Title

A model of coffee berry borer population growth and susceptibility to control by birds

Authors

Muccio, Kaitlin R

Crone, Elizabeth E

Reed, J Michael

ORIGINAL ARTICLE

A model of coffee berry borer population growth and susceptibility to control by birds

Kaitlin R. Muccio[1] | Elizabeth E. Crone[1,2] | J. Michael Reed[1]

[1]Department of Biology, Tufts University, Medford, Massachusetts, USA

[2]College of Biological Science, University of California, Davis, California, USA

Correspondence
Kaitlin R. Muccio, Department of Biology, Tufts University, Medford, MA 02155, USA.
Email: kmuccio1@gmail.com

Abstract

Insectivorous birds can provide ecological and economic services by decreasing pest populations in agricultural systems, but the magnitude of effect is often debated. We modeled the capacity for birds to suppress pest population growth using a common tropical coffee pest, the coffee berry borer (CBB) (*Hypothenemus hampei*) as a study system. Previous field experiments show that birds play a role in suppressing CBB infestations through predation, but the degree to which birds can suppress population growth enough to control infestations is unknown since CBB are only vulnerable to predators when gravid females disperse. Using previously published data on CBB life-stage survivability, we constructed a female-only, daily time-step, deterministic Leslie matrix and projected CBB population growth for a single breeding season. Our goal was to assess the plausibility of CBB suppression by birds as a function of avian energy requirements, reported avian densities on coffee farms, prey composition of avian diets, estimated a caloric value of CBB, and the initial starting population size. Our model showed CBB population growth became exponential ($\lambda_{daily} = 1.042$) and that at low, but not medium or high population sizes, were birds able to reduce population growth by 50%. In general, birds exert predation pressure on insect populations, but the ability to control infestations is complex, and is likely dependent on the initial CBB population size.

KEYWORDS
agroecology, biological control, coffee, ecosystem services, population projection matrix model

1 | INTRODUCTION

Wild birds provide many ecosystem services that are economically, ecologically, and culturally important to humans (Díaz-Siefer et al., 2022; Şekercioğlu, 2006; Şekercioğlu et al., 2016). One especially important service is suppression of insect populations in agricultural systems (Evenden, 1995). On a global scale, insectivorous birds consume an estimated 400–500 million tons of insects annually (Nyffeler et al., 2018) and have the capacity to decrease arthropod populations and increase

crop yields of both temperate and tropical farms (Díaz-Siefer et al., 2022). While these beneficial effects are not always observed (Grass et al., 2017; Martínez-Núñez et al., 2021), attention has focused on promoting avian diversity and abundance on farms to leverage these benefits (Garcia et al., 2020).

The fact that birds consume agricultural pests does not ensure that they can control them, in the sense of substantially reducing densities of rapidly-growing pests. Here, we evaluate the capacity of birds to suppress agricultural pests, specifically the coffee berry borer, an

invasive pest found in almost every coffee-producing region worldwide. The coffee berry borer (CBB) (*Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae)) is one of the most economically significant pests of coffee worldwide (Duque & Baker, 2003; Vega et al., 2009), causing an estimated annual global loss of US \$500 million (Vega et al., 2002). These small beetles (<2 mm) damage coffee crops when a female bores into a coffee cherry and excavates chambers for larvae to grow, consuming the coffee bean. Control of CBB can be accomplished by spraying fungal bioinsecticide *Beauvaria bassinia*, increasing harvest frequency or continually removing, by hand, over-ripe and fallen cherries, which serve as reservoirs for infestations (Aristizábal et al., 2016; Jaramillo et al., 2006). The last, and most laborious, control method appears to be the most economically effective (Cure et al., 2020) In addition to human-mediated control, natural predators such as ants, parasitoid wasps, and nematodes are being explored as potential biocontrol agents (Espinoza et al., 2009; Infante et al., 2013; Larsen & Philpott, 2010; Manton et al., 2012; Morris et al., 2015).

Birds have also been identified as a significant biological control agent of CBB (Johnson et al., 2010; Karp et al., 2013; Kellermann et al., 2008; Martínez-Salinas et al., 2016, 2022). Field experiments in Central America have shown that CBB infestation dramatically decreases when birds are present (Johnson et al., 2010; Karp et al., 2013; Kellermann et al., 2008; Martínez-Salinas et al., 2016). For example, Karp et al. (2013) reported that bird predation suppresses CBB infestation (i.e., reduces CBB population size) by 50% and saves farmers US \$75–310/ha per year; another estimate values bird predation at US \$584/ha (Martínez-Salinas et al., 2022). Suppression is done by both resident foliage-gleaning insectivores, such as rufous-capped warblers (*Basileuterus rufifrons*), and Neotropical migrants like the yellow warbler (*Setophaga petechia*). Similar to other agriculture systems, avian abundance is higher on farms with heterogenous landscapes in close proximity to native habitat (Boesing et al., 2017; Redlich et al., 2018), suggesting low-intensity shade coffee farms are better not only for supporting biodiversity, but also in providing pest-mediating ecosystem services (Johnson et al., 2010; Maas et al., 2016; Perfecto et al., 1996).

Several lines of evidence support the notion that birds depredate CBB in coffee plantations, and that their effects are biologically significant. Firstly, we know that a variety of bird species consume CBB from assays of avian fecal and regurgitant samples (Karp et al., 2013; Martínez-Salinas et al., 2016; Sherry et al., 2016), though the detection rate is quite low (1.7%–3.3% of birds sampled). Low detection rates might be due to low consumption

rates; detectability of DNA in feces depends on number of CBB eaten, and time since feeding, as well as fecal mass (Karp et al., 2014). Secondly, bird and bat exclosure experiments are associated with greater CBB infestation within enclosures (Karp et al., 2013; Martínez-Salinas et al., 2016).

At the same time, it is not clear how birds can effectively suppress CBB at most sites, and throughout the season. Exclosure experiments that report avian suppression appear to be at sites with relatively low CBB infestations (proportion of coffee cherries with borer entry holes <15%), whereas coffee-producing regions with more recent introduction of CBB have infestations of up to 500,000 CBB in a season (Johnson & Manoukis, 2021). We also do not know whether suppression is effective throughout the reproductive cycle of the CBB, or just when abundances are relatively low. Finally, CBB field traps often capture large numbers of CBB, even in the presence of birds (Aristizábal et al., 2015, 2017; Martínez-Salinas et al., 2016). Consequently, while there is clear evidence that birds consume CBB, the degree to which CBB populations can be suppressed is less clear, particularly because of the species' population growth potential (Mariño et al., 2021; this study).

Here, we use a CBB population growth model to assess the capacity of birds at naturally occurring densities to reduce CBB populations, as a function of a starting infestation size. We created an age-based population growth model for CBB using data from a life-stage transition matrix published by Mariño et al. (2021). We converted their matrix into a female-only, daily time-step, deterministic Leslie matrix; we could not estimate population growth directly from the original matrix because it did not use a common time step (Kendall et al., 2019). We incorporated a skewed adult sex ratio to mimic real populations (Vega et al., 2015), and added a life-stage for dispersing females, the stage at which CBB are vulnerable to predation by birds. Since the entire CBB lifecycle occurs within the coffee cherry, CBB are vulnerable to predation by birds for a short time window (hours) when adult females disperse (males are flightless) between plants and burrow into a new cherry (Baker, Barrera, & Rivas, 1992; Vega et al., 2015). Birds do not eat coffee cherries, with the exception of the Jacu (dusky-legged guan, *Penelope obscura*) (Raveendran & Murthy, 2021), which is found in southeastern South America. Consequently, we assumed that only adult CBB females are vulnerable to bird predation.

With our Leslie matrix, we projected population growth for a closed population during a single CBB breeding season. We projected growth at three levels (low, medium, and high) of initial starting populations of CBB (i.e., the number of gravid females at the beginning

—WILEY┘
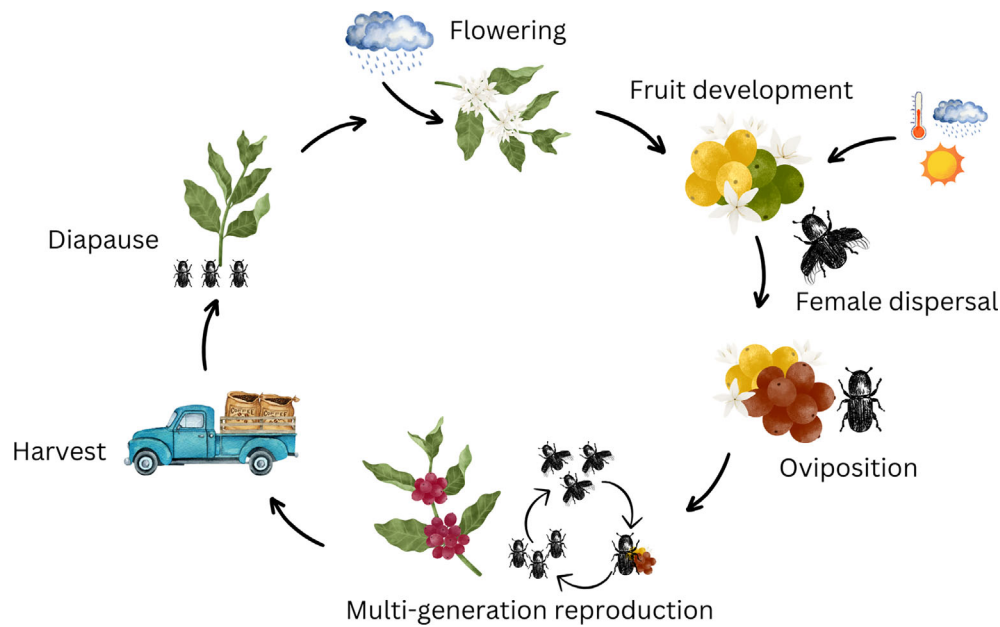
FIGURE 1 Annual cycles of coffee and the coffee berry borer. In early March, rainfall following a period of drought can initiate coffee flowering, with coffee cherry development immediately following. Borer dispersal is triggered by environmental factors (rain, relative humidity, etc.), starting in May. Females bore into cherry and oviposit once cherries are at optimal condition. Overlapping developmental stages off CBB and available berries yield multiple generations within a single season from June through December. There is continuous egg-laying, development, and female dispersal until cherries are no longer being produced. Once harvest ends in December, female CBB cease reproduction and remain in old cherries left on the ground or on trees until the next coffee season. Noted months for each life cycle are representative for the coffee season in Costa Rica.

of a new infestation), calculated from published estimates of CBB densities from alcohol lure traps (Aristizábal et al., 2015, 2017; Martínez-Salinas et al., 2016) in coffee farms from Colombia, Hawaii and Costa Rica. We then determined the degree to which dispersing female survival rate would have to be decreased (via bird predation) to result in a 50% depression in the adult population size at the end of the coffee season at all three infestation levels. Finally, we assessed the plausibility of this degree of CBB suppression by birds as a function of avian energy requirements, reported avian densities on coffee farms, prey composition of avian diets, estimated caloric value of CBB, and the starting population size of CBB females.

2 | METHODS

2.1 | Coffee phenology

Coffee phenology is directly related to rainfall patterns that differ among coffee producing regions, leading to distinct seasons, and timing of harvest(s). Our model assumes environmental conditions of Costa Rica, and thus describe the coffee phenology of this region. In regions of Costa Rica with marked seasonality, coffee flowering is triggered during the dry to wet season

transition by the onset of acute precipitation (Figure 1) (Alvim, 1960). Areas with relatively consistent rain patterns have more continuous flowering events and a longer harvest season (DaMatta et al., 2007; Martínez-Salinas et al., 2016; Rodríguez et al., 2011) In the Central Valley of Costa Rica, flowering typically begins in March, with three flowering events spread over a month (Karp et al., 2013). Flowers are short-lived, lasting only a few days before fruit (cherries) begin to develop. Maturation of coffee cherries is slow, with immature green cherries taking up to 240 days to develop into red, ripe fruit that is ready for harvest in mid-October through January (Baker, Barrera, & Rivas, 1992). After harvest, coffee plants are left to recuperate until flowering is initiated again the following year by the next onset of rain.

2.2 | Coffee berry borer phenology

Following the coffee flowering period and initiation of cherry growth, adult female CBB emerge and disperse via flight in search of new cherries to colonize (Figure 1). Timing of emergence appears to be driven primarily by relative humidity and temperature, with dispersal peaks occurring around the end of the coffee harvest, from December through March (Aristizábal et al., 2016; Baker,

Ley, et al., 1992; Jaramillo et al., 2010; Johnson & Manoukis, 2021; Martínez-Salinas et al., 2016). Females begin ovipositing in chambers carved out of the coffee endosperm roughly 120–150 days after coffee flowering, when the dry content of the seed is 20% or higher (Baker, 1984; Baker, Barrera, & Rivas, 1992; Ruiz-Cárdenas & Baker, 2010). It is this dispersal period, and subsequent drilling into the coffee cherry, when CBB are vulnerable to predation by birds, as the remainder of the CBB life cycle occurs within the coffee cherry.

There are five main CBB developmental stages: egg, larva, pupa, juvenile, and adult. Females can oviposit daily for up to 40 days, averaging 1–2 eggs per day (summarized by Vega et al., 2015). After a week, eggs hatch and larva take 17 days to develop into pupa. Following pupation (∼7 days), juveniles emerge and reach sexual maturity after about 4 days (Mariño et al., 2021). The length of the CBB life cycle can be slowed and accelerated depending on average temperature (Hamilton et al., 2019); the developmental times used here are based on 25°C rearing conditions (see also Section 4). Offspring sex ratio is skewed toward females, ranging from 1:5 to 1:494 (summarized by Vega et al., 2015). Since males are flightless, mating occurs between siblings within the natal cherry. Fertilized females then disperse to colonize other cherries, though multigenerational oviposition within the natal cherry is possible. The prolonged maturation of the coffee crop (∼7 months) allows continual reproduction, with 2–8 CBB generations feasible in a single season if environmental conditions and food availability be favorable (Jaramillo et al., 2010; Vega et al., 2015). With the removal of cherries during harvest, adult CBB will enter diapause in coffee cherries that remain on the plant or fall to the ground (Figure 1).

2.3 | Bird community

Since birds do not eat coffee cherries, biocontrol by birds would only occur during the brief dispersal period when CBB are vulnerable. There is a rich bird community during this period of time as both resident and migratory birds are present (Karp et al., 2013). Neotropical migrants are potentially more abundant on coffee farms than resident species that may prefer forest habitat due to higher prey abundances (Komar, 2006; Şekercioğlu et al., 2023). Many migratory warbler species of the *Setophaga* genus that frequent coffee farms have been confirmed as CBB predators, as have resident bird species such as the rufous-capped warbler (*B. rufifrons*) and common tody flycatcher (*Todirostrum cinereum*) (Karp et al., 2014; Sherry et al., 2016) Overall, insectivorous birds are the most abundant on coffee farms and hold great potential

as biocontrol of many insect pests (Komar, 2006). Details on bird densities on Costa Rica coffee farms used in the model are expanded on below (see Section 2.5).

2.4 | Coffee berry borer population growth model

We created a deterministic Leslie matrix for coffee berry borers with one-day time steps using data reported by Mariño et al. (2021) for an artificially infested coffee farm. Mariño et al. (2021) estimated the amount of time in each life stage (see CBB Phenology), each of which had a narrow window, and calculated transition probabilities between stages. We converted each of the stage-transition probabilities (G_i) into daily transition (survival) probabilities as $G_i^{\frac{1}{d}}$, where d = the number of days in a life stage. We assumed that mortality was evenly distributed across days within each life stage. Similarly, fecundity (F_1) estimated by Mariño et al. (2021) for a seven-day period was converted to daily egg laying rate, assuming eggs are produced at a constant rate. To account for the female skewed sex ratio, the new daily F_i was multiplied by 0.9 to model a conservative 10:1 F:M sex ratio. Lab experiments show fecundity decreases when multiple ovipositing females cohabitate (Vega et al., 2011). However, it is rare to find a cherry bored by more than one female, likely due to the high abundance of coffee cherries in the field. Therefore, we assumed density-independent growth.

Since all developmental stages of CBB occur within the coffee cherry and are assumed to be protected from predation by birds, we added a dispersal life stage to the population growth matrix, and limited bird-related mortality to this life-stage. The dispersal life stage includes the time a gravid adult female emerges from the natal cherry, disperses via flight, and the initial stages of boring into a new cherry to oviposit, while part of its body is still exposed, outside the cherry. Coffee berry borers are weak flyers (P. S. Baker, Barrera, & Rivas, 1992) and boring into the cherry and reaching the endosperm can take 2–8 h (F. Vega et al., 2015). Consequently, we estimated the disperser life stage to last 1 day.

2.5 | Modeling bird predation needed to suppress CBB population

To our knowledge, there is little information about population densities of CBB in coffee plantations at the start of the growing season. We first initialized the coffee berry borer population model (day 0) with 100 dispersing females (Stubben & Milligan, 2007). The start of CBB reproduction

commenced 120 days after coffee flowering and continued until 305 days after flowering, yielding a 185-day CBB breeding season. We confirmed CBB reproduction was possible within this period for Central Valley Costa Rica (mid-June through December) using degree day calculations from Jaramillo et al. (2009) based on CBB thermal tolerance. We then calculated how much the dispersing adult survival rate would have to be reduced to cause a 50% reduction in adult female borer population size on day 185. To determine how many CBB would need to be consumed by birds to achieve this goal, we found the difference between daily borer population sizes of unsuppressed and suppressed populations and summed the differences across the CBB reproductive season. We used sensitivity analysis to estimate the degree to which changes in each vital rate affects population growth rate (Silvertown et al., 1996). All models were implemented using the popbio (Stubben & Milligan, 2007) package in R (R version 12.0). R code for all analyses is provided in the Supporting Information (S1).

We also wanted our model to project CBB population growth that represented "low" and "high" infestations observed in the field. To start, we estimated probable CBB densities using data on the number of dispersing females collected in alcohol-lure traps. At peak dispersal, CBB numbers have been recorded as high as 1000–6120 CBB/trap/week (Aristizábal et al., 2015, 2017) to as low as 50–105 CBB/trap/week (Aristizábal et al., 2015; Martínez-Salinas et al., 2016). Using these trap counts, we calculated potential CBB densities per hectare via reported trap densities and converted weekly capture estimates to the number of daily dispersers to complement our daily population model. We used a density independent model, a standard first step in many population models. However, note that we would need to divide CBB numbers by plant density to evaluate the impacts of CBB population growth on yield. We also would need empirical data on how the demography of CBB populations change with coffee-plant density to implement a revised model, and we are unaware of published data on this. Consequently, this analysis is beyond the scope of this paper (see also Section 4).

Using data from Aristizábal et al. (2015), we selected a high peak dispersal count from farms with large infestations (17%–28% berry infestation, with up to 6120 CBB/trap/week) and a low peak dispersal count from farms with small infestations (>2.5% berry infestation, with up to 105 CBB/trap/week) to represent peak dispersal on Day 185 in our model. We then back calculated the initial population sizes (Day 0) that would yield those ultimate densities. We used our calculated values of 269 and 5 as our "high" and "low" initial population sizes of gravid females at the start of the coffee season and used 100 CBB to represent "medium" initial population size.
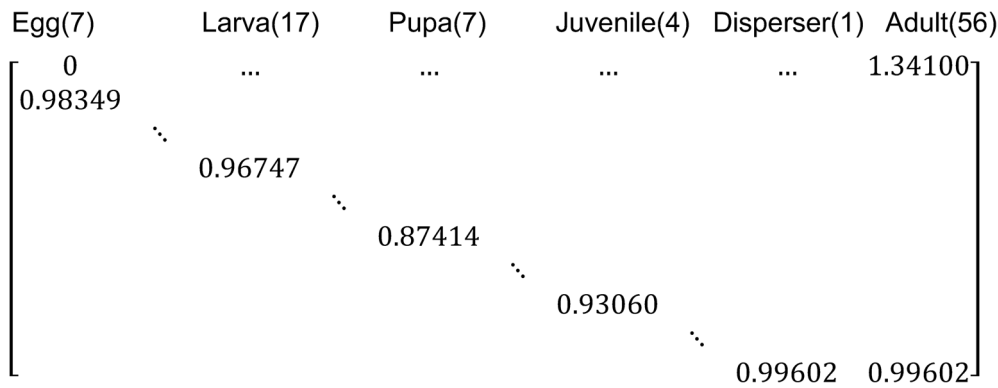
2.6 | Estimating potential predation pressure by birds

The mass, in dry weight, of a female adult CBB was determined from the weighted average of CBB (unspecified sex) using midpoint values for weight ranges from Moore et al. (1990, see tab. 3). We estimated the caloric content of a single CBB using the average energy value (cal/g dry weight) of Coleoptera species in the adult stage (Cummins & Wuycheck, 1971). Using our estimated CBB caloric content, we calculated the number of CBB required to make up 5% and 10% of an average bird's daily diet (Sherry et al., 2016).

We calculated daily energy requirements (M, in kcal) for birds under field conditions as $M = (129 \, W^{0.724}) \times 2.5$, where W is the weight (kg) of an average insectivorous bird on coffee farms (Nyffeler et al., 2018). We calculated the weight of an average insectivorous bird by averaging body masses of 33 insectivorous resident and migrant bird species (Dunning Jr., 2007) reported to consume CBB on Jamaican and Costa Rican coffee farms (Karp et al., 2013; Martínez-Salinas et al., 2016; Sherry et al., 2016), or predicted to consume CBB based on morphology and diet breadth (Karp et al., 2014). Sherry et al. (2016) found that CBB made up 5%–10% of the diet of three Neotropical migratory warblers by number of individuals consumed; we used these percentages to estimate how many calories, and therefore how many CBB, birds potentially eat. Avian consumption rate of CBB was constant, with even effort across the coffee season. For avian densities, we used estimates from Karp et al. (2013) of 3 (in low shade) to 14 (in high shade) birds per ha, because these densities include known CBB predators on coffee farms in Costa Rica.

3 | RESULTS

Parameters for our Leslie matrix for coffee berry borers are broadly consistent with expectations and general knowledge (Figure 2). For example, our conversion of fecundity to a daily value, $F_1 = 1.341$, is consistent with published literature stating that 1–2 eggs are laid per day by CBB (Waterhouse & Norris, 1987). Model projections showed that across a 185-day CBB breeding period starting at the point of first ovipositing, an initial population size of 100 female dispersers would produce 1.3 million offspring, resulting in a new adult population of 70,245 females (Figure 3). Assuming ~99% of colonizing females successfully bore and oviposit in a coffee cherry on Day 0, the first generation of new dispersing females does not appear until day 37. At Day 38, the adult population begins to increase, and continues to do so exponentially.

Egg(7)   Larva(17)   Pupa(7)   Juvenile(4)   Disperser(1)   Adult(56)

$$\begin{bmatrix} 0 & \cdots & \cdots & \cdots & \cdots & 1.34100 \\ 0.98349 & & & & & \\ & 0.96747 & & & & \\ & & 0.87414 & & & \\ & & & 0.93060 & & \\ & & & & 0.99602 & 0.99602 \end{bmatrix}$$

FIGURE 2 Leslie matrix for coffee berry borer in one-day time steps without bird predation. The parenthetic number following each life stage label is the number of days in that life stage. Data used to calculate the vital rates, as well as time spent in each life stage, come from Mariño et al. (2021). An expanded version of this matrix is in the Supporting Information (Table S1).
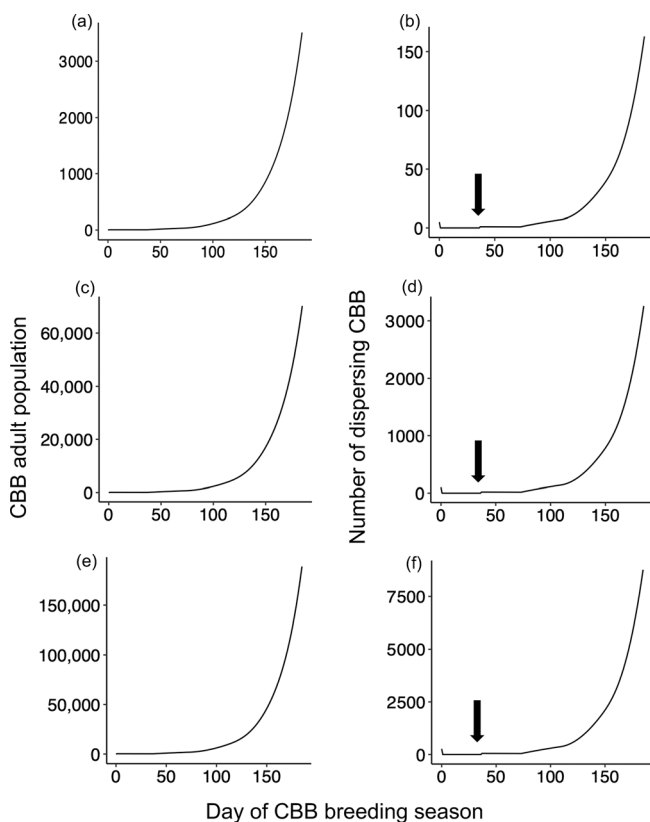

FIGURE 3 Population projections for adult female population size at (a) low $N_0 = 5$, (c) medium, $N_0 = 100$, and (e) high $N_0 = 269$ initial population sizes. From these population estimates, the number of dispersing female coffee berry borers across the coffee growing season (185 days) is also measured at (b) low, (d) medium, and (f) high initial population sizes. Arrows indicate the days that the first generation of female offspring disperse, initiating growth of the CBB adult population.

The daily growth rate (λ) of this population converged on 1.042. Sensitivity analysis revealed that survival of adult females had the largest impact on overall population growth (0.388), followed by daily survival of pupa (0.020), juveniles (0.019), eggs and larvae (0.018) and dispersing females (0.017).

In addition to modeling growth with 100 initial colonists (N_0), we projected the population growth of low ($N_0 = 5$) and high ($N_0 = 269$) starting populations calculated from observed weekly alcohol-lure trap catches during peak dispersal (Aristizábal et al., 2015). Comparing the three population projections, peak number of dispersers at Day 185 varied considerably, with 162, 3259, and 8768 daily dispersers for low, medium, and high colonizing populations, respectively. In the high population projection, the adult population (individuals that survived dispersal) toward the end of the growing season reached over 18,800 individuals. Note that because these are density-independent models, the number of CBB does not depend on plant density. However, the impacts of the CBB population on yield would depend on coffee plant density.

To reduce the final adult population by 50%, the daily survival rate of dispersing females would have to be reduced from 0.99602 (adult survival) to 0.83202. This change represents a 16.4% reduction in daily survival when dispersing. The number of CBB that birds need to eat (y) to reduce the adult population at this rate was driven by the initial population size as a straight line, $y = 79.23 N_0$ (Figure 4). At medium starting population ($N_0 = 100$), birds need to consume 7628 CBB during the borer breeding season, while at high starting population ($N_0 = 269$), about 20,500 dispersing CBB must be consumed by birds. Daily consumption rates by birds would have to increase over time as the CBB population grows and could vary from 15 to 750 CBB being consumed a day, depending on starting population size (Figure 4). Overall, we calculated that for every female CBB in the initial colonization, birds need to consume 79 CBB to reduce the end of season population by half.
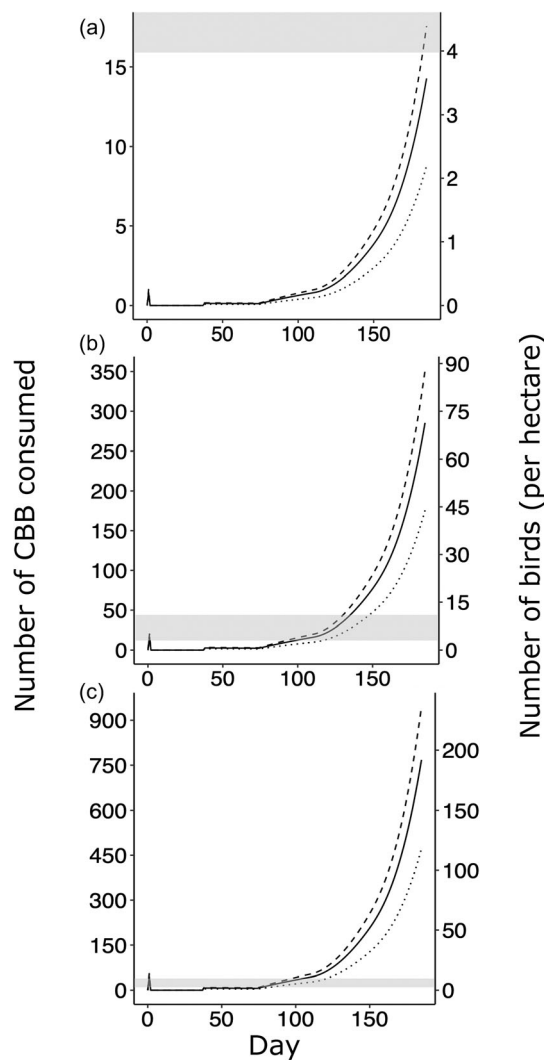
FIGURE 4 Right-hand Y axis, and associated solid black line on the plots, depicts the modeled number of CBB that need to be consumed to achieve 50% reduction in CBB numbers by day 185, based on low (a), medium (b) and high (c) initial CBB population sizes (consistent with Figure 2). The left-hand Y axis, and associated lines on the plots, indicate that number of birds required to achieve 50% reduction of CBB, based on CBB contributing 5% (dashed) or 10% (dotted) of avian diets. Gray shading represents reported range of densities of avian predators of CBB on coffee farms (Karp et al., 2013).

We estimated that the caloric content of a 195 μg adult CBB to be 1.09 calories per gram dry weight, or 0.00109 kcal. At 5%–10% of a bird's daily diet based on number of prey items, birds would consume <7 CBB per day. This represents 0.03%–0.05% of daily caloric requirements of our average insectivorous bird. At these feeding rates, our models suggest that by the time of peak dispersal, 4, 88, and 236 birds are required at low, medium, and high starting population sizes, respectively, to reduce CBB populations by 50% on day 185 (Figure 4).

4 | DISCUSSION

Our model suggests that avian predation is likely to be effective at reducing CBB populations by 50% only during small infestations (maximum adult population ∼3500, Figure 3), or during the early stages of larger infestations (maximum adult population ∼35,000–188,000, Figure 3). Birds appear unable to successfully suppress medium and large infestations because the number of CBB that need to be eaten in a season (∼7600–20,500) requires higher bird densities than are reported in the literature. Karp et al. (2013) estimated 4–12 birds/ha of species that are confirmed or suspected CBB predators. Flocks of migratory birds on coffee farms are estimated at 19/ha (McDermott & Rodewald, 2014) and 24/ha (Greenberg et al., 1997), but these values are also short of our estimates of necessary densities for suppressing larger CBB outbreaks.

One caveat to our conclusions is that our calculations were based on CBB accounting for 5%–10% of a bird's daily diet (Sherry et al., 2016). This assumption meant birds would only eat a set maximum of 7 CBB per day. Sherry et al. (2016) reported up to 116 CBB in the stomach contents of a single warbler, suggesting under certain circumstances in the field, birds eat more CBB. Generalist insectivores, particularly Neotropical migrants, have flexible foraging preferences (Bell, 2011; Parrish, 2000; Sherry et al., 2016) and would likely feed opportunistically on CBB in response to dramatic dispersal peaks. Therefore, birds might be expected to increase feeding rates as CBB disperser abundances increase, though it may depend on the relative abundances of other prey. Better data on CBB consumption rates by birds under different circumstances would improve our estimates of the circumstances under which birds can control CBB populations.

A second caveat is that bird densities used in the model may not represent the potential for CBB control because bird densities depend on the structure of the agricultural landscape, which the current model does not consider. On coffee farms, birds are more abundant when native tree cover is highest and natural forests are close by (Karp et al., 2013; McDermott & Rodewald, 2014). Across tropical and temperate regions, the propensity for birds to forage on farms, and thus exert pressure on agricultural pests, is correlated with the physical complexity and diversity of the agroecosystem (Boesing et al., 2017). For example, birds make more frequent foraging trips to apple orchards with high native tree coverage (García et al., 2018). In alfalfa fields, edge habitat complexity supports greater avian richness leading to lower pest abundances (Kross et al., 2016). Under some circumstances, the density of birds foraging in certain areas may be

higher than average densities would imply, leading to greater control potential than our models suggest.

More generally, our CBB population model is density independent and assumes environmental conditions and sufficient resources to allow CBB populations to increase without restriction. As a result, our model is limited, as it does not consider localized effects of weather and temperature fluctuations on CBB developmental time (Hamilton et al., 2019; Jaramillo et al., 2010), nor characteristics of coffee farms (e.g., area, percent shade, coffee tree density, etc.) that influence both CBB infestation and bird density. We assumed maximal capacity for CBB population growth (based on varying starting population sizes) and used estimates of bird densities from the literature that only included birds known to consume CBB, perhaps underestimating the potential for avian control. Models are an important tool for estimating population dynamics, but as with any species, the growth potential for CBB and availability of its predators, is context-dependent.

Our study echoes Kendall et al.'s (2019) conclusion that, even though errors in model construction are common, these seldom change qualitative conclusions. From our population matrix, CBB daily growth rate converged on $\lambda_{daily} = 1.042$ around day 124, with an observed rate of population change across the entire coffee-growing season of 705 (= N_{185}/N_0). Our λ_{daily} is higher than Mariño et al.'s (2021) reported lambda of 1.32 over ~50–56 days, which corresponds to $\lambda_{daily} \approx 1.006$ (i.e., $1.0056^{50} \approx 1.32$). Part of this discrepancy may come from the fact that Marino et al. combined vital rates across life stages with different time steps. Nonetheless, both models are consistent in predicting rapidly growing populations. Observed CBB population growth rates are similar to ours: Baker, Barrera, & Rivas, (1992) calculated a 1.067 growth rate in wild populations and Ruiz-Cárdenas and Baker (2010) reported 1.047 in CBB reared in laboratory settings. In their sensitivity analysis, Mariño et al. (2021) reported that adult female survival, and transitions from larva to pupa and pupa to juvenile had high sensitivity in contributing to population growth rate, with adult survival the highest (0.32–0.38). We found a similar peak sensitivity value for female adult survival in our matrix (0.388), supporting the idea that CBB population growth is most sensitive to adult survival rate. Interestingly, dispersal survival from our matrix was estimated to have low impact on population growth (0.017), even though this life stage is when CBB are vulnerable to bird predation. Thus, our analysis superficially suggests that population control once CBB are established should focus on reducing adult survival rather than on trapping dispersing females (e.g., Benton & Grant, 1999), if the same impact on numbers could be achieved. However,

dispersing females are much more accessible to control methods like spraying fungal bioinsecticide than are adult females, which are inside the coffee cherries, so despite the tremendous difference in sensitivity values, management of an established population is likely to be more cost effective by continuing to focus on dispersing females (cf. Manlik et al., 2018; Reed et al., 2009).

Population models specific to CBB have been criticized for not being representative of wild populations, since more generations are estimated through modeling than are observed in field studies (Baker, Barrera, & Rivas, 1992). We analyzed CBB population growth using a deterministic model, with an even distribution of dispersal and a fixed predation pressure. While CBB dispersal is continuous, there can be dramatic intra-seasonal peaks in numbers that were not captured by our model (Aristizábal et al., 2017). In addition, reported longevity of female CBB varies widely from 55 to 380 days, though some studies looked at CBB reared on artificial diet (Vega et al., 2015). Refinements of survival in natural settings would, therefore, improve models of CBB population growth, and the potential for control by birds. If field data on CBB vital rate stochasticity become available, and bird densities opportunistically increase during CBB peak numbers, it could affect our conclusions about the capacity of birds to control larger CBB outbreaks.

Based on our analyses, there is a population density of CBB above which their capacity to produce more adults exceeds the ability of birds to control their numbers, at least to limit the population size by 50%. This positive density-dependent relationship between population growth and density is an Allee effect (Berec et al., 2007), and escape from predation is one mechanism for this phenomenon (Liebhold & Bascompte, 2003). In general, predator-driven Allee effects can occur when predators are the main driver of prey dynamics and when predators are generalists as are insectivorous Neotropical migrants (Gascoigne & Lipcius, 2004). Additionally, predators can exert strong pressure when prey availability is not temporally or spatially limited—a potential limiting factor in the coffee system, since CBB are only available to birds during dispersal. The degree to which birds exert an Allee effect on CBB might depend on the starting population size of the pest. Variation in starting population size is likely dependent on how recently CBB have colonized in an area, timing of trapping (early vs. later in the growing season), the size of the farm (Aristizábal et al., 2015), and the extent to which farmers used control measures the previous year (Cure et al., 2020). We found that only under very low initial population sizes of CBB could birds be expected to suppress pest numbers by 50%. We note that earlier, stronger CBB suppression by birds would lead to lower infestation numbers later in the

—WILEY 9

coffee season, but this might require selective foraging by birds, depending on relative abundances of other prey species.

In conclusion, our models suggest that birds can control CBB under some circumstances, depending on the relative size of the starting CBB population and existing local bird density. To put this idea into practice it is important to remember that managing farms for bird habitat does not always result in pest reduction. Birds may not prey on the pest of interest (Martínez-Núñez et al., 2021) or birds might cause pest numbers in increase by preying on insect predators that normally regulates the pest population (Grass et al., 2017). Aside from predators, pest species are also impacted by the agricultural environment directly (e.g., monoculture provides ample host plants but a polyculture would reduce the density of hosts, decreasing the degree to which infestations can grow). In fact, on coffee farms where bird densities are higher in shade, CBB infestations are also higher (Mariño et al., 2016; Oliva et al., 2023), possibly because CBB native range is in humid, shade forests of Africa (Vega et al., 2015). It is important that future modeling include such habitat-specific factors to understand Our research helps quantify the densities under which birds have the potential to control CBB populations. Putting these numbers into practice will require understanding how management practices affect both bird and CBB densities.

ACKNOWLEDGMENTS

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ORCID

Kaitlin R. Muccio https://orcid.org/0009-0008-8891-2536

REFERENCES

Alvim, P. d. T. (1960). Moisture stress as a requirement for flowering of coffee. *Science*, *132*, 354. https://doi.org/10.1126/science.132.3423.354

Aristizábal, L. F., Bustillo, A. E., & Arthurs, S. P. (2016). Integrated pest management of coffee berry borer: Strategies from Latin America that could be useful for coffee farmers in Hawaii. *Insects*, *7*(1), E6. https://doi.org/10.3390/insects7010006

Aristizábal, L. F., Jiménez, M., Bustillo, A. E., Trujillo, H. I., & Arthurs, S. P. (2015). Monitoring coffee berry borer, *Hypothenemus hampei* (Coleoptera: Curculionidae), populations with alcohol-baited funnel traps in coffee farms in Colombia. *Florida Entomologist*, *98*(1), 381–383. https://doi.org/10.1653/024.098.0165

Aristizábal, L. F., Shriner, S., Hollingsworth, R., & Arthurs, S. (2017). Flight activity and field infestation relationships for coffee berry borer in commercial coffee plantations in Kona and Kau districts, Hawaii. *Journal of Economic Entomology*, *110*(6), 2421–2427. https://doi.org/10.1093/jee/tox215

Baker, P. (1984). Some aspects of the behavior of the coffee berry borer in relation to its control in southern Mexico (Coleoptera, Scolytidae). *Folia Entomológica Mexicana (México)*, *61*, 9–24.

Baker, P. S., Barrera, J. F., & Rivas, A. (1992). Life-history studies of the coffee berry borer (*Hypothenemus hampei*, Scolytidae) on coffee trees in southern Mexico. *Journal of Applied Ecology*, *29*(3), 656–662. https://doi.org/10.2307/2404473

Baker, P. S., Ley, C., Balbuena, R., & Barrera, J. F. (1992). Factors affecting the emergence of *Hypothenemus hampei* (Coleoptera: Scolytidae) from coffee berries. *Bulletin of Entomological Research*, *82*(2), 145–150. https://doi.org/10.1017/S000748530005166X

Bell, C. P. (2011). Resource buffering and the evolution of bird migration. *Evolutionary Ecology*, *25*(1), 91–106. https://doi.org/10.1007/s10682-010-9383-4

Benton, T. G., & Grant, A. (1999). Elasticity analysis as an important tool in evolutionary and population ecology. *Trends in Ecology & Evolution*, *14*(12), 467–471. https://doi.org/10.1016/S0169-5347(99)01724-3

Berec, L., Angulo, E., & Courchamp, F. (2007). Multiple Allee effects and population management. *Trends in Ecology & Evolution*, *22*(4), 185–191. https://doi.org/10.1016/j.tree.2006.12.002

Boesing, A. L., Nichols, E., & Metzger, J. P. (2017). Effects of landscape structure on avian-mediated insect pest control services: A review. *Landscape Ecology*, *32*(5), 931–944. https://doi.org/10.1007/s10980-017-0503-1

Cummins, K. W., & Wuycheck, J. C. (1971). Caloric equivalents for investigations in ecological energetics. Mitteilungen. *Internationale Vereinigung fuer Theoretische und Angewandte Limnologie*, *18*, 1–158.

Cure, J., Rodríguez, D., Gutierrez, A. P., & Ponti, L. (2020). The coffee agroecosystem: Bio-economic analysis of coffee berry borer control (*Hypothenemus hampei*). *Scientific Reports*, *10*, 12262. https://doi.org/10.1038/s41598-020-68989-x

Díaz-Siefer, P., Olmos-Moya, N., Fontúrbel, F. E., Lavandero, B., Pozo, R. A., & Celis-Diez, J. L. (2022). Bird-mediated effects of pest control services on crop productivity: A global synthesis. *Journal of Pest Science*, *95*(2), 567–576. https://doi.org/10.1007/s10340-021-01438-4

DaMatta, F. M., Ronchi, C. P., Maestri, M., & Barros, R. S. (2007). Ecophysiology of coffee growth and production. *Brazilian Journal of Plant Physiology*, *19*, 485–510. https://doi.org/10.1590/S1677-04202007000400014

Dunning, J. B., Jr. (2007). *CRC handbook of avian body masses*. CRC Press.

Duque, O. H., & Baker, P. S. (2003). *Devouring profit: The socio-economics of coffee berry borer IPM*. The Commodities Press—Cenicafé. https://biblioteca.cenicafe.org/handle/10778/4331

Espinoza, J. C., Infante, F., Castillo, A., Pérez, J., Nieto, G., Pinson, E. P., & Vega, F. E. (2009). The biology of *Phymastichus*

coffea LaSalle (Hymenoptera: Eulophidae) under field conditions. *Biological Control*, 49(3), 227–233. https://doi.org/10.1016/j.biocontrol.2009.01.021

Evenden, M. D. (1995). The laborers of nature: Economic ornithology and the role of nirds as agents of biological pest control in North American agriculture, ca. 1880–1930. *Forest & Conservation History*, 39(4), 172–183. https://doi.org/10.2307/3983958

García, D., Miñarro, M., & Martínez-Sastre, R. (2018). Birds as suppliers of pest control in cider apple orchards: Avian biodiversity drivers and insectivory effect. *Agriculture, Ecosystems & Environment*, 254, 233–243. https://doi.org/10.1016/j.agee.2017.11.034

Garcia, K., Olimpi, E. M., Karp, D. S., & Gonthier, D. J. (2020). The good, the bad, and the risky: Can birds be incorporated as biological control agents into integrated pest management programs? *Journal of Integrated Pest Management*, 11(1), 11. https://doi.org/10.1093/jipm/pmaa009

Gascoigne, J. C., & Lipcius, R. N. (2004). Allee effects driven by predation. *Journal of Applied Ecology*, 41(5), 801–810. https://doi.org/10.1111/j.0021-8901.2004.00944.x

Grass, I., Lehmann, K., Thies, C., & Tscharntke, T. (2017). Insectivorous birds disrupt biological control of cereal aphids. *Ecology*, 98(6), 1583–1590. https://doi.org/10.1002/ecy.1814

Greenberg, R., Bichier, P., & Sterling, J. (1997). Bird populations in rustic and planted shade coffee plantations of eastern Chiapas, México. *Biotropica*, 29(4), 501–514. https://doi.org/10.1111/j.1744-7429.1997.tb00044.x

Hamilton, L. J., Hollingsworth, R. G., Sabado-Halpern, M., Manoukis, N. C., Follett, P. A., & Johnson, M. A. (2019). Coffee berry borer (*Hypothenemus hampei*) (Coleoptera: Curculionidae) development across an elevational gradient on Hawaiʻi Island: Applying laboratory degree-day predictions to natural field populations. *PLoS One*, 14(7), e0218321. https://doi.org/10.1371/journal.pone.0218321

Infante, F., Castillo, A., Pérez, J., & Vega, F. E. (2013). Field-cage evaluation of the parasitoid *Phymastichus coffea* as a natural enemy of the coffee berry borer, *Hypothenemus hampei*. *Biological Control*, 67(3), 446–450. https://doi.org/10.1016/j.biocontrol.2013.09.019

Jaramillo, J., Borgemeister, C., & Baker, P. (2006). Coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae): Searching for sustainable control strategies. *Bulletin of Entomological Research*, 96, 223–233. https://doi.org/10.1079/BER2006434

Jaramillo, J., Chabi-olaye, A., & Borgemeister, C. (2010). Temperature-dependent development and emergence pattern of *Hypothenemus hampei* (Coleoptera: Curculionidae: Scolytinae) from coffee berries. *Journal of Economic Entomology*, 103(4), 1159–1165. https://doi.org/10.1603/EC09408

Jaramillo, J., Chabi-Olaye, A., Kamonjo, C., Jaramillo, A., Vega, F. E., Poehling, H. M., & Borgemeister, C. (2009). Thermal tolerance of the coffee berry borer Hypothenemus hampei: predictions of climate change impact on a tropical insect pest. *PLoS One*, 4(8), e6487.

Johnson, M. A., & Manoukis, N. C. (2021). Influence of seasonal and climatic variables on coffee berry borer (*Hypothenemus hampei* Ferrari) flight activity in Hawaii. *PLoS One*, 16(12), e0257861. https://doi.org/10.1371/journal.pone.0257861

Johnson, M. D., Kellermann, J. L., & Stercho, A. M. (2010). Pest reduction services by birds in shade and sun coffee in Jamaica.

Animal Conservation, 13(2), 140–147. https://doi.org/10.1111/j.1469-1795.2009.00310.x

Karp, D. S., Judson, S., Daily, G. C., & Hadly, E. A. (2014). Molecular diagnosis of bird-mediated pest consumption in tropical farmland. *Springerplus*, 3(1), 630. https://doi.org/10.1186/2193-1801-3-630

Karp, D. S., Mendenhall, C. D., Sandí, R. F., Chaumont, N., Ehrlich, P. R., Hadly, E. A., & Daily, G. C. (2013). Forest bolsters bird abundance, pest control and coffee yield. *Ecology Letters*, 16(11), 1339–1347. https://doi.org/10.1111/ele.12173

Kellermann, J. L., Johnson, M. D., Stercho, A. M., & Hackett, S. C. (2008). Ecological and economic services provided by birds on Jamaican Blue Mountain coffee farms. *Conservation Biology*, 22(5), 1177–1185. https://doi.org/10.1111/j.1523-1739.2008.00968.x

Kendall, B. E., Fujiwara, M., Diaz-Lopez, J., Schneider, S., Voigt, J., & Wiesner, S. (2019). Persistent problems in the construction of matrix population models. *Ecological Modelling*, 406, 33–43. https://doi.org/10.1016/j.ecolmodel.2019.03.011

Komar, O. (2006). Priority contribution. Ecology and conservation of birds in coffee plantations: A critical review. *Bird Conservation International*, 16(1), 1–23. https://doi.org/10.1017/S0959270906000074

Kross, S. M., Kelsey, T. R., McColl, C. J., & Townsend, J. M. (2016). Field-scale habitat complexity enhances avian conservation and avian-mediated pest-control services in an intensive agricultural crop. *Agriculture, Ecosystems & Environment*, 225, 140–149. https://doi.org/10.1016/j.agee.2016.03.043

Larsen, A., & Philpott, S. M. (2010). Twig-nesting ants: The hidden predators of the coffee berry borer in Chiapas, Mexico: Arboreal ants and coffee berry borer. *Biotropica*, 42(3), 342–347. https://doi.org/10.1111/j.1744-7429.2009.00603.x

Liebhold, A., & Bascompte, J. (2003). The Allee effect, stochastic dynamics and the eradication of alien species. *Ecology Letters*, 6(2), 33–140.

Maas, B., Karp, D. S., Bumrungsri, S., Darras, K., Gonthier, D., Huang, J. C.-C., Lindell, C. A., Maine, J. J., Mestre, L., Michel, N. L., Morrison, E. B., Perfecto, I., Philpott, S. M., Şekercioğlu, Ç. H., Silva, R. M., Taylor, P. J., Tscharntke, T., Van Bael, S. A., Whelan, C. J., & Williams-Guillén, K. (2016). Bird and bat predation services in tropical forests and agroforestry landscapes. *Biological Reviews of the Cambridge Philosophical Society*, 91(4), 1081–1101. https://doi.org/10.1111/brv.12211

Manlik, O., Lacy, R. C., & Sherwin, W. B. (2018). Applicability and limitations of sensitivity analyses for wildlife management. *Journal of Applied Ecology*, 55(3), 1430–1440. https://doi.org/10.1111/1365-2664.13044

Manton, J. L., Hollingsworth, R. G., & Cabos, R. Y. M. (2012). Potential of *Steinernema carpocapsae* (Rhabditida: Steinernematidae) against *Hypothenemus hampei* (Coleoptera: Curculionidae) in Hawaiʻi. *Florida Entomologist*, 95(4), 1194–1197. https://doi.org/10.1653/024.095.0452

Mariño, Y. A., Bayman, P., & Sabat, A. M. (2021). Demography and perturbation analyses of the coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae): Implications for management. *PLoS One*, 16(12), e0260499. https://doi.org/10.1371/journal.pone.0260499

Mariño, Y. A., Pérez, M.-E., Gallardo, F., Trifilio, M., Cruz, M., & Bayman, P. (2016). Sun vs. shade affects infestation, total population and sex ratio of the coffee berry borer (*Hypothenemus*

hampei) in Puerto Rico. *Agriculture, Ecosystems & Environment*, *222*, 258–266. https://doi.org/10.1016/j.agee.2015.12.031

Martínez-Núñez, C., Rey, P. J., Manzaneda, A. J., García, D., Tarifa, R., & Molina, J. L. (2021). Insectivorous birds are not effective pest control agents in olive groves. *Basic and Applied Ecology*, *56*, 270–280. https://doi.org/10.1016/j.baae.2021.08.006

Martínez-Salinas, A., Chain-Guadarrama, A., Aristizábal, N., Vilchez-Mendoza, S., Cerda, R., & Ricketts, T. H. (2022). Interacting pest control and pollination services in coffee systems. *Proceedings of the National Academy of Sciences*, *119*(15), e2119959119. https://doi.org/10.1073/pnas.2119959119

Martínez-Salinas, A., DeClerck, F., Vierling, K., Vierling, L., Legal, L., Vílchez-Mendoza, S., & Avelino, J. (2016). Bird functional diversity supports pest control services in a Costa Rican coffee farm. *Agriculture, Ecosystems & Environment*, *235*, 277–288. https://doi.org/10.1016/j.agee.2016.10.029

McDermott, M., & Rodewald, A. (2014). Conservation value of silvopastures to Neotropical migrants in Andean forest flocks. *Biological Conservation*, *175*, 140–147. https://doi.org/10.1016/j.biocon.2014.04.027

Moore, D., Abraham, Y. J., & Mills, N. J. (1990). Effects of competition in the coffee berry borer, Hypothenemus hampei (Ferrari) (Col., Scolytidae). *Journal of Applied Entomology*, *109*(1-5), 64–70.

Morris, J. R., Vandermeer, J., & Perfecto, I. (2015). A keystone ant species provides robust biological control of the coffee berry borer under varying pest densities. *PLoS One*, *10*(11), e0142850. https://doi.org/10.1371/journal.pone.0142850

Nyffeler, M., Şekercioğlu, Ç. H., & Whelan, C. J. (2018). Insectivorous birds consume an estimated 400–500 million tons of prey annually. *The Science of Nature*, *105*(7), 47. https://doi.org/10.1007/s00114-018-1571-z

Oliva, M., Rubio, K. B., Chinguel, D., Carranza, J., Bobadilla, L. G., & Leiva, S. (2023). Coffee berry borer infestation and population per fruit relationship with coffee variety, shade level, and altitude on specialty coffee farms in Peru. *International Journal of Agronomy*, *2023*, e6782173. https://doi.org/10.1155/2023/6782173

Parrish, J. (2000). Behavioral, energetic, and conservation implications of foraging plasticity during migration. *Studies in Avian Biology*, *20*, 52–70.

Perfecto, I., Rice, R. A., Greenberg, R., & Van der Voort, M. E. (1996). Shade coffee: A disappearing refuge for biodiversity: Shade coffee plantations can contain as much biodiversity as forest habitats. *Bioscience*, *46*(8), 598–608. https://doi.org/10.2307/1312989

Raveendran, A., & Murthy, P. S. (2021). New trends in specialty coffees—"The digested coffees". *Critical Reviews in Food Science and Nutrition*, *20*(17), 4622–4628. https://doi.org/10.1080/10408398.2021.1877111

Redlich, S., Martin, E. A., Wende, B., & Steffan-Dewenter, I. (2018). Landscape heterogeneity rather than crop diversity mediates bird diversity in agricultural landscapes. *PLoS One*, *13*(8), e0200438. https://doi.org/10.1371/journal.pone.0200438

Reed, J. M., Fefferman, N., & Averill-Murray, R. C. (2009). Vital rate sensitivity analysis as a tool for assessing management actions for the desert tortoise. *Biological Conservation*, *142*(11), 2710–2717. https://doi.org/10.1016/j.biocon.2009.06.025

Rodríguez, D., Cure, J. R., Cotes, J. M., Gutierrez, A. P., & Cantor, F. (2011). A coffee agroecosystem model: I. Growth and development of the coffee plant. *Ecological Modelling*, *222*(19), 3626–3639. https://doi.org/10.1016/j.ecolmodel.2011.08.003

Ruiz-Cárdenas, R., & Baker, P. (2010). Life table of *Hypothenemus hampei* (Ferrari) in relation to coffee berry phenology under Colombian field conditions. *Scientia Agricola*, *67*, 658–668. https://doi.org/10.1590/S0103-90162010000600007

Şekercioğlu, Ç. H. (2006). Increasing awareness of avian ecological function. *Trends in Ecology & Evolution*, *21*(8), 464–471. https://doi.org/10.1016/j.tree.2006.05.007

Şekercioğlu, Ç. H., Fullwood, M. J., Cerling, T. E., Brenes, F. O., Daily, G. C., Ehrlich, P. R., Chamberlain, P., & Newsome, S. D. (2023). Using stable isotopes to measure the dietary responses of Costa Rican forest birds to agricultural countryside. *Frontiers in Ecology and Evolution*, *11*, 1086616. https://doi.org/10.3389/fevo.2023.1086616

Şekercioğlu, Ç. H., Wenny, D. G., & Whelan, C. J. (2016). *Why birds matter: Avian ecological function and ecosystem services*. University of Chicago Press.

Sherry, T. W., Johnson, M. D., Williams, K. A., Kaban, J. D., McAvoy, C. K., Hallauer, A. M., Rainey, S., & Xu, S. (2016). Dietary opportunism, resource partitioning, and consumption of coffee berry borers by five species of migratory wood warblers (Parulidae) wintering in Jamaican shade coffee plantations. *Journal of Field Ornithology*, *87*(3), 273–292. https://doi.org/10.1111/jofo.12160

Silvertown, J., Franco, M., & Menges, E. (1996). Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. *Conservation Biology*, *10*(2), 591–597.

Stubben, C., & Milligan, B. (2007). Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software*, *22*, 1–23. https://doi.org/10.18637/jss.v022.i11

Vega, F. E., Kramer, M., & Jaramillo, J. (2011). Increasing coffee berry borer (Coleoptera: Curculionidae: Scolytinae) female density in artificial diet decreases fecundity. *Journal of Economic Entomology*, *104*(1), 87–93.

Vega, F., Infante, F., & Johnson, A. (2015). The genus *Hypothenemus*, with emphasis on *H. hampei*, the coffee berry borer. In *Bark beetles: Biology and ecology of native and invasive species* (pp. 427–497). Elsevier. https://doi.org/10.1016/B978-0-12-417156-5.00011-3

Vega, F. E., Franqui, R. A., & Benavides, P. (2002). The presence of the coffee berry borer, *Hypothenemus hampei*, in Puerto Rico: Fact or fiction? *Journal of Insect Science*, *2*(13), 3.

Vega, F. E., Infante, F., Castillo, A., & Jaramillo, J. (2009). The coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae): A short review, with recent findings and future research directions. *Terrestrial Arthropod Reviews*, *2*, 129–147.

Waterhouse, D. F., & Norris, K. R. (1987). *Biological control Pacific prospects*. Inkata Press.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.