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ARTICLE

Birds and bats enhance cacao yield despite suppressing arthropod mesopredation

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Abstract

Bird- and bat-mediated biocontrol benefits the productivity of tropical commodity crops such as cacao, but the ecological interactions driving these ecosystem services remain poorly understood. Whereas birds and bats prey on herbivorous arthropods, they may also prey on arthropod mesopredators such as ants, with poorly understood consequences for pest biocontrol. We used a full-factorial experiment excluding birds, bats, and ants to assess their effects on (a) the abundance of multiple arthropod groups; (b) predation pressure on arthropods evaluated through artificial sentinel caterpillars; and (c) cacao yield over 1 year in shaded agroforestry systems of native cacao varieties in Peru. Birds and bats increased cacao yield by 118%, which translates in smallholder benefits of ca. US $959 ha^{-1} year^{-1}. Birds and bats decreased predation by ants and other arthropods, but contributed to the control of phytophagous taxa such as aphids and mealybugs. By contrast, ant presence increased the abundance of these sap-sucking insects, with negative impacts for cacao yield. Notably, high abundances of the dominant ant *Nylanderia* sp., known to attend sap-sucking insects, were associated with lower cacao yield along a distance gradient from the closest forest edge. According to these results, arthropod predation by birds and bats, rather than mesopredation by arthropods, was most responsible for increases in cacao yield. Moving forward, detailed research about their trophic interactions will be necessary to identify the cause of such benefits. Retaining and restoring the large benefits of birds and bats as well as minimizing disservices by other taxa in cacao agroforests can benefit from management schemes that prioritize preservation of shade trees and adjacent forests within agroforestry landscapes.

Carolina Ocampo-Ariza, Justine Vansynghel, and Denise Bertleff contributed equally to this work.

KEYWORDS
ants, biological pest control, cacao agroforestry, ecosystem services, multitrophic interactions, native cacao, Peru

INTRODUCTION

Ecosystem services provided by animals contribute significantly to the production of multiple crops and the maintenance of ecological stability of agroecosystems (Dainese et al., 2019; Garibaldi et al., 2018; Zhang et al., 2007). Notably, arthropod predation services can reduce the costs associated with pest control and enhance crop productivity through top-down effects on fruit set and harvest (Taylor et al., 2018; Whelan et al., 2008). The predation of herbivorous or frugivorous arthropods can help prevent leaf damage (Cassano et al., 2016; Van Bael et al., 2007) and improve the quantity and quality of harvested fruits (Maas et al., 2016). However, the contribution of different predatory groups to top-down regulation of potential crop pests varies across land-use types, levels of disturbance, and regions (Roslin et al., 2017; Schwab et al., 2021). Therefore, local assessments are needed to identify the main providers of arthropod predation services and their relative contribution to crop yield.

Sustained productivity of neotropical cacao agroforestry systems is hindered by multiple constraints during the cacao life-cycle, including low pollination success, leaf and flower herbivory, and other pests and diseases reducing crop yields (Vansynghel, Ocampo Ariza, et al., 2022). Among arthropod pests, caterpillars of the pod and bark borers *Carmenta foraseminis* and *C. theobromae* (Lepidoptera: Sesiidae), and the mirid *Monalonion dissimulatum*, are considered to cause the most important yield losses (e.g., Carabalí Muñoz et al., 2018; Vargas et al., 2005). Caterpillars in the Pyralidae and Pterophoridae families have been also identified as relevant leaf eaters, whereas aphids and mealybugs are the most abundant sap-sucking taxa on cacao trees (e.g., Castillo, 2013). However, the effects of these groups on crop yield have not been quantified, and the identities of their natural enemies remain unclear.

The presence of key predators of herbivorous arthropods—notably birds, bats, and ants—has been linked to a decrease of ecosystem disservices such as leaf herbivory (Cassano et al., 2016; Van Bael et al., 2007) and significant improvements in cacao productivity (Gras et al., 2016; Maas et al., 2013). However, the relative contribution of different predator taxa to biological control and intraguild interactions among predators remain poorly understood (Gras et al., 2016; Ritchie & Johnson, 2009; Wielgoss et al., 2014). This prevents the identification of key agroforestry management strategies toward biodiversity-derived benefits for smallholder farmers, which comprise 70% of cacao producers worldwide (Voora et al., 2019).

Biocontrol of herbivorous arthropods is often affected by intraguild interactions between top and intermediate predators (Ritchie & Johnson, 2009; Schmitz, 2007; Tscharntke, 1997). Top predators, such as birds and bats, consume not only pest insects, but also predatory arthropods such as ants or spiders (hereafter "mesopredators"), potentially weakening pest control (Grass et al., 2017; Karp & Daily, 2014; Martin et al., 2013). Conversely, the combined predatory activity of multiple groups may have additive or even synergistic effects on the control of herbivorous arthropods (Williams-Guillén et al., 2008). Exclusion experiments have proven to be useful tools to evaluate the separate and combined role of different taxa in arthropod predation, and other ecological functions which may impact plant productivity (Clough et al., 2017; Ferreira et al., 2023; Maas et al., 2019; Martin et al., 2013; Wielgoss et al., 2013). However, so far few studies have successfully used exclusion experiments to disentangle the effects of diurnal and nocturnal vertebrate predators on arthropod populations and crop yield (Maas et al., 2019); and the ecosystem services and potential disservices provided by each group vary across studies (Karp & Daily, 2014; Maas et al., 2013; Williams-Guillén et al., 2008). Consequently, studying the separate and combined contribution of top predators and mesopredators has the potential to clarify their trophic roles in the cacao life cycle and how these contribute to productivity.

Ants play major and diverse ecological roles in tropical agroecosystems, including predation, herbivory, and mutualisms with crop pests (e.g., Clough et al., 2017; Philpott & Armbrecht, 2006; Wielgoss et al., 2013). These ecological roles may have divergent or even completely opposite effects on crop yield: whereas mesopredation may favor crop yield by reducing the impact of herbivorous insects, the assistance of crop pests by ants may result in significant issues for plant growth and productivity. Despite these contrasts, current evidence indicates that ants can have an overall positive effect on pest control, herbivory suppression, and crop yield, outweighing the contribution of other mesopredatory arthropods (e.g., Sam et al., 2022; Wielgoss et al., 2013). Moreover, the high densities of ants in tropical agroforestry make them appropriate for exclusion experiments, since changes in their relative abundances are quickly observed and may be linked to other ecological changes. For example, ant exclusion experiments combined with arthropod diversity surveys may allow assessing the overall contribution of the ant community to crop productivity, and the control of other arthropod taxa.

Artificial sentinel caterpillars are a useful tool to simultaneously evaluate arthropod predation by multiple taxa in the field (Howe et al., 2009). This passive and non-invasive method provides a way to monitor the activity of arthropod natural enemies, including top and meso-predators and parasitoids (Lövei & Ferrante, 2017), and distinguish among them. In spite of some limitations, such as being unspecific to represent precise prey species (Nurdiansyah et al., 2016) and mostly attracting predators and parasitoids guided by visual, rather than chemical cues or movement, the method provides a cost-efficient alternative for making general estimations of predation pressure on non-flying arthropods in different habitats (e.g., Howe et al., 2009; Lövei & Ferrante, 2017; Roslin et al., 2017). Recent studies using artificial caterpillars in agroecosystems have shown that birds and ants are dominant arthropod predators (Maas et al., 2015; Schwab et al., 2021), that predation pressure in farmland is lower than in natural habitats, and that the identity of the main arthropod predators varies greatly in function of landscape and management variables, as well as across the year (Low et al., 2014; Molleman et al., 2016). Ant marks have been found to represent up to 69% of predation rates on artificial caterpillars in agroforests in Madagascar (Schwab et al., 2021), despite ants being mostly guided toward prey through chemical cues (Molleman et al., 2016). Combining sentinel prey experiments with selective predator exclusions can help identify the main arthropod predators, disentangle the roles of top and intermediate predators on biocontrol, and identify the best management strategies at agroforest and landscape scales to maximize their activity.

We set up a full-factorial experiment excluding birds, bats, and ants from cacao trees to assess the relative contribution of each taxon to arthropod predation and yield in Peruvian agroforestry systems. The study was developed along gradients of distance to forest and canopy cover, to account for local and landscape variables known to impact the diversity and activity of animal taxa that affect cacao yield, including potential pests and arthropod predators (Gras et al., 2016; Ocampo-Ariza et al., 2022). We evaluated arthropod abundances and arthropod predation rates (the frequency or percentage of predation attacks found on artificial sentinel caterpillars) at the time of flowering and early fruit development of cacao fruits, considered as the most critical stage for yield success (Bos et al., 2007; Maas et al., 2013). We assessed cacao yield over the course of one full year. We hypothesized that (1) birds and bats would have a comparable contribution to cacao yield (Maas et al., 2019); (2) bird and bat exclusion would result in mesopredator release, reflected in higher predatory activity of mesopredators on artificial caterpillars and lower densities of phytophagous arthropods within exclosures than outside of them (Gras et al., 2016); and (3) ants would play a role as mesopredators, but simultaneously enhance the presence of phytophagous insects, given the mutualistic interaction between ants and sap-sucking insects (Way, 1963; Wielgoss et al., 2014). We discuss the relevance of our results for the management of ecosystem services in cacao agroforests, and the study of ecological interactions within agroecosystems.

METHODS

Study area

The study was performed in 12 cacao agroforests in the surroundings of the community of La Quemazón, Piura, Peru (5°18′48.03″ S, 79°43′12.02″ W). The agroforests were located in the seasonally dry tropical forest biome, along a gradient of distance to secondary forest ranging from 56 to 964 m. Canopy closure in the agroforests was medium to high, ranging between 39% and 84%, and dominated mostly by *Inga* spp. (Hanf-Dressler, 2020). This canopy cover gradient did not appear to have a major influence in arthropods or yield and was not included in our data analyses. Cacao agroforests ranged in size between 0.4 and 1.92 ha, with an average age of 10 years, representative of agroforests in the study area.

Seasonally dry tropical forests are known for their extreme climatic conditions, including a dry season which extends for ~8 months, and extremely low annual rainfall (Linares-Palomino et al., 2011). Cacao agroforests in this region require irrigation to meet the water needs of the crop, and of the shade trees intercropped with cacao. The phenology of cacao plants in the region of Piura is characterized by year-round production, with a marked flowering peak from September to October, and a consequent harvesting peak 6 months later, between March and April. Cacao trees are pruned yearly or twice a year, some weeks before the flowering peak. Pruning maintains cacao plants at a maximum height of ~4 m, to facilitate harvesting.

All the agroforests included in this study are predominantly composed of the native cacao variety "*Cacao blanco de Piura*," considered to have a high-quality flavor profile (i.e., "fine flavor variety," Tscharntke et al., 2023), which fetches considerably higher prices than those of bulk cacao varieties. All agroforests belong to cacao smallholders associated in the agrarian cooperative Norandino Ltda. Associated smallholders benefit from the marketing of fine or flavor cacao both by its higher price and other socio-ecological gains derived from cooperativism (Maas et al., 2020; Villar et al., 2021).

Exclosure experiments

We established three vertebrate exclusion treatments and one control treatment inside each of the 12 cacao agroforests in September 2019, during the flowering peak of cacao, and monitored them over the course of approximately 1 year, until October–November, 2020. Each treatment included two cacao trees, one of which was subject to an ant exclusion treatment, consisting of a plastic cone located at the base of the trunk, covered with Schacht insect sticky glue, to prevent ants from accessing the plant from the ground. Additionally, the density of ants present on the trees was reduced by applying some drops of Atoxin 15 EC at the entrance of all observed ant nests. Vertebrate exclosures consisted of cages with dimensions of 2 m wide, 5 m long and 3 m high (Figure 1). The frames of the structure were built using bamboo poles, and fishing mesh of 2.5 cm opening was used to cover all sides and roof of the cage, selectively preventing the entrance of birds and bats. Selectivity was ensured by differential opening times of each treatment: (1) bird exclosures were kept closed during the day (6:00–18:00) and open during night (18:00–6:00), to allow the access of nocturnal vertebrates; (2) bat exclosures were kept open during the day to allow access of diurnal vertebrates, and closed during the night; (3) full exclosures were permanently closed; (4) control treatments consisted of two plants left permanently accessible to vertebrates and without a cage constructed around them (Maas et al., 2019).

Yield evaluations

We performed yield evaluations every other week starting in November, 2019, over a 1-year period. Fresh cacao beans in our study area are typically delivered by farmers to the cooperative's facilities directly after harvesting. All pods infested by fungal diseases (only six cacao pods), or attacked by squirrels (52 cacao pods) were discarded by farmers upon observation, and were not incorporated in our assessments of yield, which included a total of 596 cacao pods (Vansynghel, Ocampo-Ariza, et al., 2022). In contrast, damage by mirids frequently does not reach the endocarp of cacao pods, and fruits are harvested as normal. During our experiment, we only found two cacao pods severely damaged by mirids.

After harvesting, the cacao beans are fermented and dried following a similar protocol to the one described by Laura et al. (2021), guaranteeing high quality standards. Fermenting requires large volumes of freshly harvested cacao, which we did not have in our bi-weekly evaluations. Therefore, we only counted the number of harvested pods, and sun-dried the beans at the facilities of Norandino Ltda. In La Quemazón. We weighed the dry beans, summed all harvesting rounds per tree and

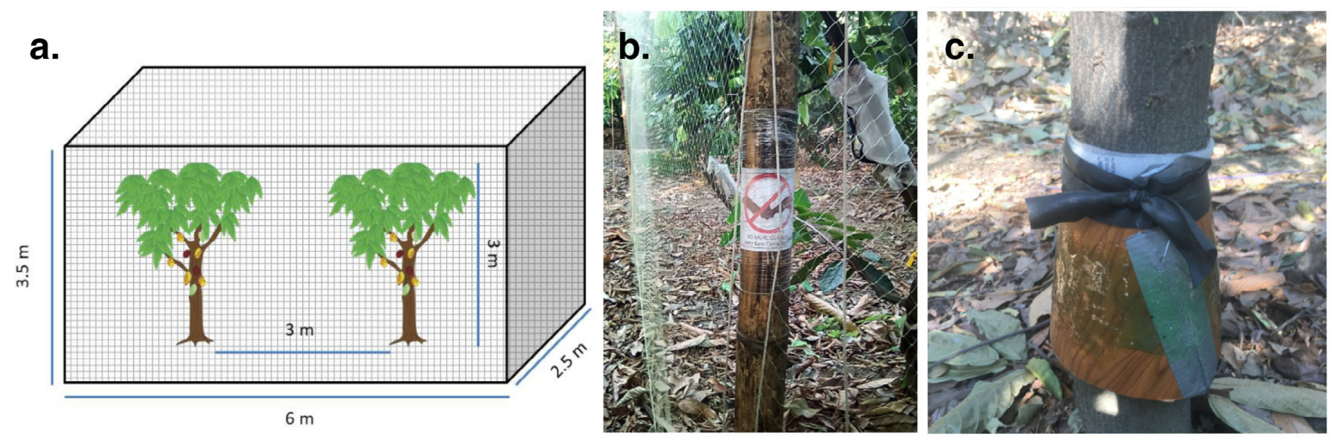

FIGURE 1 Experimental set-up of ant, bird, and bat exclusions, and ant baiting experiments in cacao agroforests of Peru. (a) Schematic representation of exclusion experiments to prevent the access of birds and bats to cacao plants. Each exclusion consisted of fishing mesh covering a surface area of 6 × 2.5 m, which included two cacao plants. The distance between cacao plants as well as their height are averages from the conditions found in all the field sites. (b) Image of the bird exclusion experiment in Piura, Peru (Photo by Carolina Ocampo-Ariza). (c) Ant exclusions using cones covered with insect sticky glue, to prevent the access to the tree by ants from the ground (Photo by Justine Vansynghel).

multiplied the total dry weight of cacao by the number of trees per hectare typically found in our study area (1100 cacao trees, at a planting distance of 3×3 m), to obtain an estimated yearly yield value in kg/ha.

Arthropod predation assessments

We used sentinel plasticine caterpillars to assess arthropod predation on each of our study trees. The caterpillars were made from green plasticine with a mechanical clay extruder and had a standard size of 35×5 mm (Figure 2). We performed a total of four rounds of sampling between November 2019 and March 2020. However, due to coronavirus disease 2019 (COVID-19) related restrictions, the sampling could only be completed on a subset of nine of our 12 study plantations. During each sampling round, we placed two caterpillars on each experimental cacao plant: one on a leaf (Figure 2c), and a second one either close to a flower or on a cacao pod (Figure 2b), for a total of 16 caterpillars placed in each agroforest. Consequently, the total sampling effort consisted of 576 sentinel caterpillars, on 72 cacao plants.

We glued the caterpillars to the plants using instant glue early in the morning (06:00–10:00) and left them unsupervised for 48 h. After this time, we registered the presence or absence of all caterpillars, and inspected all remaining caterpillars for bite marks. We registered the number of markings on each caterpillar, took pictures of all bitten caterpillars using a digital SLR camera, and collected caterpillars with unidentified markings for later analysis. We identified the potential predator that caused biting marks using pictures and identification keys from literature (Schwab et al., 2021; Tvardikova & Novotny, 2012), and confirmed ant markings through direct observation of *Crematogaster crinosa* and *Monomorium* sp. biting the caterpillars (Figure 2f). We sorted the markings into the following predator categories: birds (Figure 2d), ants (Figure 2f), or other unidentified arthropods, presumably other ant species, Coleoptera and rare Orthoptera, based on our observations of arthropod diversity (Figure 2e). Mammal (likely squirrels, Figure 2a) and other unidentified markings were rare and excluded from further analyses.

We calculated overall predation rates (%), as the total number of predation events found per sampling round

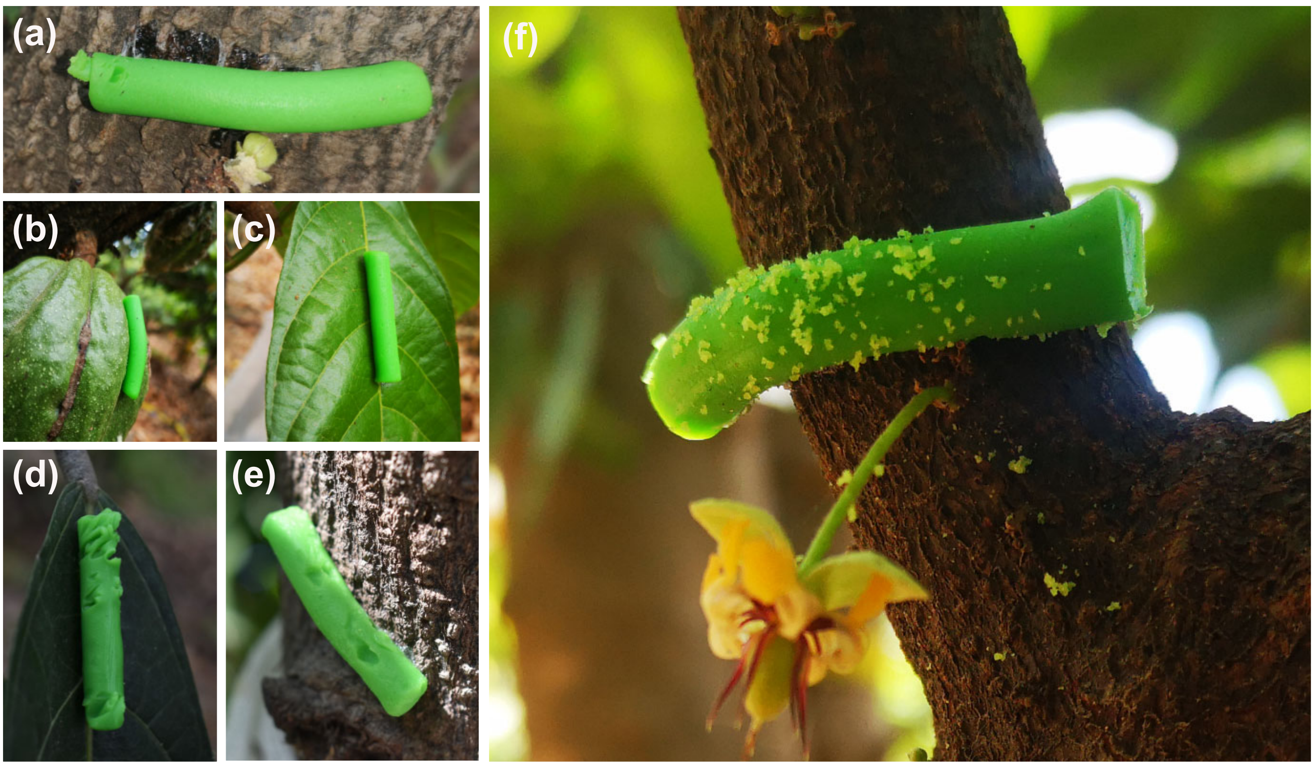

FIGURE 2 Plasticine sentinel caterpillars used to assess arthropod predation rates on cacao agroforests of Peru. The caterpillars were located either on or close to a reproductive structure (a, f: close to a flower; b, directly on a cacao pod) or on a leaf (c, d). (d–f) Display the most common predation marks found on the caterpillars: (d) birds, (e) unidentified arthropods, and (f) ants, characterized by the removal of small portions of plasticine from the underside of the caterpillars, which were then visibly spread on the upper side of the caterpillar and along the surface of the cacao plant. The caterpillar on figure (a) shows rodent marks. All photos by Denise Bertleff.

on all caterpillars recovered per tree, excluding caterpillars that fell on the ground. Moreover, we calculated the predation intensity for each predator category, as the total number of markings found per tree, divided by the overall number of caterpillars recovered per round. Distance to forest in this subset of plantations ranged between 187 and 901 m.

Arthropod assessments

We performed three arthropod monitoring surveys during the local cacao flowering peak and early fruit set, which coincides with the end of the dry season, between November 2019 and January 2020. During each arthropod monitoring survey, we visited all experimental plants twice, performing day (7:00–11:00) and night (19:00–00:00) assessments of arthropod diversity. Each visit consisted of a 25-min survey during which we observed the entire tree and registered all arthropods on its surface. To do so, we surveyed all parts of the tree without touching it, using ladders to observe the upper part of the canopy (see Maas et al., 2013 for a detailed description). We excluded insects on flight, except in cases in which it was evident that they had visited or were visiting the plant (e.g., overflying a flower). We identified all arthropods to morphospecies at the maximum possible level of taxonomic detail without collecting them, using pictures, taxonomic keys (Gibb & Oseto, 2006; Nieves-Aldrey et al., 2006; Zucchi, 1995), and the platform iNaturalist (https://www.inaturalist.org/). We summed abundance values for the day and night sampling rounds, and performed analyses using the cumulative abundance of each arthropod group.

We classified all observed arthropods into groups with known and unequivocal dietary preferences. Within phytophagous taxa, we selected the most abundant groups, namely aphids (Hemiptera: Aphididae), mealybugs (Hemiptera: Pseudococcidae), leaf-chewing beetles (Coleoptera: Chrysomelidae), and sap-sucking Homoptera from the suborder Auchenorryncha (plant hoppers, leafhoppers, treehoppers, including Acanaloniidae, Cicadellidae, Cixiidae, Delphacidae, Derbidae, Flatidae, Membracidae, and Psyllidae).

Within mesopredatory insects, we classified spiders as "weavers" or "hunters," based on their morphology and taxonomy. Other mesopredatory taxa or natural enemies of arthropods, for example, parasitic or predatory wasps, were recorded only a few times during our surveys and were therefore excluded from further analyses.

We focused on the two most abundant ant species to perform additional analyses, that is, *Nylanderia* sp., and *Brachymyrmex* sp. These two ant genera are considered to be omnivorous and have been seen caring for insects that produce honeydew and other sugar sources, which they use as food, as well as scavenging and eating other insects (California Academy of Sciences, 2022). We confirmed that specimens of *Nylanderia* sp. were not the tawny crazy ant (*Nylanderia fulva*), known to be an invasive species in the Americas.

Data analysis

All analyses were performed in R 4.0.5 (R Development Core Team, 2021). We used pair-wise *t*-tests to assess whether the number of predation events differed between caterpillars placed on reproductive parts of the plant, and on the leaves. We used generalized linear mixed effects models (GLMMs) in the package glmmTMB (Magnusson et al., 2017) to evaluate the effects of vertebrate exclusion, ant exclusion, and distance to forest on all our response variables—namely cacao yield (kg/ha), predation rates, and abundance of different arthropod groups. For each response variable, we built a global model including all possible two-way interactions, and the identity of each cacao agroforest as a random effect. We then used the "dredge" function from the MuMIn package (Bartón, 2014) to select the best models derived from each global model, based on AIC_c comparison ($\Delta AIC_c \leq 2$). The subset of best models was averaged using the "model.avg" function to obtain one final model. We report the conditional average outputs from these final models. When the averaged model indicated a significant effect of our exclusion experiment on the response variable, we performed additional post hoc comparisons among all pairs of exclusion treatments using Tukey HSD tests in the package emmeans (Russell, 2019).

We repeated our analysis for overall predation rates separately for the two most dominant predator groups identified from the sentinel caterpillars: ants and other unidentified arthropods. Moreover, we evaluated whether the abundance of either ants or herbivorous insects, and their interaction with distance to forest, had significant effects on cacao yield. In this last case, the identity of cacao agroforests was once again included as a random effect. Given the low number of predation markings from birds ($n = 11$), we did not use these data for any further analyses.

Model diagnostics were evaluated using the package DHARMa (Hartig, 2018), and the distribution of models was adapted accordingly. We used a hurdle-gamma distribution (ziGamma) for cacao yield and predation rates, in order to allow non-constant error and zeroes in continuous data (Magnusson et al., 2017). All abundances followed a Poisson distribution, with cases of overdispersion accounted for through negative binomial distributions (Zuur et al., 2009). We used the package effects (Fox & Hong, 2010) to obtain average effects ± SE of significant predictors from the best model selected. We used these data to plot results in the ggplot2 package (Wickham, 2009), and to calculate the monetary gains derived from birds and bats on cacao yield. To do so, we calculated the difference between the yield in control treatments and that in the different exclusion treatments. We then transformed this into a percentage, and used this percentage to estimate gains based on the average productivity of cacao agroforests in our study area. We assumed an average productivity of 618 kg/ha year^{-1}, and an average price per kilogram of dry cacao of 10 PEN (3.5 USD), reported by Villar et al. (2021) for associated farmers in the region of Piura in the year 2020. Therefore, the economic gains we report here should be considered specific to the case of *Cacao blanco de Piura* in our study region in the 2020 campaign. The data and code used for these analyses are available at the OSF (Ocampo-Ariza et al., 2022).

RESULTS

Arthropod predation rates

We retrieved 97.6% of the sentinel caterpillars from our arthropod predation assessments ($n = 563$ caterpillars), of which 38.54% ($n = 146$ caterpillars) had identifiable predation markings on them ($n = 217$ predation marks). Caterpillars located on fruits or close to flowers were predated significantly more than those on cacao leaves ($t = -2.84$, $p = 0.004$). Markings by unidentified arthropods were the most common on sentinel caterpillars, representing 72% of all identified markings, followed by ants (19%) and birds (9%). We found that overall predation rates were 10% higher in the presence than absence of ants, independently of bird and bat exclusion (Appendix S1). Predation by unidentified arthropods also increased when ants were present (Appendix S1). This led us to believe that such unidentified marks might have been caused by other unidentified ant species or crawling arthropods which were also excluded within ant exclusions. Bird exclusions significantly increased overall arthropod predation rates on dummy caterpillars (45.29 ± 5.97%), in comparison to controls in which both birds and bats were present (30.12 ± 4.11%). Numbers of biting marks by unidentified arthropods and by ants were also significantly higher in the absence of birds than when birds and bats were present (Appendix S1, Figure 3a). Bat exclusions and full exclusions also increased overall predation rates, as well as attacks by unidentified arthropods, (Figure 3a), but the change was not significant (Appendix S1).

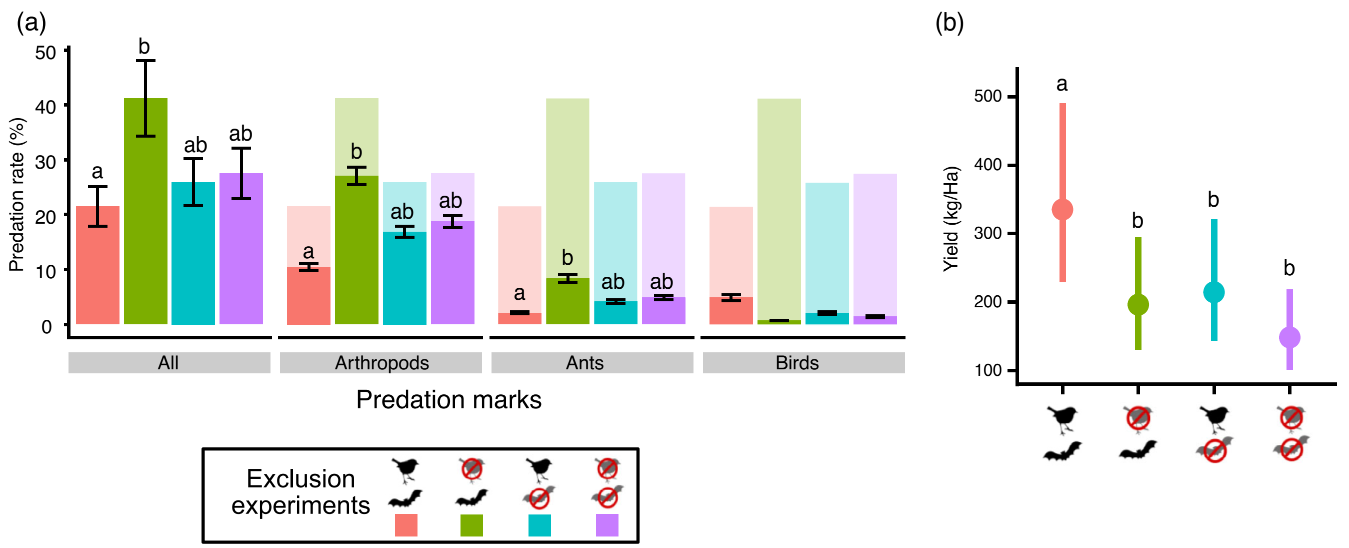

FIGURE 3 Effects of vertebrate exclusion treatments on predation rates on dummy caterpillars (a) and on yearly cacao yield per hectare (b) in 12 experimental cacao agroforests in Peru. Bars in (a) indicate the percentage of recovered artificial sentinel caterpillars with predation marks of any type (All), or from three different predators: birds, ants, and other unidentified arthropods. The bars from all predation marks are replicated as shades on subplots of individual predators for reference of the percentage from the total predation marks covered by each predator. Error bars in (a) indicate means ± SE. Figure (b) displays predictions from generalized linear mixed models (GLMMs), with bars indicating 95% CIs. Different letters above error bars indicate significant differences between exclusion treatments. When letters are absent, differences among exclusions were not assessed given the low number of predation events. Colors in (a) and (b) distinguish four exclusion treatments of birds and bats: pink, control; green, bird exclusion; blue, bat exclusion; and purple, full (bird and bat) exclusion.

Effects of top predators on cacao yield

Cacao yield was higher in the presence of birds and bats than in any of the vertebrate exclusions (Appendix S2, Figure 3b). In comparison to full exclusions (136.24 ± 0.217 kg/ha), yield was on average 119% higher in control treatments where birds and bats were present (298.18 ± 0.217 kg/ha). In other words, the presence of birds and bats accounted for an average of 54% of cacao production in study trees of the control treatments. Considering an average productivity of 618 kg/ha/year at 3.5 USD/kg for the study region (Villar et al., 2021), pest predation services by birds and bats represented a gross economic value of US \$958.94 ± 71.23 ha^{-1} $year^{-1}$ for cacao smallholders in our study area. Separate bird (186.06 ± 0.221 kg/ha) and bat exclusions (192.69 ± 0.219 kg/ha) also decreased yield, but the change in comparison to control treatments was only significant for the bird exclusion (Appendix S2, Figure 3b).

Arthropod abundance

During our arthropod surveys, we observed 40,487 diurnal and nocturnal insects, belonging to 18 orders, 114 families and 360 morphospecies. Aphids were the most abundant group, representing 54% of all observations, followed by mealybugs (Hemiptera: Pseudococcidae), with 8%.

Arthropod abundance: Ants and spiders

We recorded a total of 4737 ants, belonging to 11 morphospecies (Appendix S3). Two species represented 58% of all our ant observations: *Nylanderia* sp. (40.17%), *Brachymyrmex* sp. (18%). As expected, the abundance of all ants, as well as those of the two most abundant species were significantly reduced within ant exclusions (Appendix S4). However, vertebrate exclusions had no significant effect on either the entire ant community, nor on the abundance of either one of the single species. The abundance of *Brachymyrmex* sp. decreased in cacao plantations at larger distances from the forest.

We found 42 spider morphospecies, of which 17 were weaving spiders, 24 were free hunters, and 1 was unidentified. The abundances of both weaving and free hunting spiders were similar among vertebrate exclusions (Appendix S4).

Arthropod abundance: Herbivorous insects

As expected, the abundances of most herbivorous arthropods, such as aphids (Figure 4a), mealybugs (Figure 4b), and sap-sucking Homoptera (Figure 4d) increased in the absence of birds or bats, but changes were not statistically significant for Homoptera (Appendix S4). Leaf beetles were less abundant when birds and bats were absent (Figure 4c). Against our expectations, we observed the cacao bug *Monalonion dissimulatum* (Heteropitera, Mirdae) only 11 times during our arthropod surveys (0.027% of all arthropod observations), and recorded only two other individuals of the Miridae.

We found that aphid abundance was significantly lower in ant exclusions when bats and birds were present. In the presence of ants, aphid abundance remained on a similar level in all vertebrate exclusions, whereas the combination of ant and vertebrate exclusions resulted in the highest aphid abundance. Simultaneous exclusions of birds and bats resulted in comparable abundance of aphids than simultaneous exclusion of ants and either of the two vertebrate groups (Figure 4a, Appendix S4). We found no significant effect of distance to forest on the abundance of any herbivorous insect group.

Arthropod effects on yield

In the presence of ants, cacao yield significantly decreased by almost 50% in agroforests at larger distances from the forest, in comparison to those on the forest edge (Figure 5b). When looking at the effect of single species, we found that *Nylanderia* sp. ants significantly affected cacao yield along the gradient of distance to forest. At low (mean − 1SD) and medium (mean) abundances of *Nylanderia* sp., yield increased along the distance to forest, while high abundances (mean + 1SD) resulted in a significant decrease in cacao yield along the same gradient (Figure 5c,d, Appendix S5). None of the other arthropod species in this study had significant direct effects on cacao yield, except for ants (Appendix S5, Figure 5d).

DISCUSSION

Our study supports previous evidence of the crucial role that birds and bats have for sustaining cacao productivity, and identifies arthropod species that may be negatively affecting it. We found that the presence of birds and bats more than doubled the cacao yield observed for trees from which they were excluded. By contrast, when the ant *Nylanderia* sp., which are known to attend plant suckers, was present in large abundances, this caused a decrease in cacao yield at increasing distances from the forest. Excluding birds and bats from cacao trees increased the abundance of phytophagous taxa such as

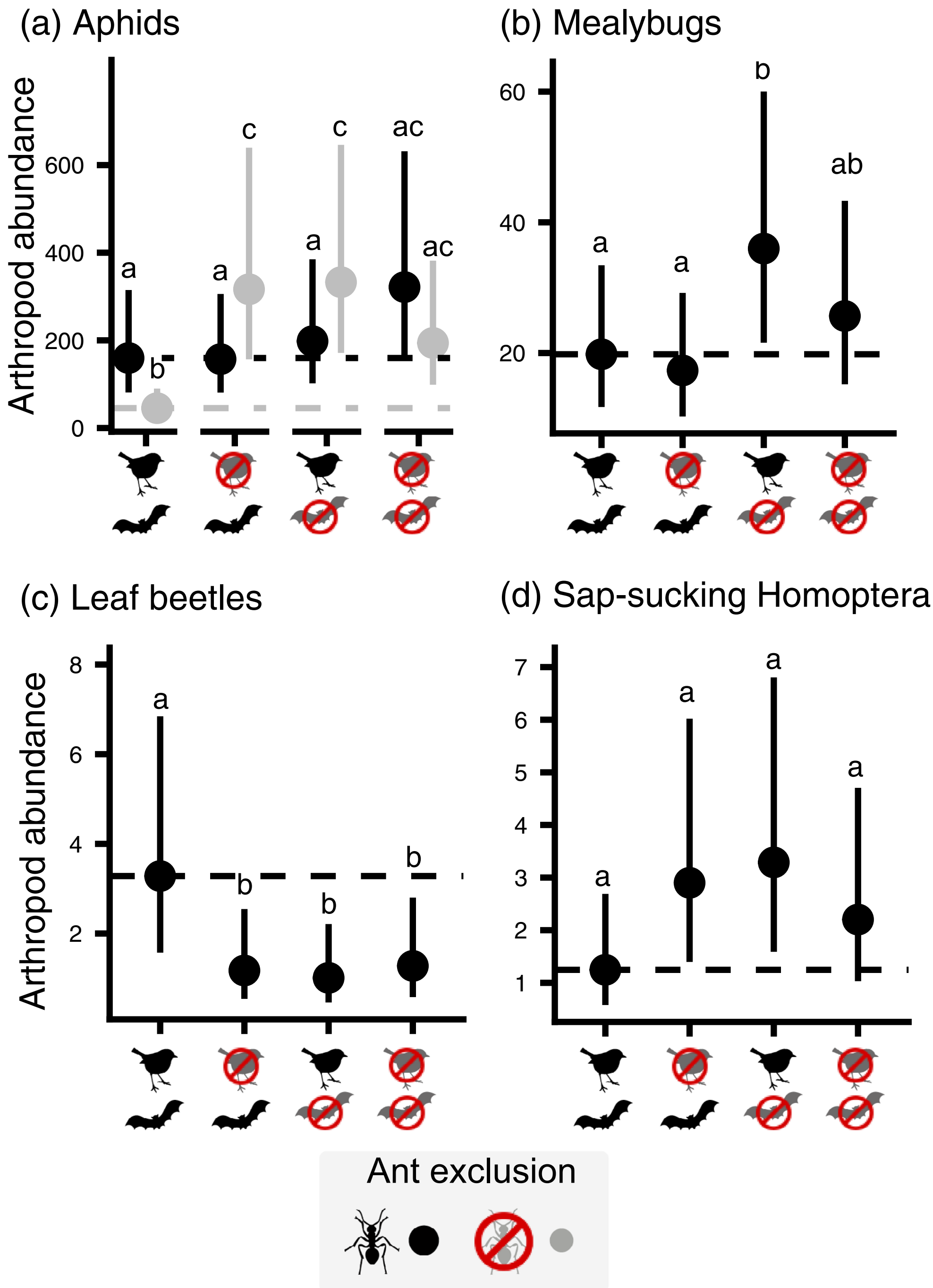

FIGURE 4 (a–d) Effects of vertebrate (birds and bats) exclusions and ant exclusions (black = ants, gray = no ants; in cases with significant differences between treatments) on the abundance of arthropod groups found on cacao plants from agroforestry systems in Peru (leaf beetles = Coleoptera, Chrysomelidae; aphids = Hemiptera, Aphididae; mealybugs = Hemiptera: Pseudococcidae). Abundances were assessed through observation surveys, and effects were assessed through generalized linear mixed models (GLMMs) and model selection through multi-model inference and model averaging. Significant differences between groups are indicated by different letters above the lines, and assessed through post hoc Tukey HSD tests. Horizontal dashed lines mark the mean of control treatments, as a reference for changes within exclusion experiments.

aphids and mealybugs. We discuss the relevance of our results for the management of biodiverse cacao agroforests in tropical dry forest areas, and for the study of multitrophic interactions in these agroecosystems.

Exclusion of birds resulted in an increase of arthropod predation rates, which partially confirmed our hypothesis of a mesopredator release, whereby the removal of top predators enables mesopredators—such as

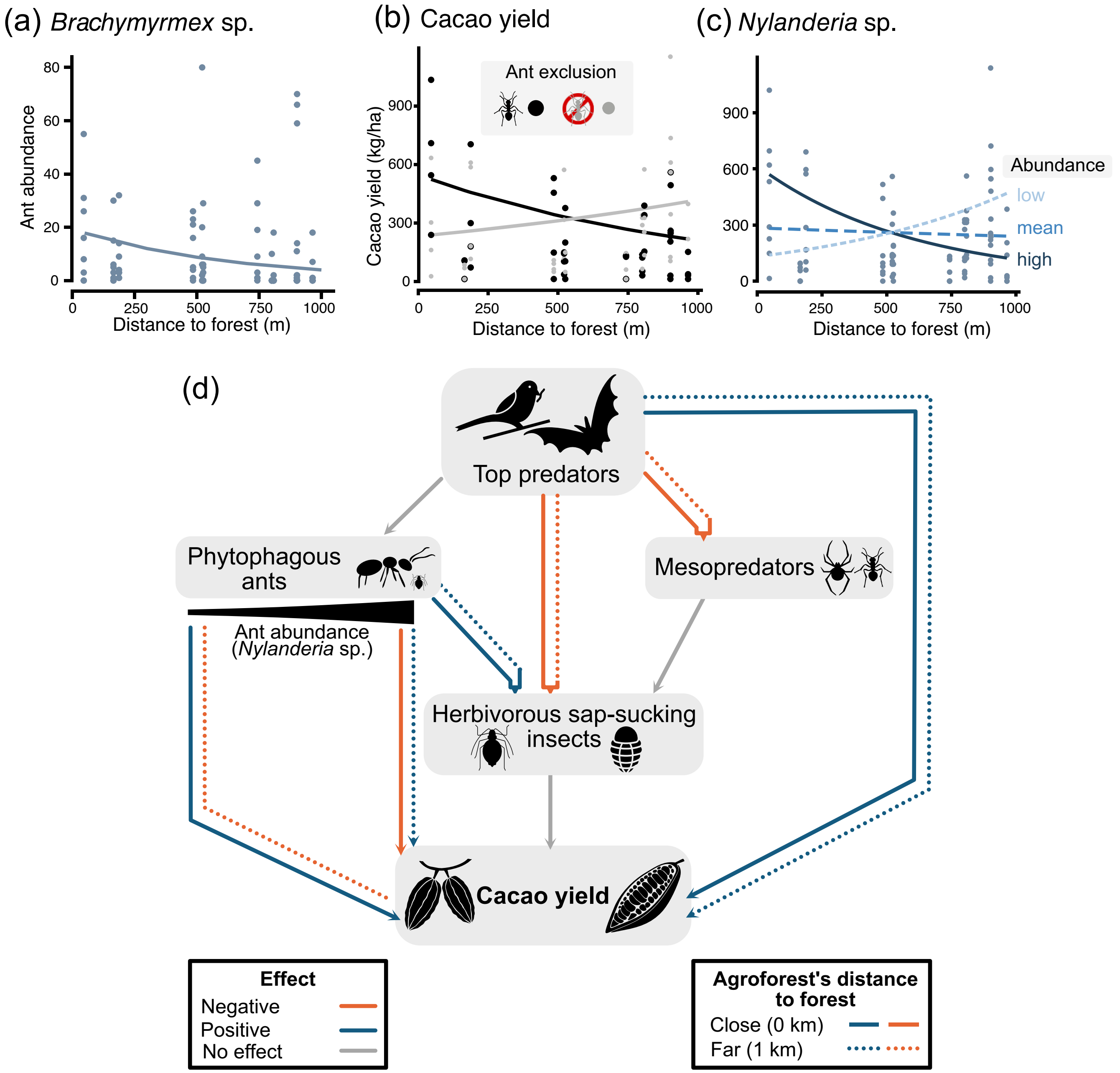

FIGURE 5 Changes in the abundance of arthropod groups (a, c, d) and yield (b, d), explained by distance to forest in cacao agroforests. (c) The effect of the interaction between distance to forest and abundance of the ant *Nylanderia* sp. (Low = mean − 1SD; High = mean + 1SD) on cacao yield. (d) A conceptual map of all observed and expected effects of top predators on multiple arthropod groups and cacao yield, and how such effects varied with forest distance. Effects were assessed through generalized linear mixed models (GLMMs) and model selection through multi-model inference and model averaging. For summary tables of the models see Appendices S2 and S4.

ants and other arthropods—to rapidly increase their foraging activity and populations. However, excluding only bats or joint exclusion of both top predator groups did not change mesopredation. This may indicate that birds drive mesopredator suppression in our study area more than bats, and is in line with previous assessments of differential contributions of these two groups to arthropod control (Karp & Daily, 2014). However, against our expectations, predation rates in full exclosures were not significantly different from controls. This suggests that the effects of birds and bats were not additive, and that intraguild interactions among mesopredators (i.e., mesopredators predating each other; Sitvarin & Rypstra, 2014) likely neutralized the mesopredator release observed in the single bird exclusions. Predation pressure on sentinel prey was higher when they were placed on or nearby flowers and fruits rather than on leaves of cacao plants, which may indicate that arthropod prey availability, likely including relevant pests, is higher around reproductive organs. This supports earlier hypotheses of the crucial role of flower herbivory in reducing cacao yield (Maas et al., 2013; Wielgoss et al., 2013).

Contrary to previous studies reporting mesopredator releases which showed an increase in abundances of predatory arthropods (Cassano et al., 2016; Ferreira et al., 2023; Gras et al., 2016; Maas et al., 2013), we only found an increase in their predatory activity, but not in their abundances. As these changes in predation rates were also not connected to effects on herbivorous insects or cacao yield (Figure 5d), we conclude that vertebrate predators (birds and bats) were much more important for promoting cacao yield than the mesopredators.

Indeed, the presence of top predators was related to a significant increase in cacao productivity compared to when they were excluded, and we confirmed our hypothesis that the benefits provided by birds and bats would be comparable. We found that phytophagous insects, mostly sap-suckers like aphids and mealybugs, but not mesopredators, were the taxa most favored by the absence of top predators. However, only in the case of mealybugs we observed a differential effect of bat- in comparison to bird exclusions. The absence of bats resulted in a significant increase in mealybug abundance on cacao trees, similar to recent findings in African cacao agroforestry (Ferreira et al., 2023). Because bats are mostly unattracted to sessile prey, it seems likely that the changes observed here are due to an indirect interaction with mealybugs whereby bats consume other taxa that directly affects these insects. Nevertheless, recent evidence shows that gleaning bats may indeed be able to consume sap-sucking insects, even though these are largely sessile (Ingala et al., 2021). As mealybugs are relevant crop pests and known vectors of cacao diseases in other parts of the tropics (Ameyaw et al., 2014), the biocontrol role of bats in these agroecosystems may be worth considering in the development of wildlife-friendly management strategies.

In the case of ants, and in contrast to our third hypothesis, we found that their mutualism with sap-sucking insects was more relevant than their potential role as mesopredators. We found that ants were important mesopredators in our artificial sentinel caterpillar experiment, but this did not translate in significant decreases of potential cacao pests, nor benefits for crop yield. This is opposing to previous evidence from cacao agroforests in Indonesia, where ants did reduce the abundance of herbivorous insects (Gras et al., 2016). On the contrary, the access of ants to cacao trees in our study was related to a significant decrease in cacao yield at increasing distances from forest. Presumably, ants provide protection against predators and parasitoids, enhancing the abundance and harmful activity of herbivorous insects such as mealybugs. This contrast between mesopredation benefits and negative effects of ants' mutualisms emphasize the need to study ants at detailed taxonomic and functional levels that allow to disentangle these tradeoffs. Indeed, through separate analyses of the most abundant ant taxa we revealed that the effects of ants on cacao yield and sap-sucker abundance were driven by the dominant ant species *Nylanderia* sp. High abundances of *Nylanderia* sp. had negative consequences for cacao yield at increasing forest distance. This ant genus is known to have a generalist diet and has been documented to assist mealybugs and aphids with negative impacts in North American crop yields (Holt et al., 2022; Sharma et al., 2013), and it is therefore likely that its interactions with sap-sucking insects drive negative effects on cacao yield as well.

We found that forests adjacent to cacao plantations are relevant to maximize the biodiversity benefits on cacao yield, while minimizing potential disservices. Yield decreased with increasing forest distance in the presence of ants, likely due to weakened pest control by birds, who are known to become less abundant along the gradient of distance to forest mostly in the rainy season (Ocampo-Ariza et al., 2022).

Our study provides the first assessment of bird, bat, and ant contribution to cacao yield in seasonally-dry tropical forests of Peru. We found that the prevalence and abundance of typical pest and diseases of cacao in South America was lower than in previous reports. For example, the cacao mirid *Monalonion dissimulatum* was rarely encountered in our arthropod surveys, in contrast to its abundance and negative effects on cacao yield in other parts of South America (Vargas et al., 2005). It seems likely that seasonality plays a large role in these differences and that increases in insect population are limited to wet season, when sufficient resources for reproduction are available (Silva et al., 2012; Vasconcellos et al., 2010). Similarly, the abundance of top predators in cacao agroforests varies between seasons, and local migrants may contribute to pest control in precise times of the year (Ocampo-Ariza et al., 2022). Further studies in dry tropical forest areas should account for this variation in trophic interactions during the year, across years and due to climate change, when drought and high temperatures may impact the biomass and abundance of predators and their prey (Karp & Daily, 2014; Newell et al., 2023; Ocampo-Ariza et al., 2022).

Plant-arthropod interactions limiting cacao productivity at different stages of its life cycle are complex, geographically variable and remain largely unclear

(Toledo-Hernández et al., 2017; Vansynghel, Ocampo Ariza, et al., 2022). The combination of multiple methodologies allowed us to connect the presence of top predators and ants with multiple functions within agroecosystems, but a detailed understanding of trophic interactions within agroecosystems likely requires additional approaches. Using artificial caterpillars, we identified arthropods as the most relevant insect predators in our study area, were unable to distinguish them at fine taxonomic levels. Such constraint of sentinel prey experiments is well recognized and changes in color and shape of the prey seem to be of little use to improve their specificity (Nurdiansyah et al., 2016; Weissflog et al., 2022). However, the predation rates and proportion of identified markings reported here are comparable to previous experiments with this technique (Maas et al., 2015; Schwab et al., 2021). Moreover, the trophic link guaranteeing benefits from top predators for cacao productivity remains unclear. Therefore, it is urgent to use alternative approaches that provide a more direct assessment of top predators' trophic preferences, such as detailed characterizations of predators' diets through molecular analyses (Ingala et al., 2021; Lance et al., 2022; Tiede et al., 2020). This will be essential to identify both the main arthropod groups controlled by birds and bats, and the key species providing biocontrol, which should become a focus of research and conservation efforts within cacao agroforestry.

CONCLUSIONS

Our study shows that birds and bats can significantly increase yields of the native *Cacao blanco de Piura* in tropical dry forest landscapes, despite their suppression of mesopredators such as ants and other predatory insects. Forest vicinity is crucial to maintaining high yields, if ants are not experimentally excluded, presumably because bird diversity peaks near forests (Ocampo-Ariza et al., 2022) and may minimize the negative effects of these insects. In contrast, far from the forest, high abundances of the ant *Nylanderia* sp., which is known to attend plant-sucking insects, reduced cacao yield. Bird and bat exclusion reduced the abundance of two main sap-sucking insects on cacao trees, which may be due to direct predation and indirect effects that require further research. In view of the key role that nearby forests play to maintain top predators and minimize the negative effects of some arthropods, conservation and restoration of native forest in the vicinity of cacao agroforests, in addition to the maintenance of intermediate canopy covers in agroecosystems, should become part of a management scheme toward sustainable cacao agroforestry landscapes.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Ocampo-Ariza, 2023) are available in the Open Science Framework at http://doi.org/10.17605/OSF.IO/XAESN.

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SUPPORTING INFORMATION

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

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