reduction in the use of fungicides to control the disease (De Bellaire et al. 2010). Additionally, at all sites polyethylene bags impregned with a mix of Buprofezin (2% by mass) and Bifenthrin (0.1% by mass) were used to cover the developing banana fruits.

Table 1
Pesticides used for insect and nematode control, insecticide use intensity and weed management at the six sampling sites on the Caribbean slope of Costa Rica.

Site	**Pesticides used***	**Insecticide use intensity**	**Weed management**
1	None	Low	Herbicides
2	Pyriproxyfen, Oxamyl	High	Herbicides
3	PSFA**, Terbufos	High	No herbicides
4	Horticultural oil, Oxamyl	High	No herbicides
5	Sulfur, Fluopyram, Oxamyl	High	No herbicides
6	None	Low	No herbicides
*For insect and nematode control, ** Potassium Salts of Fatty Acids			
Insect identification			

Parasitoids were identified to genus level using keys to genera of Aphelinidae (Hanson 1995) and Encyrtidae (Noyes 1980). *Plagiomerus* (Encyrtidae) was identified to species level using Noyes (2023). Specimens were sexed by observing morphological differences in antennae and presence/absence of an ovipositor. The sex ratio was calculated as the proportion male/female. *D. boisduvalii* identification was performed using molecular techniques, where scales recovered during field sampling were stored in absolute ethanol and cold preserved (Morse and Normack 2006).

DNA extraction was performed according to Brandfass and Karlovsky (2008), from four samples containing a single female scale insect and six samples containing groups of five females. Oligonucleotide primers were used to amplify regions of the EF1α gene, where the sense primer EF-1a(a) (GATGCTCCGGGGGACAYAGA) was paired with the antisense primer EF2 (ATGTGAGCGGTGTGGCAATCCAA) and the D2 and D3 expansion segments of the 28S gene by pairing the s3660 sense primer (GAGAGAGTTMAASAGTACGTGAA-AC) with the antisense primer 28b (TCGGAAGGAAGGAACCAGCTACTA), as proposed by Morse and Normack (2006), and by standard PCR protocols using a Veriti® programmable thermal cycler (Applied Biosystems, USA). Sequencing was done by Macrogen Inc, sequence editing was done by using the BioEdit program, and the consensus strand obtained was copied to the NCBI (National Center for Biotechnology Information) "Blast" web page to obtain the molecular identification and identity percentage with previously reported sequences.

Parasitism determination

Sampling was done randomly, but in a well distributed manner; twenty pseudopetioles were collected from the oldest pseudoleaf of banana plants infested with scale insects at each of the six banana plantations. This process was conducted at monthly intervals for five months, resulting in a total of 100 samples per site and 600 analyzed samples in total. The initial number of live healthy adult *D. boisduvalii* females with the third nymphal exuvia present in each pseudopetiole fragment (55 cm2) was recorded. These specimens were then stored in well-ventilated glass tubes and monitored daily for parasitoid emergence (Abell and Van Driesche 2012), identification, and determination of percent parasitism. The determination of percent parasitism was calculated by assessing the number of adult parasitoid insects from each species that emerged and comparing it to the total number of host scale insects initially present in the sample (Abd-Rabou et al. 2014, Wiese et al. 2005). For parasitism by *Aphytis* sp., a correction of 3 parasitoids per female scale insect was applied. This correction factor was utilized because *Aphytis* sp. is a gregarious ectoparasitoid, and the findings indicated an average of 3 pupae per host (Table 2).

Data analysis

To test predictions regarding the relationships between weed management and intensity of insecticide use on parasitism of *D. boisduvalii*, a series of generalized linear models (glm) were developed. In these models, weed management and intensity of insecticide use served as predictors, while scale insect parasitism was the response variable, using a binomial distribution because of overdispersion in the dependent variable. The 'glm' function and likelihood ratio test/ANOVA type II for significance testing were performed. To improve the generalized linear models, parasitism was analyzed as proportion data of discrete counts and analyzed with logistic regression (Mangiafico 2016). Furthermore, to determine statistical differences between treatments, estimated marginal means were determined from glm models using the *emmeans* package 1.5.5 (Lenth 2022) and all pairwise comparisons of means were separated ($p < 0.05$) through 'cld' function using the Šidák correction with the *multcompView* package 0.1-8 (Graves et al. 2019). All statistical analyses were performed in R 4.2.2 (R Core Team 2023).

Results

Four species of parasitoids from two families were identified: a gregarious ectoparasitoid *Aphytis* sp., a solitary endoparasitoid *Coccobius* sp., a very rare hyperparasitoid *Ablerus* sp. (all three belonging to the family Aphelinidae), and a solitary endoparasitoid *Plagiomerus peruviensis* (Encyrtidae). *Aphytis* sp. showed an average of 3 pupae per host, with a range of 1–6. In general, percent parasitism of *D. boisduvalii* showed a high dispersion with an average of 5.66% (range of 0-83.05%) by *P. peruviensis*, 9.28% (range of 0-75.76%) by *Coccobius* sp. and 1.07% (range of 0-42.11%) by *Aphytis* sp. (Table 2)

Table 2
Number of parasitoid pupae per female scale insect, parasitism (%) and type of development for each of the primary parasitoid species of *Diaspis boisduvalii* in Costa Rican banana plantations.

Parasitoid	**Parasitoid pupae / female scale**			**Development**	**Parasitism (%)**	
	n	**Mean (Sd)**	**Range**		**Mean (Sd)**	**Range**
Plagiomerus	15	1	-	Solitary endoparasitoid	5.66 (12.61)	0–83.05
Coccobius	15	1	-	Solitary endoparasitoid	9.28 (11.71)	0–75.76
Aphytis	35	3 (± 1.28)	1–6	Gregararious ectoparasitoid	1.07 (4.18)	0–42.11
Sd = Standard deviation of the mean						

Sites with high insecticide use and no herbicides showed the lowest percent parasitism with an average of 10.41%. The highest rate of parasitism was at sites with low insecticide use and with use of herbicides ($p > 0.05$), these sites having an average parasitism of 27.46%. However, there was no statistical difference between sites with high insecticide use and no herbicides versus high insecticides plus herbicide use ($p < 0.05$). In the same manner, there was no statistical difference between sites with low insecticide use and no herbicides versus low insecticides plus herbicide use (Fig. 2, Appendix: Table S2). In general, there was a statistical difference between sites with low and high insecticide use with an average percent parasitism of 24.94% and 11.35%, respectively (Appendix: Table S1).

Parasitism remained consistently low in sites with high insecticide use, with a percent parasitism of 10.41 and 14.99% without and with herbicide use, respectively (Fig. 2, Appendix: Table S2-3), and no significant differences were observed in the percent parasitism by each species due to herbicide use at these sites ($p = 0.173$, $p = 0.314$, and $p = 0.114$ for *P. peruviensis*, *Coccobius* sp. and *Aphytis* sp., respectively; Appendix: Table S4). However, in sites with low insecticide use, the use of herbicides dramatically reduced the percent parasitism by *Coccobius* sp. ($p < 0.001$), i.e. 0.89 and 18.76% with and without herbicide use, respectively (Fig. 3b, Appendix: Table S4). In contrast, in areas where herbicides were used as a weed management method, a highly significant positive effect was observed on percent parasitism by *Plagiomerus peruviensis* ($p < 0.001$), i.e. 26.52 and 1.17% with and without herbicide use, respectively (Fig. 3a, Appendix: Table S4). Percent parasitism by *Aphytis* sp. on *D. boisduvalii* showed no significant differences with respect to herbicide use and remained low, with no parasitism recorded in sites where herbicide was used (Fig. 3c, Appendix: Table S4).

The sex ratios (male/female) of parasitoid adults emerging from adult female *D. boisduvalii* exhibited notable variation between parasitoid species. Only 15% of the emerging *Coccobius* sp. were male, signifying a highly skewed sex ratio towards females. *Plagiomerus peruviensis* displayed an extremely low sex ratio, with just 1% of the emerging adults being male. In contrast, *Aphytis* sp. exhibited a higher proportion of males, with a sex ratio of 27% males, and *Ablerus* sp. displayed a balanced sex ratio, with 1.06 males for every female (Fig. 4).

Discussion

Insecticides remain the most common pest management tool globally (Guedes et al. 2016). These compounds are applied in the environment to reduce target species populations, either by increasing mortality or decreasing fecundity (Guedes et al. 2016; Sánchez-Bayo 2021). The predominant method of banana cultivation in Costa Rica is through an agricultural monocrop system and depends on extensive use of synthetic pesticides that impact ecosystems (Brühl et al. 2023). In order to control pest populations such as *D. boisduvalii* and other banana pests, insecticides are commonly employed. This is done by using polyethylene bags to cover the banana fruit during its growth, these bags being impregnated with a mixture of insecticides, or by applying insecticides at ground level. In many cases, both methods are utilized. Additionally, at least two applications of insecticides or nematicides are used annually to regularly control nematode populations in almost all banana plantations (Polidoro et al 2008). Pesticides have adverse effects on living organisms, particularly impacting non-target species such as natural enemies of insect pests (Theiling and Croft 1988; Guedes et al. 2016; Schmidt-Jeffris 2023). This effect was dramatically observed in this study, where the intensity of insecticide use significantly affected the percent parasitism of *D. boisduvalii*; parasitism varied from 24.94–11.35% in sites with low and high insecticide use, respectively (Fig. 2, Appendix: Table S1).

Insecticides are the most toxic pesticides to natural enemies, followed by herbicides (Theiling and Croft 1988). As mentioned above, insecticides negatively affected all parasitoids of *D. boisduvalii*, which was expected. However, the species-specific response among *D. boisduvalii* parasitoids in relation to herbicide use (Fig. 3, Appendix: Table S4) was quite unexpected and is diffiucult to explain. Both *Plagiomerus* and *Coccobius* are koinobiont endoparasitoids, and therefore presumably pro-ovigenic and relatively short-lived. These two parasitoids might thus be expected to respond similarly to herbicides, which was not the case. Perhaps *Plagiomerus* is less affected by herbicides due to differences in its physiology or behavior, and its scarcity in herbicide-free plantations is simply an artifact. Interspecific competition can play a role in shaping community structure of parasitoids (Cusumano et al. 2016), but it seems unlikely that this explains the results for *Plagiomerus* given the relatively low levels of parasitism.

In addition to their toxic effects, herbicides also have indirect effects by reducing the diversity of nectar resources upon which adult parasitoids depend (Shaw 2006; Wäckers et al. 2008; Snart et al. 2018; Zaviezo and Muñoz 2023). Mealybugs (Hemiptera: Pseudococcidae) are present in Costa Rican banana plantations (Palma-Jiménez et al. 2019), and honeydew from these insects could possibly serve as a sugar source for *Plagiomerus* in environments where associated plants are scarce, such as those where herbicides were used for weed management (Wäckers et al. 2008; Neerbos et al. 2019).

Parasitoids of *D. boisduvalii* in banana plantations showed strikingly different sex ratios (Fig. 4). In the vast majority of Hymenoptera males develop from unfertilized (haploid) eggs, a phenomenom known as arrhenotokous parthenogenesis, while females develop from fertilized (diploid) eggs. The relatively low proportion of males in *Aphytis* sp. and *Coccobius* sp. might indicate the existence of local mate competion, whereby mating occurs between siblings prior to dispersal (Hamilton 1967). However, further investigation is required to test this possibility. On the other hand, the near absence of males in *P. peruviensis* suggests the existence of thelytokous parthenogensis, i.e. unmated females producing only daughters. The bacterial symbiont *Cardinum* has previously been implicated in thelytokous parthenogenesis in another species of *Plagiomerus* (Matalon et al. 2007), and it would be interesting to examine whether this is also the case in *P. peruviensis*. Whether thelytokoy could explain the better performance of *P. peruviensis* in environments with herbicides is an open question.

In conclusion, our study revealed a significant impact of insecticides on the parasitoids of *D. boisduvalii* in Costa Rican banana plantations as well as species-specific responses of the parasitoid species with respect to herbicide use. The latter result was surprising and further research is required to determine if indeed *P. peruviensis* is less affected by herbicide use than are *Aphytis* sp. and *Coccobius* sp. If this finding is confirmed, there remains the interesting question of what factors or mechanisms underlie the different susceptibilities to herbicides. It is also important to explore interactions between mealybugs, *D. boisduvalii* and parasitoid populations, as well as the influence of plant community composition. Studying the selectivity of each pesticide used in banana plantations to parasitoids is crucial for preserving natural enemies. Mitigating nontarget effects of pesticides and increasing vegetation diversity within banana agroecosystems are essential for the success of biological control and conservation.

Declarations

Author contribution

All authors conceived and designed the research. MSG and CG conducted the research. PH contributed with insect identification. MSG carried out data analysis. MSG and PH wrote the manuscript. All authors reviewed and approved the manuscript.

Acknowledgements

The authors thank Marcos Rojas, Julio Rodríguez and Pedro Ávila for their help with field work. Authors also thank Miguel González and Jorge Sandoval from the Corporación Bananera Nacional de Costa Rica (CORBANA) for their support so that the research could be carried out.

Funding

This work was fully funded by the Corporación Bananera Nacional de Costa Rica (CORBANA), Department of Entomology.

Data Availability

The dataset and code generated in this study are available from the corresponding author.

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Figures

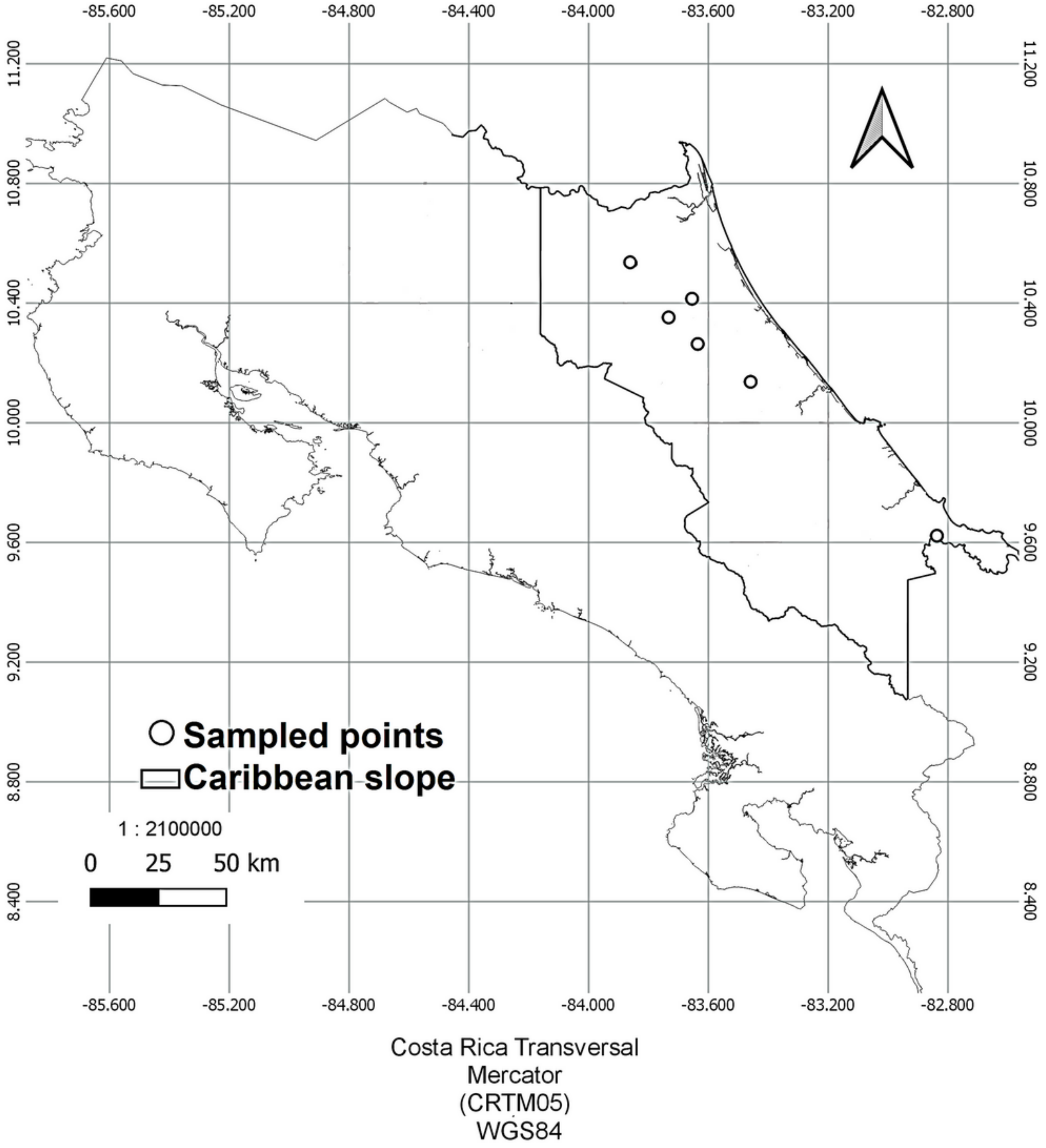

Figure 1

Sampling sites. Highlighted area represents the Caribbean slope where bananas are grown and small circles indicate sites that were sampled.

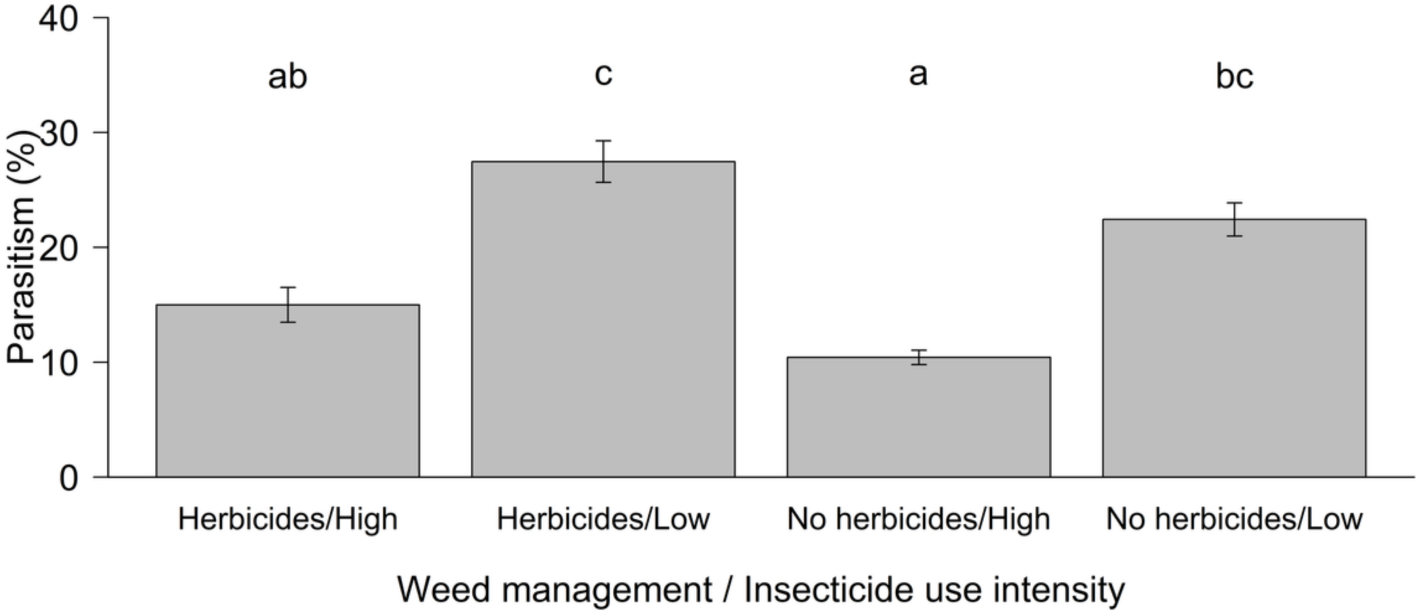

Figure 2

Effect of weed management (herbicide use) and insecticide use on percent parasitism of *Diaspis boisduvalii* in Costa Rican banana plantations. Error bars represent standard error of the mean and different letters indicate significant statistical differences between treatments ($p < 0.05$).

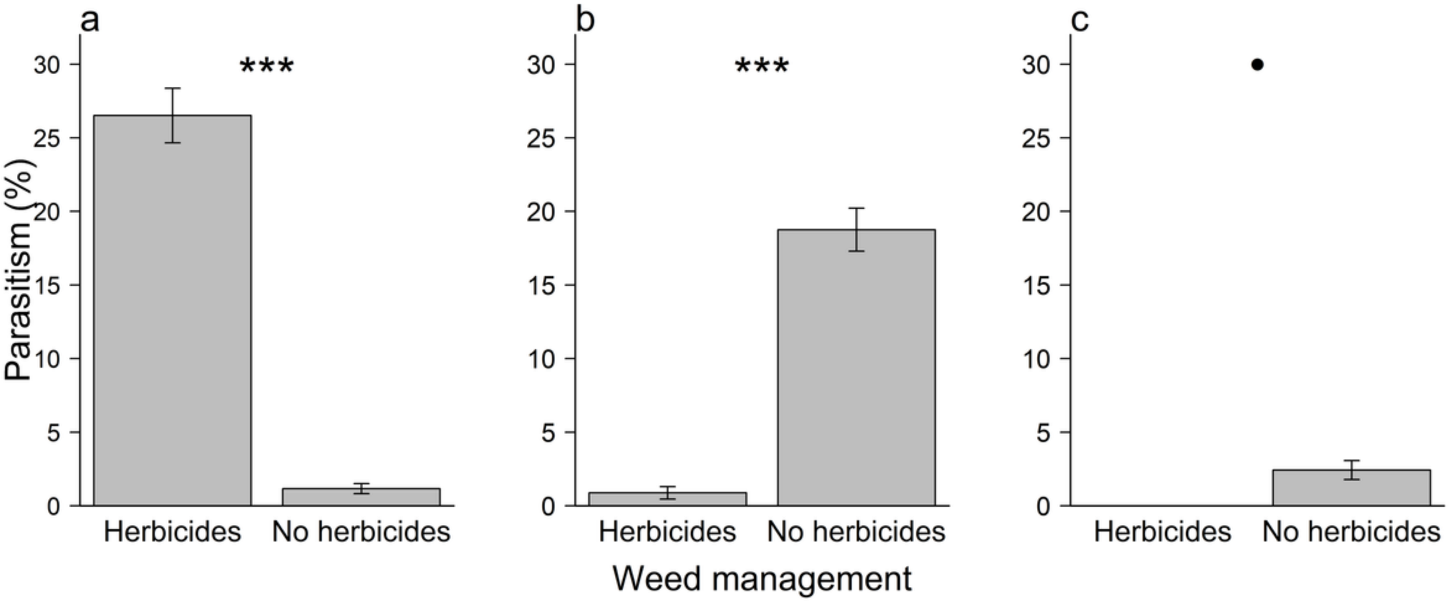

Figure 3

Effect of herbicide use on percent parasitism of *Diaspis boisduvalii* in banana plantations with low insecticide use. a) *Plagiomerus peruviensis* b) *Coccobius* sp. c) *Aphytis* sp. Error bars represent standard error of the mean, • $p < 0.1$, *** $p < 0.001$.

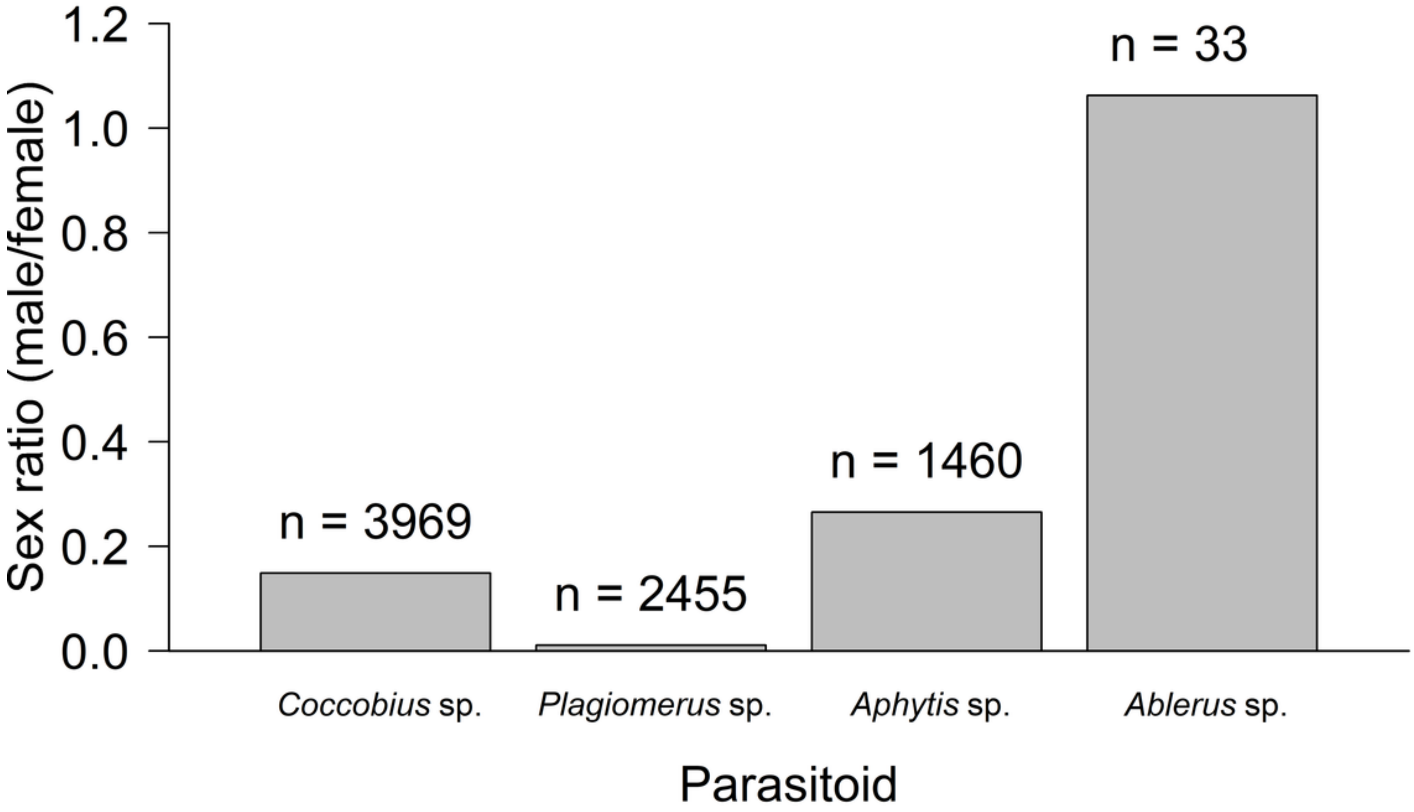

Figure 4

Sex ratio for each of the parasitoid species of *Diaspis boisduvalii* in Costa Rican banana plantations.

Supplementary Files

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