

RESEARCH ARTICLE

Fewer pests and more ecosystem service-providing arthropods in shady African cocoa farms: Insights from a data integration study

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Abstract

1. Agricultural intensification is leading to conversion of cocoa agroforestry towards monocultures across the tropics. In the context of cocoa agriculture, arthropods provide a range of ecosystem services and dis-services. Arthropod pests (e.g., mirids and mealybugs) can cause major damage to crops, whilst pollinators and natural enemies (e.g., predatory insects and parasitoids) have the potential to enhance agricultural yields. Understanding how intensification of cocoa farming affects different arthropod groups is therefore important in maximising the abundance of beneficial arthropod taxa and reducing pest burdens. However, little is known about the influences of agricultural intensification on tropical arthropod communities, especially in Africa, where ~70% of the world's cocoa is produced.
2. Most research on arthropod communities considers data from different sampling methods separately, as proxies of abundance; whilst these proxies can be informative, estimating true abundance enables direct comparison between arthropod taxa, and therefore the study of community dynamics. Here, we develop a Bayesian hierarchical model that integrates data from three common arthropod survey techniques to estimate population size of arthropod orders and to investigate how arthropod community composition responds to farm shade cover (an indicator of management intensity).
3. Our results show that eight of 11 arthropod taxa responded to farm shade cover; importantly, brown capsids (the primary pest of cocoa in Africa), Coleoptera pests and Hemiptera pests decreased with increasing farm shade cover, whilst Araneae

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(natural enemies) and Diptera (potential pollinators) were more abundant in shady farms.

4. *Synthesis and applications.* To achieve lower pest burdens and higher abundances of potential pollinators and natural enemies, African cocoa farms should maintain a dense canopy of shade trees. The current shift towards high-intensity cocoa farming in Africa could result in long-term losses due to pest infestations and loss of arthropod-mediated ecosystem services.

KEYWORDS

Afrotropics, agroforestry, arthropods, community composition, hierarchical modelling, population size, sampling methods

1 | INTRODUCTION

In agroecosystems, effective management requires detailed knowledge of arthropod communities, including the population sizes of pests (Deutsch et al., 2018), the time of year at which pest populations peak (Mahob et al., 2011) and how they are influenced by environmental covariates (Babin et al., 2010; Bisseleua et al., 2009; Janssen & Rijn, 2021). This requirement is even more important when economic resources are limited, for instance in tropical regions where most agricultural production is carried out by small-scale farmers living below the poverty line (Niether et al., 2020; Tscharnkte et al., 2012). Currently, many tropical farmers are being encouraged to intensify agriculture on the basis that it will increase their yields; however, in the absence of expensive chemical inputs, intensified farms may quickly experience increases in arthropod pests, leading to long-term yield declines (Ordway et al., 2017; Tscharnkte et al., 2011). Additionally, intensified farms may suffer from a reduction in beneficial arthropods, such as pollinators, natural enemies and other ecosystem service providers (Bisseleua et al., 2013; Toledo-Hernández et al., 2021). Thus, to identify the optimal approach to sustainable management, we must better understand the effect of agricultural intensification on arthropod communities (Janssen & Rijn, 2021; Niether et al., 2020).

Agroforestry, the practice of growing crops under a canopy of shade trees is a common form of food production in tropical regions, partly because agroforestry systems are relatively cheap to establish, requiring just the thinning of existing rainforest and planting of crops beneath the canopy (Clough et al., 2009; Tscharnkte et al., 2012). A prime example of an agroforestry-grown crop is cocoa, the fastest expanding export-oriented crop in the Afro-tropics (Ordway et al., 2017). Although cocoa is traditionally grown under shady conditions, the past decades have seen a shift towards more intensively managed monocultures, in which cocoa trees are planted in clear-cut patches of land (Armengot et al., 2016; Tscharnkte et al., 2011). This expansion and intensification of cocoa agriculture have led to extensive deforestation in countries such as Côte d'Ivoire (Barima et al., 2016; Maclean, 2017). Whilst there is evidence supporting the increase in yields in sunny farms compared to their shady counterparts (Bisseleua et al., 2013), there is also evidence that shaded cocoa

farms have a longer productive lifespan and suffer lower pest burdens, making long-term yields comparable (Ahenkorah et al., 1974, 1987; Niether et al., 2020; Tscharnkte et al., 2011).

In Africa, the main cocoa pests are the brown capsid *Sahlbergella singularis* (Hemiptera: Miridae; Ambele et al., 2023; Bagny Beilhe et al., 2018), as well as other Hemipteran groups such as mealybugs (Hemiptera: Pseudococcidae) and mosquito capsids (Hemiptera: Afropeltis). These pests are still among the most important factors limiting cocoa production, causing annual crop losses of 25%–40% (Wessel & Quist-Wessel, 2015). Hemipteran bugs tend to occur at higher abundances in sunnier farms, though evidence supporting this is still limited (Ambele et al., 2023; Bagny Beilhe et al., 2018). Whilst pests decrease agricultural productivity, several arthropod groups provide ecosystem services in cocoa farms, such as pollination and pest suppression. There is still very limited information available on cocoa pollinators in Africa, but in Indonesia, pollination is thought to be accomplished primarily by small Dipterans (Toledo-Hernández et al., 2021). The effect of shade cover on potential pollinators of cocoa is still largely unknown, especially in the Afrotropics (Ambele et al., 2023; Toledo-Hernández et al., 2021). Natural enemies such as ants and spiders may provide pest suppression in cocoa agroforestry, and there is some evidence that these groups prefer shadier farms (Anjos et al., 2022; Bisseleua et al., 2017).

Our understanding of arthropod communities in agroecosystems is limited due to the methodological challenge of studying such a diverse group of animals; one survey method is rarely suitable to survey whole communities, and field data therefore often result in taxon-specific proxies of abundance. The use of proxies rather than absolute abundances limits the applications of these data; of special importance is the study of community dynamics, which requires data on species' densities which must consequently be standardised between taxa (Curtsdotter et al., 2019). In complex agroecosystems containing diverse arthropod taxa, which play varying roles in the provision of ecosystem services or dis-services, and interact between each other (predation, competition, parasitism), the cascading effects of management on communities can be complex and hard to predict without a fully parametrised community model (Janssen & Rijn, 2021). The limited number of studies that have applied community modelling approaches to species' density data in agricultural

habitats show that pest population control measures can have unexpected long-term outcomes as a result of interactions between species. For instance, pest populations may resurge after pesticide application due to the collapse of predator populations (Janssen & Rijn, 2021; Trumper & Holt, 1998). Other studies applying community models to different food-web systems have also shown unpredictable effects of changes in species' densities, due to direct and indirect interactions between species (Burt et al., 2018; Dexter et al., 2020; Vial et al., 2011). This type of community modelling requires data on species' densities or population sizes that are comparable across taxa.

Here, we overcome the challenge of generating comparable population size estimates for arthropods by combining data from three methods (malaise traps, sweep netting and visual surveys) using a data integration approach. We chose these specific methods because they are broadly complementary in terms of target taxonomic groups and field effort (Montgomery et al., 2021). We applied the data integration technique to our field data, collected in Afrotropical cocoa agroforestry systems on a gradient of shade cover. In cocoa agroforestry, shade cover is an indication of shade tree farm management; more intensively managed ('sunny') farms have open canopies, whilst traditional ('shady') agroforests have closed canopies (Tschardt et al., 2011). Using data collected across this gradient, we aimed to (1) generate comparable estimates of population size across the arthropod community; and (2) investigate the effect of shade management and season on the main arthropod orders found in the farms, including service-providers and pest groups.

2 | MATERIALS AND METHODS

2.1 | Field sites

We conducted arthropod surveys in 28 cocoa farms located across the Centre, East and South regions of Cameroon (Appendix S1). Farms were selected based on shade cover (to form a gradient), size (>1.5 ha, mean = 4.9, SD = 3.8) and logistical feasibility, and were separated by more than 500 m (Jarrett et al., 2021, 2022). We measured shade cover at each farm by taking pictures of the canopy above the cocoa tree crowns (using a camera on an extendable pole), and then calculating the percentage of vegetation cover in each picture. The shade cover value for each farm is a mean of 10 pictures taken following a transect in the farm (Jarrett et al., 2021): shade cover in our farms ranged from 20% to 98% (Appendix S1). We surveyed arthropods in these farms over four visits in Jan–Feb and Aug–Sept 2019–2020. Not all sites were visited in all field campaigns, so the number of visits per site ranged from 2 to 4 (mean = 2.6). Our visits captured both the dry season (Jan–Feb) and the rainy season (Aug–Sept), with each farm visited at least once in each season, allowing us to assess the effect of rainfall seasonality on arthropod populations (Molua, 2006). These visits captured the start of the cocoa harvest season (Aug–Sept) and the period of initial fruit development (Jan–Feb; Ferreira, Jarrett, et al., 2023).

2.2 | Arthropod surveys

We used three different sampling methods to survey arthropods: sweep netting, malaise traps and visual surveys (Figure 1; Jarrett, 2023). For all observations of a given survey type, the observer was the same researcher.

During each visit, the observer conducted two sweep netting sessions, one at dawn (~6:30) and one at dusk (~18:30). Each session consisted of walking a 240 m transect through the farm, sweeping the closest available vegetation at chest height once every 6 m, alternating left and right (total 40 sweeps per session). Transects always crossed the centre of the farm and avoided edges (minimum 20 m from boundary). At the end of the session, the observer transferred the contents of the sweep net to a plastic bag containing a wad of cotton wool soaked in 50% ETOH. Once the arthropods had stopped moving, and upon return from the field each day, the observer removed them from the bag, identified individuals to order level, and counted them. For the analyses, we considered the sum of morning and evening counts.

The evening before the dawn sweep netting session, we set up two malaise traps (NHBS; height = 0.9 m [short end]–1.7 m [tall end]; width = 1.2 m; length = 1.9 m) at each farm. They were placed at least 20 m from the farm boundary and were separated by a minimum of 50 m. The malaise traps were unbaited, with the collection jars containing 50% ETOH. The traps were left standing for 24 h so that they were collecting at the same time as the sweep netting occurred. At the end of the 24 h we collected the traps and identified and counted the specimens in the collecting jars to order level.

We carried out two different types of visual surveys: full tree visual surveys and pest counts (henceforth 'visual surveys' refers to both, 'tree visual surveys' refers to the former and 'pest counts' to the latter). Within 2 weeks (mean = 8 days) of the sweep netting and malaise trapping, we conducted the tree visual surveys. Whilst sweep netting and malaise traps were used at each visit to each farm, tree visual surveys were conducted in a sub-sample of farms, due to effort constraints (Figure 1). The tree visual surveys consisted of a 25-min survey of all arthropods found in a specific cocoa tree. In each of the 8 farms in which the tree visual surveys were conducted, we chose two cocoa trees that were ~3 m high and of the same age and type. The 25 mins were divided into five 5-min periods, one of which was dedicated to the tree trunk, and each of the other four dedicated to one quarter of the crown (following Ferreira, Jarrett, et al., 2023). The observer used a ladder to reach the higher parts of the crown, and stopped the watch when the count or identification to order level was not instantaneous.

The pest counts (conducted in same 24-h period as sweep netting and malaise traps) adopted similar methodology to the tree visual surveys, but with several important distinctions. First, the pest counts disregarded other arthropods (Table 1). We considered as pests any arthropods found visibly damaging cocoa trees, whether it be the pods themselves or the leaves, shoots or trunks. Additionally, we counted all brown capsids, aphids and scale insects as pests following Bagny Beilhe et al. (2018). This classification possibly results

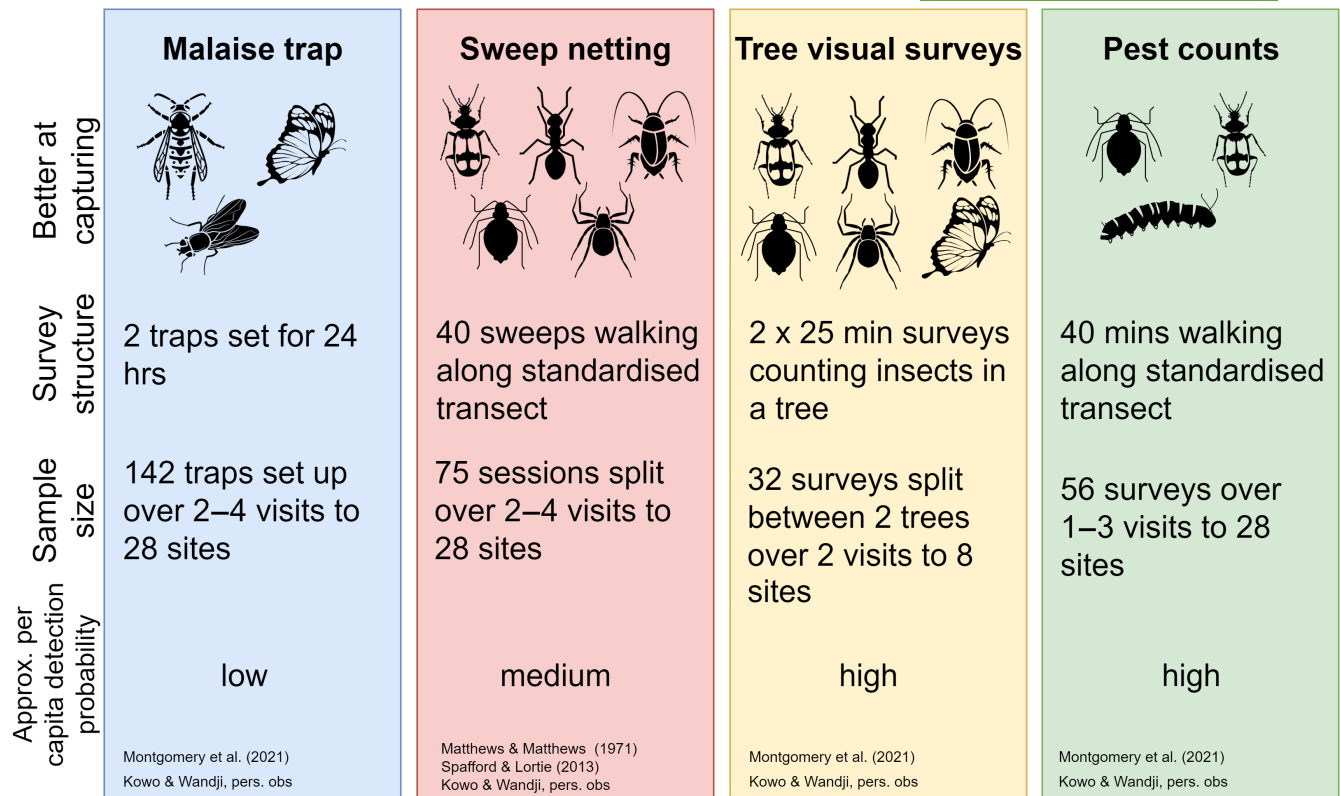


FIGURE 1 Summary of sampling methods used in the field. Created with diagrams.net (for details on artwork see Appendix S5).

TABLE 1 Taxa considered in model, and taxonomic coverage of each survey method.

Taxa	Surveyed by sweep netting and malaise traps (subscript j^*)	Surveyed by tree visual surveys (subscript j^*)	Surveyed by pest counts (subscript p)
Araneae	Araneae	Araneae	
Blattodea	Blattodea	Blattodea	
Coleoptera non-pest	Coleoptera (non-pest + pest)	Coleoptera (non-pest + pest)	
Coleoptera pest			Coleoptera pest
Diptera	Diptera	Diptera	
Hemiptera non-pest	Hemiptera (non-pest + pest)	Hemiptera (non-pest + pest)	
Hemiptera pest			Hemiptera pest
Hymenoptera	Hymenoptera	Hymenoptera	
Lepidoptera non-pest	Lepidoptera (non-pest + pest)	Lepidoptera (non-pest + pest)	
Lepidoptera pest			Lepidoptera pest
Brown capsid		Brown capsid	Brown capsid

Note: Sweep nets, malaise traps and tree visual surveys did not distinguish pests and non-pests, and therefore considered the sum of both, whilst pest counts only considered pests.

in an overestimation of the number of pests, as some individuals observed actively damaging cocoa (and consequently counted as pests) may have been opportunistically feeding but do not cause significant damage to the crop. We settled on this broad definition of pest because identification of arthropods to species level increases handling time considerably and may not be possible without close examination in the laboratory. Additionally, though the main pests of

cocoa in Africa are well known (e.g., brown capsid), other secondary pests are less well documented (Bagny Beilhe et al., 2018).

Second, the observer did not utilise a ladder and therefore only observed the trunk of the tree or any branches at or below eye-level; this trade-off streamlined survey logistics (many more trees could be surveyed) whilst covering a search area containing most cocoa pods (and pests) in our farms (Romero Vergel et al., 2022).

Rather than focussing on just one tree, the observer undertook a 40-min walk through the site stopping at each tree on-route to identify and count any pest arthropods. The number of trees visited was on average 50 per site. Pests were identified to order level with the exception of brown capsid, which was counted separately. Whenever the identification or count of arthropods was not instantaneous (e.g., if there was a large group of individuals, or if the observer needed to consult a reference book), the observer would stop the watch, and then re-start it once surveying recommenced. The pest counts were conducted at dawn, because brown capsids become less active during the sunniest hours of the day and tend to move higher up in the branches (Bagny Beilhe et al., 2018).

All field sampling was conducted in collaboration with the International Institute of Tropical Agriculture under the research permission granted by the Government of the Republic of Cameroon in their Headquarters Agreement.

2.3 | Arthropod grouping

For our study, we considered the following 11 taxa: Araneae, Blattodea, brown capsid (primary pest of cocoa), Coleoptera non-pest, Coleoptera pest, Diptera, Hemiptera non-pest, Hemiptera pest (other than brown capsid), Hymenoptera, Lepidoptera non-pest and Lepidoptera pest (Table 1). These groupings represent the orders most captured across trapping methods. The field data from sweep netting, malaise traps and tree counts were sorted to order level without distinguishing pest from non-pests whilst the pest count data considered only pests (Table 1).

2.4 | Modelling framework

Our model integrated count data from the three different survey techniques into a joint likelihood to estimate population size.

2.4.1 | Determinants of population size

We considered an arthropod community made up of 11 taxa (Table 1). Our estimates of population size are at the spatial scale of one cocoa tree: N_{jiv} refers to the population size (i.e., total number of individuals) of each taxon j at site i and visit v per cocoa tree. We modelled population size from a Poisson-Gamma (i.e., Negative Binomial) process with rate λ_{jiv} and a scale parameter h_j (Greene, 2008).

$$N_{jiv} \sim \text{Poisson}(\lambda_{jiv} h_j), \quad (1)$$

$$h_j \sim \text{Gamma}(\theta_j, \theta_j). \quad (2)$$

We used a Poisson-Gamma distribution to allow for overdispersion resulting from stochastic variation in species population sizes;

the scale parameter h_j allows the relaxation of the Poisson assumption of variance equals mean. To ensure that the magnitude of the scale parameter h_j did not dilute all the signal in our data, we implemented a shrinkage tendency towards Poisson dispersion by setting the following prior for θ_j (Equation 3).

$$\theta_j = \max(100 - \Theta_j, 10) \text{ where } \Theta_j \sim \text{Exponential}\left(\frac{1}{200}\right), \quad (3)$$

λ_{jiv} was modelled as a log-linear function with a guild-specific intercept (γ_{j0}) and two covariates: a guild-specific effect of shade cover (continuous variable, centered and standardised) on population size ($shade_i$) and a guild-specific seasonal categorical covariate ($season_v$, where $season_v = 1$ if Dry and 0 otherwise; Equation 4). Importantly, we assumed that response to shade cover was order-specific, so that orders that contained both pests and non-pests shared the parameter for shade cover. The exception to this rule were brown capsids, which, despite being in the order Hemiptera, were not assumed to respond similarly to shade cover. We made this distinction because brown capsids are the primary cocoa pest in West Africa and therefore of exceptional interest in terms of management outcomes.

$$\log(\lambda_{jiv}) = \gamma_{j0} + \gamma_{j1} shade_i + \gamma_{j2} season_v. \quad (4)$$

2.4.2 | Observation component

During each visit, separated by at least 5 months, we sampled the arthropod community using sweep netting, malaise traps, tree visual surveys and pest counts. We assume that the different survey methods functioned independently so that the probability of being detected by one method did not influence the probability of being detected by the other methods. We assumed that the population of each taxon available for detection by method m was proportional (but not necessarily equal) to N_{jiv} (Miller et al., 2019).

Sweep netting, malaise traps and tree visual surveys did not distinguish between pests and non-pests. Therefore, groups Hemiptera, Coleoptera and Lepidoptera included both pests and non-pest individuals (henceforth, we use subscript j^* to represent $nonpest_j + pest_j$; Table 1). We modelled the number of individuals (c_{mj^*iv}) found of each taxon j^* by each method m from a Poisson-Gamma distribution with a mean of μ_{mj^*iv} and a scale parameter d_{mj^*iv} (Equations 5 and 6). The mean μ_{mj^*iv} was given by population size N_{j^*iv} multiplied by a taxon- and method-specific per-capita capture rate $\exp(\beta_{mj^*})$ (Equation 7).

$$c_{mj^*iv} \sim \text{Poisson}(\mu_{mj^*iv} d_{mj^*iv}), \quad (5)$$

$$d_{mj^*iv} \sim \text{Gamma}(\psi_{mj^*}, \psi_{mj^*}), \quad (6)$$

$$\mu_{mj^*iv} = N_{j^*iv} \exp(\beta_{mj^*}). \quad (7)$$

For the scale parameter d_{mj^*iv} we implemented a shrinkage tendency, as in Equation (3). We set normally distributed priors for

capture rates β_{mj} , parametrised according to knowledge of the groups best targeted by each method, as well as the overall capture efficiency of each method (Montgomery et al., 2021). For visual surveys we assumed a high capture rate (mean of prior for capture probability = 0.8; Table 2), and this effectively calibrated the capture rates of the other methods; by assuming that visual surveys detected the majority of arthropods present, we could estimate capture rates of the other methods. Importantly, we assumed that the capture rate of visual surveys held a maximum value of 1, in other words, it was not possible to count more individuals than were present (Table 2).

The pest counts sampled only pests, and therefore only considered the subset of groups (p) that contained this type (Table 1). These data allowed us to estimate population size of pests only, in addition to the total estimates of population size derived from the other surveys methods. Consequently, we could estimate the population size of non-pests for Coleoptera, Hemiptera and Lepidoptera by subtracting the pests from the total population size.

We modelled the pest count data for each visit (c_{piv}) from a Poisson-Gamma distribution with a mean of μ_{piv} and a scale parameter d_{piv} (Equations 8 and 9). The mean μ_{piv} was given by population size N_{piv} multiplied by a group-specific per-capita capture rate (Equation 10). Per unit area, the capture rates for pest counts were considered the same as the capture rates for tree visual surveys for the corresponding groups (Table 2). However, as the pest counts covered a different surface area compared with the tree visual surveys (for tree visual surveys 1 entire tree, for pest counts a fraction of 50 trees), we scaled the capture rates β_{j3} by a parameter a which represented the ratio of surface area covered by both methods.

$$c_{piv} \sim \text{Poisson}(\mu_{piv} d_{piv}), \quad (8)$$

$$d_{piv} \sim \text{Gamma}(\psi_p, \psi_p), \quad (9)$$

$$\mu_{piv} = N_{piv} \exp\left(\frac{\beta_{j3}}{a}\right). \quad (10)$$

We set the same prior for ψ_p as described in Equation (3).

TABLE 2 Priors set on parameter β for each taxon and sampling method.

Taxa	Sweep netting			Malaise traps			Tree visual surveys		
	Mean	SD	Exp(β)	Mean	SD	Exp(β)	Mean	SD	Exp(β)
Araneae	-1	2	0.36	-1	2	0.36	-0.2 T(,0)	0.1	0.82 T(,1)
Blattodea	-1	2	0.36	-1	2	0.36	-0.2 T(,0)	0.1	0.82 T(,1)
Coleoptera	-1	2	0.36	-1	2	0.36	-0.2 T(,0)	0.1	0.82 T(,1)
Diptera	-2	2	0.14	1.2	2	3.3	-0.2 T(,0)	0.1	0.82 T(,1)
Hemiptera	-1	2	0.36	-1	2	0.36	-0.2 T(,0)	0.1	0.82 T(,1)
Hymenoptera	-1	2	0.36	-1	2	0.36	-0.2 T(,0)	0.1	0.82 T(,1)
Lepidoptera	-2	2	0.14	1.2	2	3.3	-0.2 T(,0)	0.1	0.82 T(,1)
Brown capsid							-0.2 T(,0)	0.1	0.82 T(,1)

Note: All priors were normally distributed, and summarised here with mean and SD. Because β is the log of capture rate (Equation 6), for ease of interpretation we also present the exponential of β , which can be interpreted as a taxon- and method- specific per-capita capture rate. For tree visual surveys, we truncated β at 0 (indicated in table with 'T'), i.e., maximum capture rate of tree visual surveys = $\exp(0) = 1$. For pest counts, capture rate was considered equal to tree visual surveys but scaled by survey area (Equation 10).

2.5 | Analyses

We fit the integrated model to the field data and evaluated precision of the posteriors using Bayesian credible intervals (BCIs). We performed model validation by generating simulated data with known parameters using Equations (1)–(10), fitting the integrated model and then comparing simulated and estimated parameters (Appendix S2). To assess the robustness of results to prior distributions, we run the model under varying scenarios of prior certainty (Appendix S3). Additionally, we compared detected trends in population size with shade cover between our integrated model and a more commonly used General Mixed Model approach (Appendix S4): overall, the GLMs of individual survey method data only detected trends in the arthropod groups they sampled most effectively (Appendix S4).

We fit all models using Bayesian inference with the JAGS 4.3.0 software (Plummer, 2017) executed using the runjags package (Denwood, 2016) in the R statistical computing environment (R Core Team, 2022). We ran each model for 50,000 iterations, with 10,000 burn-in iterations, and convergence was assessed visually by monitoring trace plots and with the Gelman-Rubin R-hat diagnostic, with convergence presumed when R-hat < 1.1.

3 | RESULTS

3.1 | Estimates of population size

Under simulation, our integrated model was able to accurately estimate model parameters relating to detection rates and population size (Appendix S2). When fit to data from the field, the integrated model predicted that the arthropod community in cocoa trees was dominated in abundance by Hymenoptera, followed by non-pest Hemiptera (Figures 2–4). The least abundant group was brown capsid, with mean population sizes of 1.6 individuals per tree (95% CIs = 0.52, 3.4). Pest groups made up 1.5%–3% of the arthropod community, depending on shade cover and season (Figure 4).

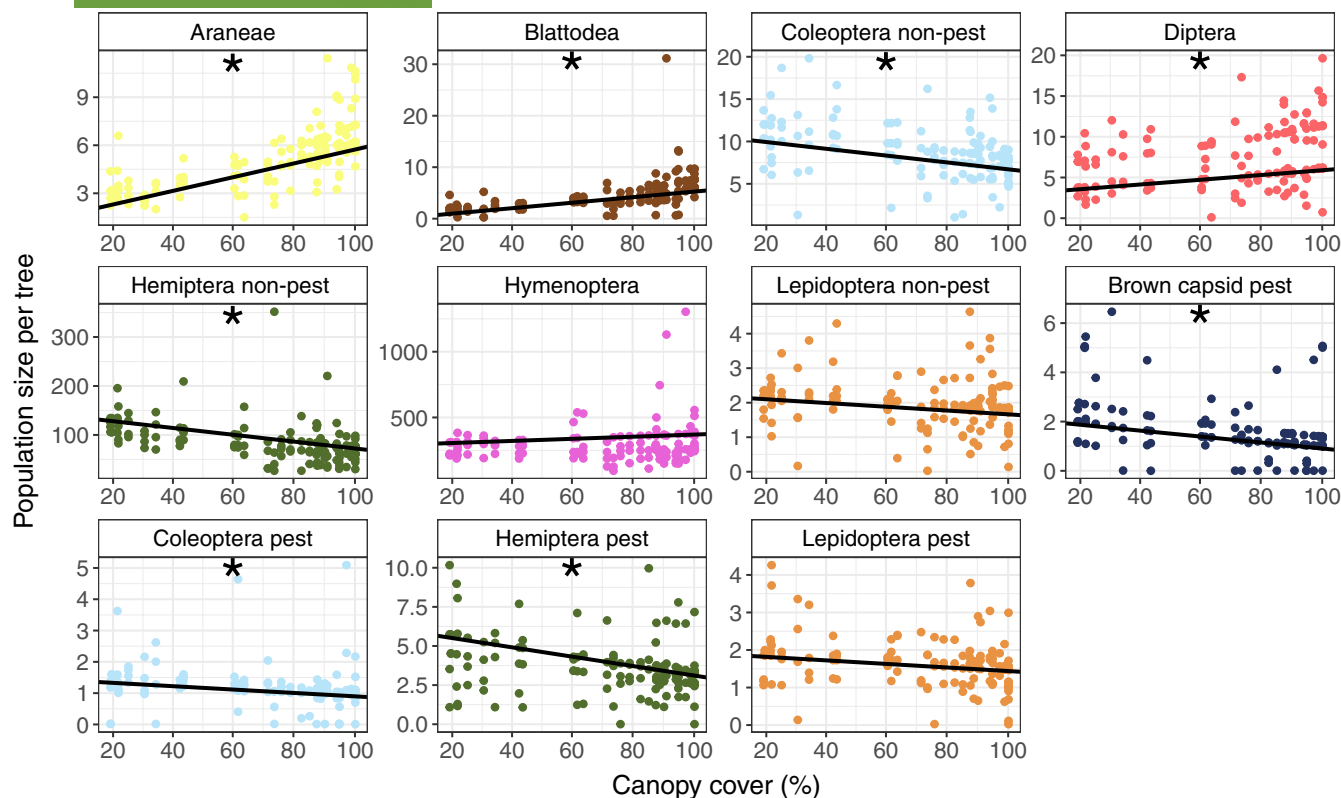


FIGURE 2 Effect of shade cover (%) on population size of different arthropod groups. Points are the mean of posteriors for population size at each site and visit, and the line is the coefficient describing the effect of shade cover on population size, as estimated by model (parameter γ_{ji}). Asterisks indicate that the 95% BCIs of the posterior did not overlap 0.

3.2 | Effects of management and season

Our model detected an effect of shade cover on the population size of eight out of 11 arthropod groups (Figures 2 and 4). Araneae, Blattodea and Diptera increased with increasing shade cover, with populations in shady farms estimated to be approximately double the size of populations in sunny farms. Population size of brown capsids was four times higher in sunny farms than in shady farms. Coleoptera and Hemiptera decreased in population size with increasing shade cover, with approximately twice the number of Hemipteran and Coleopteran pest individuals in sunny farms compared to shady ones.

Season had an effect on five out of 11 groups (Figures 3 and 4): Diptera and brown capsid were more abundant in the rainy season, with brown capsids doubling in population size from the dry season to the wet season. Hemiptera were significantly more abundant in the dry season than the wet season, and a similar trend was true for Hymenoptera.

4 | DISCUSSION

We used integrated analysis of data from several common arthropod survey techniques to estimate the population size of arthropod taxa in cocoa agroforestry systems. We investigated the effect of

shade cover and season on these groups, finding that arthropod communities in shadier farms consisted of more service-providers and natural enemies, whilst communities in sunnier farms had higher pest abundances.

Our results showed that Araneae, Blattodea and Diptera were positively associated with shade cover in African cocoa systems, likely due to a preference for dark and damp microhabitats (Bisseleua et al., 2013; Djuideu et al., 2020; Sonwa et al., 2019; Toledo-Hernández et al., 2021). Araneae may be more abundant in shady farms also due to higher prey availability; the lower abundances of pests in shaded farms could therefore in part be due to higher predation pressures (Ferreira, Jarrett, et al., 2023). A higher abundance of Dipterans in shady farms could result in higher pollination rates, which is extremely relevant in cocoa as it is a pollination-limited crop (Toledo-Hernández et al., 2020, 2023). Small midges known as ceratopogonids (Diptera) are widely acknowledged as the most common cocoa pollinators (Mortimer et al., 2017), but it is likely that other taxa (Cecidomyiidae, Drosophilidae) play a role in pollination as well (Ambele et al., 2023; Toledo-Hernández et al., 2021). For now, the relative efficiency of cocoa pollinators is widely unknown. Together, our findings indicate that shadier African cocoa farms have higher availability of pollinators, as well as higher abundance of spiders that can act as natural enemies.

We found that farms with less shade cover had higher abundances of Hemiptera, Coleoptera and brown capsids. Whilst both

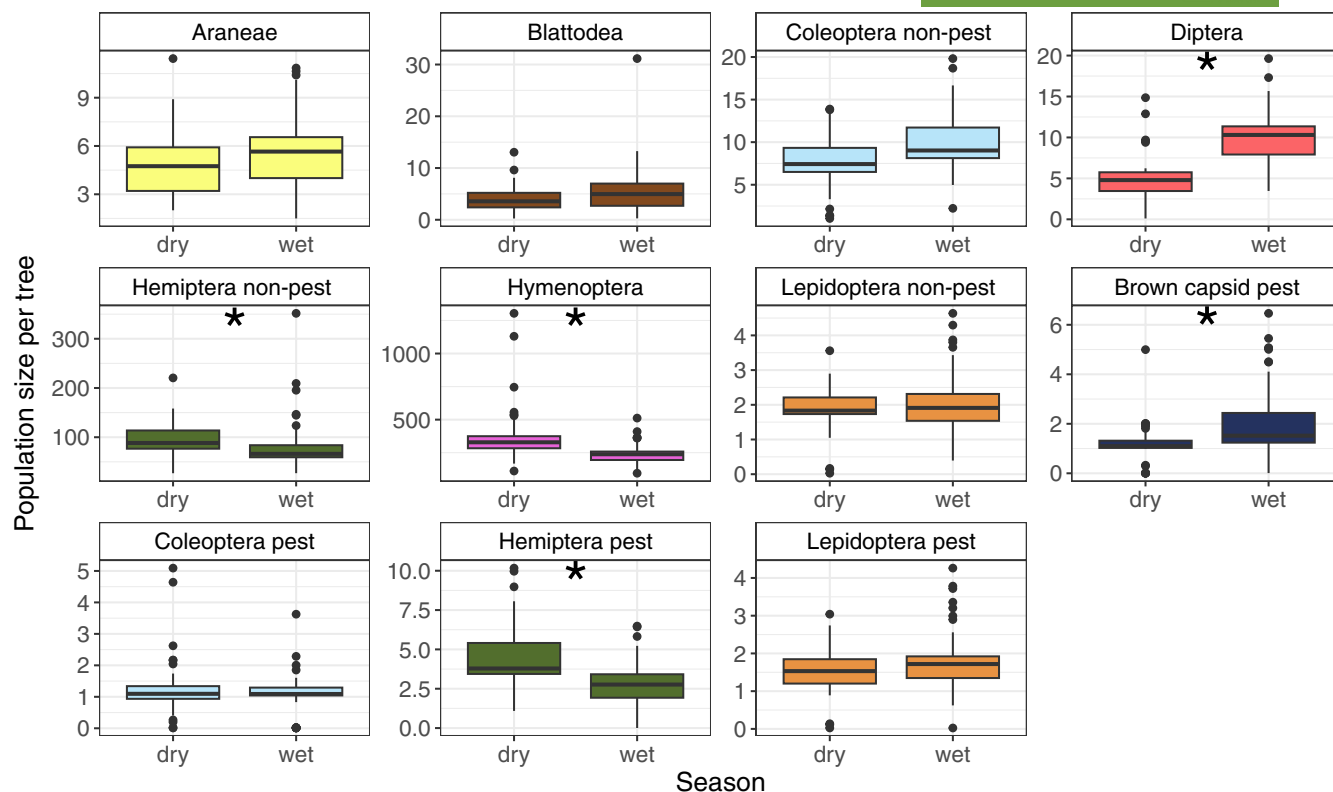


FIGURE 3 Effect of season (dry or wet) on population size of different arthropod groups. Boxplot summary statistics were calculated using the mean of the posterior distribution for population size at each site & visit. Asterisks indicate that the 95% BCIs of the posterior of parameter γ_{j2} (coefficient for the effect of season on population size) did not overlap 0.

Hemiptera and Coleoptera consist in a range of species with varying ecological roles (herbivores, predators, detritivores), they also contain pest groups. Mealybugs (Hemiptera: Pseudococcidae), for instance, can occur at high abundances in cocoa farms and are responsible for spreading cocoa swollen shoot virus in the Afrotropics (Bagny Beilhe et al., 2018). The increased abundance of Hemipteran and Coleopteran pests in sunny farms agrees with Ahenkorah et al. (1974, 1987) and Klein et al. (2002), and may be a reason behind the shorter productive life-spans of sunny farms in the Afrotropics (Ambele et al., 2023).

We investigated populations of brown capsids (a Hemipteran) at the species level, as this species is considered the primary pest of cocoa in Africa. We found that brown capsids occur at very low densities, averaging 1.6 individuals per tree. This estimate is similar to previous estimates of 2.1 individuals per tree (Babin et al., 2010) and <1 individual per tree (Bisseleua et al., 2011), and above the economic threshold for phytosanitary intervention (0.7 individuals/tree in Cameroon; Ambele et al., 2023; Babin et al., 2010). Additionally, we found a significant decrease in capsid abundance with increasing shade cover, in accordance with Babin et al. (2010) and Bagny Beilhe et al. (2018). Together, the findings on Hemipteran and Coleopteran pests and brown capsids indicate an important risk incurred in the current push towards more intensified cocoa production in Africa (Armengot et al., 2016).

Our results show no effect of shade cover on Hymenopteran or Lepidopteran abundance, likely due to species-specific responses to microclimate (e.g., Peters et al., 2011), resulting in an overall net-zero effect. Both these highly diverse orders include pests and ecosystem service providers: ants, the most common Hymenopteran family in our system, predate on pest insects in agroforestry (Bisseleua et al., 2013, 2017), and may play a role as potential pollinators (Toledo-Hernández et al., 2021). Many parasitic wasps (e.g. Braconidae, Ichneumonidae) are natural enemies of pests (Ambele et al., 2023; Bisseleua et al., 2013; Sperber et al., 2004). However, there is also evidence showing that certain ant groups can damage cocoa crops by acting as mechanical vectors of disease (Bisseleua et al., 2017).

The predictions from our model indicate that shady low-intensity cocoa farming supports an arthropod community with more service-providing taxa, and lower pest abundances. Conservation and adoption of such shady agroforestry practices can therefore result in a reduced need for chemical inputs, thus benefitting farmers' health whilst simultaneously reducing input costs (Niether et al., 2020). Additionally, these systems can provide new opportunities for local stakeholders. First, shaded cocoa farms are buffered from the extreme temperatures expected to occur more frequently with climate change (Blaser et al., 2018). Second, shaded cocoa plantations can contribute significantly to

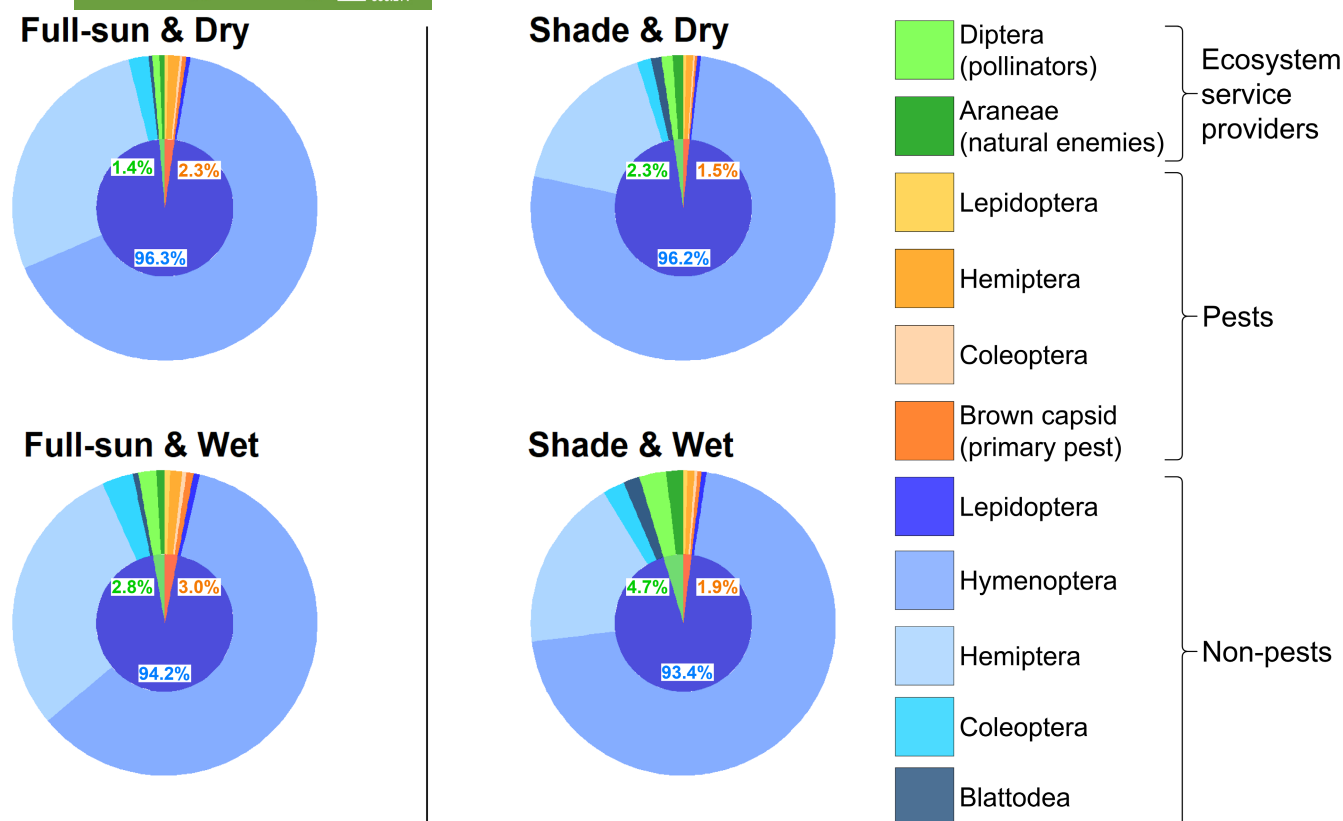


FIGURE 4 Arthropod community composition in cocoa trees under four different scenarios: full-sun farm (20% shade cover) in the dry and wet season, and shade farm (90% shade cover) in the dry and wet season. Shades of green represent ecosystem service providers, shades of orange/yellow represent pests, and the remaining taxa appear in blue. Proportional community composition predicted from the model is summarised using the mean of the posterior distribution of population size.

the conservation of species, including especially vulnerable taxa such as rainforest birds (Jarrett et al., 2021) and bats (Ferreira, Darling, et al., 2023). Recent evidence from African cocoa shows that under shady conditions, these bird and bat populations contribute considerably to farm yields through pest suppression services (Ferreira, Jarrett, et al., 2023). We are only beginning to grasp the diversity of insects in the Afrotropics, but with an estimated 1 million species present and 80% undescribed, and amidst general insect declines worldwide, conservation of such biological diversity should be prioritised (Stork, 2018). A biodiversity-friendly cultivation system in turn could constitute a new market opportunity for farmers, with fairer revenues and improved livelihoods achieved through certification.

Integrating data from the different survey types in this study allowed us to correct for the detection biases of each method and assess the effects of shade cover and season on a broad range of arthropod groups. The main limitation to our data integration approach is that the population size estimation depends considerably on having a subset of data from a 'gold-standard' sampling approach with high detectability (in our case, the visual surveys). Without these data, the model would be unable to distinguish population size from capture rates. Consequently, inaccuracy in population size estimates could result from over-estimating the capture probability of the gold standard method. Another

important limitation of this study is the level of taxonomic aggregation; whilst grouping species to order level facilitated model estimation, it may also obscure intra-order variability in effects of management. With taxa grouped to order level, conclusions about the ecology of the system are tentative; for instance, whilst we detected a positive effect of shade cover on Diptera, we cannot be certain that this applies to pollinator groups. We encourage future in-depth studies of each arthropod group and their associated services and dis-services. Finally, it could have been beneficial in this study to add a sampling method that considered ground-dwelling or below-ground-dwelling taxa, as certain ecosystem service-providers (e.g., dung beetles) may have been overlooked with our sampling methods.

In conclusion, the differences in arthropod community composition driven by shade management may lead to rapidly declining yields in intensive cocoa farms (Blaser et al., 2018; Jagoret et al., 2011; Obiri et al., 2007), an important issue when considering the general trend towards intensification of cocoa agriculture in Africa (Ordway et al., 2017; Tschardt et al., 2011). Our analyses provided a method to generate comparable estimates of population size across taxa, the first step towards being able to study community dynamics of arthropods in cocoa farms. It is essential to understand such dynamics, as intensification of cocoa agriculture, wide-spread in the Afrotropics, may be an unsustainable

trajectory leading towards a crash in productivity induced by increasing pest burdens and loss of ecosystem services (Clough et al., 2009; Tscharnkte et al., 2011).

AUTHOR CONTRIBUTIONS

Crinan Jarrett, Daniel T. Haydon, Andreanna J. Welch, Luke L. Powell and Jason Matthiopoulos conceived the ideas and designed methodology; Crinan Jarrett, Kowo Cyril, Christel Alain Wandji, Luke L. Powell and Diogo F. Ferreira collected the data; Crinan Jarrett analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Figshare Digital Repository <https://doi.org/10.6084/m9.figshare.21968318.v1> (Jarrett, 2023).

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SUPPORTING INFORMATION

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

Appendix S1: Map of study sites.

Appendix S2: Simulation.

Appendix S3: Prior sensitivity analysis.

Appendix S4: Comparison with GLMs.

Appendix S5: Artwork credits.

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