



Birds and bats enhance yields in Afrotropical cacao agroforests only under high tree-level shade cover

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ABSTRACT

Central/West Africa is one of the most biodiverse regions on earth and one of the largest producers of cacao, producing about 68.4 % of the world's chocolate. Here, cacao pests and diseases can cause losses of \$761 million annually. However, no studies from Africa have quantified the role of flying vertebrates as pest suppressors in cacao plantations. We used an exclusion experiment to prevent access of bats and birds to cacao trees for 12 months and quantified how their absence affected arthropod communities, herbivory, and cacao crop yield. Overall, important pests such as mealybugs and other hemipterans were more abundant in enclosures (9 and 1.6 times increase, respectively), despite potential multitrophic interactions with simultaneously increasing predatory arthropods such as spiders and mantis. Under heavy shade (90 %), cacao trees with flying vertebrate enclosures had 3.9 times fewer flowers and 3.2 times fewer large pods than control trees, corresponding to estimated losses on average of \$478 ha⁻¹y⁻¹. Under low tree-level shade cover (10 %) however, the opposite pattern was evident: enclosure trees had 5.2 times more flowers and 3.7 times more large pods than control trees, corresponding to estimated savings on average of \$796 ha⁻¹y⁻¹. We demonstrate that the enormous potential of African flying vertebrates as pest suppressors in cacao plantations is dependent on local shade tree management and only economically relevant above 50 % of shade. Despite higher productivity at low shade levels, our findings encourage African policymakers and farmers to adopt more high shade cacao agroforestry systems to maximize pest suppression services provided by bats and birds.

1. Introduction

Agricultural expansion is the main driver of tropical deforestation, especially in Central/West Africa (Curtis et al., 2018). Research on the balance between agriculture and biodiversity is needed to optimise crop production benefits without adding more pressure to convert primary forests to farmlands (Clough et al., 2011). Most of the scientific research linking trade-offs between biodiversity conservation and agriculture focuses on temperate regions, and studies on highly biodiverse areas are mostly in the Neotropics, leaving agroecological research from the

African continent largely unexplored (Maas et al., 2019, 2016).

Nature-based solutions to enhance agricultural production, like natural pest suppression, are often more cost-effective and sustainable than conventional interventions (Lindell et al., 2018), but knowledge about maximizing crop yields via managing ecosystem services remains limited (Rusinamhodzi, 2019). Agroforestry, an agricultural technique that combines crops and trees, may offer a path forward to preserve biodiversity and ecosystems services, while maintaining livelihoods of local farmer communities (De Beenhouwer et al., 2013; Maas et al., 2020).

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Cacao (*Theobroma cacao* L., 1753) is a cash crop of global importance and a tropical understory plant depending on shade trees for cultivation (Tscharntke et al., 2011). Traditional cacao plantations, i.e., cacao trees grown under a dense canopy of various shade trees, are a good model of agroforestry as they contribute more to the preservation of ecosystem integrity and diversity compared with more intensively managed cacao systems (De Beenhouwer et al., 2013). Further, cacao's global trade represented \$8.6 billion in 2017 (Voora et al., 2019) with 68.4 % of the world's cacao being produced in Central/West Africa nowadays (FAO-STAT, 2020). Although cacao is considered the fastest expanding export-oriented crop across Central/West Africa (Ordway et al., 2017), cacao productivity is decreasing in many producing countries due to problems like degraded soils, pests, and diseases (Armengot et al., 2020; Blaser et al., 2018). For example, full-sun plantations, where shade trees are entirely missing, can reduce the long-term resistance and resilience of the system jeopardizing cacao sustainability (Tscharntke et al., 2011).

Worldwide, cacao pests and diseases can cause losses of 761 million dollars annually (Bowers et al., 2001). Cacao pests such as the brown capsid *Sahlbergella singularis* Haglund, 1895 (Hemiptera: Miridae), the major insect pest in the cacao belt of Central/West Africa (Bagny Beilhe et al., 2018), and the mealybug (Hemiptera: Pseudococcidae spp.), responsible for spreading the Cacao Swollen Shoot Virus Disease (Andres et al., 2018), are still among the most important factors limiting cacao production (Wessel and Quist-Wessel, 2015). In some cases, these pests can cause annual crop losses of about 25–40 % (Wessel and Quist-Wessel, 2015) and even evolve resistances to chemical pesticides (Tabashnik and Johnson, 1999). Additionally, pesticides and other types of agrochemicals not only affect human health but can also cause negative collateral effects on the communities of insect pollinators (Nicolopoulou-Stamati et al., 2016; Vanbergen, Initiative, the I.P., 2013), which are fundamental for cacao pollination and productivity (Tolado-Hernández et al., 2020, 2017). Furthermore, Janssen and van Rijn (2021) showed that when natural enemies of pests are present, pesticides did not significantly reduce pest densities, highlighting the importance to consider nature-based solutions.

Flying vertebrates (i.e., bats and birds) contribute to a great variety of ecosystem services worldwide (Kunz et al., 2011; Whelan et al., 2008). They are of great importance for the suppression of insect populations, including agricultural pests (e.g. Maas et al., 2016; Librán-Embú et al., 2017). In one of the few studies to date focusing on these taxa in cacao plantations (Maas et al., 2016), enclosure experiments from Indonesia revealed that insect predation by bats and birds increased yield by 31 % and saved farmers 730 dollars per ha annually (Maas et al., 2013). Although this shows the potential of bats and birds as cacao pest suppressors, the African bird, bat and arthropod communities and their trophic interactions are entirely different from those found in Southeast Asia (Bagny Beilhe et al., 2018; del Hoyo, 2020; Taylor and Tuttle, 2019; Tscharntke and Hawkins, 2002) and no study has yet been conducted in Central/West Africa, even though most cacao is produced in this region.

Exclusion experiments can be powerful manipulations that allow monitoring of arthropods communities and yields when a specific animal group is not present, helping also to understand potential effects of biodiversity decline caused by agricultural intensification (Maas et al., 2019). Hence, in this study, we used an exclusion experiment to understand the role of bats and birds for pest suppression and crop production in differently managed cacao agroforestry systems in Cameroon, Central Africa. Specifically, we investigated how arthropod abundance, herbivory, pod damage, and cacao production varied between enclosure and control trees, and how these differences were affected by the degree of tree-level shade cover, which is influenced by shade cover management intensity. Finally, we were interested in shade cover at tree-level, instead of the typically used plantation-level shade cover, because the variation of light is likely to influence arthropod distribution within plantation, with the main pest *S. singularis* generally aggregating in the sunniest areas/trees of a plantation (Babin et al., 2010).

2. Material and methods

2.1. Study area

Our experiment was based in Cameroon (Central Africa; 7.3697° N, 12.3547° E), one of the six African countries that harbours the second largest tropical rainforest in the world, the Congo Rainforest (Fisher et al., 2013). The study was conducted in eight cacao plantations situated in three landscapes dominated by primary/secondary forest in the central region of Cameroon. Cacao plantations were spread through three landscape/localities (Ayos, Elat and Ngoumou; Fig. 1). Since cacao shade management is highly variable, we selected cacao plantations representing a gradient of minimum shade to high shade (see Table A.1). All plantations were > 1.5 ha large (see Table A1) and at least 800 m apart when situated in the same locality.

2.2. Cacao tree selection and characteristics

In each plantation, we selected two pairs of similar trees (e.g., variety and/or age, based on farmer's knowledge) separated by at least 20 m from each other and at a distance of at least 20 m from the plantation edge. To account for differences in cacao tree size that could affect our results, we used the BIOMASS package (Réjou-Méchain et al., 2017) to calculate cacao tree biomass (Table A.1). To account for differences in light conditions between cacao trees within a plantation, we measured shade cover above each control and enclosure tree. As mentioned above, we used tree-level shade cover measure instead of plantation-level shade cover because shade tree species vary in density and size causing a considerable heterogeneity of light conditions within plantation (Babin et al., 2010). We considered tree-level shade cover as it is broadly representative for plantation-level shade cover (Fig. A.3). Tree-level shade cover measurements ranged from 91 % in the least intensively managed plantation to 12 % in the most intensively managed (Table A.1); See Section 1 in Appendix for more details on methodology.

2.3. Exclusion experiment set-up

In each plantation, we excluded bats and birds from one tree of each pair and used the other tree as a control, making a total of 16 enclosure and 16 control trees. Following Maas et al. (2019), enclosure trees were covered using fishing nets (20 mm² mesh) attached to a bamboo scaffold to avoid contact between the tree's foliage and net (Fig. A.1). The selected mesh size for the fishing net was small enough to prevent access by even the smallest bat and bird species that occur in Cameroon but large enough to allow access by pests and most arthropods groups (ACR, 2019; del Hoyo, 2020). The exclusion treatment was installed in February 2020 after fruit harvesting and maintained for 12 months.

2.4. Arthropod and tree monitoring

To correlate the absence of bats and birds with the increase/decrease of a specific arthropod group and cacao production, we monitored each cacao tree once per month. Our monitoring was divided into three components: pest/arthropod communities, tree productivity, and pods/leaf damage.

Pest/arthropod sampling focused on all arthropods, including cacao pests (*S. singularis* and mealybugs) above (~2 mm). Each tree was divided into five parts (main trunk, right and left middle section, right and left top section; Fig. A.2) and all components on each part (flowers, fruits, leaves, and branches) were monitored for five minutes. During those 25 min we visually inspected and counted all arthropods. We identified arthropods to order, ants to family level and pests to their respective group. When groups were very abundant, we estimated numbers by eye (i.e., we counted the number of arthropods on one leaf and then multiplied by the total number of leaves where they were present in similar quantity; Firempong, 1976). Arthropods groups were

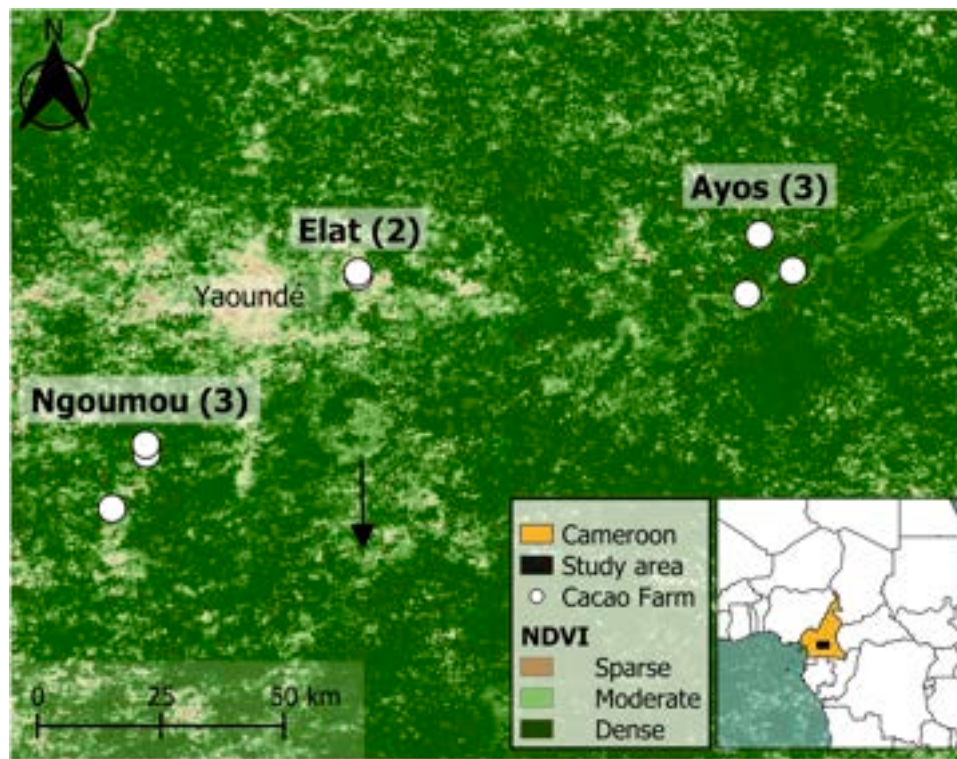


Fig. 1. Map of central Cameroon showing the eight plantations where the exclusion experiment was set up. Closer plantations were separate by 800 m. The base map shows eMODIS Normalised Difference Vegetation Index (NDVI), as an indicator of vegetative land cover (accessed from <https://earlywarning.usgs.gov/>).

classified as pests (mealybug and *S. singularis*), phytophagous, predatory, or potential pollinators depending on their main diets and roles in cacao plantations (Cassano et al., 2016; Toledo-Hernández et al., 2017; Wessel and Quist-Wessel, 2015). For logistical reasons we were not able to conduct the arthropod monitoring as in Maas et al. (2013), thus we only sampled trees between 8 AM and 5 PM in each landscape. However, sampling always occurred at the same time of the day for each tree to avoid differences due to arthropods' activity patterns between visits (Awudzi et al., 2017; Azhar, 1986) and to be able to look for consistent patterns throughout the 12 months. Also, we visited each pair of trees at similar times (difference of 30 min) and the two pairs within a plantation were monitored always one after the other (1 h difference between pairs) to mitigate potential effects of activity differences between controls and exclusions in the data. Nevertheless, three out of the eight plantations (one per locality) were sampled in the afternoon.

To measure tree productivity and pod damage, we counted all cacao flowers and fruits, as well as presence/absence of pest and disease symptoms on each pod. Following Gras et al. (2016), we classified fruits into small (0–9 cm), large (> 9 cm) and ripe categories according with their sizes and colour. We divided pod damage into six categories: Black Pod Disease, Capsid Pest Feeding, Dead Black Tissue, Cherelle Wilt, Immature Ripening, and vertebrate feeding (see Section 2 in Appendix for more details).

To quantify herbivory, we selected and marked a group of ten new cacao leaves in each cacao tree at the beginning of the experiment. Each leaf was then photographed every visit (approx. every 30 days), using a whiteboard and scale. When one of the marked leaves fell, become dry or had more than half of its area eaten, we selected a new leaf to replace it and repeated the process. Following Cassano et al. (2016) we used the software ImageJ (Schneider et al., 2012) to measure foliar area and area damaged between 1st and last picture of each leaf (ranging from 1 to 12 months) and thus estimated a rate of herbivory per tree over the period of one year.

2.5. Statistical analysis

To test the effects of the exclusions on pest/arthropod populations, tree productivity, and pod/leaf damage, we used general linear mixed-effects models (GLMMs). We used as response variables the abundance per tree and visit of the different arthropod groups (13 groups), number of flowers and pods (two categories) per visit, presence/absence of pod damage (for five categories), and herbivory per tree (%). We only used arthropod groups that had more than 30 counts (Table A.2). For count data (arthropods, flowers, pods, and pods damaged) we used a Poisson distribution. However, when data were overdispersed or overdispersed with excess of zeros we used negative binomial and generalised Poisson distribution, respectively (Table A.3; Yadav et al., 2021). Because herbivory was modelled as the percentage of leaf area loss, we used a beta regression with a zero-inflation component to allow for zeros in the dataset. All global models contained treatment, tree-level shade cover and tree biomass as covariates, and an interaction between treatment and tree-level shade cover to compensate for possible differences between trees. Models included random effect terms to account for the nested sampling design (i.e., cacao trees within plantation) and to minimise possible differences between plantations sampled in the morning and afternoon. We excluded the first month of our exclusion experiment from our models to account for initial abundance fluctuations of arthropods, flowers, and pods. Finally, for pod damage we used an offset with total pods collected per tree and visit to compensate for differences in number of pods between trees. We performed backwards model selection using likelihood ratio tests on fully nested models (LRTs, cut-off probability $P > 0.1$) and then used minimal adequate models to estimate coefficients. Model evaluation was conducted using the package DHARMA (Hartig and Hartig, 2017). All GLMMs were run using the package glmmTMB (Brooks et al., 2017) in R v4.0.3 software (R Core Team, 2020).

2.6. Cacao yield

Due to travelling issues associated to the pandemic during the harvesting season, where visits to the farms needed to be more constant and occur more often to be able to collect ripe pods before they became rotten, we were not able to collect all pods from all trees. Hence, to link the results of our flying vertebrate enclosure experiment and corresponding effects on crop yields to economic values, we used 264 ripe fruits that we were able to harvest from 25 of our 32 cacao trees and from seven of our eight plantations (although not even from these trees we were able to collect all pods) as reference for mean productivity values for large pods (see Table A.1 for more details). We measured the length and diameter of each cacao fruit, before we extracted, dried, and weighed its beans.

Fruit length and weight of dry/marketable cacao beans showed a Pearson correlation coefficient of 0.5 (Fig. A.4). Thus, we conducted a linear model (Gaussian distribution) with pod length as predictor and dry bean weight per pod as a response variable. By using the mean length of the 264 collected pods as a proxy of the size of the large pods

from our plantations, we estimated the dry bean weight within a pod with the size of our large pods. After having the mean dry bean weight, we converted to dry weight the rounded mean number of large pods estimated by our enclosure model to be save/lost in enclosures and controls with different levels of tree shade cover (Table A.3). Finally, we converted the dry bean weight into cacao yield in dollars and CFA (Cameroon currency) per ha/year, considering the ICCO daily price for cacao beans on January 3rd 2022 (<https://www.icco.org/statistics/>) and 900 cacao trees per hectare (mean number of cacao trees for our eight plantations; Table A.1). Monetary values were estimated for cacao trees with a low shade value (higher yield production), mid shade value (potential win-win scenarios) and high shade value (higher biodiversity metrics) (Bennett et al., 2021; Blaser et al., 2018; Clough et al., 2011; Jarrett et al., 2021; Waldron et al., 2015, 2012).

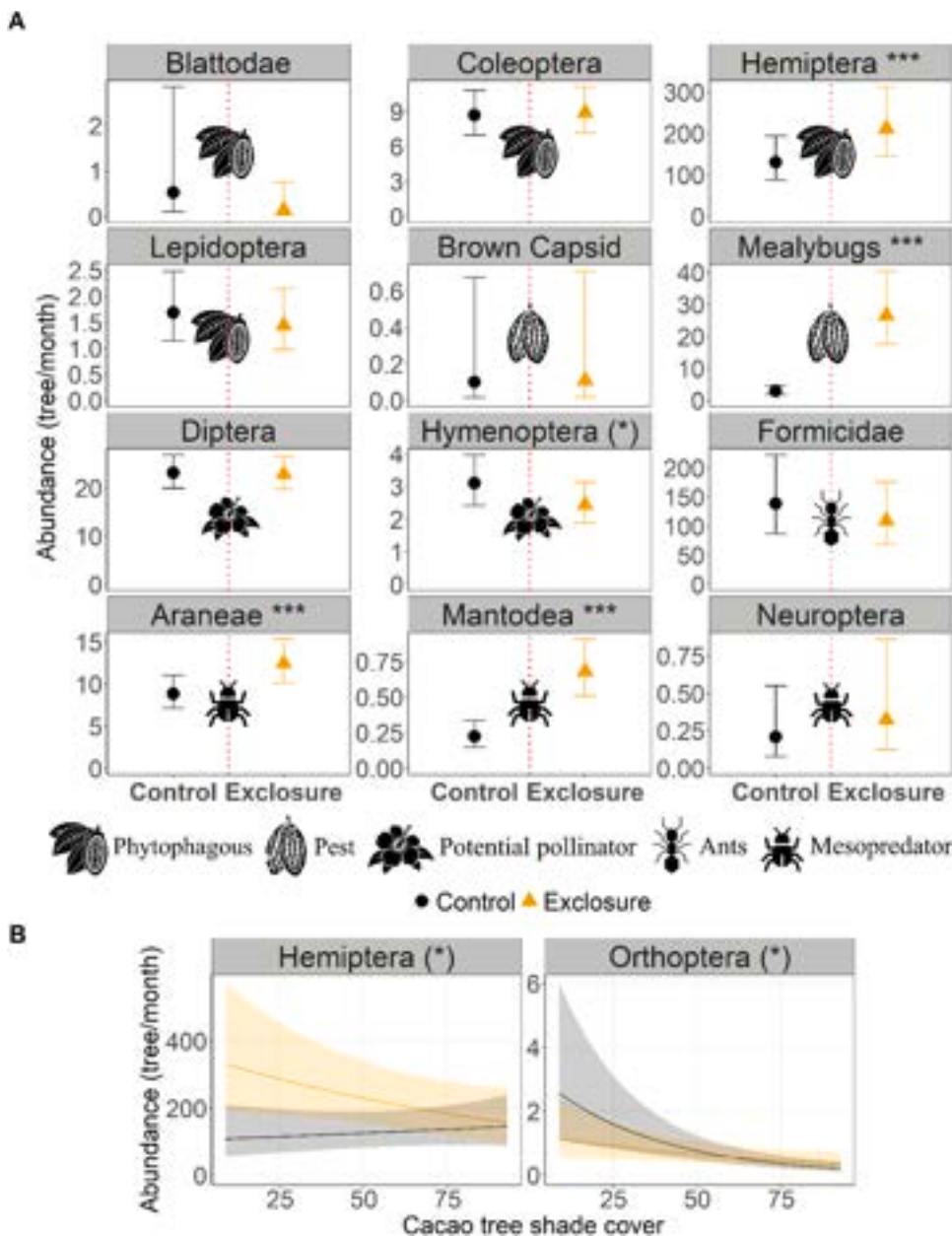


Fig. 2. – Mean abundance of arthropods (\pm CI) for (A) treatment and (B) the interaction between treatment and tree-level shade cover on the monthly abundance of each arthropod group per cacao tree. Hemiptera group includes all insects of that order minus brown capsid and mealybugs. Control represents trees where bats and birds were not excluded, while enclosure represent trees where these groups were excluded. Shaded areas represent CIs. Values indicate mean abundances per tree/month predicted by the minimum adequate model (Table A.3). In plot A, treatment covariate was retained in all models to illustrate its effect sizes. Significance levels are indicated as *** $p < 0.001$ and (*) $p < 0.1$.

3. Results

3.1. Pest/arthropod populations

We recorded 183,011 arthropods belonging to 13 orders in all cacao trees: 74,424 from 13 orders in control trees and 108,587 from 13 orders in exclusion trees (Table A.2). Plant-sucking insects (order Hemiptera) were the most abundant group, followed by ants (family Formicidae, order Hymenoptera). Mealybugs (*Pseudococcidae* spp., order Hemiptera) were the most abundant pest, with 535 records in control trees and 4569 records in exclusion trees. Brown Capsids (*S. singularis*, order Hemiptera) occurred in very low abundance, having 91 records in just 11 of 32 trees and 4 of 8 farms, with 64 records in control trees and 27 records in exclusion trees (see Table A.2).

Arthropods responses to the absence of bats and birds were group specific (Fig. 2A; Table A.3). Within phytophagous arthropods, other Hemiptera and mealybugs showed significant increases in the absence of bats and birds, with populations of mealybugs increasing by 89.31 % in exclusions, and other Hemiptera by 38.57 %. However, the effect of our exclusions on the abundance of other Hemiptera was dependent on tree-level shade cover, with higher abundance in treatments with low shade. Also, the response of Orthoptera to treatment type was marginally dependent on tree-level shade cover, with higher abundance in controls compared to exclusions at low shade and similar patterns at high shade (Fig. 2B; Table A.3). The other phytophagous arthropods (Blattodea, Coleoptera and Lepidoptera) showed no significant change within treatments. All predatory arthropods populations also increased in exclusion trees, with results being significant for Araneae and Mantodea. Potential pollinators (Hymenoptera, such as bees and parasitic wasps) responded marginally positively (significant at a 0.1 significance level) to the presence of bats and birds. Finally, the responses of arthropod groups to tree biomass and tree-level shade cover independently of treatment were group specific (Table A.23). Most groups responded negatively to biomass (Araneae, Coleoptera, Diptera, Hymenoptera, Lepidoptera and Orthoptera), with Formicidae responding positively (Fig. A.5). For tree-level shade cover, Coleoptera and Neuroptera responded positively, while Orthoptera responded negatively (Fig. A.6; see Section 3 in appendix for a detailed discussion on these results).

3.2. Herbivory and pod damage

Capsid pest feeding was the type of pod damage recorded most often ($n = 2120$, 47.05 % of all pods), followed by 642 events of Cherelle Wilt (22.09 % of all small pods) and 639 events of Black Pod Disease (14.18 % of all pods; 'event' refers to a count of pod damage that could be repeated from previous visits; Table A.4). We did not find any significant differences between control and exclusions for any of these types of pod damage (Fig. 3A). However, we found fewer events of Immature Ripening in exclusions than in controls, 54 (1.86 %) to 217 (7.47 %), though the effect was only marginally significant (Fig. 3A; Table A.3). During the study, we only detected one pod (in a control tree) with feeding marks by a vertebrate animal (likely a rodent). Responses to tree biomass and tree-level shade cover varied between response variables, with capsid pest feeding and dead black tissue being lower with increasing tree-level shade cover (Fig. A.5 and A.6; Table A.3).

Leaf damage was estimated based on 575 leaves. Almost 75 % of the leaves ($n = 425$) had less than 1 % of area loss. Values ranged from 0 % to 42.9 % in control trees and from 0 % to 33.7 % in exclusion trees (Table A.5). Marginally more herbivory occurred in the control trees (Fig. 3B; Table A.3).

3.3. Tree productivity

During the 11 sampling visits, we counted a total of 14,969 flowers, 2906 small fruits and 1600 large fruits (as above, pods could be counted

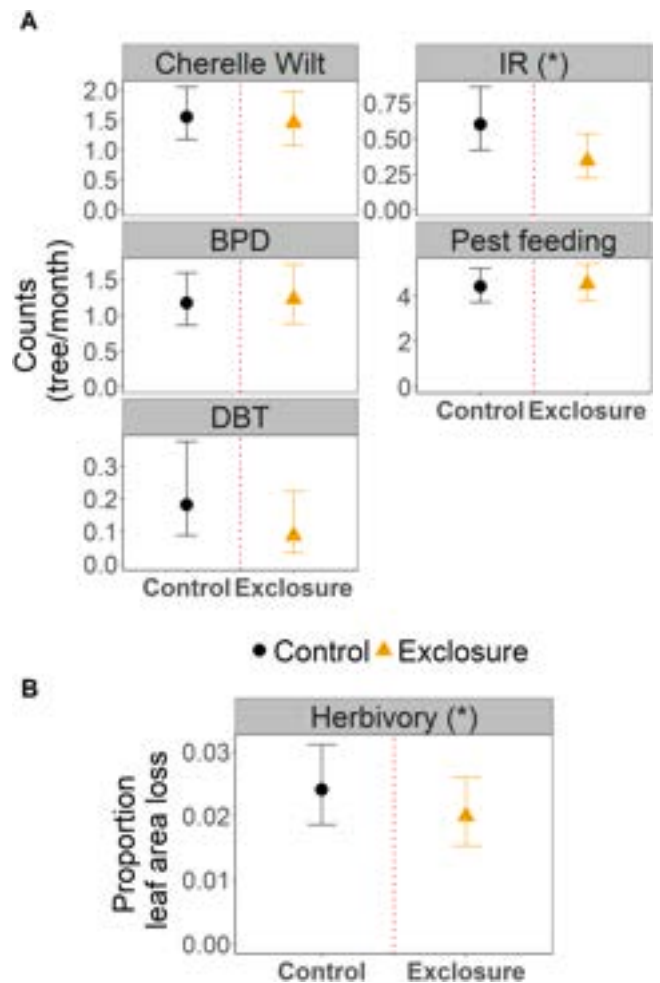


Fig. 3. Mean counts/proportion (\pm CI) for full exclusions on (A) the number of monthly events detected of Cherelle Wilt, Immature Ripening (IR), Black Pod Disease (BPD), Capsid Pest Feeding marks and Dead Black Tissues (DBT), and on (B) the proportion of leaf area loss per cacao tree. Control represents trees where bats and birds were not excluded, while exclusion represent trees where these groups were excluded. Values indicates mean counts/proportions per tree/month predicted by the minimum adequate model (Table A.3). In plot A treatment covariate was retained in all models to illustrate effect sizes. Marginal significance levels are indicated as (*) $p < 0.1$.

multiple times on different sampling visits). Of these, 39.35 % of flowers, 46.56 % small pods and 41.25 % of large pods were counted on exclusion trees (Table A.4). The absence of bats and birds affected the number of flowers and pods observed in the trees, with flowers only being marginally significant (Fig. 4; Table A.3). Responses of flowers and large pods to treatment type were dependent on tree-level shade cover – with more flowers and large pods inside exclusions at low shade levels, while at high shade levels, there were more flowers and large pods in controls compared with exclusions (Fig. 4B). Large pods also increased significantly with increasing tree biomass (Fig. A.5; Table A.3).

3.4. Cacao yield

We predicted a dry bean weight for the mean large pod size (15.33 cm) of 72.84 g per pod (95 % CI of 71.084, 74.596; Fig. A.7). However, because responses of large pods to treatment type depended on tree-level shade cover (see mean and CI number of large pods in Fig. 4B), cacao yield also varied with shade (Table 1). According to these results, we found that in cacao trees with high levels of shade cover

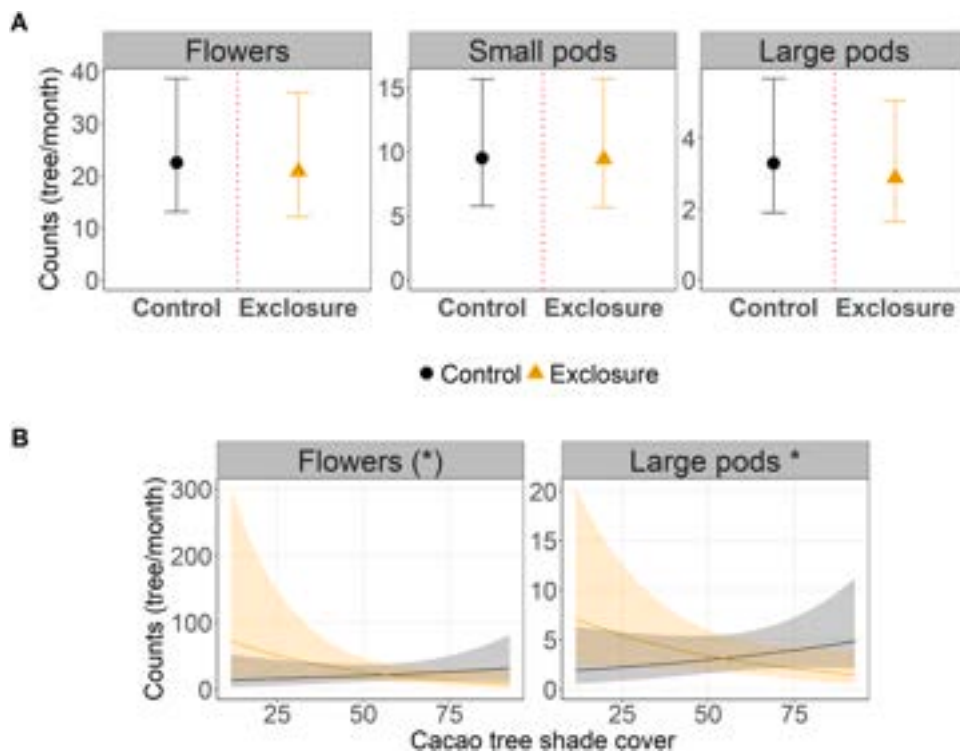


Fig. 4. - Mean counts (\pm CI) for (A) full exclusions and (B) its interaction with tree-level shade cover on the monthly number of flowers and pods categories per cacao tree. Control represents trees where bats and birds were not excluded, while exclusion represent trees where these groups were excluded. Shaded areas represent CIs. Values indicates mean counts per tree/month predicted by the minimum adequate model (Table A.3). In plot A treatment effect sizes. Significance levels are indicated as * $p < 0.05$, and (*) $p < 0.1$.

Table 1

Table showing the conversion of the rounded mean number of pods predicted by the large pod model to cacao yield revenues in CFA (Fig. 4B). Conversion was done for very low levels (~10 %), intermediary levels (~50 %) and high levels (~90 %) of tree-level shade cover.

Tree-level shade cover	Treatment	Mean number of large pods (tree)	Predicted Dry Weight (kg/tree)	95 % CI Dry Weight (kg/tree)	Revenue in CFA (ha/year)	Revenue range in CFA (ha/year)
10 %	Control	2	0.146	0.142; 0.149	183,037	178,624; 187,449
	Treatment	7	0.510	0.498; 0.522	640,628	625,184; 656,072
50 %	Control	3	0.219	0.213; 0.224	274,555	267,936; 281,174
	Treatment	3	0.219	0.213; 0.224	274,555	267,936; 281,174
90 %	Control	5	0.364	0.355; 0.373	457,592	446,560; 468,623
	Treatment	2	0.146	0.142; 0.149	183,037	178,624; 187,449

Note: We assumed 900 cacao trees/ha, cacao bean price of 1396.027 CFA/kg and currency exchange of \$1 = 574.64CFA

(about 90 % or higher) bats and birds may save farmers 267,936 CFA (\$466) to 281,174 CFA (\$489) per ha and year. However, we also found that in plantation with cacao trees with low levels of shade cover (~10 %) bats and birds could contribute to reducing farmers' profit between 446,560 CFA (\$777) and 468,623 CFA (\$816). When tree-level shade cover was intermediary (50 %), we found no relevant gains or losses between exclusions and controls (Table 1).

4. Discussion

Our study demonstrates, for the first time, how birds and bats contribute to pest suppression services in African cacao agroforestry systems. In accordance with our predictions, the absence of bats and birds significantly increased the populations of phytophagous arthropods (9.4 times for mealybug pest and 1.6 times for other Hemipteran insects) and predatory arthropods (1.4 times for spiders and 3 times for mantis), whereas the populations of one potential pollinator group marginally decreased (1.3 times for Hymenoptera; Fig. 2). Contrary to our expectations, the absence of bats and birds did not affect the populations of brown capsids.

4.1. Effects on arthropods

Similar to an exclusion experiment conducted by Maas et al. (2013) in Indonesia, which found differences in yield between treatments but no differences in the abundance of the main pests and their pod damage, the main cacao pest in our study system, *S. singularis*, did not vary significantly with the absence of bats and birds (Fig. 2A). However, this species is particularly difficult to detect, occurring normally in densities of two adult individuals per tree and being mostly active around sunrise (Babin et al., 2010). Therefore, the discrepancy between the very low numbers of brown capsids that we recorded and the more than 2000 pods with capsid feeding marks that we counted (Table A.4) could indicate that the pest damage was caused by other insect groups (e.g., other Hemipteran insects), or that we need full-day monitoring protocols to be carried out to detect *S. singularis* populations. On the other hand, we detected 9.4 times more mealybugs in exclusions compared to control trees (Fig. 2A). Mealybugs are responsible for carrying Swollen Shoot Virus Disease, a disease that only occurs in Central/West Africa that can cause total tree destruction and crop losses of several million dollars (Andres et al., 2018). However, because no outbreaks of this virus have been registered in Cameroon (Andres et al., 2017), we did not consider signs of this disease in our sampling. We did, however, observe mealybugs feeding directly on young cacao leaves on many occasions.

Hence, it is not possible to know if the differences in production observed were associated to this pest or other factors. We need more studies focusing on mealybugs in Cameroonian cacao plantations.

In accordance with Cassano et al. (2016), we did not find a significant increase in the number of leaf-eating chewing insects (Coleoptera, Lepidoptera and Orthoptera) in the absence of bats and birds. Although herbivory was marginally higher in control trees, from 2.4 % total leaf area loss in controls to 1.9 % in enclosures, the magnitude of this difference was very low and unlikely to affect production, which is in line with findings from other studies (Maas et al., 2019, 2016). Because predatory arthropod (Araneae and Mantodea) abundance increased in the absence of bats and birds, there may be a redundancy in the biological control services provided by flying vertebrates and predatory arthropods, which could explain the low rates of herbivory (Cassano et al., 2016). In our study, only mealybugs and other Hemipteran insects increased significantly in numbers in enclosures (Fig. 2A). Hemipteran insects are sap-sucking insects with economic significance since they can be pests of various crops across the world, like aphids in kale plantations (Ndang'ang'a et al., 2013) and tea mosquito bug in tea plantations (Roy et al., 2015). Although we counted mealybugs and *S. singularis* independently from other Hemipterans, other species not considered by us because they are not common cacao pest in Cameroon, such as *Distantiella theobroma* (Distant, 1909; Babin et al., 2010), could also be affecting cacao production. However, like Maas et al. (2013), we did not find any evidence of a significant increase of capsid feeding marks in enclosures (Fig. 3A) to claim that other capsid secondary pests could be more important in our study area than previously assumed. Hence, future studies should try to define protocols that focus not only on main cacao pests for the area, but also on all known secondary pests and their respective damage (CABI plantwise, 2019). Only by doing this can we shed light on the missing link between bird/bat predation, pest pod damage and cacao production in Cameroon and other parts of the world.

Bats and birds appeared to provide an ecosystem service by reducing mealybug pest numbers, but they may have also provided a disservice by significantly reducing the populations of spiders and mantises (Fig. 2A). However, the increase of spiders and mantis in enclosures could likely be a mesopredator-release effect, where populations of medium-sized predators rapidly increase in an ecosystem after the removal of larger, top predator (Ritchie and Johnson, 2009). Nevertheless, a study conducted in Indonesian cacao plantations showed that even though predatory arthropods decreased with the presence of bats and/or birds, there was still a reduction in pest numbers and an increase in production (Maas et al., 2013), corroborating our results. This indicates that responses of specific arthropods groups to the absence of flying vertebrates seem to be dependent not only on overall arthropod communities and their net balance, but also on the characteristics of those predatory vertebrates (e.g., the community of bats in Cameroon is composed by several aerial hawking and leaf-gleaning bats species that can capture flying and non-flying insects; ACR, 2019). We speculate that the increase of predatory arthropods in our trees was strong enough to maintain the balance of leaf-eating chewing insects and other arthropods orders, but not of pest populations that occur at high densities like mealybugs. In addition, we observed some bird species (e.g., *Cyanomitra olivacea* [Smith, 1840]) feeding on mealybugs in our plantations (Powell & Jarrett pers. obs.). Thus, follow up work should focus on the diet of these animals to see if indeed they are eating these pests.

4.2. Effects on tree productivity

The number of flowers marginally decreased in enclosures and increased in controls with increasing tree-level shade cover (Fig. 4B). This could be associated with the increases of Coleoptera larvae populations with increasing tree-level shade cover (Fig. A.5), which could lead to higher rates of herbivory in cacao flowers when flying vertebrate predators are not present (Maas et al., 2013). However, the high number of flowers in low shade cacao trees in enclosures may also indicate that

other management variables, such as habitat management or unaccounted tree factors, may be responsible for the differences observed, especially if we consider that Coleopteran flower visitation rate in cacao is very low (Toledo-Hernández et al., 2017; Vansynghele et al., 2022). We also found marginally more Hymenoptera in control trees, which may be pollinators of cacao (e.g., small parasitic wasps and bees; Toledo-Hernández et al., 2017). Also, an exclusion experiment conducted in Peru showed that the presence of bats and birds improved cacao yields by improving fruit set (Vansynghele et al., 2022). However, we found similar numbers of small pods between enclosures and control trees (Fig. 4A), indicating similar levels of fruit set between treatments. This may indicate that differences observed in cacao production are probably not associated with pollination (going from flower, fruit set to small pod) and most likely with pod development (going from small to large pod). Nevertheless, because we were not directly measuring fruit set is hard to disentangle these patterns. We recommend for future studies in African cacao plantations to investigate in more detail the role of bats and birds in limiting fruit set by monitoring directly flowers and conduct enclosures at the flower level.

Cacao production usually decreases with increasing plantation-level shade cover, with studies pointing to a maximum of 30–40 % shade to maintain partial win-win scenarios for farmers and biodiversity (Blaser et al., 2018; Clough et al., 2011; Gras et al., 2016). In our study, we recorded a constant decrease in the number of large pods with increasing tree-level shade cover in enclosures but an increase when bats and birds were present (Fig. 4B). Although we could not find a direct link between pod damage and cacao yield, bats and birds are known to increase productivity through pest suppression in different agroforestry systems (Maas et al., 2016), with these services being higher in plantations with high plantation-level shade cover and forest proximity (Gras et al., 2016; Librán-Embido et al., 2017). However, none of pest groups studied here increased in numbers with increasing tree-level shade cover and even the Hemipteran insects showed the opposite pattern, decreasing in enclosures and increasing in controls with increasing tree-level shade cover (Fig. 4B). Also, pest feeding marks decreased significantly with increasing tree-level shade cover independently of bats and birds being present (Fig. A.5). Nevertheless, studies conducted in some of the same cacao plantations as our study showed that insectivores bats and birds increased in abundance with increasing plantation-level shade cover (Jarrett et al., 2021; Ferreira et al., unpublished data). So, it is very likely that the differences observed in productivity are associated to a pest (e.g., mealybugs or another non-targeted pest). We need more studies to determine if this increase in number of pods in control trees with increasing tree-level shade cover is associated to that or other underlying mechanism, such differences in shade tree species composition (Asitoakor et al., 2022) or physiological/management conditions that limit flowering/fruit set (Toledo-Hernández et al., 2017), and if the same patterns are observed when shade cover is considered at the plantation-level.

Contrary to other exclusion experiments studies conducted in cacao plantations from South America (Cassano et al., 2016; Vansynghele et al., 2022) and South-East Asia (Maas et al., 2013), tree-level shade cover in our plantations influenced the responses to the absence of flying vertebrates. However, because those studies used shade cover at plantation-level, while in our study we used at tree-level, comparisons about the importance of shade cover to regulate top-down effects by bats and birds between these regions are difficult to infer. In addition, Maas et al. (2013) had few plantations with high shade (only one and two plantations out of 15 with shade cover higher than 70 % and 60 %, respectively), making it difficult to compare results of the role of flying vertebrates at very high levels of shade (90 %). Nevertheless, our bat and bird communities seem to be compensating for expected decreases in production with increasing tree-level shade cover, but production was still higher in enclosure trees with very little shade than in control trees with a lot of shade (mean of 7 large pods versus 5 pods; Fig. 4B). Niether et al. (2020) in a meta-analysis showed that even though full-sun

plantations have higher cacao yields than agroforestry systems, when these systems are managed properly and all the systems' yields are considered (e.g., by-crops from shade trees), they can be economically as viable as full-sun plantations. In addition, agroforestry cacao systems are more ecologically stable and have longer productive lifetime (Niether et al., 2020), which can help farmers to have stable revenues across long periods (Jagoret et al., 2011). This is especially important when we consider that cacao agroforestry systems have greater resilience to climate change and the potential to mitigate it due to a higher carbon sequestration (Blaser et al., 2018; Niether et al., 2020), something that could help address the problems that African farmers will face with the future climate change scenarios (Müller et al., 2011).

5. Conclusions

In recent years, there has been a strong pressure from the Cameroonian government to increase cacao production through the development of low shade/full-sun hybrid cacao systems (Ordway et al., 2017). Although our results do not directly link pest suppression, pod damage and cocoa yield, they seem to indicate that bats and birds may help farmers save on average 274,555 CFA (\$478) per ha per year when tree-level shade cover is maintained at high levels and can cost farmers 457,592 (\$796) at low levels of shade. However, if we consider that low shade/full-sun systems are not sustainable in the long term and do not offer resilience against future climate scenarios, our results (assuming that tree-level shade cover is a broadly representative for plantation-level shade cover) support the assumption that bats and birds can help mitigate some of the losses in production caused by going from a full-sun to a more traditional cacao system. In addition, we showed that these taxa have the potential to act as pest suppressors in African cacao plantations by reducing the populations of mealybugs and other Hemipteran pests.

Our findings highlight the need to conduct more targeted research in this region due to the lack of transferability of some results between Africa, South America, and Asia (Maas et al., 2019, 2016), which is of paramount importance when considering how underrepresented is the research from Central/West Africa (Maas et al., 2021; Pettorelli et al., 2021). Finally, our findings encourage African farmers with high pest incidence in their plantations (especially mealybugs and other Hemipterans) to increase tree-level shade cover to maximise pest suppression, and thus avoid at the same time high-intensity farming and degradation of tree diversity, with additional co-benefits for climate change mitigation and human well-being.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Diogo F. Ferreira reports financial support was provided by Bat Conservation International. Diogo F. Ferreira reports financial support was provided by Rufford Foundation. Crinan Jarrett reports financial support was provided by British Ornithologists' Union.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.108325.

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