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Interacting pest control and pollination services in coffee systems

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Biodiversity-mediated ecosystem services (ES) support human well-being, but their values are typically estimated individually. Although ES are part of complex socioecological systems, we know surprisingly little about how multiple ES interact ecologically and economically. Interactions could be positive (synergy), negative (trade-offs), or absent (additive effects), with strong implications for management and valuation. Here, we evaluate the interactions of two ES, pollination and pest control, via a factorial field experiment in 30 Costa Rican coffee farms. We found synergistic interactions between these two critical ES to crop production. The combined positive effects of birds and bees on fruit set, fruit weight, and fruit weight uniformity were greater than their individual effects. This represents experimental evidence at realistic farm scales of positive interactions among ES in agricultural systems. These synergies suggest that assessments of individual ES may underestimate the benefits biodiversity provides to agriculture and human well-being. Using our experimental results, we demonstrate that bird pest control and bee pollination services translate directly into monetary benefits to coffee farmers. Excluding both birds and bees resulted in an average yield reduction of 24.7% (equivalent to losing US$1,066.00/ha). These findings highlight that habitat enhancements to support native biodiversity can have multiple benefits for coffee, a valuable crop that supports rural livelihoods worldwide. Accounting for potential interactions among ES is essential to quantifying their combined ecological and economic value.

biodiversity | ecosystem services | synergies | coffee production | economic valuation

Ecosystem services (ES), the multiple benefits humankind obtains from biodiversity, are critical to sustaining human life on earth. Still, there are significant knowledge gaps related to the mechanisms through which species provide ES, notably for regulating services (1). These gaps hinder our capacity to manage ES effectively (2) and develop policies that positively impact biodiversity conservation and the provision of ES (3).

In particular, how multiple ES interact, both ecologically and economically, is an area that has received little attention. Most studies have focused on one ES at a time, and those focusing on multiple ES typically assess them separately (4), without accounting for ecological interactions among them (but see ref. 5). ES can produce positive interactions (i.e., synergies, in which increasing the provision of one ES increases the provision of others), negative interactions (i.e., trade-offs, in which increasing the provision of one ES reduces the provision of others), or have no interactions (i.e., additive or complementary effects, in which services have independent effects) (6, 7). Considering the ecological and economic implications of ES, understanding how they interact is vital to inform biodiversity conservation and landscape management.

Animal-mediated regulatory ES such as pollination and pest control benefit crop production (4). Worldwide, 87.5% of flowering plants (8)—including 75% of major crops (9)—depend on animal pollination to different degrees, with a greater proportion of tropical plants being animal-pollinated in comparison with those in temperate zones (8). Likewise, a diversity of natural enemies suppresses pests in important global food crops (10). Both pollination and pest control provide benefits to the agricultural sector worth billions of US dollars, either by increasing productivity or avoiding replacement costs from ensuring pollination and suppressing pests in other ways (11–13).

Coffee is one of the most important crops across the world's tropical regions because of its economic value, contributions to biodiversity conservation, and cultural linkages (14). Coffee production also supports rural livelihoods, with small farmers worldwide supplying nearly 70% of its global production (14). In 2012, total coffee exports reached US$24 billion, a three-fold increase over 2002, because of steady increases in production and consumption over the last 50 y (15). Optimal coffee production regions overlap closely with critical areas for biodiversity conservation (16). However,

Significance

Food production depends on biodiversity and ecosystem services (ES) such as pest control and pollination. Our knowledge about biodiversity benefits to crop production has increased in recent decades, but most studies treat ES separately and then add up their values. Ignoring that these services, being part of the same system, likely interact is blinding us to potential synergies and trade-offs. Our field experiment shows, at realistic field scales, that pest control and pollination can interact positively. This synergy translates directly to improved yields and income for coffee farmers, who produce a global commodity worth $24 billion per year. Our findings highlight the need to study interactions to understand the linkages between biodiversity, ES, and farmers' livelihoods.

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current intensification trends (i.e., moving from coffee agroforestry systems to coffee monocultures) hamper coffee systems' potential to support biodiversity and reduce ES provision (4, 16).

Bees and birds are critical ES providers to coffee systems. For instance, Arabica coffee (*Coffea arabica*) plants can self-pollinate, but native and nonnative pollinators improve coffee productivity by increasing fruit set, fruit size, and overall yield (17), with direct impacts on revenues (18–20). Similarly, birds are essential pest control providers (12, 21) and can also contribute to pollination to a lesser degree (12, 22). In particular, birds suppress the coffee berry borer or broca (*Hypothenemus hampei* Ferrari) (Coleoptera: Curculionidae: Scolytinae) (23), one of the most damaging pests to coffee crops worldwide (24). Broca suppression by birds translates into direct economic benefits to farmers (25–27).

Despite the importance of these and other ES to agriculture, we know little about how they interact ecologically and economically (7, 28) with most studies considering multiple ES conducting their assessments in parallel (i.e., assess each ES independently) but not testing for actual interactions between them. A recent review reported the existence of only 16 studies on ES interactions in agriculture, covering 10 crops and 9 countries, none of them in Latin America (7). Similarly, a review focused on pollination and pest control in coffee systems (29) found only one published study related to the interaction of these ES (30), also included in Garibaldi et al. (7). Without understanding potential interactions among ES, it is difficult to estimate and manage nature's contributions to coffee and other agroecological systems worldwide.

Here, we directly test interactions between two critical ES to agriculture, using manipulative experiments at realistic field scales (Fig. 1). We focus on coffee systems in Latin America and ask three specific questions. How much do pest control and pollination services contribute to coffee productivity? Are there synergies, trade-offs, or no interactions between these two ES? What is the economic value of these two ES as inputs to coffee production, both individually and in combination?

Results

Our field experiments (Fig. 1) revealed that birds and bees interact positively (i.e., synergistically) increasing coffee production. Their combined effects are larger than their individual contributions. This is true, in part, because they affect different fruit parameters that relate to yield. Throughout the results, we refer to the treatment in which only birds were allowed access as "bird activity alone," when only bees were allowed access as "bee activity alone," when both were allowed access as "bird and bee activity," and when birds and bees were both excluded as "neither activity."

Fruit Set. Bird activity alone did not change fruit set relative to excluding both birds and bees. In contrast, bee activity alone significantly increased proportional fruit set from 0.50 to 0.56 (representing an 11.0% increment) (Fig. 2*A* and Table 1). We found a significant interaction between bird and bee activity (Table 1), indicating synergistic effects between the pest control and pollination services. The combined effects of bird and bee activity on fruit set were significantly greater than their individual effects (Fig. 2*A* and Table 1), jointly increasing proportional fruit set from 0.50 to 0.62 (representing a 24.0% increment) compared to the neither activity treatment.

Fruit Weight. Both bee activity and fruit condition (i.e., bored vs. not bored) influenced average fruit weight, while bird activity alone did not (Table 1). Compared to treatments without bees, bees increased fruit weight from 1.41 to 1.47 g (representing a 4.2% increment). The same increment was found between bored and not-bored fruits. We found significant interactions between bird and bee activity for average fruit weight, as well as significant interactions between bee activity and fruit condition (Table 1 and Fig. 2 *B* and *C*). Fruits weighed more when they were not bored and came from branches where bees had access (1.53 g) compared to all other treatments (1.41 g), representing an 8.5% increment (Fig. 2*B*). Moreover, independently of fruit condition, average fruit weight was higher with bird and bee activity compared to all other treatments (0.09 g difference, representing a 6.6% increment) (Fig. 2*C*).

We also evaluated bird and bee activity effects on fruit weight uniformity, as measured by the fruit weight coefficient of variation (CV). We found no individual effects of bird activity, bee activity, or fruit condition on fruit weight uniformity but the interaction between bird and bee activity was significant (Table 1). We observed greater fruit weight uniformity on fruits from branches where both birds and bees had access, compared to all other treatments (Fig. 2*D*).

Bird and Bee Activity Effects on Proportion of Bored Fruits. We found a significant interaction between birds, bees, and time affecting the observed proportion of bored fruits (Table 1). The proportion of bored fruits differed across treatments, and these differences changed as fruits matured (Fig. 3). In November, when the main harvest took place, the proportion of bored fruits was significantly lower in branches where birds were present (Fig. 3). Specifically, at this time, we observed the highest broca infestation rate when neither birds nor bees were present (0.14 proportion) and the lowest broca infestation rate when birds were present but bees were absent (0.07 proportion), resulting in a 52.8% reduction.

Economic Value of Pest Control and Pollination Services. We estimated average coffee yield for our 30 study farms to be 12,889 kg/ha (±1,832) under natural conditions (i.e., bird and bee activity treatment). This potential yield translates to an expected gross income of US$4,317/ha (±614). Our experiments indicate that, with birds excluded, average yield would be reduced by 13.5% or 1,744 kg/ha (95% confidence interval [CI], 1,237 to 2,251), due to the combined effects on fruit set and fruit mass. This represents a financial loss of US$584/ha (95% CI, US$414 to 754). With bees excluded, average yield would be reduced by 24.5%, 3,161 kg/ha (95% CI, 2,242 to 4,080), representing a loss of US$1,059/ha (95% CI, US$751 to 1,367). Finally, we found the greatest reduction in average yield with both birds and bees excluded: 24.7% reduction, equivalent to losing 3,183 kg/ha (95% CI, 2,255 to 4,110) or US$1,066/ha (95% CI, 755 to 1,377). See *SI Appendix* for additional coffee yield and income calculations.

Discussion

Our field experiments showed that pest control and pollination services provided by birds and bees contribute to coffee production by increasing fruit set (Fig. 2*A*) and fruit weight (Fig. 2 *B*–*D*) and by decreasing broca infestation (Fig. 3). Most importantly, we found significant positive interactions between the effects of birds and bees (Table 1), indicating synergy between the two ES these taxa provide. Fruit set, fruit weight, and fruit uniformity were all highest when birds and bees were both allowed to visit coffee plants (Fig. 2). These ES contribute substantially to farmer income, both individually and together.

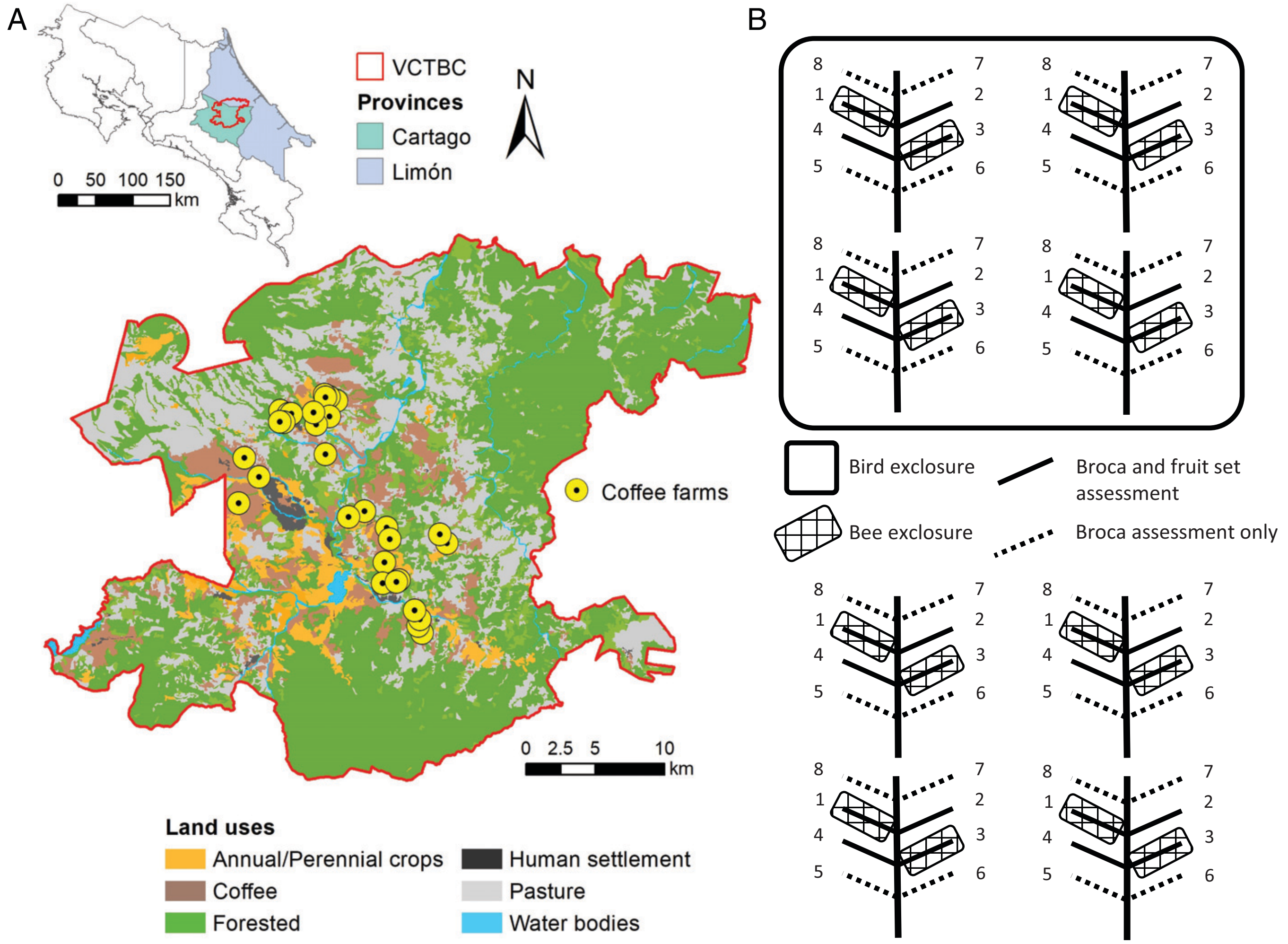

Fig. 1. Study area and experimental design. (*A*) Location of the VCTBC (red silhouette) proportional to Costa Rica and main land uses present within the VCTBC. Yellow circles with black centers show individual location of coffee farms ($n = 30$). (*B*) Full-factorial experimental design of bee and bird exclosure treatments to assess the potential interacting contributions of pollination and pest control. By selecting eight coffee plants and excluding a group of four coffee plants from birds, and two branches in each plant from bees, we set up four exclosure treatments at the branch level: i) in which only birds were allowed access (bird activity alone), ii) where only bees were allowed access (bee activity alone), iii) where both were allowed access (bird and bee activity, i.e., control treatment), and iv) where birds and bees were both excluded (neither activity). In branches 1 to 4, we assessed fruit set (i.e., pollination service) and the proportion of bored fruits (i.e., pest control service). In branches 5 to 8, we further assessed only the proportion of bored fruits.

Although *C. arabica* is considered to be self-compatible, we found that coffee benefits from bee activity by developing more fruits from initial flowers (i.e., fruit set) and increasing fruit weight (Fig. 2). These results align with other studies which have found positive effects on yield from visits by both native and nonnative bees, reporting fruit set increments between 9 and 50% (17–19, 31, 32) and fruit weight increments between 7 and 27% (30). Thus, *C. arabica* is likely amphicarpic, i.e., some flowers require cross-pollination while others can self-pollinate (31). A higher diversity of bees more effectively deposits pollen on stigmas of coffee flowers (32), which is critical to boosting coffee productivity. Bee cross-pollination also contributes to coffee quality by reducing the frequency of misshapen seeds, fruit drop, increasing pollen genetic diversity (19, 33, 34), and as seen here by increasing fruit weight uniformity (Fig. 2*D*).

Coffee also benefits from bird activity by a reduction in broca infestation. Both gleaners and aerial-hawking insectivorous birds, as well as migrants and year-long residents, are proven broca predators (23). Additional evidence of broca predation by other groups such as hummingbirds (27) indicates that increases in bird diversity might positively impact bird-mediated pest control service delivery. Broca suppression by birds varies between 1 and 58% in coffee plants where birds are allowed to forage (23, 25–27). Bird-mediated pest control services may also improve fruit set by regulating floral and foliar herbivores thereby preventing resource allocation from reproductive to vegetative organs (30). Finally, coffee yield benefits from bird-mediated pest control since higher broca infestation is related to lower fruit weight and early fruit drop (24).

We found significant interactions between pest control and pollination services in coffee (Table 1), indicating synergy between these two ES (35). Previous studies have found interactions between these services in other crops, such as red clover and oilseed rape (6, 36, 37). However, only one study (30) has evaluated interactions between pest control and pollination in coffee systems. They found additive instead of synergistic effects. Importantly, no studies have found negative interactions between bird and bee activity and their ES.

How might pollination and pest control interact synergistically? Previous work raises several hypotheses. First, grazing by herbivore pests may modify floral display or the quality of floral rewards, thus reducing the attractiveness of plants for pollinators (7). The role of birds and other vertebrates in controlling

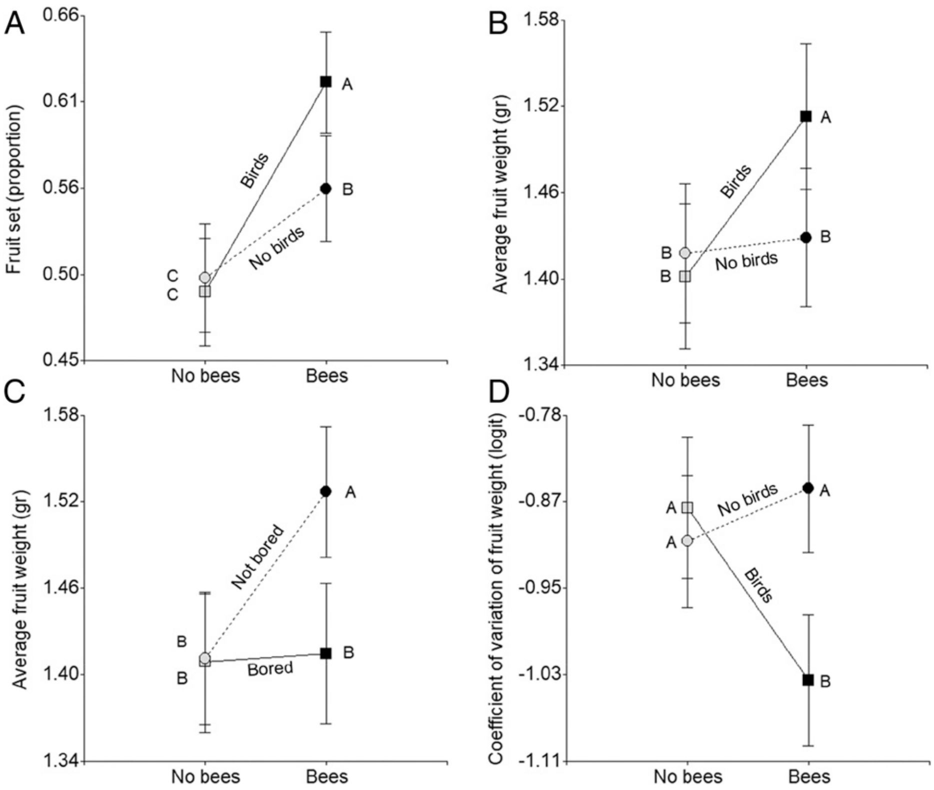

Fig. 2. Interacting effects of bee and bird activity on coffee production. (*A* and *B*) Effects of bee and bird activity on fruit set and fruit weight. (*C*) Effects of bee activity and fruit condition (i.e., bored vs. not bored) on fruit weight, and (*D*) effects of bee and bird activity on fruit weight CV as a measure of fruit uniformity. Statistics are presented in Table 1. Different letters denote statistically significant differences.

arthropod abundance and plant damage in coffee has been well-established in previous studies (38, 39). In cucumber and radish crops, herbivory has been associated with fewer pollinator visits due to the reduced number, size, and flower lifetime (40). Pest control also boosts seed set and yield in red clover (6) and oilseed rape (36), suggesting that improved pest control also benefits pollination services. Second, broca infestation may trigger metabolically expensive defensive reactions in plants (41), creating resource limitations that can reduce fruit set and seed size. As a result, reducing pest pressure by promoting bird activity will allow the plant the resources to respond fully to improved pollination. In coffee, there is evidence that excluding birds and bats increased herbivory, reducing fruit set and suggesting that herbivory may trigger resource allocation from reproductive to vegetative organs (30). Third, this and other studies have shown that bee-pollinated coffee flowers appear to receive higher resource investment from the plant, resulting in higher fruit sets (31) and larger fruits (30). These resource allocation trade-offs may also result in fruits and seeds that are better chemically defended against pests with cross-pollination. Thus, pollination services may help reduce broca infestation, adding to the effect of bird activity. While each of these hypotheses is ecologically plausible, establishing the specific mechanism for the positive interactions we observed is beyond the scope of this study.

We also found evidence of positive effects of ES on crop quality, which has been less studied than yield effects per se. Pollination services have been found to increase uniformity and shelf life in strawberry and blueberry crops (42, 43), and improve apple size, shape, commercial value, and firmness in orchards (44). In our study, bird-mediated pest control and bee pollination services increased the uniformity of coffee fruit weight, an important crop quality metric. We observed the lowest variation in fruit weight, i.e., greatest uniformity, when both birds and bees visited coffee plants (Fig. 2*D*). Broca infestation also reduces coffee quality in several ways, and we found the lowest broca infestation when birds were present (Fig. 3). Broca infestation affects coffee quality by damaging seeds directly, but also by facilitating secondary bacterial infections (45), negatively impacting coffee aroma, flavor, and acidity (46). Broca is also a carrier of several fungal species, including *Aspergillus ochraceus* that produces the mycotoxin ochratoxin known to be nephrotoxic and carcinogenic (47). Amounts of ochratoxin content in roasted coffee are controlled under European Union regulations (46), potentially impacting these markets' access.

Unexpectedly, our pollination treatments also affected broca infestation rates. Early in fruit development, we observed significantly more bored fruits on branches where bees were allowed to visit (Fig. 3, May). Broca beetles naturally follow aggregated distribution patterns, but are capable of short and long dispersion flights (48). We speculate that this is another potential mechanism involved in the synergistic effects we observed, suggesting that ES interactions could occur at very fine scales (i.e., branch level). First, by increasing the total number of fruits per branch, pollinators may reduce the need for broca individuals to move among branches, limiting the spread of infestation (24). However, late in fruit development (i.e., Fig. 3, November), the interaction between bird presence and bee absence lowered broca infestation, most likely resulting from having fewer available fruits and influencing broca to disperse more. Similarly, the treatment with bird and bee absence resulted in the greatest number of bored fruits. Perhaps because of fewer available fruits which combined with the aggregated nature of the broca beetle and the lack of predation from birds contributed to an increase in infestation. Second, broca use olfactory and visual cues to find hosts (49), perhaps at earlier stages of

Table 1. Mixed effect models testing the effects of BeeEx, BirdEx, and their interaction on fruit set, fruit weight, and proportion of bored fruits

Fixed effect	*df*	*F* value	*P*
Fruit set			
BirdEx	1	1.83	0.1790
BeeEx	1	402.48	**<0.0001**
BirdEx × BeeEx	1	67.06	**<0.0001**
Fruit weight (g)			
BirdEx	1	0.87	0.3584
BeeEx	1	15.05	**0.0002**
BOR	1	7.97	**0.0054**
BirdEx × BeeEx	1	10.12	**0.0018**
BirdEx × BOR	1	0.01	0.9327
BeeEx × BOR	1	12.18	**0.0006**
BirdEx × BeeEx x BOR	1	0.01	0.9184
Fruit weight CV			
BirdEx	1	2.71	0.1106
BeeEx	1	1.56	0.2142
BOR	1	0.06	0.8071
BirdEx × BeeEx	1	5.65	**0.0190**
BirdEx × BOR	1	0.59	0.4438
BeeEx × BOR	1	1.37	0.2443
BirdEx × BeeEx × BOR	1	0.01	0.9315
Proportion of bored fruits			
BirdEx	1	2.54	0.1119
BeeEx	1	74.34	**<0.0001**
Time	3	769.83	**<0.0001**
BirdEx × BeeEx	1	1.11	0.2924
BirdEx × Time	3	10.91	**<0.0001**
BeeEx × Time	3	92.37	**<0.0001**
BirdEx × BeeEx × Time	3	3.12	**0.0259**

We also evaluated the effect of fruit condition (bored vs. not bored) (BOR) and its interaction with bird exclosure (BirdEx) and bee exclosure (BeeEx) on fruit weight, as well as the effect of time (Time) and its interaction with bird and bee exclosure on the proportion of bored fruits. See *Materials and Methods* for a detailed description of explanatory variables, response variables, and statistical models. Bold denotes statistical significance.

fruit development those fruits pollinated by bees with greater quality (size, color) might be more attractive to broca.

Finally, by measuring the change in coffee production when ES are removed, we estimated the monetary value of pest control and pollination. We found the synergistic effect of bird pest control and bee pollination services translate directly into monetary benefits to coffee farmers. Excluding birds and bees resulted in an average yield reduction of 24.7% (equivalent to losing a gross income of US$1,066.00/ha). Our experimental design allowed us to assess the economic contribution of each service and their combined monetary values in coffee systems, which was greater than the estimation of either pest control or pollination services alone. Our average estimate of broca reduction (US$584/ha) is higher than those previously reported by other studies in coffee farms in Jamaica and Costa Rica (US$44 to 310/ha) (25–27), while our estimate of the pollination value (US$1,059/ha) falls between those previously reported in coffee (US$17 to 1,861/ha/y) (18, 20). Bird pest control and bee pollination services, better together than individually, increase coffee fruit set and uniformity and reduce coffee yield losses. These services can represent real economic benefits for farmers—at least a quarter of the calculated gross incomes are protected/gained thanks to these services. Finally, even though a complete cost-benefit analysis is beyond the scope of this article, accounting for costs of coffee production would allow an estimate of net benefits and avoid overestimating ES values (20).

Our findings highlight that habitat enhancements to support native biodiversity can have multiple benefits for agriculture. A better understanding of potential interactions among ES is long overdue. Identifying these ecological and economic synergies and trade-offs among ES will be essential to quantifying their collective values accurately and managing them effectively.

Materials and Methods

Study Area and Farm Selection. We conducted the study within the Volcanica Central Talamanca Biological Corridor (VCTBC) in Costa Rica. The VCTBC constitutes a heterogeneous landscape where productive lands interact with forest remnants within and outside protected areas across 1,146.3 km^2. In 2010, the area dedicated to coffee cultivation covered ∼8.5% of the total landscape, third in expanse after forests (51.1%) and pastures (25.3%) (Fig. 1*A*). We selected 30 coffee farms that represent local variation in shade, management and elevation (672 to 1,110 m above sea level) (Fig. 1*A*). Most farms were owned by smallholders with a coffee cultivated area ranging from 0.35 to 6 ha (only two farms had coffee cultivated area slightly greater than 20 ha). All farmers cultivated *C. arabica* L., most often the Caturra variety, but also varieties such as Obatá, Catimor, Catuai rojo, CR95, and Marsellesa (see *SI Appendix* for additional information on farm characteristics).

Plant Selection and Experimental Design. To assess the potential interacting contributions of pest control and pollination services to coffee productivity, we established a full-factorial experiment of bird and bee exclosure treatments (Fig. 1*B*). Before coffee flowering, between January and February 2019, we selected eight coffee plants of similar height and vigor in each coffee farm. All selected plants were located on the same coffee lot and planted at close distance, thus sharing location, and environmental and management conditions.

To assess bird pest control services, we enclosed four out of the eight coffee plants with a plastic mesh small enough to exclude foliage gleaning birds but large enough to allow bees and other small animals (20-mm mesh size) (23). A frame made of bamboo poles was used to maintain the plastic mesh in place, resulting in a permanent exclosure. The remaining four coffee plants were left open (i.e., not enclosed), allowing birds to forage freely. To assess bee pollination services, we selected four similar branches in each of the eight coffee plants (hereafter: experimental branches 1 to 4). We excluded bees using fine nylon mesh gauze bags in two out of these four branches (1 mm mesh size; handmade by a seamstress). We placed the bags over selected branches before the main flowering event and removed them once the flowering ended. In rare cases when we found opened flowers before setting the bags, we removed those flowers. The other two branches on each plant served as open controls to measure productivity under natural pollination. This full-factorial design resulted in four different treatments at the branch level (Fig. 1*B*): i) only birds were allowed access (bird activity alone), ii) only bees were allowed access (bee activity alone), iii) both were allowed access (bird and bee activity, i.e., control treatment), and iv) birds and bees were both excluded (neither activity). Furthermore, to make sure we accurately assessed broca infestation rates, we randomly selected four additional branches distributed in the upper and lower parts of the same eight plants (hereafter: branches 5 to 8) (Fig. 1*B*). We did not test for the effects from the experimental manipulations themselves from which there is inconsistent evidence (50). Finally, we checked bird exclosure nets regularly while the experiment was deployed to repair or replace nets if necessary and to make sure birds have been effectively excluded.

Fruit Counting and Fruit Parameters. In May 2019, 12 to 18 wk after the main flowering event, we removed pollinator exclosures (i.e., nylon mesh gauze bags) and counted the number of early fruits at each experimental branch's eight most distal nodes. We also estimated the number of flowers that opened at each node by adding the number of fruits to the number of flower scars and abnormal flowers (flowers that did not appear healthy/functional).

We visited every farm three more times between July and November 2019, and counted the total number of fruits and bored fruits present in all branches (i.e., experimental branches 1 to 4 and additional branches 5 to 8 used for broca assessment only). In branches 5 to 8, we counted fruits in all existing fruiting nodes (i.e., not limited to the eight most distal nodes). We collected all

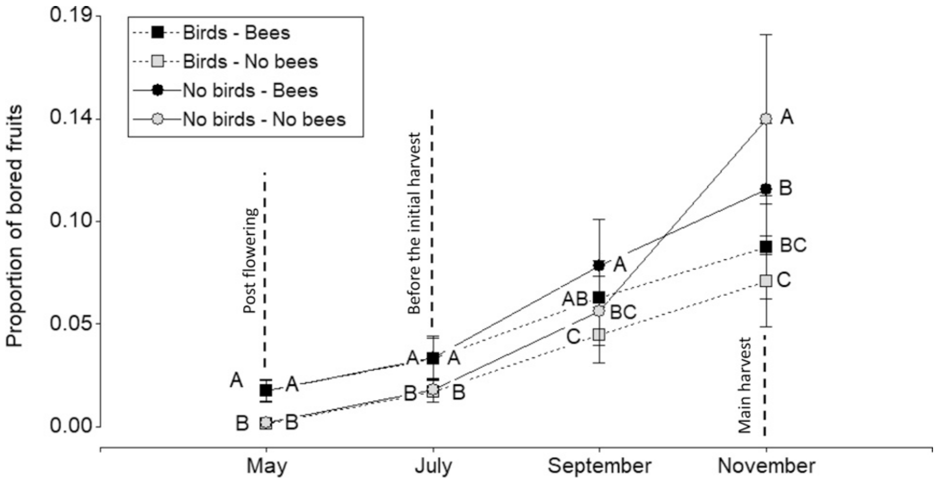

Fig. 3. Interacting effects of bee activity, bird activity, and time on the proportion of bored fruits. Fruit counts were conducted every 2 mo postflowering (May) until main harvest (November). Statistics are presented in Table 1. Different letters denote statistically significant differences within each time.

harvestable (ripe) fruits present in our experimental branches from the second visit onward. Immediately after harvesting, we measured fresh (wet) weight from each fruit individually and visually inspected for broca marks presence or absence. Due to weather conditions and differences in phenology, the period between visits differed among farms.

We calculated fruit set, average fruit weight, fruit weight CV (as a measure of fruit weight uniformity, a desirable condition for marketing and roasting), and proportion of bored fruits for each experimental treatment. Proportion of bored fruits was calculated based on information from branches 1 to 8. We calculated fruit set as the number of coffee fruits recorded in the second count (i.e., just before the initial harvest) divided by the number of initial flowers. We calculated the average and the CV of fruit weight for each treatment using the recorded mass of all harvested fruits of all experimental branches per treatment. Finally, we calculated broca infestation rate per treatment as the fraction of harvested fruits with broca marks. We acknowledge that broca might create a mark and be predated upon before causing seed damage; however, since we are focusing on differences among treatments, we assume this effect is consistent among them such that comparisons are valid. Also, we further inspected all fruits with broca marks and found that 81% showed evidence of effective broca colonization and seed damage.

Data Analysis. To analyze the effect of bird and bee exclosure treatments on fruit set, we used generalized linear mixed models (glmer function in R package lme4). We included the number of initial flowers as an offset in this model to account for variation in flower and fruit counts and potential effects on fruit set, assuming a binomial distribution. We fitted the model with bird exclosure, bee exclosure, and their interaction as fixed effects, where a significant positive interaction is a signal of synergism (35). To meet the hierarchical sampling unit structure of the study design, we identified farm and bird exclosure sampling units nested within the farm as random effects.

To analyze the effect of bird and bee exclosure treatments and bored condition on the average fruit weight, we used linear mixed models (lme function in R package nlme). We identified farm and bird exclosure sampling units nested within the farm as random effects to meet the hierarchical study design. To assess the effects on fruit weight uniformity, we used the CV of fruit weight as a response variable following the same analytical approach.

To analyze the effect of bird and bee exclosure treatments on the proportion of bored fruits (i.e., fruits infested by broca from branches 1 to 8), we used generalized linear mixed models. Assuming a binomial distribution, we included the total number of fruits as an offset in this model to account for variation in fruit counts and potential effects on the proportion of bored fruits. Because we counted the number of bored fruits across time, we fitted this model with bird exclosure, bee exclosure, time, and all possible interactions as fixed effects. To account for nonindependence in the study design, we identified farm, bird and bee exclosure sampling units as nested random effects.

Economic Analyses. We calculated expected yield and farmer income based on fruit set, proportion of bored fruits, and fruit weight parameters from our exclosure experiment. This allowed us to calculate the economic benefits of current pest control and pollination services across coffee farms. To estimate average productivity per farm and exclosure treatment, we first estimated the average number of fruits on the four unmanipulated plants by counting all fruiting nodes in each plant. Then, we randomly selected three branches per plant and estimated the average number of fruits per node by counting the total number of nodes and the total number of fruits. Next, we estimated the average number of fruits per plant by multiplying the total number of nodes by the estimated number of fruits per node, and averaged using the information from all four plants. We then estimated average per plant productivity (in kilograms) per treatment considering the results from our exclosure experiment. To do so, we first calculated the number of harvestable fruits per plant in each farm by multiplying the average number of fruits per plant by the mean proportional fruit set from our statistical model for each treatment. Then, to calculate the number of bored harvestable fruits, we multiplied the total harvestable fruits per plant by the mean proportion of bored fruits from our statistical model for each treatment. The number of healthy fruits resulted from the difference between total harvestable fruits per plant and the number of bored harvestable fruits. To calculate kilograms of harvestable fruits per plant per treatment, considering differences in fruit weight between healthy and bored fruits, we individually multiplied the number of healthy and bored harvestable fruits per plant by their mean weight from our statistical model for each treatment, and summed them.

We then scaled up to farm-level estimates of coffee productivity (in kilograms per hectare), using plant density per hectare data estimated from a 10- × 10-m plot in each farm. We calculated yield in kilograms per hectare per farm for each exclosure treatment by multiplying the number of estimated plants per hectare by the estimated average per plant productivity (in kilograms) per exclosure treatment. Finally, we multiplied the average price that coffee mills paid per kilogram of coffee (US$0.33) in the Turrialba region during the year 2019 to obtain expected income per hectare for each treatment assuming all fruits were marketable, even if bored. This differs from methods used in other studies (25, 27) but reflects the reality of the Turrialba region where all fruits are weighed and paid for regardless of infestation (see *SI Appendix* for step-by-step calculations and formulas).

Data Availability. Data from bird and bee exclosure experiments on coffee farms and data on coffee productivity can be found in Figshare (https://doi.org/10.6084/m9.figshare.19394063) (51).

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