Biological Control - Parasitoids and Predators

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A Host–Parasitoid Model for *Aspidiotus rigidus* (Hemiptera: Diaspididae) and *Comperiella calauanica* (Hymenoptera: Encyrtidae)

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Abstract

The outbreak of the coconut scale insect *Aspidiotus rigidus* Reyne (Hemiptera: Encyrtidae) posed a serious threat to the coconut industry in the Philippines. In this article, we modeled the interaction between *A. rigidus* and its parasitoid *Comperiella calauanica* Barrion, Almarinez, Amalin (Hymenoptera: Encyrtidae) using a system of ordinary differential equations based on a Holling type III functional response. The equilibrium points were determined, and their local stability was examined. Numerical simulations showed that *C. calauanica* may control the population density of *A. rigidus* below the economic injury level.

Key words: modeling, biological control—parasitoids and predators, host–parasitoid interactions

Pest infestation has been a problem since the beginning of agriculture. Two common reasons for pest outbreaks are the introduction of foreign species and the absence of natural enemies (David 2000). This was the case when a species of armored scale insect invaded the coconut farms in South Luzon, Philippines, in 2014. A proportion as high as 70% of the farms were affected by the infestation (Ganzon 2013). The armored scale insect was identified as *Aspidiotus rigidus* Reyne (Hemiptera: Encyrtidae) (Watson et al. 2014). It attaches to a host plant and uses it for food. *A. rigidus* has a wide range of host plants but has high preference for coconut trees. Typically, *A. rigidus* attaches itself to the lower surface of the leaf, but during pest outbreaks, it occupies the fruit and leaves of a coconut tree. It sucks the sap out of the tree and the result is the yellowing of leaves, a decrease in crop yield, reduced copra content and nut production, and tasteless or slightly sour coconut water (Reyne 1948). In severe infestations, the tree dies in 6 mo or less (Watson et al. 2014).

A. rigidus has several natural enemies, but none of them has so far proved its ability to control the pest (Reyne 1948, 1947; Watson et al. 2014). A new species that has shown potential as a biological control agent against *A. rigidus* is *Comperiella calauanica* Barrion, Almarinez, Amalin (Hymenoptera: Encyrtidae). It was first observed in Calauan, Laguna, Philippines, on 4 April 2014 in coconut trees parasitizing *A. rigidus* and field samples from the region of Southern Luzon showed up to 80% parasitization of *A. rigidus* by *C. calauanica* (Almarinez et al. 2015).

The use of a natural enemy to control pest outbreak is highly encouraged because it is host specific, environmentally sustainable, and preserves other biological control agents (David 2000). Some successful applications of the use of a biological control agent in suppression of the growth of the pest population are as follows: control of corn borer *Ostrinia nubilalis* (Hubner) (Lepidoptera: Crambidae) on maize by the release of *Trichogramma evanescens* Westwood (Hymenoptera: Trichogrammatidae) (Burgio and Maini 1995), *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) against whitefly *Trialeurodes vaporariorum* Westwood (Hymenoptera: Aleyrodidae) on tomatoes (van Lenteren et al. 1996, Grasman et al. 2001), vedalia beetle *Rodolia cardinalis* (Mulsant) (Coleoptera: Coccinellidae) against the cottony cushion scale, *Icerya purchase* Maskell (Hemiptera: Monophlebidae) (Weseloh and Hare 2009), among others.

Literature on *A. rigidus* and its natural enemies are scarce. Prior to Watson et al. (2014), the last known study of *A. rigidus* was that of Reyne (1948), where a full account of the biology of *A. rigidus* is provided. It was only after the devastating infestation in the coconut farms in the Philippines in 2013 that interest in *A. rigidus* was renewed. In the present study, the use of *C. calauanica* as a biological control agent of *A. rigidus* is assessed. Toward this end, we describe the interaction between the coconut scale insect *A. rigidus* and its parasitoid *C. calauanica* using a mathematical model.

Mathematical models describing host–parasitoid systems generally have two basic frameworks. Models that use difference equations, e.g., Nicholson and Bailey (1935) and May (1978), belong to the discrete-time framework. Models that use differential equations, e.g., Ives (1992), Blas et al. (2016), and Blas and David (2017), belong to the continuous-time framework. The first continuous-time differential equation model for host–parasitoid interaction is attributed to Lotka in 1926 and Volterra in 1925, though initially their work was intended to describe a vertebrate predator-prey interaction. The Lotka–Volterra model may be modified to incorporate density dependence into either host or parasitoid population, functional responses of parasitoids to density of the host, age structure, parasitoid aggregation, time delays in maturation, and host refuges (Mills and Getz 1996). In this study, we model the interaction of *A. rigidus* and *C. calauanica* using a system of differential equations.

Studies of host–parasitoid interactions have produced significant contributions in the field of pest management. Barlow and Goldson (1993) showed that the parasite *Microctonus aethiopoides* Loan (Hymenoptera: Braconidae) is responsible for the decline in abundance of the pest *Sitona discoideus* Gyllenhal (Coleoptera: Curculionidae), suggesting that the parasite is able to control the density of the pest for the long term and that the interaction is stable. Grasman et al. (2001) used a two-coupled differential equation model of the parasitoid *E. formosa* and the greenhouse whitefly *T. vaporariorum* to devise a system of inundative release of the parasitoid to limit the growth of the whitefly population. Rafikov and Silveira (2014) investigated the interaction between the sugarcane borer *Diatraea saccharalis* (F.) (Lepidoptera: Crambidae) and the parasitoid *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) and proposed a system for introducing the parasitoid to the environment based on optimal control theory.

In this study, we modified the model of Rafikov and Silveira (2014) to reflect the interaction of *A. rigidus* and *C. calauanica*. Equilibrium points of the model were derived and conditions for existence were obtained. Local stability analysis for each equilibrium was performed, and inequality conditions were established (see Supp Mater [online only]). The parameter estimates were computed based on available data. Two outcome variables were defined: the maximum and the final host density. Sensitivity analysis was done by calculating partial rank correlation coefficients (PRCC) between the parameters and the outcome variables. To check model sensitivity with respect to the initial conditions, the initial host and parasitoid density were varied using the Latin hypercube sampling scheme. A control strategy by liberation of high densities of *C. calauanica* was explored by numerical simulation.

Materials and Methods

We used ordinary differential equations to describe the dynamics of the population interaction of *A. rigidus* and its parasitoid *C. calauanica*. The model follows the Lotka–Volterra continuous-time framework and consists of three coupled ordinary differential equations similar to the model of Rafikov and Silveira (2014), which includes a parasitized host stage, representing the population of the parasitized host. For simplicity, we only considered the population of female *A. rigidus*. The following are the assumptions used in the model:

1. In the absence of the parasitoid, the growth of *A. rigidus* population follows the logistic growth model.
2. The host will be incapable of reproducing after it is attacked by the parasitoid.
3. The parasitoid depends entirely on the host population. In the absence of the host, the parasitoid is expected to die out.
4. Parasitism arises from random encounters between host and parasitoid.
5. Parasitized hosts still compete for space with unparasitized hosts.

It is assumed that both larvae and adult hosts are susceptible to parasitoid attack. Although it is true that for most *Comperiella* spp. the most preferred host stage to parasitize usually includes the third instar, *C. calauanica* also parasitizes the mature *A. rigidus*, especially if third instar scales are scarce. This was observed not only in lab-reared and nursery-reared colonies, but also in field-collected samples. In fact, more *C. calauanica* had been parasitized at maturity than in the second instar. Only mature male, *C. calauanica* is invulnerable as it is already winged and can fly away.

We assumed that the parasitoid's response to host density follows the sigmoidal Holling type III functional response given by $f(H) = bH^2 / (w^2 + H^2)$, where H denotes host density and b, ω are parameters. According to Holling (1959), this type of response assumes the existence of a host threshold density. The rate of parasitism increases slowly when the host density is below the threshold and increases significantly once the density goes over the threshold. The increase in the attack rate eventually slows as the host approaches maximum population.

Fig. 1 shows the interaction of *A. rigidus* and its parasitoid *C. calauanica*. The susceptible host, parasitized host, and adult parasitoid have density H, I, and P, respectively.

The following equations describe the dynamics of the system.

$$\frac{dH}{dt} = bH\left(1 - \frac{H+I}{k}\right) - \frac{\gamma H^2 P}{\beta^2 + H^2} - d_1 H \tag{1a}$$

$$\frac{dI}{dt} = \frac{\gamma H^2 P}{\beta^2 + H^2} - nI - d_2 I \tag{1b}$$
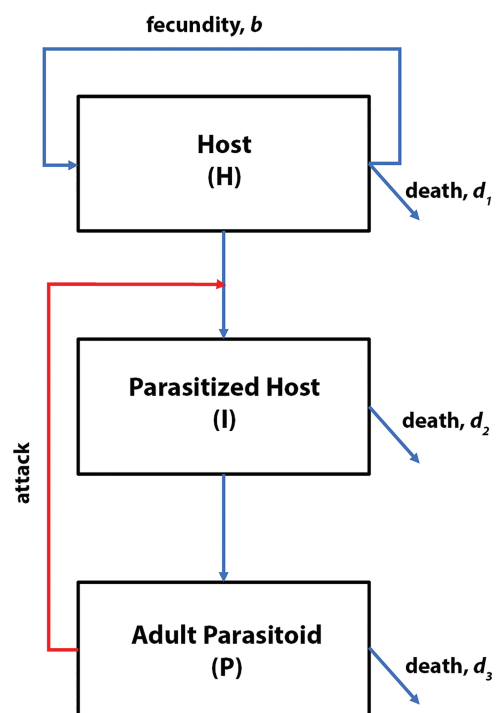
$$\frac{dP}{dt} = rnI - d_3 P \tag{1c}$$

Fig. 1. Schematic diagram of the host–parasitoid interaction.

In the above model, the intrinsic birth rate of *A. rigidus* is denoted by b, the female host mortality rate is d_1, and k is the carrying capacity, which is related to the density of foliage of the coconut tree. The host H may die due to natural mortality, denoted by d_1 in the model, or from being attacked by parasitoids, where the maximum rate of parasitism is denoted by γ. The half-saturation constant or the required density of hosts present for parasitism rate to reach half its maximum is denoted by β. Once the host has been attacked by the parasitoid, it is then moved to the parasitized host stage, where it becomes food to the young parasitoid. The rate at which the parasitized host produces a new parasitoid is n, with each parasitized host producing r number of parasitoids. The prematurely infected host dies at rate d_2, and adult parasitoids have a mortality rate d_3.

We introduce the following dimensionless quantities,

$$t^* = bt, \ H^* = \frac{H}{k}, \ I^* = \frac{I}{k}, \ P^* = \frac{\gamma P}{bk} \quad (2)$$

$$\alpha = \frac{\beta}{k}, \ \phi_1 = \frac{d_1}{b}, \ \eta = \frac{n}{b}, \ \phi_2 = \frac{d_2}{b}, \ \omega = \frac{r\gamma}{b}, \ \phi_3 = \frac{d_3}{b} \quad (3)$$

Substituting equations (2) and (3) in equation (1) and dropping the asterisks, we obtain the dimensionless system (see Supp Mater [online only]):

$$\frac{dH}{dt} = H(1 - H - I) - \frac{H^2 P}{\alpha^2 + H^2} - \phi_1 H, \quad (4a)$$

$$\frac{dI}{dt} = \frac{H^2 P}{\alpha^2 + H^2} - \eta I - \phi_2 I, \quad (4b)$$

$$\frac{dP}{dt} = \omega \eta I - \phi_3 P. \quad (4c)$$

System (4), together with the initial conditions,

$$H(0) = H_0 > 0, \ I(0) = I_0 \geq 0, \ P(0) = P_0 > 0 \quad (5)$$

forms an initial value problem, which models the host–parasitoid system. We obtained the equilibrium points of the system (4), and each equilibrium point was subjected to local stability analysis. We then performed a numerical simulation of the model to show the dynamics of the host–parasitoid interaction.

In the numerical simulation, system (1) was used to determine the model parameters. We used number of host/200 m² as a unit of density. The reference value 200 m² is based on the available leaf area of a single coconut tree (Reyne 1948). For the parameter k, or the maximum density of the host that a single coconut tree can support, we noted that in severe infestations, the observed density of *A. rigidus* is 20–30 insects/cm² (Reyne 1948). By accounting for the total leaf area of the coconut tree, the number of the host insects per tree would be 40–60 million. Taking the average, we used 50 million *A. rigidus* per coconut tree as the value of k.

On average, it was observed that a single adult female *A. rigidus* can lay and hatch 50.32 eggs (B. J. M. Almarinez et al., unpublished data). Sex ratio usually varies for different seasons, but in most cases, 25–50% of an *A. rigidus* colony consists of males (Reyne 1948). Thus, the average number of male *A. rigidus* is 37.5% of the total *A. rigidus* population and the estimated proportion of females is 62.5%. To satisfy Fisher's principle, a 50% proportion of female *A. rigidus* was also used in the simulations. The duration of the development of immature female *A. rigidus* is around 48 d, and adults can live up to 19.67 d (B. J. M. Almarinez et al., unpublished data). So, we assumed that the life expectancy of a female *A. rigidus* is 67.67 d.

Due to the absence of age structure in the model, intrinsic birth rate will be calculated as constant in all ages of female *A. rigidus*.

Consequently, the dynamics of *A. rigidus* population will be faster (e.g., population stabilizes earlier compared with the actual time). The intrinsic growth rate is computed as follows:

$$
\begin{aligned}
b &= \frac{\text{Total number of eggs laid}}{\text{life expectancy}} \times \text{percent of female population} \\
&= \frac{50.32}{67.67} \times 0.625 \\
&= 0.4648 \, \text{eggs/d}
\end{aligned}
$$

and following Fisher's principle, $\frac{50.32}{67.67} \times 0.50 = 0.3718 \, \text{eggs/d}$.

The life expectancies of *A. rigidus* and adult *C. calauanica* are 67.67 and 5.58 d, respectively. Then, $d_1 = 1/67.67 \approx 0.0148$ and $d_3 = 1/5.58 = 0.1792$. We also assumed that $d_2 = 0$, i.e., the development of *C. calauanica* from egg to adult is always successful. Moreover, based on laboratory observation, we assumed a single *C. calauanica* emerges from a single host, hence, $r = 1$ (B. J. M. Almarinez et al. unpublished data).

It was observed that the development of *C. calauanica* from egg to maturity is around 21–24 d (B. J. M. Almarinez et al., unpublished data). We used the median of this (22.5 d) for the duration of the development from egg to emergence of adult. The rate at which the parasitized host produce a new parasitoid n is $1/22.5 \approx 0.0444$. The maximum parasitism rate γ is the number of ovarian eggs divided by the life expectancy of adult *C. calauanica*, and we obtained $\gamma = 9.33/5.58 \approx 1.6720.$. There is currently no data that can be used as basis for the value of the half-saturation constant β. For this study, we assumed that the base rate of parasitism is half its maximum when host density is $0.5\,k$ (or half its carrying capacity), thus $\beta = 0.5\,k$. Different values of β were tested during sensitivity analysis.
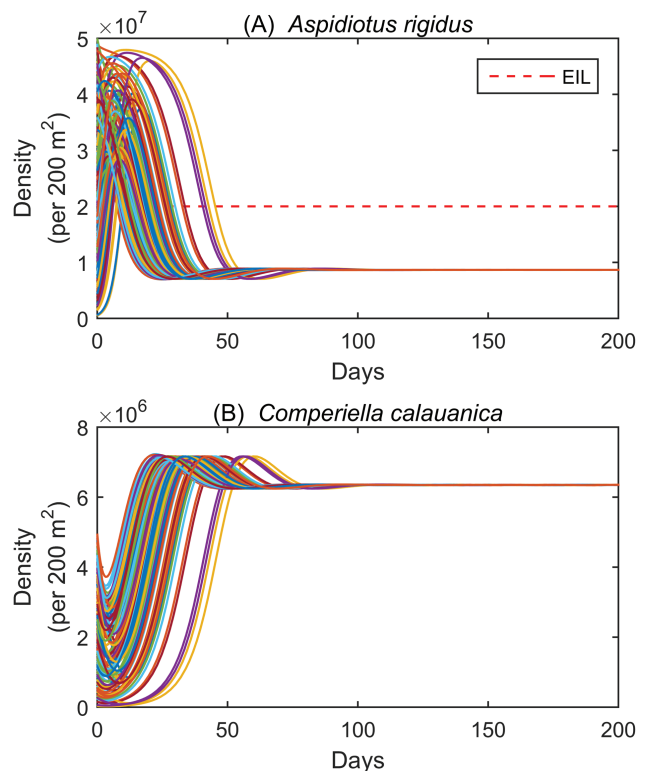

Fig. 2. Population dynamics of (A) *Aspidiotus rigidus* and (B) *Compceriella calauanica* using the parameter values in Table 1 and 100 possible combinations of initial densities. Regardless of initial condition, the population densities of each species stabilized at a specific value.

According to Tang and Cheke (2008), economic injury level (EIL) refers to the lowest population density of pest that will cause economic damage. In this paper, we used EIL = 2×10^7 *A. rigidus* (Reyne 1948). All simulations were computed using the built-in ordinary differential equation solver in MATLAB (Mathworks, Natick, MA).

Due to the uncertainty of the parameter values, we carried out sensitivity analysis using PRCC to identify which parameters significantly affected the outcome variable (see Supp Mater [online only]). PRCC quantifies the statistical relationship between an input parameter and an outcome variable while keeping all other input parameters constant at their expected value (Blower and Dowlatabadi 1994).

Results and Discussion

Equilibrium Points

The system has three equilibrium points:

$$E_0 = (0,0,0)$$
$$E_1 = (1 - \phi_1, 0, 0)$$
$$E^* = (H^*, I^*, P^*)$$

where

$$H^* = -\sqrt{\frac{\phi_3(\eta + \phi_2)}{R}}, \quad R = \eta\omega - \phi_3(\eta + \phi_2),$$

$$I^* = \frac{\alpha^2 \phi_3(\phi_2 + \eta + 1 - \phi_1)(R) + \alpha(\alpha^2 \phi_3 + [1 - \phi_1]R)\sqrt{\phi_3(\phi_2 + \eta)(R)}}{R([\phi_2 + \eta]R - \alpha^2 \phi_3)},$$

$$P^* = \frac{\omega\eta}{\phi_3} I^*.$$

The trivial equilibrium point E_0 exists regardless of the values of the parameter. When the mortality rate of *A. rigidus* is greater than its intrinsic birth rate, E_0 becomes locally asymptotically stable and both species die out. For the parasitoid-free equilibrium E_1 to exist, the death rate of *A. rigidus* must be less than its intrinsic birth rate. It becomes locally asymptotically stable once the parasitoid dies at a rate faster than its growth and eventually leads to parasitoid elimination. Herbivore–parasitoid coexistence E_3 exists only if the growth rate of the parasitoid exceeds its mortality rate. The stability condition of E_3 is given in Supp Mater [online only].

Numerical Simulation

Our simulations show that although the parameter values are kept constant, varying initial densities did not affect the terminal densities of both *A. rigidus* and *C. calauanica* (see Fig. 2). Fig. 2 also suggests that the stability of the equilibrium point $E^* = H^*, I^*, P^*$ depends only on the values of the parameters and not on the initial conditions.

The sensitivity analysis using PRCC showed four parameters out of seven were critical in predicting the maximum host density. Death rate d_1 and intrinsic birth rate b of *A. rigidus* contributed most ($P < 0.001$) toward the uncertainty of the prediction. Parameters β and n had lower but statistically significant contributions. Increasing the values of the parameters n, d_1, and b decreased (PRCC < 0) and increased (PRCC > 0) the maximum host density, respectively (see Fig. 3A).

The parameter intrinsic birth rate of *A. rigidus* b, maximum parasitism rate γ, half-saturation level β, death rate of *A. rigidus* d_1, death rate of premature parasitized host d_2, and death rate of *C. calauanica* d_3 were all statistically significant ($P < 0.001$) in predicting terminal host density

Table 1. Summary of the parameters including the biological interpretations, estimated values, and units

| Parameters	Biological interpretations	Estimated values	Units
k	Carrying capacity of a coconut tree	5×10^6	h $(200\ m^2)^{-1}$
b	Eggs laid per female host	0.4648; 0.3718	$(d)^{-1}$
γ	Maximum parasitism rate	1.6720	$hp^{-1}\ d^{-1}$
β	Density of host at which the γ is half	$0.5\ k$	h
n	Development rate of young parasitoid	0.0444	d^{-1}
r	Number of parasitoid that emerged from one parasitized host	1	ph^{-1}
d_1	Mortality rate of host	0.0148	d^{-1}
d_2	Mortality rate of young parasitoid	0	d^{-1}
d_3	Mortality rate of adult parasitoid	0.1792	d^{-1}

h (host), p (parasitoid).
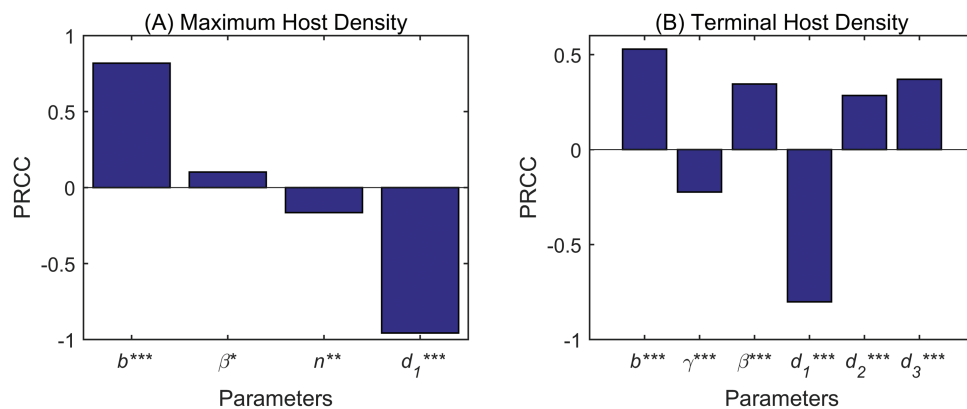
Fig. 3. Sensitivity analysis of the parameters against two outcome variables (A) maximum host density and (B) terminal host density. The results are significant at the 0.05 level (*), the 0.01 level (**), or the 0.001 level (***).

Table 2. Initial conditions used in the numerical simulation

Simulation	Initial condition	Values
S1	a) Suppose that on day 0 we have 1,000 female *A. rigidus* and 100 female *C. calauanica*.	$H_0 = 1{,}000$, $I_0 = 0$, $P_0 = 10$
	b) Suppose that on day 0 we have 1.5×10^7 female *A. rigidus* and 1,000 female *C. calauanica*.	$H_0 = 1.5 \times 10^7$, $I_0 = 0$, $P_0 = 1{,}000$
	c) Suppose that on day 0 we have 3×10^7 female *A. rigidus* and 2,000 female *C. calauanica*.	$H_0 = 3.0 \times 10^7$, $I_0 = 0$, $P_0 = 2{,}000$
S2	d) Suppose that initial density of *A. rigidus* equals the EIL and vary the initial parasitoid density.	$H_0 = 2.0 \times 10^7$, $I_0 = 0$, $P_0 = 5.0 \times 10^7$ $P_0 = 6.0 \times 10^7$ $P_0 = 9.0 \times 10^7$
S3	e) Suppose that initial density of *A. rigidus* equals the EIL and single release of 9.0×10^6 parasitoid.	$H_0 = 2.0 \times 10^7$, $I_0 = 0$, $P_0 = 9.0 \times 10^7$
	f) Suppose that initial density of *A. rigidus* equals the EIL and two releases of 9.0×10^6 parasitoid. Timing of releases varies either every 5 or 15 d.	$H_0 = 2.0 \times 10^7$, $I_0 = 0$, $P_0 = 4.5 \times 10^6$, another 4.5×10^6 after 5 d
	a.	$H_0 = 2.0 \times 10^7$, $I_0 = 0$, $P_0 = 4.5 \times 10^6$, another 4.5×10^6 after 15 d
	g) Suppose that initial density of *A. rigidus* equals the EIL. Three releases of 9.0×10^6 parasitoid. Timing of releases varies either every 5 or 15 d.	$H_0 = 2.0 \times 10^7$, $I_0 = 0$, $P_0 = 3.0 \times 10^6$, another 3.0×10^6 after 5 and 10 d
	a.	$H_0 = 2.0 \times 10^7$, $I_0 = 0$, $P_0 = 3.0 \times 10^6$, another 3.0×10^6 after 15 and 30 d
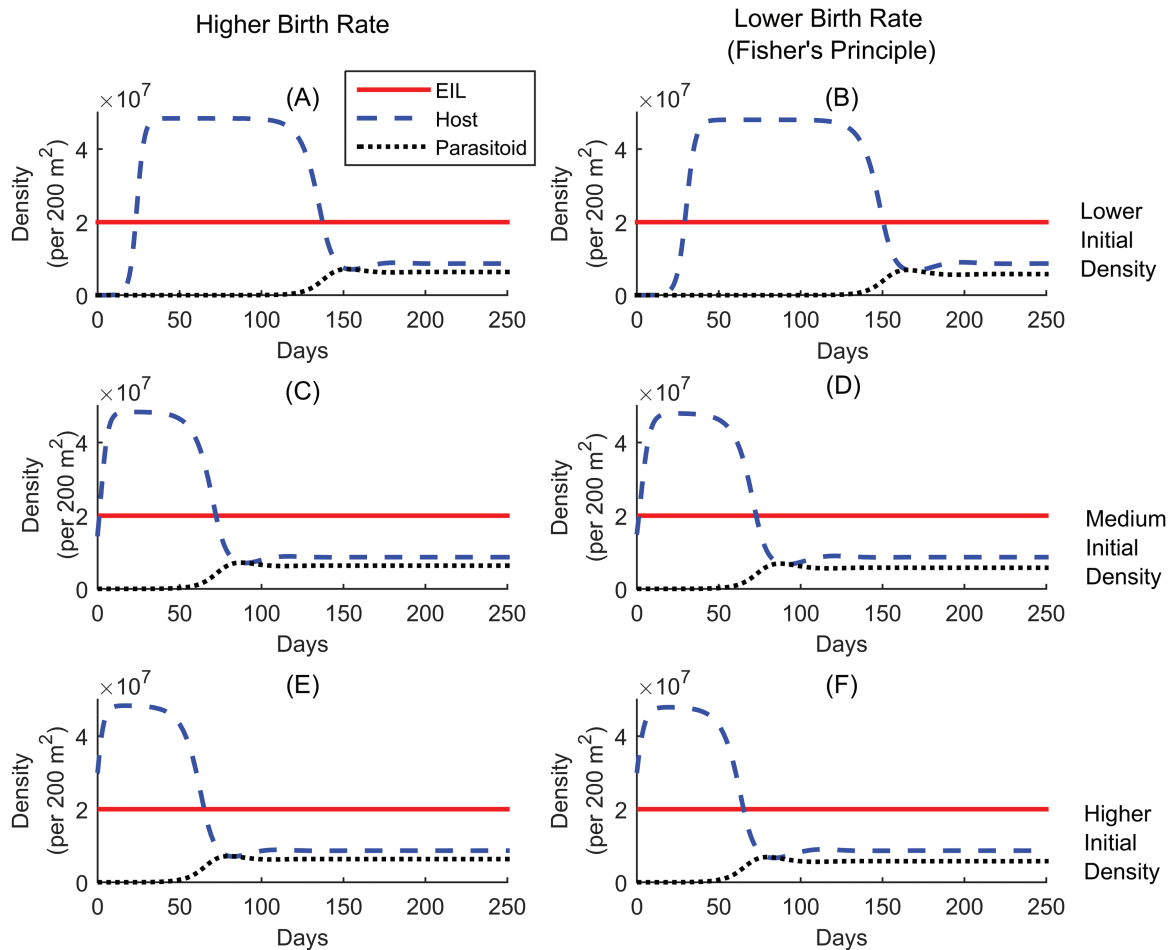
Fig. 4. Population dynamics of *Aspidiotus rigidus* and *Comperiella calauanica* using the parameter values from Table 1 with variation in intrinsic birth rate and initial densities. All scenarios showed that the host density stabilized at a value lower than EIL regardless if it started below (i.e., A, B, C, D) or above (i.e., E, F) EIL.

(see Fig. 3B). Higher values of b, d_2, and d_3 caused an increase in host density. Higher intrinsic birth rate of *A. rigidus* b indicated faster host population growth, and higher values of d_2, d_3 corresponded with lower values of the parasitoid, resulting in slower parasitism. The half-saturation level β is vital in the parasitoid functional response. Higher values of β indicated slow increase in parasitism, as it took a longer time to reach the half maximum parasitism rate. Note that to reduce the terminal host

density, we should consider the parameters γ and d_1. The PRCC value of d_1, which is a strong negative, reflects the objective of any control strategy that aims to reduce pest density. Though it is unlikely to control the maximum parasitism rate γ, the control strategy should analyze how to increase the rate at which the parasitism rate approaches its maximum.

For the dynamics of *A. rigidus* and *C. calauanica*, we ran the model using the parameter values in Table 1 and the initial conditions

of Simulation S1 in Table 2. Although the initial host densities in Figs. 4A–D were below the EIL, the density of *A. rigidus* still reached the EIL. Fig. 4 illustrates the coexistence of all species despite the changes in initial conditions. The same figure shows that the equilibrium E^* is asymptotically stable and the density of *A. rigidus* eventually stabilizes below the EIL. Similar pattern was found when we performed the same simulation with varying value of β into either $0.2\,k$, $0.3\,k$, $0.8\,k$, or $0.9\,k$. Thus, given sufficient time, the coconut scale insect infestation will resolve itself without the need for human intervention. However, the lack of immediate action on the first signs of infestation may result in economic damages. Pest control is still imperative because recovery of infected coconuts will last beyond the end of the outbreak.

Suppose that the pest density already attained the EIL (see Simulation S2 in Table 2). By trial and error method, we found out that the smallest number (in multiples of one million) of parasitoid that will immediately suppress and maintain the population density of *A. rigidus* below the EIL is 9×10^6 *C. calauanica* per coconut tree (see Fig. 5). It must also be pointed out that any initial density of *C. calauanica* between 9×10^6 in the system will eventually control the population of *A. rigidus*. For instance, the liberation of 5×10^6 *C. calauanica* did not immediately reduce the population of *A. rigidus*. Instead, a rise was observed followed by a descent until it maintained the population density of *A. rigidus* below the EIL.

Let us consider the scenario of inundative release of the 9×10^6 parasitoid (see Simulation S3 in Table 2). We explore five cases: 1) Scenario 1—a one-time release of 9×10^6 parasitoid at day 0 (same as Fig. 5); 2) Scenario 2a—two releases of 4.5×10^6 *C. calauanica* with 5-d interval starting from day 0, Scenario 2b—two releases of 4.5×10^6 *C. calauanica* with 15-d interval starting from day 0; and 3) Scenario 3a—three releases of 3×10^6 *C. calauanica* with 5-d interval starting from day 0, Scenario 3a—three releases of 3×10^6 *C. calauanica* with 15-d interval starting from day 0. Fig. 6 suggests that if the objective is to stop the *A. rigidus* density from growing beyond EIL, then Scenario 1 is the best approach among the three scenarios. It can be observed that inundative releases by dividing 9×10^6 parasitoids into two or three consecutive releases reduced the duration of pest outbreak but did not immediately control the pest population. It can be deduced that the density of the parasitoid during initial release is more important than frequency of releases. Nevertheless, in any case, a great number of *C. calauanica* is needed to cause an immediate decline in the *A. rigidus* population.
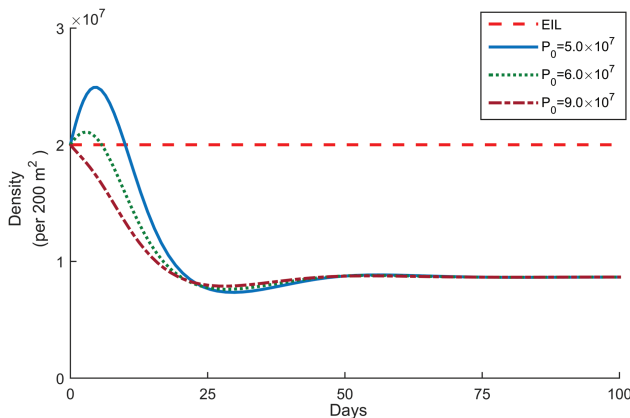
Conclusion

We presented a mathematical model that describes the interaction of the scale insect *A. rigidus* and its parasitoid *C. calauanica*. The model showed the possible population dynamics of both species. The equilibrium points were determined and the conditions for their existence were discussed. A local stability analysis was performed for each equilibrium point. It showed that the population of both species collapsed if the death rate of *A. rigidus* was greater than its intrinsic birth rate, and coexistence is likely if *C. calauanica* grows at a rate faster than its death rate. Inequality conditions for stability of other equilibrium points were also analyzed.

Sensitivity analysis was carried out to evaluate the uncertainty and influence of the parameter values with the two model outputs: maximum and terminal host density. PRCC values indicated that the model was most sensitive to both intrinsic birth rate and death rate of *A. rigidus*. The dynamics of the population of *A. rigidus* and *C. calauanica* depended less on the initial densities and more on the values of the parameter. Hence, the results of the sensitivity analysis emphasized the need for a better estimate of the parameter values (Table 3).

Numerical simulations were performed to assess the possible application of *C. calauanica* as a biological control for the pest *A. rigidus*. It was observed that the parasitoid *C. calauanica* can be efficient in keeping the population density of the scale insect *A. rigidus* below the EIL. It is concluded that the biological control application by liberation of high densities of *C. calauanica* may control the coconut scale insect *A. rigidus*.

The lack of pertinent information about the population dynamics of both species was a major challenge for this study. It is strongly
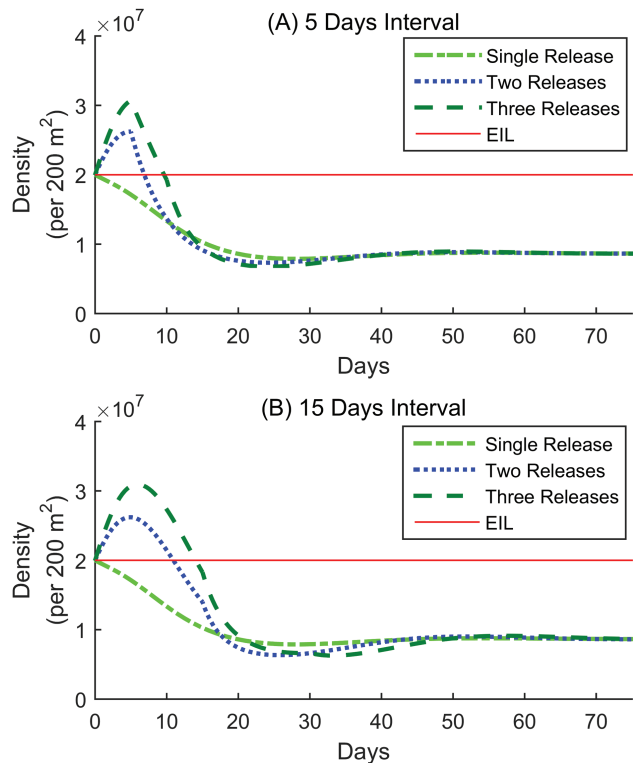
Fig. 6. Population dynamics of *Aspidiotus rigidus* where its initial density is $H_0 = 2.0 \times 10^7$ where 9.0×10^6 *Comperiella calauanica* are released once; 4.5×10^6 and 3.0×10^6 *C. calauanica* are released in two and three times, respectively, at an interval of (A) 5 d and (B) 15 d. In multiple release, the shorter the interval of release the quicker the pest infestation ends.

Fig. 5. Population dynamics of *Aspidiotus rigidus* where its initial density is $H_0 = 2.0 \times 10^7$ at different initial densities of *Comperiella calauanica* P_0. The least number of parasitoids (in multiple of one million) that immediately suppresses the growth of the host is 9.0×10^6.

Table 3. Partial rank correlation coefficients

Maximum host density		Final host density	
Parameter	PRCC	Parameter	PRCC
b	0.8185***	b	0.5289***
γ	0.0072	γ	−0.2235***
β	0.1020*	β	0.3451***
n	−0.1648**	n	0.0474
d_1	−0.9570***	d_1	−0.8016***
d_2	0.0524	d_2	0.2848***
d_3	0.0337	d_3	0.3700***

The results are significant at the 0.05 level (*), the 0.01 level (**), or the 0.001 level (***).

recommended that an experimental study be done to generate population data detailing the dynamics of both species within a specific time frame. It is also important to verify the functional response of *C. calauanica* on its host *A. rigidus*. Further studies should be done to assess the effect of abiotic factors as well as the inclusion of an invulnerable age class of the host.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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